POPULATION BIOLOGY OF SNAIL HOSTS FOR *SCHISTOSOMA HAEMATOBIUM* ON THE KENYA COAST

by

J.H. O'KEEFFE B.Sc. (East Anglia)

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Department of Pure and Applied Biology
Imperial College
Silwood Park
Ascot
Berkshire

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ABSTRACT

Fourteen freshwater bodies on the Kenya coast were examined for schistosomiasis intermediate host snails. All but two were found to contain either Bulinus globosus (in permanent water bodies) or Bulinus nasutus (in temporary pools). B. globosus were found to be shedding Schistosoma haematobium in four dams. The overall prevalence of B. globosus with mature S. haematobium infections was 0.28%, with seasonal peaks in individual sites up to 11.8%.

A detailed sampling programme was conducted in two dams (known as Benes and Nguni) over two years, using plastic sheet traps and mark-recapture techniques. Captive cohorts were raised in netted boxes in the dams to investigate the effects of different feeding regimes and densities on population growth.

Growth rates were measured for B. globosus using marked snails and were found to vary considerably throughout the year and between sites. Life tables were constructed using as many growth curves as could be calculated separately. Proportional reproduction in different age classes was measured from cohorts in boxes and used to allocate m_x values for field samples. Values for the intrinsic rate of natural increase (r_m) were calculated for weekly cohorts in both dams.

Benes dam is a large (3 Ha) water body and therefore water depth and chemistry fluctuates less than in the smaller Nguni dam. Conditions in Benes dam were less suitable for B. globosus as measured by lower average survival and lower maximum value of r_m. Temperature appears to regulate r_m in both dams, with no positive values above a mean water temperature of 28.5 °C. Rainfall and associated variables (water depth and chemistry) condition the habitats, so that in both dams, population growth rose fastest and to the highest levels when large amounts of unseasonal rain fell during the coolest months. Different feeding regimes in boxes caused marked differences in growth, reproduction and survivorship, and therefore r_m. Field values for these parameters correlated with those for the least effective feeding regimes in boxes, and indicated that food quality may have been limiting field populations. Reproduction in natural populations was strongly density dependent (as were growth rates and survival in box-kept snails) and at low density levels was correlated (in Nguni dam) with the prevalence of a sterilising heterophyid trematode infection. Values of r_m in Benes dam were significantly depressed by high snail densities.

Benes dam was the main transmission site for S. haematobium but the above measurements indicate that the dam is a comparatively sub-optimal habitat. It is therefore suggested that "low level" snail control (such as vegetation clearance), might be sufficient to reduce the transmission potential of the dam.

TABLE OF CONTENTS

	PAGE
ABSTRACT	2
LIST OF TABLES	9
LIST OF FIGURES	13
LIST OF APPENDICES	17
CHAPTER 1 INTRODUCTION	18
1.1 Schistosomiasis	18
1.2 Control Methods for Schistosomiasis..	19
1.2.1 Snail control	24
1.2.2 The identification of research priorities	26
1.3 Population Biology of Host Snails: The State of the Art	28
1.4 The Aims of This Project	36
CHAPTER 2 STUDY SITES	38
2.1 Description of the Study Area	38
2.1.1 Benes dam	41
2.1.2 Nguni dam	46
2.2 Climate	49
2.3 Population Fluctuations of Bulinus globosus in Benes and Nguni Dams	49
CHAPTER 3 GENERAL METHODS	54
3.1 Introduction	54
3.1.1 Sampling methods	55
3.1.2 Plastic sheet snail traps.	58

PAGE

3.1.2 Choice of trap sites.. 60

3.2 The Sampling Regime 63

3.2.1 Colonisation rate 63

3.2.2 Intersample time 65

3.2.3 Sample uniformity 66

3.2.3.1 Trap underside v. upperside. 66

3.2.3.2 Top v. bottom traps. 66

3.2.3.3 Trap aging 68

3.2.4 Trap calibration 69

3.2.4.1 Absolute density 69

3.2.4.2 Man-time samples 76

3.2.4.3 Small snail sampling 78

3.3 Snail Measuring 79

3.4 Estimation of Snail Maturity. 81

3.5 The Mark-Recapture Programme. 90

3.5.1 Underlying assumptions of mark-recapture population estimates 94

3.5.1.1 No mark induced mortality and no mark loss 94

3.5.1.2 Equal catchability.. 102

3.5.1.3 Time intervals between samples.. .. 104

3.5.1.4 Equal probability of surviving the sampling period. 104

3.6 Snail Boxes 105

3.6.1 Design and purpose 105

3.6.2 Initial tests of snail boxes.. 113

3.6.3 1981/82 box treatments 114

3.6.4 Hatching boxes 119

PAGE

3.7 Laboratory Aquaria 123

3.8 Testing for Infections 124

3.9 Environmental Measurements 129

3.9.1 Temperature and basic water chemistry measurements in the dams.. 129

3.9.2 Rainfall and atmospheric temperature readings 131

3.9.3 Detailed water chemistry.. 131

CHAPTER 4 GROWTH RATES 132

4.1 Introduction 132

4.2 Growth Curves from Marked Snails. 137

4.3 Growth Curves from Box Snails 145

4.3.1 Feeding and density effects on box snail growth 153

4.4 Growth Curves from Sample Modes.. 153

4.5 Discussion 156

4.5.1 Factors influencing growth 167

CHAPTER 5 SURVIVAL 169

5.1 Introduction 169

5.2 Field Survival 171

5.2.1 Survival from trap samples 171

5.2.2 Survival from marked snails 180

5.3 Survival from Box-Kept Snails 186

5.4 Discussion 190

5.4.1 Factors causing mortality. 190

5.4.2 Differences between field and box snail mortality 193

PAGE

5.4.3 Comparisons of results with those from previous studies 195

CHAPTER 6 REPRODUCTION 200

6.1 Introduction 200

6.2 Results 202

6.2.1 The relationship of size and age to maturity and reproduction. 202

6.2.2 Hatch time 205

6.2.3 Hatch success 207

6.2.4 Numbers of eggs per egg mass.. 209

6.2.5 Adult recruitment size 209

6.2.6 Feeding and density effects on reproduction 213

6.2.7 Size specific reproduction in snail boxes 213

6.3 Discussion 218

6.3.1 The calculation of m_x values.. 223

CHAPTER 7 LIFE TABLES AND THE INTRINSIC RATE OF NATURAL INCREASE 226

7.1 Introduction 226

7.1.1 The intrinsic rate of natural increase 226

7.1.2 Estimating r 228

7.2 Life Tables and r_m from Boxes 231

7.3 Life Tables and r_m from Trap Samples. 234

7.4 Discussion 240

7.4.1 The interpretation of r_m and comparisons with previous studies. .. 245

PAGE

CHAPTER 8 INFECTIONS 252

8.1 Introduction 252

8.2 Schistosome Infections 254

8.2.1 Seasonality and age distribution of schistosome infections. 258

8.3 Heterophyid Infections 260

8.4 Discussion 263

CHAPTER 9 THE ENVIRONMENT 275

9.1 Introduction 275

9.2 Results 278

9.2.1 Chemical constituents of the water .. 278

9.2.2 Total dissolved salts. 280

9.2.3 pH and oxygen 282

9.2.4 Water temperature 282

9.2.5 Rainfall 286

9.2.6 Relationships between environmental variables and snail population parameters 289

9.3 Discussion 294

CHAPTER 10 CONCLUSIONS 299

10.1 The Distribution of *Bulinus* 299

10.2 The Sampling Methods 300

10.3 *Bulinus globosus* in Nguni and Benes dams. .. 301

10.3.1 Population regulation 302

10.4 Further Research 306

PAGE

10.5 Schistosomiasis Transmission 307

10.5.1 Snail control measures 308

ACKNOWLEDGEMENTS 310

REFERENCES 311

APPENDICES 331

LIST OF TABLES PAGE

1.1 Field population studies on Schistosome host snails and related species 29

2.1 Freshwater sites between Bamburi and Vipingo .. 39

3.1 Comparison of snail densities on each side of the traps 67

3.2 B. globosus densities on traps compared to those on natural vegetation 72

3.3 Comparison of numbers of B. globosus on vegetation traps and plastic traps. 75

3.4 Comparison of numbers of B. globosus (>3mm) collected per 15 minute search and per trap .. 77

3.5 The onset of reproduction compared to time of adult recognition in box-kept snails 89

3.6 Previous studies on aquatic snails using mark-recapture techniques 91

3.7 Comparison of marked v. unmarked snails 96

3.8 The effect of the marking process on snail mortality 99

3.9 Mark durability 101

3.10 Test for independence of mark status 103

3.11 Egg count accuracy 122

3.12 Testing the efficiency of the mass screening method used for detecting patent infections .. 128

4.1 Time specific data from growth increments of marked snails 138

4.2 Summary of growth parameters fitted to snail growth in boxes 151

LIST OF TABLES (Cont) PAGE

4.3 The results of factorial analysis of variance for mean growth performance 154

4.4 Growth parameters from field sample mode sizes. 161

4.5 Growth parameters for two dams during two years 162

5.1 Summary of average weekly mortality estimates from trap sample data 178

5.2 Survival estimates for Nguni dam 1981/82 from marked snails 181

5.3 Summary of recapture rates over different time periods for all sizes of B. globosus 187

5.4 The results of factorial analysis of variance for survival of B. globosus in boxes 188

5.5 Survival and mortality in box-kept snails after ten weeks 189

5.6 Summary of average weekly mortality rates measured by different methods 196

5.7 Test for the difference between average weekly mortality from 0 to 10 weeks and from 0 to 20 weeks 197

6.1 Comparison of age and size at maturity and initial reproduction 204

6.2 Summary of mean hatch times 206

6.3 Mean % hatch success 208

6.4 The results of factorial analysis of variance for mean reproductive performance of B. globosus in boxes 216

LIST OF TABLES (Cont) PAGE

6.5 Proportional reproduction by snails of different size classes in boxes 217

6.6 Comparison of different aspects of reproduction 220

6.7 A hypothetical example of the method used to allocate eggs to size classes in field samples. 225

7.1 r_m values calculated from cohorts of box-kept B. globosus 232

7.2 The results of factorial analysis of variance for r_m of B. globosus in boxes 233

7.3 Comparison of r_m and r_c for Nguni trap samples, 1981/82 239

7.4 Summary of r_m values measured for box-kept and free-living B. globosus 242

7.5 Values for r/week from previous field studies.. 249

8.1 Results of a schistosome egg survey from primary schoolchildren at Gongoni village.. .. 255

8.2 Numbers of B. globosus tested for cercarial shedding 257

8.3 Differences in observed prevalence of snails shedding heterophyid cercariae from B. globosus kept in boxes in Nguni dam during 1981/82.. .. 262

8.4 The onset of heterphyid shedding in box-kept snails 264

9.1 Chemical constituents of Benes dam water 279

9.2 Nitrogen and calcium concentrations in Nguni dam during 1981/82. 281

LIST OF TABLES (Cont) PAGE

9.3 Autocorrelations between environmental variables 291

9.4 The results of multiple linear regressions and correlations on r_m of cohorts with environmental variables 293

9.5 Significant partial correlation coefficients between r_m and environmental measures.. 295

LIST OF FIGURES PAGE

1.1 The schistosome life cycle 21

2.1 Map of the project area 40

2.2 Benes dam. A typical water contact site 43

2.3 Map of Benes dam 45

2.4 Nguni dam vegetation 47

2.5 Map of Nguni dam 48

2.6 Mean monthly rainfall 50

2.7 Mean monthly air temperatures.. 51

2.8 Fluctuations in numbers of B. globosus and egg masses in Nguni and Benes dams. 52

3.1 Plastic sheet snail trap 59

3.2 A multiple trap sampling site.. 62

3.3 The rate of colonisation of snail traps 64

3.4 Comparison of the relative attraction of new v. old traps 70

3.5 Comparison of B. globosus densities on vegetation and trap plastic 73

3.6 Snail trap constructed of Typha latifolia leaf. 74

3.7 Field measurement of B. globosus 82

3.8 Field recognition of maturity in B. globosus .. 84

3.9 The development of the accessory reproductive glands of B. globosus 86

3.10 The assessment of maturity in B. globosus . .. 88

3.11 The effect of marking on snail mortality 98

3.12 Mean survival by size from mark-recapture data. 107

3.13 Snail boxes 111

3.14 Hatching boxes 120

LIST OF FIGURES (Cont) PAGE

3.15 The portable system used for environmental measurements 130

4.1 Estimation of a cohort growth curve 135

4.2 Mean growth rates at different mm size classes. 139

4.3 Average time-specific growth curves for B. globosus in Nguni dam during 1981/82 140

4.4 Average time-specific growth curves for B. globosus in Nguni dam during 1980 142

4.5 Average time-specific growth curves for B. globosus in Benes dam during 1980 143

4.6 Cohort growth curves for B. globosus during 1981 in Nguni dam 144

4.7 Modified von Bertalanffy curves fitted to growth data from box snails 148

4.8 Feeding effect on growth rate.. 149

4.9 Mean cohort growth rates from box-kept snails.. 152

4.10 Growth rates from successive size class modes, Benes dam 1980 157

4.11 Dominant cohort growth, Nguni dam 1980. 158

4.12 Dominant cohort growth, Benes dam 1981. 159

4.13 Dominant cohort growth, Nguni dam 1981. 160

4.14 Comparison of growth performance from box snails and marked snails in Nguni dam 164

4.15 Comparison of growth rates for B. globosus from Rhodesia and this project 166

5.1 Mean survivorship curves for Nguni dam 1980 .. 172

LIST OF FIGURES (Cont) PAGE

5.2 Mean survivorship curves for Nguni dam 1981 .. 175

5.3 Mean survivorship curves for Benes dam 1980 .. 177

5.4 % recaptures of marked snails in Nguni dam by size and by time 183

5.5 % recaptures of marked snails in Benes and Nguni dams 185

5.6 Mortality rates calculated from recaptures of marked snails, trap samples and boxes.. 194

6.1 Comparison of reproductive performance of free-living and box-kept snails 203

6.2 Changes in egg mass sizes with time 210

6.3 The relationship between egg mass size and snail size 212

6.4 Mean adult recruitment size 214

6.5 The change in average size at adult recruitment with time 215

6.6 Mean proportions of total reproduction allocated to each size class 219

6.7 Snail density effects on reproduction.. 221

7.1 r_m values for weekly cohorts in Nguni dam, 1980/81 236

7.2 r_m values for weekly cohorts in Benes dam, 1980/81 237

7.3 r_m values for weekly cohorts in Nguni dam, 1981/82 238

7.4 Mean r_m values for box-kept snails. 244

LIST OF FIGURES (Cont) PAGE

7.5 Comparison of a theoretical stable age distribution (from box-kept snails) with the actual distribution from trap samples.. 247

8.1 Distribution of B. globosus shedding schistosome cercariae 259

8.2 Proportions of B. globosus in boxes shedding heterophyid cercariae 265

8.3 Proportions of snails showing mature heterophyid infections by month 266

8.4 Size-specific prevalence of heterophyid shedding B. globosus in Nguni dam during 1981/82 267

8.5 Data from Fig. 8.4 transformed to age prevalence 268

8.6 The relationship between mature heterophyid infections and reproduction 274

9.1 Total dissolved salts in Benes and Nguni dams.. 283

9.2 pH fluctuations in Benes and Nguni dams 284

9.3 Oxygen saturation in Benes and Nguni dams.. .. 285

9.4 Mean maximum and minimum water temperatures in Benes and Nguni dams 287

9.5 Rainfall from January 1980 to February 1982 .. 288

9.6 Water level fluctuations in Benes and Nguni dams 290

9.7 The relationship of r_m to mean water temperature 296

LIST OF APPENDICES

PAGE

A. Weekly Bulinus globosus samples from Nguni and Benes dams, separated into mm size classes, and adults and juveniles 331

B. A program (written in BASIC language for use on a Hewlett-Packard 9845B desktop computer), to calculate weekly growth rates 335

C. A program (written in BASIC language for use on a Hewlett-Packard 9845B desktop computer), to allocate reproduction to sample size classes, and calculate life tables and r_m values for weekly cohorts 337

D. Life tables for weekly cohorts 340

CHAPTER 1 INTRODUCTION

1.1. Schistosomiasis

Three species of the digenean genus Schistosoma (S. mansoni, S. haematobium and S. japonicum), are responsible for one of the most widespread parasitic infections of man, second only in socioeconomic and public health importance to malaria in tropical and sub-tropical areas (Iarotski and Davis, 1981). Between 125 (Iarotski and Davis, 1981) and 200 million (Webbe, 1981) people are infected with schistosomiasis and over 500 million are exposed to the risk of infection.

Although there is evidence from hieroglyphs and papyrus fragments that the Egyptians recognised a worm related disease causing haematuria as early as the second millenium B.C. (Farooq, 1973), it was not until 1851 that the first schistosome was described.

This was S. haematobium, discovered in the portal and mesenteric veins of a man at autopsy in Cairo by the German surgeon Theodor Bilharz (Wright, 1981). Despite considerable background knowledge (such as the full life cycle of Fasciola hepatica) it was more than sixty years before unequivocal evidence of a schistosome life cycle was produced. In 1913, Miyairi and Suzuki showed that S. japonicum developed in the hydrobiid snail Oncomelania nosophora (Wright, 1981). The complete life cycle of a typical human host schistosome is

shown in Fig. 1.1. In 1915 the British parasitologist R.T. Leiper established the separate identities of S. haematobium and S. mansoni, and raised two hitherto obscure genera of planorbid snails into the limelight, implicating Bulinus as the host for S. haematobium and Biomphalaria for S. mansoni.

By 1918 attempts were being made to control schistosomiasis by chemotherapy (tartar emetic) and by snail eradication, using lime as a molluscicide (in Japan). In 1937, environmental control of snails was initiated, C.H. Barlow advocating weed clearance in canals in Egypt (Farooq, 1973). By the 1930's, field studies on transmission patterns were being initiated, with attempts to quantify the various processes governing the prevalence of the flukes, (e.g. Gordon et al, 1934). In 1952 the World Health Organisation first became involved in a control scheme (in Egypt) and its involvement has increased ever since, until today schistosomiasis ranks second to malaria on the W.H.O.'s list of priority diseases.

1.2. Control Methods for Schistosomiasis

Anderson (1980) lists four main methods currently employed in the control of bilharziasis:

(a) Reduction in host snail density.

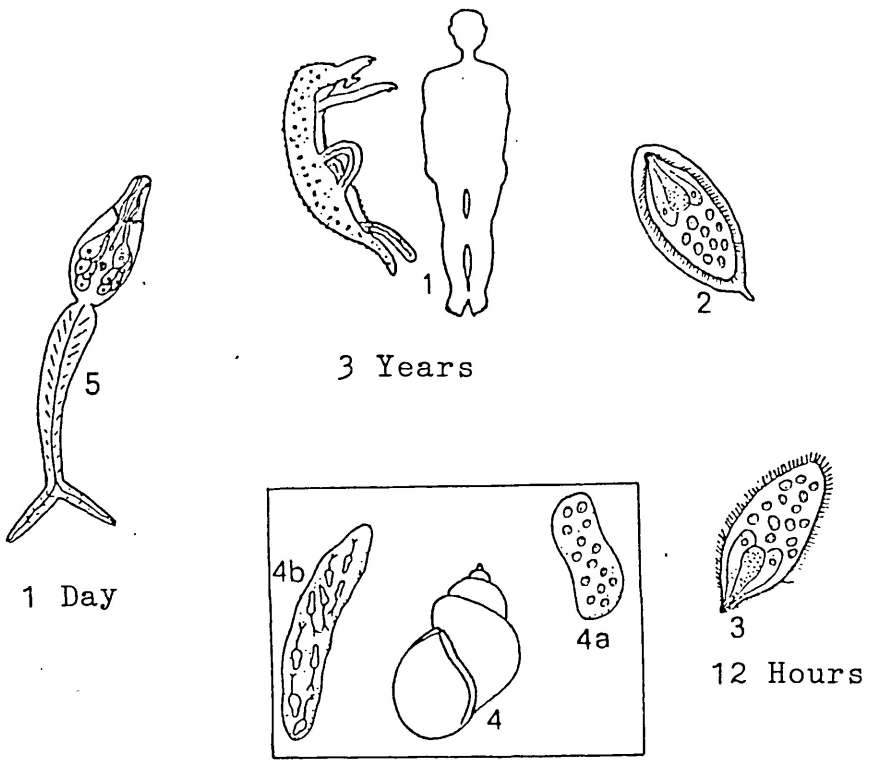
(b) Chemotherapeutic treatment of the human host.

(c) Education to reduce human contact with infected snails.

Fig. 1.1 The life cycle of Schistosoma haematobium (with approximate mean duration of each stage).

The paired adult worms (1) live in the veins and bladder wall of man. Eggs laid by the females (2) work their way through the bladder wall and are voided in the urine. They hatch in fresh water and the free-swimming ciliated miracidium (3) must find and enter a snail (4). Within the snail the miracidium becomes a mother sporocyst (4a) which gives rise to a number of daughter sporocysts (4b). These in turn give rise to the next larval stage, the free-swimming cercaria (5). The cercaria is the infective stage to man penetrating directly through the skin, shedding its tail, and migrating through the body until it arrives as a mature worm at its egg-laying site.

(Modified from Wright, 1981.)



THE SCHISTOSOME LIFE CYCLE

(d) Improvement of sanitation to reduce the release of eggs into habitats harbouring the snail intermediate hosts.

The development of safe and effective vaccines would provide the most effective approach to control, and research to produce either an attenuated cercariae vaccine or an antipathology vaccine are in progress (Webbe, 1981). However, until these are developed and made available cheaply, the four methods listed above will continue to be the major components of control. Schistosomiasis is predominantly a disease of communities living at an extremely low level of technology, and the most appropriate long term responses to the disease should probably be aimed either at low technology permanent disruption of transmission through environmental control of the snails and reduction of water contacts, or at increasing the material standards of living (particularly by providing clean water supplies and adequate sanitation). Whether there is an emphasis on either option will usually depend on the political philosophy of the country which implements the control measures. In either case, chemotherapy and molluscicides are inappropriate measures. Both are relatively high technology and neither provides long term protection unless prevalence levels can be reduced so as to permanently interrupt transmission. Nevertheless, they still provide the backbone of most control projects now in operation.

According to Jordan (1972), the prevalence of schistosomiasis was continuing to increase in many areas during the early 1970's principally because of the continuing emphasis in third world countries on construction of dams and irrigation systems for agricultural and (in the case of the major dams) industrial use. This trend will obviously continue because of the perceived priorities in most countries where schistosomiasis is endemic, which rate food supply problems more urgent than those caused by parasitic diseases (i.e. the Lake Chad irrigation project in Northern Nigeria). In spite of this, there are now control programmes operating in 71 countries, of which the World Health Organisation considers eight to be successful. (Those in Brazil, Egypt, Iran, Japan, Puerto Rico, St. Lucia, Tunisia and Venezuela; Iarotski and Davis, 1981). Whether this constitutes a worldwide decrease or a reduction in the rate of increase of numbers infected is not clear at present. The latter seems more likely.

Nearly 50% of countries in which bilharzia is endemic use more than three different methods of control simultaneously (Iarotski and Davis, 1981). This approach to control may turn out to be the most effective, but at present is more an indication that, despite a great deal of costly research on various aspects of the epidemiology and possible control procedures, there is still no general agreement on the optimum single method of control.

1.2.1. Snail control

Because of their high intrinsic rate of increase, good dispersal capabilities and great intraspecific genetic variability, it has generally been agreed that the eradication of snail hosts of schistosomiasis would be extremely difficult (Thomas, 1973). The alternative is to prevent transmission by reducing the snail population to a critical threshold level below which the parasite is unable to persist (Anderson and May, 1979).

Most workers no longer believe that snail control alone is capable of achieving this break in transmission. In general they regard it as simply an important part of integrated control. This view is supported by theoretical studies which suggest that killing snails will lead to a decline in worm burden, but is of little use as a means of eradicating schistosomiasis (Barbour, 1982).

During the 1960's, the use of molluscicides provided the only reliable approach to control of schistosomiasis, and, although integrated methods are now the favoured approach, there is ample evidence that area-wide molluscicide is successfully controlling snails in major programmes (e.g. in China and Egypt) and that focal control by molluscicides is successful in other areas (Webbe, 1981). However, molluscicide is also the most expensive form of control, must be reapplied at frequent intervals and may have undesirable side effects. More recently emphasis has

been placed on snail control by modification of the habitat (removal of vegetation, increased flow rates in streams, drainage of swamps, fluctuation of the water level in dams (Bradley and Webbe, 1978) and biological control through competitors (e.g. Marisa cornuarietis) (Negron Aponte & Jobin, 1979), predators (such as scyomyzid flies, Berg, 1964), or other trematode parasites (Lim and Heyneman, 1972). Other approaches which have been tried are control by natural inhibitors, produced by the snails themselves, (Levy et al, 1973) and by natural molluscicidal plant extracts (e.g. from Phytolacca dodecandra) (Lemma, 1970).

The major control programme in Puerto Rico, which was initiated in 1953, began by using molluscicides for snail control but is now geared to environmental modification and competitive exclusion by M. cornuarietis with considerable success, according to Negron-Apónte and Jobin (1979).

It is clearly possible but undesirable to control snails by the blanket application of molluscicides. The key to the efficient control of snails by other means is through a close understanding of the ecology of the snails. Hubendick (1958) laments the accumulation of so little precise information and the fact that so few distinct relationships had been established in snail ecology. In 1957 the World Health Organisation study group on the ecology of snail hosts of bilharziasis called for further studies on host snails (W.H.O., 1957). Although an enormous amount of research has been carried out since then, this call echoes

down the literature to the present day (Webbe, 1962a; Harrison, 1966; Hairston, 1973; Bradley and Webbe, 1978; Iarotski and Davis, 1981).

1.2.2. The identification of research priorities

"One of the principal uses of theoretical study is to highlight the areas in which we need to acquire more detailed biological data" (Anderson and May, 1979).

In 1965, Dr. G. Macdonald developed a general mathematical model of the dynamics of helminth infections which elucidated the concept of a breakpoint level of infection below which a helminth population would proceed to extinction (Macdonald, 1965). This breakpoint arises as a consequence of the need for worm burdens in the human host to exceed a certain value if sexual contact between male and female parasites is sufficient to maintain the production of transmission stages. More recent work (Anderson, 1982) suggests that such breakpoints will, in practice, be very low due to the highly aggregated nature of the distribution of worm numbers within the human host populations. Such work demonstrates the power of mathematical models in public health research. Models can provide insights into the nature of a problem and may yield predictions of the consequences of a course of action. Bailey (1967) discusses the use of simple models for clarifying problems and identifying critical areas, and more complex models for statistical fitting to data. But he deplores the trend towards mathematical papers of intrinsic interest

but of only accidental practical value (Bailey, 1975). Bradley (1982) pursues this theme of the dichotomy between theory and "practical" research, quoting "The revulsion of malariologists following Lotka's 1923 model". He concludes that the most enduring advances have been made by the few men (such as Ross and Macdonald) who have managed to combine the talents of field workers and applied mathematicians, and calls for an increased dialogue between the majority who can claim only one of these attributes.

Modelling in schistosomiasis has produced very valuable general insights (such as that of Macdonald, 1965), and specific insights (e.g. the theory of targeted chemotherapy, Fine and Lehman, 1977). Anderson and May (1979) develop an age prevalence model for schistosome infections within snail populations and identify the primary areas in which more detailed data are needed:

(a) Field estimates of infected and uninfected snail mortality rates (taking into account juvenile snail mortality).

(b) The rate of loss of infections within snail populations (or whether snails can lose their infections).

(c) If loss of infection occurs, can these snails become reinfected.

(d) Rates of snail infection within natural habitats.

At a more general level, Anderson (1980) calls for a much better data base concerning the many parameters which determine the reproductive potential of schistosome species.

Bradley and Webbe (1978) identify a number of priority research subjects. Among them are a continued increase in background knowledge and strong support for any new and penetrating ideas on molluscan ecology. Iarotski and Davis (1981) emphasize the need for research into snail ecology, particularly in the field of biological control.

1.3. Population Biology of Host Snails - The State of The Art

The term population studies means different things to different people, as a survey of the literature on schistosome host snails shows. Contributions range from the description of major population fluctuations throughout the year to meticulous and detailed investigations of population structure and processes. All of these add something to the background knowledge of snail ecology and build a further basis from which speculation and predictions arise and against which certain hypotheses can be tested. Many of the less thorough field investigations have been carried out in extremely difficult circumstances, often as a minor adjunct to primarily human epidemiological surveys. Table 1.1 takes a fairly broad definition of "population studies" and lists the species, locations and dates of publication of those which have made a contribution to the knowledge of the ecology of host snails.

Tropical aquatic snails present many difficulties to the population ecologist. Although they are slow-moving (and

Table 1.1 Field population studies on schistosome host snails and related species.

Snail species	Country	Author(s)	Date
Bulinus globosus	Ghana	McCullough	(1957)
Bulinus globosus	Tanzania	Webbe & Msangi	(1958)
Bulinus globosus	Tanzania	Pringle & Msangi	(1960)
Bulinus globosus	Kenya	Teesdale	(1962)
Bulinus globosus	Tanzania	Pringle & Raybould	(1964)
Bulinus globosus	Zimbabwe	Shiff	(1964)
Bulinus globosus	Nigeria	Hira & Muller	(1966)
Bulinus globosus	Tanzania	Otieno	(1969)
Bulinus globosus	Ghana	Paperna	(1972)
Bulinus globosus	Sierra Leone	Onambiro	(1972)
Bulinus globosus*	South Africa	Appleton	(1974)
Bulinus globosus	Liberia	Sodeman	(1979)
Bulinus ugandae	Uganda	Berrie	(1964)
Bulinus africanus	Tanzania	Webbe & Msangi	(1958)
Bulinus africanus	Kenya	Teesdale	(1962)
Bulinus nasutus	Tanzania	Webbe & Msangi	(1958)
Bulinus nasutus	Kenya	Teesdale	(1962)
Bulinus nasutus	Tanzania	Webbe	(1962a)
Bulinus abyssinicus	Somalia	Upatham et al	(1981)
Bulinus truncatus	Egypt	Barlow & Muench	(1951)
Bulinus truncatus	Ghana	McCullough	(1962)
Bulinus truncatus	Egypt	Dazo et al	(1966)
Bulinus truncatus	Ghana	Paperna	(1972)
Bulinus truncatus	Egypt	Demian & Kamel	(1972)
Bulinus truncatus	Ghana	Klumpp & Chu	(1977)
Bulinus tropicus	South Africa	Stiglingh & van Eeden	(1977)

Table 1.1 continued.

Snail species	Country	Author(s)	Date
Bulinus forskalii	Uganda	Cridland	(1957a, 1957b)
Bulinus forskalii	Ghana	McCullough	(1957)
Bulinus forskalii	Kenya	Teesdale	(1962)
Biomphalaria pfeifferi	Tanzania	Webbe	(1960)
Biomphalaria pfeifferi	Kenya	Teesdale	(1962)
Biomphalaria pfeifferi	Nigeria	Hira & Muller	(1966)
Biomphalaria pfeifferi	South Africa	Appleton	(1974)
Biomphalaria pfeifferi	Liberia	Sodeman	(1979)
Biomphalaria sudanica	Uganda	Cridland	(1957a, 1957b, 1958)
Biomphalaria sudanica	Uganda	Berrie	(1964)
Biomphalaria adowensis	Uganda	Cridland	(1957a, 1957b)
Biomphalaria alexandrina	Egypt	Dazo et al	(1966)
Biomphalaria glabrata	Puerto Rico	Jobin	(1970)
Biomphalaria glabrata	St. Lucia	Sturrock	(1973a, 1973b)
Oncomelania quadrasi	Phillipines	Pesigan et al	(1958)
Oncomelania quadrasi	Phillipines	Makiya et al	(1981)

* Identification uncertain, listed as Bulinus (physopsis) sp.

therefore easily caught), aquatic snails tend to have overlapping generations (causing age identification problems) due to a relative lack of seasonality, live in habitats which are very difficult to sample adequately and present very widely varying responses to similar conditions, (an ecological flexibility which allows them to colonise and survive in transient and unstable habitats). Schistosome host snails present the additional hazard of the disease which further restricts sampling options. In spite of these difficulties, some of the studies listed in Table 1.1 have been remarkably detailed and have provided very accurate population parameter measures and insights into the mechanisms of population changes.

Barlow and Muench (1951) bypassed many of the inherent field problems by creating their own habitat and stocking it with a cohort of Bulinus truncatus of known age. They used this population to study the life span and mortality rates of the snails. They showed that mortality was clearly age dependent (high in early and late life), and that the life span of the snails, even in a relatively protected environment, was much shorter than had originally been thought. (The mean expected life span was two months while no snails lived beyond fourteen months of age.)

Oncomelania quadrasi, the snail host of Schistosoma japonicum in the Phillipines, lives on marshy ground which can (in most cases) be sampled by standard quadrat methods. Pesigan et al (1958) pioneered most of the methods used in subsequent

projects, collecting snails over two years and using life table analysis to determine mortality and reproductive rates for O. quadrasi. The study, part of an overall epidemiological investigation of S. japonicum in the Phillipines, was designed to find out what the effects of snail control might be and what recovery timescales might be expected from different levels of control. The analysis required a knowledge of the age structure of the population, for which a field growth curve was measured, using mode size classes at successive samples. Age-specific reproduction was measured in the laboratory and age at maturity was determined by observing the minimum sizes of copulating snails in field samples. Because of the difficulties of sampling small (<1mm) snails adequately, they developed a combined index of the survival of eggs and young snails. The distribution of the snails was found to be highly aggregated and was best described by the negative binomial probability model. Field mortality rates were calculated by comparing successive sample sizes with reference to the growth curve to identify the size classes which represented survivors of smaller sized snails in the previous sample. Pesigan et al (1958) were able to predict recovery timescales for different initial kill rates which were confirmed when snail control was instigated. This study marked the beginning of an era during which snail population studies (employing basically the same methods) were used to predict the optimum time for the application of control measures and the likely frequency of repeat treatments necessary to maintain control.

Webbe (1962a) used these analytical methods to investigate the dynamics of populations of Bulinus nasutus productus in a series of temporary ponds in Tanzania. He found that the snails were capable of long periods of aestivation, and that infected snails could also survive the dry season. The study involved a detailed analysis of habitat changes through the year, from which it was concluded that rainfall and temperature were the major external factors affecting the snails. Density effects on the birth rate and mortality were thought to be the major intrinsic influences. Schistosome infections in snails were found to increase with snail density, and with the proportion of older snails in the population. Infection was also shown to have a considerable effect on snail mortality, especially in young snails.

Shiff (1964), working on Bulinus globosus in Zimbabwe, developed field methods to encompass measures of egg viability rates and to take account of differences in growth rates during different seasons (mainly due to temperature). He also calculated values for the intrinsic rate of natural increase as a measure of repopulation rates after catastrophic reductions. Once again the major environmental factors were found to be temperature (through its influence on fecundity), and rainfall. Shiff concluded that B. globosus can thrive either in large water bodies where survival is high, despite only moderate reproductive rates, or in small water bodies where high innate capacities of increase allow the snails to take advantage of short spells of optimum conditions.

Dr. N.G. Hairston, one of the primary organisers of the Phillipines project (Pesigan et al, 1958) was also involved in the comparative study of populations of Bulinus truncatus and Biomphalaria alexandrina, reported by Dazo et al (1966). The aim of this project was to predict the optimum times for molluscicide treatment of the two host snails in canals and irrigation drains. Both species were found to have separate optimum habitats (B. truncatus in large canals, B. alexandrina in the smaller drains), but densities fluctuated at similar times of the year. Field values for the intrinsic rate of natural increase were measured with a view to establishing when the population would be least able to recover from catastrophic declines.

Sturrock (1973a, 1973b) investigated several different types of habitat in St. Lucia and found that ponds and marshes were the most favourable habitat for Biomphalaria glabrata, but that higher and more persistent infection rates occurred in populations in flowing waters. Detailed analysis, with meticulous testing of growth rate measures and sampling methods, revealed that rainfall is the key factor controlling population changes. Sturrock (1973a) also showed that rainfall has an opposite effect in lentic and lotic habitats. Once again field values of r_m (the intrinsic rate of natural increase) were used to predict recovery rates. The study resulted in recommendations for seasonal treatments of stream populations of snails.

These six reports have been reviewed because they represent the evolution of field methods for snail population study. This research generated many insights into the mechanisms of population changes and it provides the basis for the present study.

Other projects have also contributed greatly to an understanding of freshwater snail ecology. Temperate freshwater snail populations are more easily studied than those in tropical climates because generations tend to be separated by severe seasonal changes. Eisenberg (1966, 1970) investigated the effects of density and feeding on Lymnaea elodes in Michigan, using pens to subdivide the population in a pond. Different density and feeding treatments gave clear indications of density regulation and of food limitations. Eisenberg refers to a "maintenance nutrition" level at which the snails stay alive but are barely capable of reproduction.

Laboratory studies of schistosome host snails have also established valuable relationships and procedures. The relative demographic performance of B. globosus and B. pfeifferi in different environments has been measured using the intrinsic rate of natural increase. The method is explained by Shiff and Husting (1966) and provides a way of establishing the range and optimum level of an environmental variable for snail population growth by reference to a single population parameter.

1.4. The Aims of this Project

Research on schistosome host snails to date has led to a good understanding of the environmental mechanisms (mainly temperature and rainfall) which control population fluctuations in the field. In addition, many more local influences have been closely investigated (e.g. the aquatic weed Ceratophyllum is known to have an important influence on the density of Bulinus truncatus in Ghana, Paperna, 1969; Odei, 1973; Chu, 1978; Klumpp and Chu, 1980). However, where relationships have been demonstrated, the processes involved are often poorly understood. Laboratory studies (e.g. Harrison and Shiff, 1966, and those reviewed in Thomas, 1973) have established the importance of many intrinsic and external influences on the growth rates, reproduction and survival of snails.

The methods used to study snail populations in the field have not progressed significantly since the early 1970's, and a major part of this project is concerned with adapting, improving and testing both the field sampling of aquatic snails and the analysis of the data collected. The life table is still the most powerful tool for organising demographic data and is used to obtain field values for the intrinsic rate of natural increase. The idea of using r_m (the potential for increase, as distinct from the actual rate of increase) as a measure of population growth potential or performance in a particular environment (Shiff and Husting, 1966) is extrapolated to field situations to

provide a measure of the suitability of a habitat in terms of a particular species. A further aim is to relate this habitat suitability to particular environmental variables, and to find out which stage of the life cycle is most affected.

The intrinsic mechanisms of population regulation are investigated both in natural populations and controlled cohorts in the field, with particular reference to the questions raised by Anderson and May (1979) (see Section 1.2.2.).

Another, and no less important aim of the investigation, was the identification of schistosomiasis transmission foci in the project area. Warren et al (1979) found that up to 84% of schoolchildren (aged 5 - 18 years) from schools around Mombasa on the Kenya coast were passing S. haematobium eggs in their urine. This indicates that high levels of transmission are being maintained in the area and it is therefore very important, from a public health point of view, to locate the transmission foci and identify the snail species acting as intermediate host, and the seasonal and spatial fluctuations in prevalence.

CHAPTER 2 STUDY SITES

2.1. Description of the Study Area

Initial surveys of freshwater bodies extended from Bamburi (8km north of Mombasa) to Vipingo (27km north of Mombasa), and from the coastline to 6km inland. The area was inspected by air and by road and any large (> 10m diameter) ponds and dams were visited to look for potential schistosome host snails. Table 2.1 lists the water bodies, map references and bulinid snails found. (*Bulinus forskalii* group snails were present in almost all water bodies, but are not considered to be potential hosts of schistosomes). Fig. 2.1 shows the project area and sites inspected.

Two dams, Nguni (No. 1) dam at Bamburi, and Benes dam at Vipingo, were chosen for detailed study and are described below. The other sites were inspected periodically and snails were collected for shedding tests (see Chapter 8). Snails were provisionally identified using W.H.O. manuals (W.H.O. 1973a, 1973b) and specimens were sent to the British Museum (Natural History) for confirmation.

All the dams were constructed by bulldozing an earth wall to dam an existing water catchment area, and measured from 50m to 550m long (Bamburi dam No. 2 and Benes dam respectively). Bamburi dams, Nos. 2, 4 and 5 were built

Table 2.1. Freshwater sites between Bamburi and Vipingo, inspected for schistosome host snails.

Location		Name	Map reference* NS	EW	Snail species
Bamburi	1	Dam 1 (Nguni)	955835	057615	Bulinus (Ph.) globosus
	2	Dam 2	955860	057595	Bulinus (Ph.) sp. unknown
	3	Dam 3	955880	057590	Bulinus (Ph.) "
	4	Dam 4	955865	057650	Bulinus (Ph.) "
	5	Dam 5	955910	057640	None
	6	Quarry Entrance Pond	955900	057720	Bulinus (Ph.) nasutus
	7	Bamburi Old Dam	956015	057700	Bulinus (Ph.) globosus
	8	Quarry Dam West	955955	057645	Bulinus (Ph.) globosus
Utange	9	Utange Pond	956160	058140	Bulinus (Ph.) nasutus
Mtwapa	10	Jumba Marsh	956610	058320	Bulinus (Ph.) nasutus
Kikambala	11	Kikambala Marsh	956970	058550	Bulinus (Ph.) nasutus
Vipingo	12	Benes dam	957760	058425	Bulinus (Ph.) globosus
	13	Chodari dam	958120	058690	None
	14	Junju dam	957625	058440	Bulinus (Ph.) globosus

* 12 figure grid references from the survey of Kenya (series Y731) (1972), sheets 198/3 and 198/4.

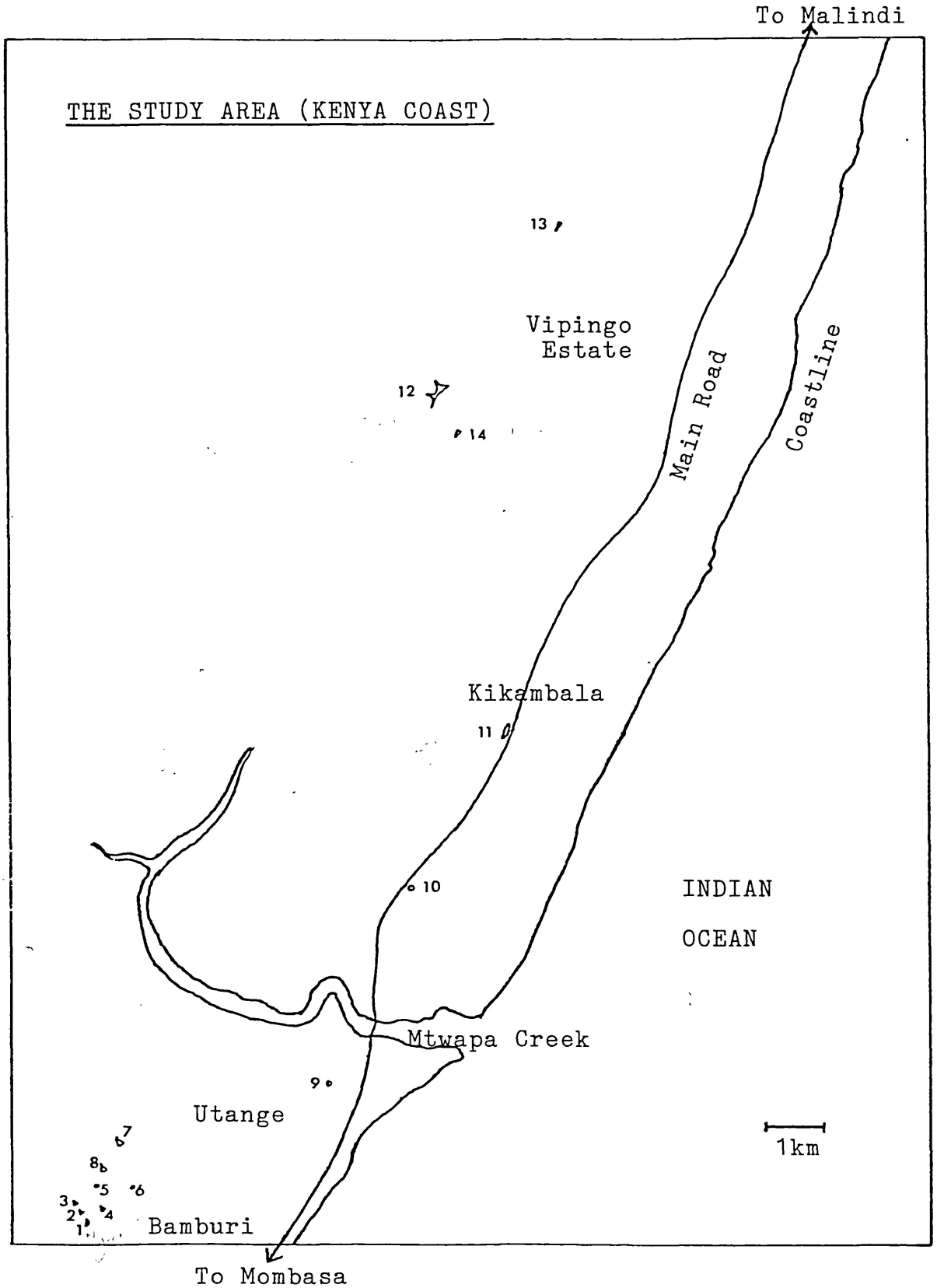


Fig. 2.1 The project area, showing sites inspected. Numbers refer to Table 2.1 which lists names and map references of the water bodies.

during the execution of this project (in February 1981). No bulinids were found in dam No. 5. One Bulinus (Physopsis) species snail was found in May 1981 in dam No. 4 but none in subsequent inspections. A few Bulinus (Physopsis) species snails were found in dam No. 2, but these had disappeared by November 1981. It is most likely that these were snails (probably Bulinus nasutus) which were previously present in the catchment areas where the dams were built, rather than examples of random dispersal colonisation. Dam No. 3 was over five years old and had been inspected in 1978 and 1979 prior to the project. It was again inspected six times during 1980/81 and on none of these occasions were bulinid snails found, although the prosobranch Cleopatra ferruginea appeared during 1980. In February 1982, 15 bulinid snails were found, indicating that the dam had been colonised between November 1981 (when the dam was last searched) and February 1982.

The remaining sites can be divided into permanent and temporary water bodies. The dams (which constituted the only permanent water bodies) formed the habitat for Bulinus globosus, whilst B. nasutus were invariably found in the temporary water bodies (see Table 2.1).

2.1.1. Benes dam

Benes dam is situated 6km inland from the coast at an altitude of 90m. It was built in a valley, using the

underlying latosolic sedimentary dark red loamy sands to dam the temporary stream in the valley bottom.

The dam covers 3.5 Ha and has a maximum depth of 4m. Although the water level fluctuates with the rainy seasons it has not dried out since it was built in 1959. It was constructed by the management of Vipingo Estates originally to irrigate the nearby sisal plantation. Because of pumping costs it has never been used for this purpose, and its only commercial use is now for stock watering. The dam serves as the main water supply for washing, laundry, fishing and drinking for the local population.

Luxuriant stands of emergent and aquatic vegetation fringe the dam for 4 to 15m and to a depth of 1.7m. The major species are:

Cyperus exaltatus
C. alternifolius
Typha latifolia
Nymphaea caerulea
N. lotus
Ipomoea aquatica
Pistia stratiotes
Najas pectinata

Fig. 2.2 shows a typical water contact site, cut through the dominant stands of Typha latifolia. Fig. 2.3 is a map of the dam, showing the position of the major sampling sites.

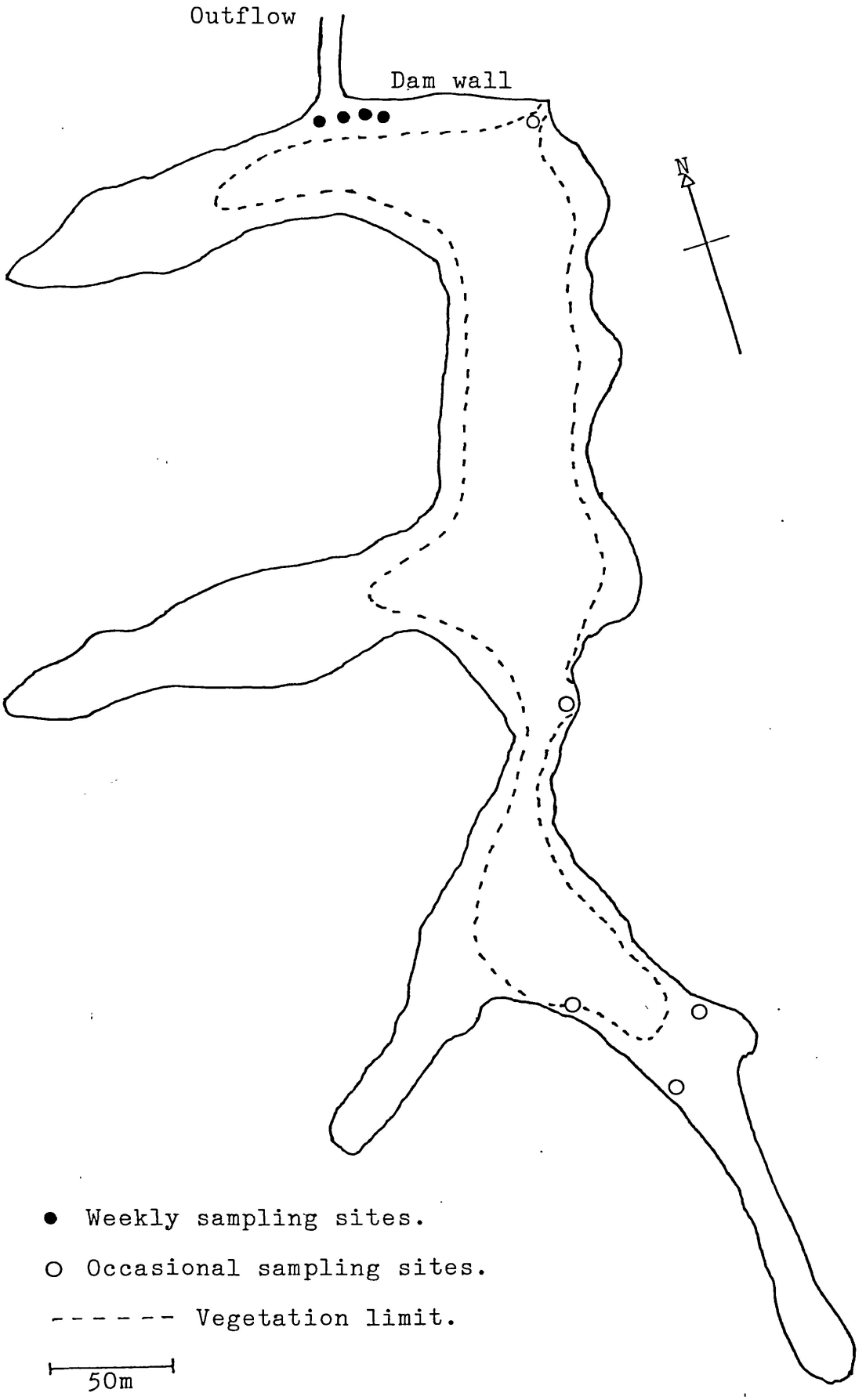


Fig. 2.2 Benes dam, showing a typical water contact site, cleared through the fringing emergent vegetation.

Fig. 2.3 Benes Dam (Vipingo).

Permanent trap sample sites were all located round the main water contact site, beside the dam outflow. Occasional snail samples were collected (for shedding tests) from other water contact sites round the dam.

BENES DAM


Outflow
Dam wall
N
● Weekly sampling sites.
○ Occasional sampling sites.
------ Vegetation limit.
50m

2.1.2. Nguni dam

Nguni dam, 19km south of Benes dam, is situated 5km inland, at an altitude of m, on brown clay derived from marine sediments. It was built in 1975 by the same method as Benes dam, in order to provide a breeding pond for tilapia (Sarotherodon niloticus) which are reared in a nearby fish farm. It is also used for stock watering (mainly sheep). To prevent interference with fish stocks the dam is patrolled by a watchman at all times, and local people are not allowed to use the water. (The nearest villages are 2km away and alternative water resources are available.)

The dam covers 0.3 Ha and has a maximum depth of 3m (sufficient to ensure that it has not dried out since it was built). The fringing vegetation is sparse compared to Benes dam, with patches of Cyperus exaltatus and isolated clumps of Nymphaea caerulea (see Fig. 2.4). During 1981, Najas pectinata, a choking weed, became established in Nguni dam and may cause significant changes in future years (especially in view of the importance of aquatic macrophytes as a substrate for B. globosus). Fig. 2.5 shows Nguni dam and the position of permanent sampling sites around the edge.

Nguni dam was chosen as a main sampling site because it is closely controlled, and interference, both to sampling equipment and the snail population is minimised. It is also



Fig. 2.4 Nguni dam (Bamburi).

NGUNI DAM

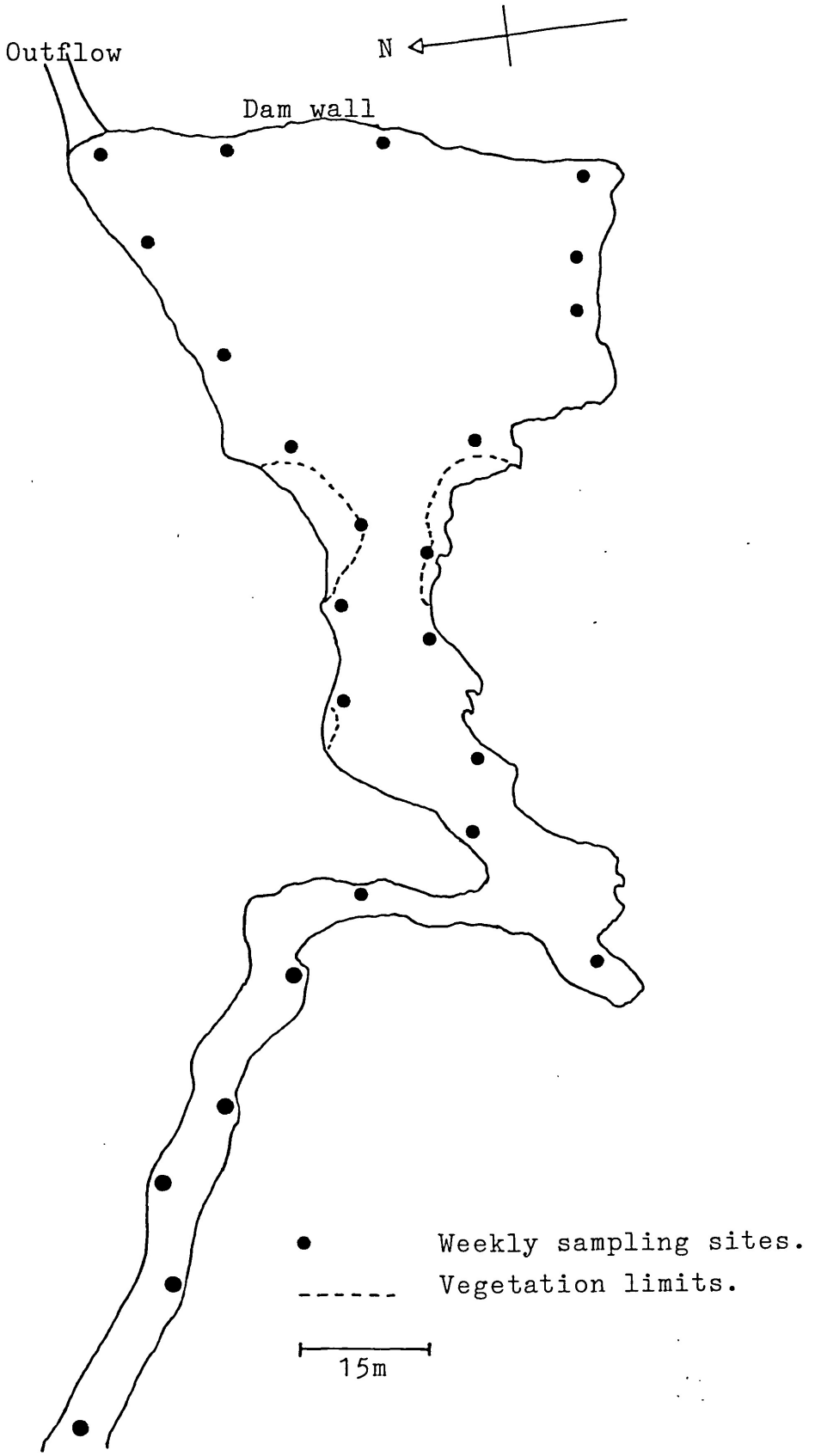


Fig. 2.5 Nguni Dam, Bamburi, showing the position of weekly sampling sites.

small enough that all parts can be sampled by one person. Benes dam, on the other hand, provided the most likely schistosomiasis transmission site in the area.

2.2. Climate

The climate on the Kenya coast is dominated by the south-west monsoon, bringing the major rainy season from April to June, and the north-east monsoon, bringing a more variable rainy season in November. December to March is hot and usually dry, whilst July to October is cooler and somewhat wetter. Figs. 2.6 and 2.7 summarise mean monthly rainfall and air temperatures. Rainfall and water temperature in the dams throughout the project are given in Chapter 9.

2.3. Population Fluctuations of Bulinus globosus in Benes and Nguni Dams

Continuous weekly sampling programmes (using methods described in Chapter 3) were carried out in Nguni and Benes dams from March 1980 to January 1981 and from June 1981 to February 1982. (Throughout the rest of this report these two periods are referred to as 1980/81 and 1981/82.)

The observed fluctuations in sample sizes of B. globosus in the two major field sites (Benes and Nguni dams) are shown in Fig. 2.8. They are included here because they are frequently referred to in succeeding chapters. Samples from

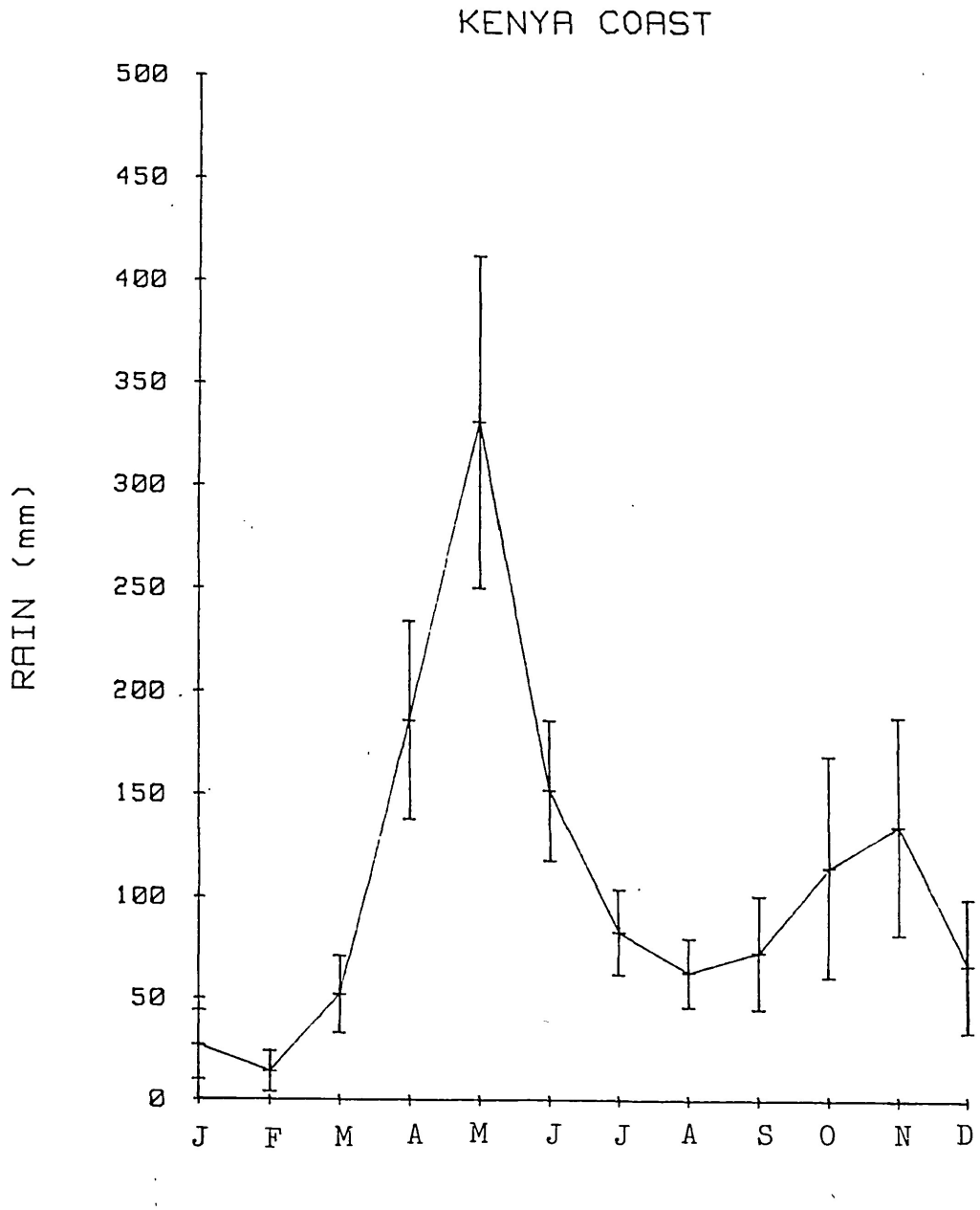


Fig. 2.6 Mean monthly rainfall (with 95% confidence limits) from data collected at Bamburi airfield 1964 - 1979.

Mean yearly total rainfall is 1247 $\pm$ 121mm.

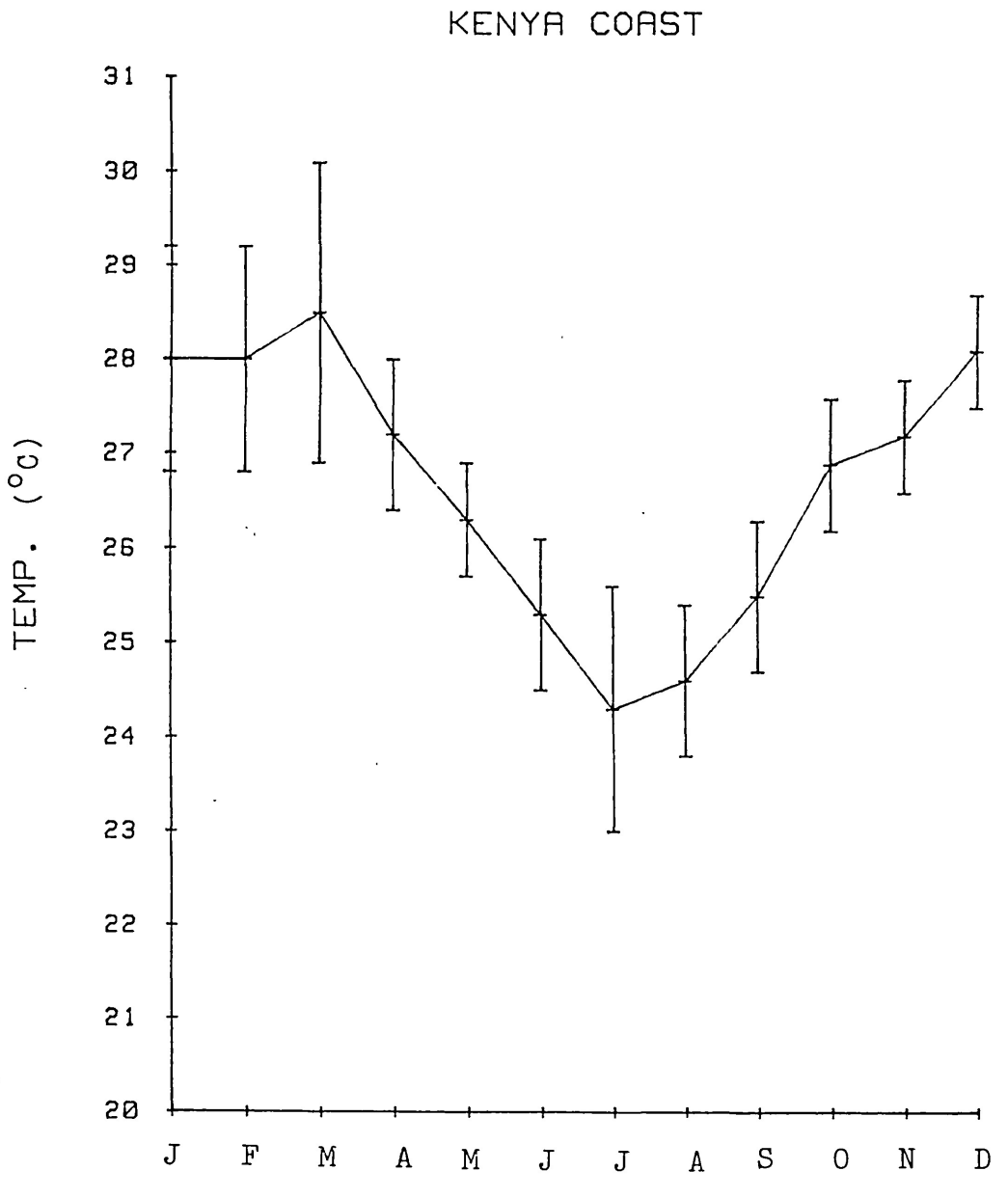


Fig. 2.7 Mean monthly air temperatures (with 95% confidence limits) from data collected at Bamburi airfield 1975 - 1981.

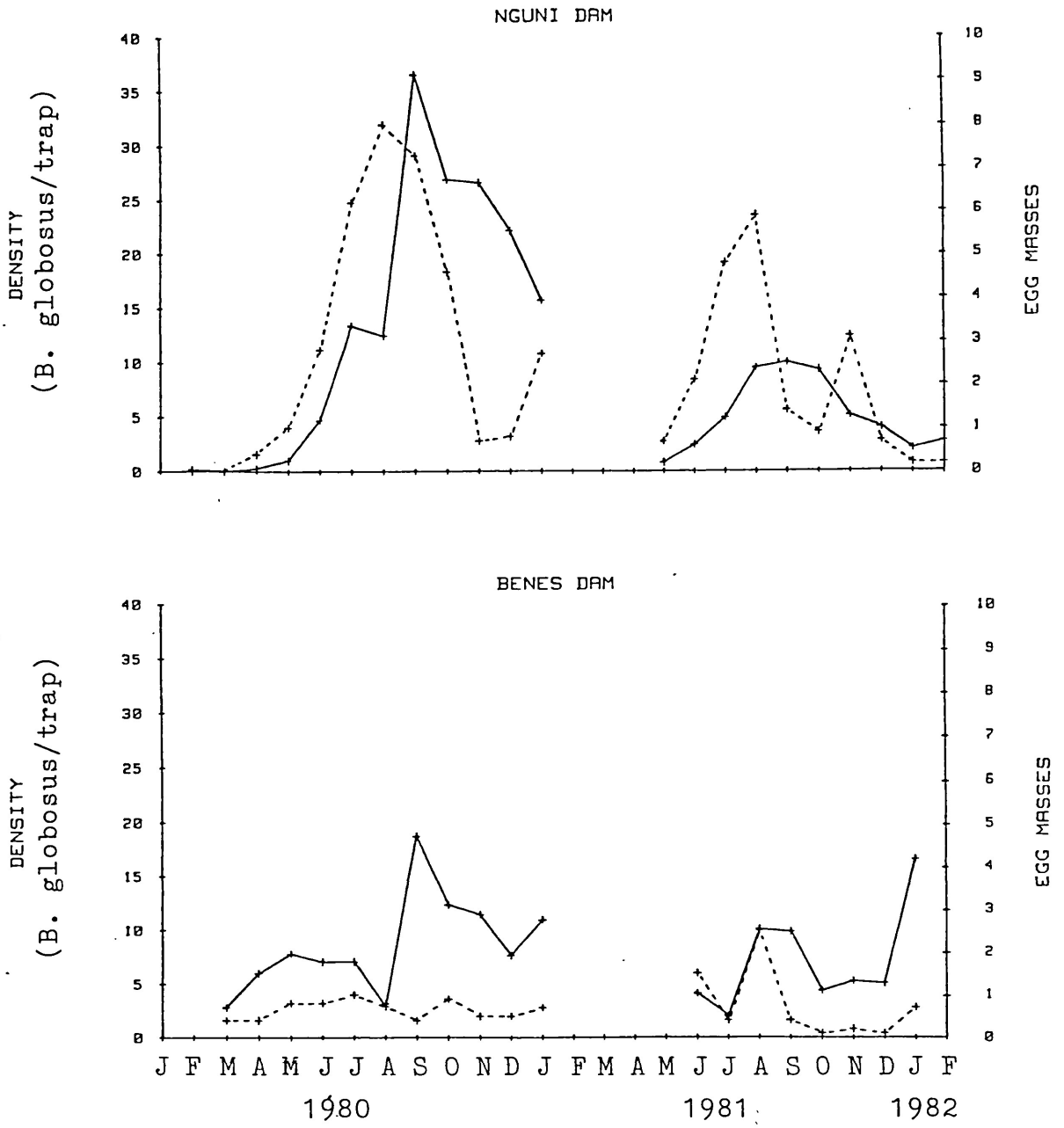


Fig. 2.8 Fluctuations in mean numbers of B. globosus per trap (+—+) and egg masses per trap (+- - -+) throughout the project in Nguni and Benes dams.

Nguni dam were taken from between 100 and 260 snail traps per month. Data from Benes dam is from 80 traps per month during 1980/81, but only from between 8 and 16 traps per month during 1981/82 when most fieldwork was concentrated on Nguni dam. Because of this reduced sampling effort for 1981/82 from Benes dam the collected data is less reliable than the other data sets, and the subsequent less detailed analysis reflects this.

Detailed weekly sample results showing numbers of snails in each size class are given in Appendix A.

CHAPTER 3 GENERAL METHODS

3.1. Introduction

In the design of a field sampling programme a variety of authors have stressed (e.g. Southwood, 1978) the need for a clear definition of the parameters which must be measured. Conflicting priorities and available time and manpower, however, will inevitably prejudice the attainment of the ideal sampling system despite great forethought in design.

Any sampling method implies a disturbance of the system, which is itself likely to have some effect on the measurements being taken. As a rule, the more rigorous the measurements, the greater the disturbance and the less likely the results are to apply to a natural system. The methods used in this project were aimed to provide a spectrum of data from laboratory studies, (in which the inputs are rigorously controlled, and total census data is obtained), to field studies (in which there is no control of the environment, and samples are measured from the real world). A third level of data was obtained from enclosures in the field, which provided some control of inputs, and total census data, but in as near to natural conditions as possible. Field measurements were taken wherever they realistically could be, but similar measurements in controlled environments were used for comparison and to investigate the effect of particular variables, as well as

for measuring those aspects which could not be observed in natural populations.

In order to construct life tables for natural snail populations, the major parameters which must be measured are:

(i) density;
(ii) growth rates;
(iii) age specific reproduction rates;
(iv) survival rates.

Previous field studies on aquatic snails have tackled the measurement of those parameters in a number of ways. Hairston et al (1958), in a paper evaluating various sampling techniques, concluded that no single method was suitable for all habitats, and that the best method also depended on the aims of the research.

3.1.1. Sampling methods

Obbe (1962a) used 10 minute searches in defined areas (a method developed by Olivier and Schneidermann, 1956, and referred to hereafter as man-time sampling) to obtain relative density estimates of Bulinus nasutus. Dazo et al (1966), working in canals, used a 25cm wide drag scoop to collect B. truncatus. Shiff (1964) employed a modified Eckman grab in ponds to collect B. globosus. Sturrock (1973a) used 3ft^2 quadrats in marshes, a mud corer in banana drains and timed searches in ponds and streams. Klumpp and

Chu (1977) and Chu and Vanderburg (1976) tested and used palm leaf mats to sample B. truncatus rohlfsi. Pringle and Msangi (1961) developed bamboo rafts sunk into the substrate which could be raised and lowered for exhaustive snail counts. Boerger (1975) stood glass plates upright on the bottom of ponds to sample Helisoma spp. snails.

In this study it was felt that sampling need not provide absolute density estimates. These would be of some interest but are difficult to compare in a heterogeneous environment. Since aquatic snails spend part of their time on the bottom, part in among emergent and aquatic vegetation, and part floating under the surface film, it is difficult to relate absolute densities to an area or volume. Should the density be regarded as per m^2 of pond bottom? or as per m^2 surface area of vegetation? or as per m^3 of water? For comparative purposes, a relative density measure is likely to be more uniform. Although both Hairston et al (1958) and Southwood (1978) point out the desirability of exhaustive sampling, it was felt that there were sufficient reasons for using a relative method. Tests during a previous pilot project (O'Keeffe, 1979) had shown that exhaustive techniques (quadrats in shallow water, corers in deeper water) were extremely time consuming to manage and very destructive to the habitat. Pesigan et al (1958) found that a core sample took 10 times as long as a quadrat sample of the same size. Habitat destruction becomes a major problem during a long term project in which frequent samples are obtained from the same site. The same problem applies to any method where

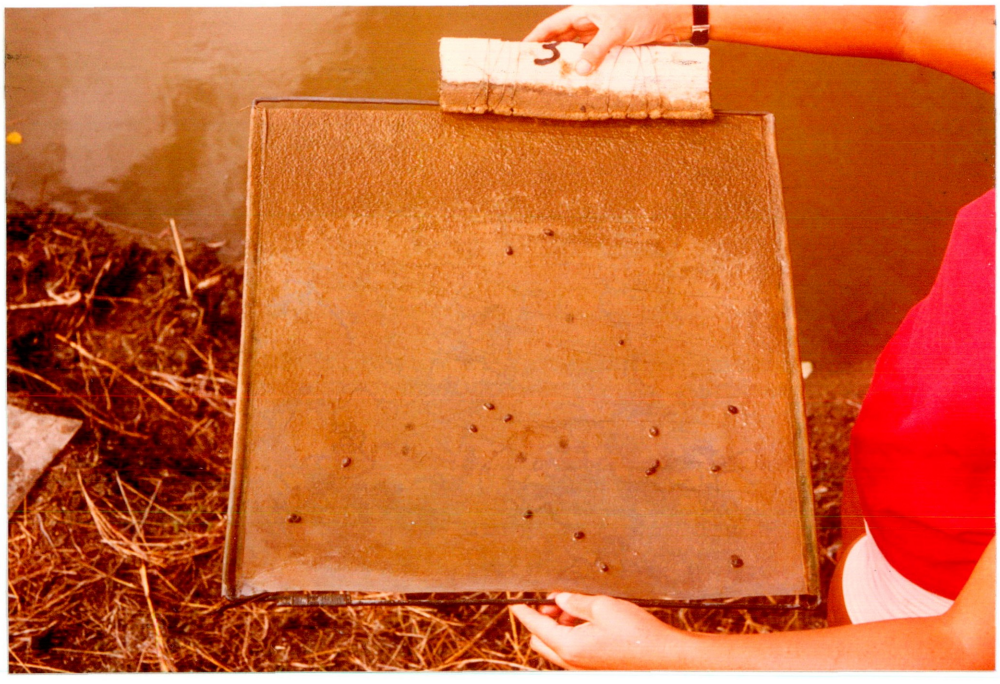
the habitat must be searched, such as man-time sampling. The ideal method to minimise disturbance is a passive trapping method such as the palm mats used by Chu and Vanderburg (1976). They found in comparisons with man-time sampling, that traps were more sensitive, especially in picking up small snails, but were more time consuming in terms of snails recovered per unit effort. Traps can also be floated to move up and down with water fluctuations while in contrast, fixed sample sites may be left high and dry. They also found that the mats needed careful handling to minimise loss when they were removed from the water (losses due to snails falling off could be as high as 30%). This is not a serious problem as long as the loss is constant for all traps (since the samples are relative anyway), but obviously more traps, and therefore more sampling effort, will be required when large numbers of snails are lost. Hairston et al (1958) thought that palm leaf traps were of little use in quantitative studies since: "their attractiveness to snails depends upon their stage of decay". Chu and Vanderburg found that fresh or decayed leaf was equally efficient in attracting snails, and used fresh leaf for convenience. During a pilot project (O'Keeffe, 1979) palm leaf mats were used and were found to be very effective in collecting snails. However, for a long term project, the state of decay of the leaves introduces uncertainties about the comparability of the data. It was therefore decided to use plastic sheeting which would not rot away (and therefore not require changing) and would be unlikely to change its surface or other characteristics through time.

3.1.2. Plastic sheet snail traps

The configuration of the traps is shown in Fig. 3.1. Heavy gauge plastic sheeting was sewn onto a metal frame using nylon thread. The plastic sheet inside the thread line constituted the sample area and at 50 x 50cm provided $0.5m^2$ per trap of substrate, taking into account both sides of the sheet. A polystyrene float was tied to the top of the trap so that the structure would float with the whole sampling surface under the water. At sites where the depth was > 50cm the traps floated vertically tethered to a stick, by nylon string. Where the depth was < 50cm the trap rested on the bottom and angled up to the surface.

Because the traps had to be left for long periods in the field, they were constructed of cheap and easily replaceable materials. The polystyrene floats came free from any firm receiving delicate goods in suitable packaging. The frames were made up at the local prison, the only skills needed were an ability to measure, bend wire and bond the two loose ends with tying wire. The cutting and sewing of the plastic was done by the local prison industry. All materials were readily available locally and the cost for 200 traps worked out to approximately 50p (U.K.) each.

Local people at the two main sites (Benes and Nguni dams) were informed of the reasons for the siting of snail traps in the aquatic habitats and appeared to be very tolerant of



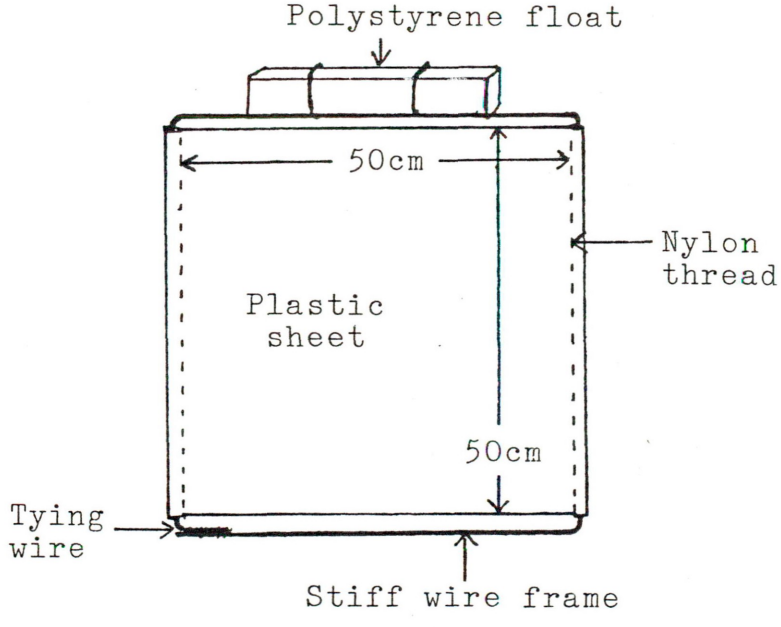


Fig. 3.1 A plastic sheet snail trap, providing $0.5m^2$ surface area for colonisation by Bulinus globosus

their presence at washing sites. None were taken away during the entire project. Fifteen traps were trampled by livestock, and this caused the closure of five sampling sites which had subsequently to be sampled using man-time methods. The traps, unless well protected, are not compatible with livestock. The only other source of loss was through flooding; sixty-three traps were washed away and damaged or lost during two major floods. This problem could have been overcome by tethering all the traps to the shore but this increases interference by animals, wild and domestic, which constantly trip over the tethers.

3.1.3. Choice of trap sites

The traps were used in the two main water bodies (Benes and Nguni dams). Since Nguni dam is much smaller than Benes, the aim was to sample all around Nguni but only at selected sites at Benes. Tests during the pilot project (O'Keeffe, 1979) had shown that the great majority of snails were confined to the emergent vegetation in Benes, at depths <2m. Trap sites were therefore confined to the edges of both dams, making sampling much easier, and allowing more samples to be collected. The edge of the dams is also, of course, where all human water contact takes place, in the absence of boats. To cope with changing water levels, sites were moveable along transect lines pointing to the centre of the water body. Sampling in each dam had to be approached rather differently: at Benes the dam is

unsupervised and during the pilot project, attempts at random sampling had been hampered because any trail through the vegetation to a sampling site becomes an invitation to use the site for washing, etc. So for this project, since the whole dam could not be sampled, it was decided to concentrate on sampling at existing water contact sites around the dam. Four sites were established at 5m intervals at the main water contact site and five other individual sites were established at contact sites between 100 and 200m apart (see Fig. 2.3).

At Nguni dam, with its 24 hour protection by a watchman, random siting of traps was possible. It was initially felt that sixty-five traps/week could be managed at Nguni, and sites were chosen on this basis. In the event, snail numbers rose much higher than expected and the number of traps processed per week was cut to thirty-six after seven months. Sites were first established with the dam roughly half full and with this circumference of water, were placed between 10 and 30m apart, the exact distance being decided with reference to random numbers. As the dam rose and fell sites moved closer and further apart.

At Benes dam, five traps were used per site, arranged as compactly as possible (see Fig. 3.2). At Nguni, all sites had two traps, and three sites had five extra, to provide a measure of within site sampling variance. As the trap sampling programme was reduced during 1981, multiple trap sites at Nguni were reduced to four traps and all sites at Benes dam were reduced to two traps.

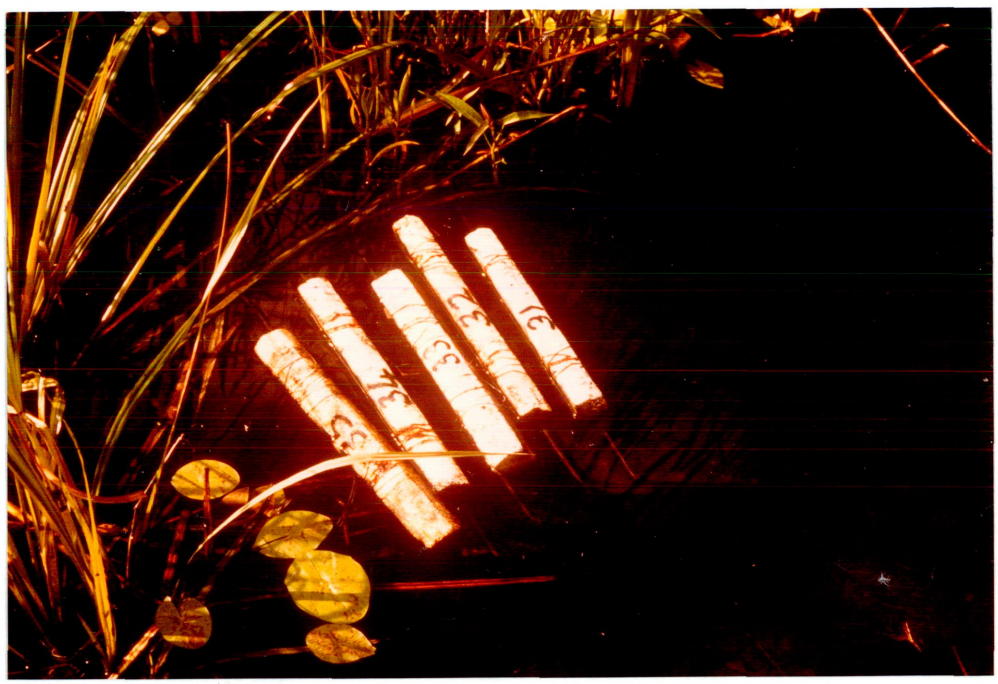


Fig. 3.2 A multiple trap sampling site.

3.2. The Sampling Regime

Having decided on the sampling method, some considerable effort was expended to test the efficiency and uniformity of the traps, and to calibrate them against other sampling methods.

3.2.1. Colonisation rate

Despite the fact that plastic is relatively inert, there was obviously going to be a time lag before colonisation by snails would be complete. Chu and Vanderburg (1976) tested their palm mats over different exposure times and found that in sparse populations, snail density reached its asymptote after two days but that for large populations, the density on mats continued to rise during the first four days.

To test the initial colonisation rate, five sets of new unweathered traps were placed at five sites in Benes dam. The traps were searched daily for the first week (except for day 5) and thereafter weekly. The trend is shown in Fig. 3.3, and indicates that colonisation is complete by two weeks after immersion. As a result of these observations traps were left in the water for at least a fortnight before any samples were taken.

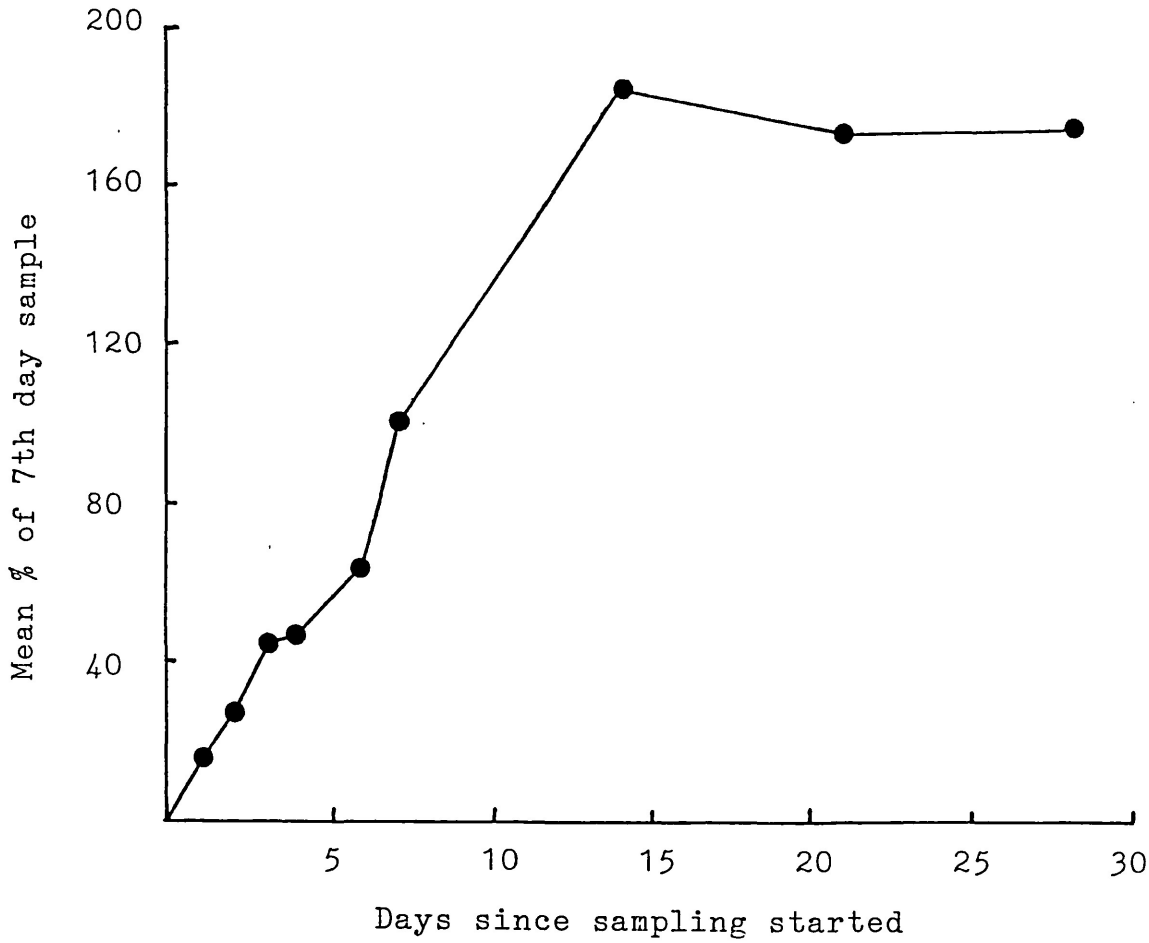


Fig. 3.3 The rate of colonisation of snail traps.

Five sets of five traps in Benes dam were inspected six times during the first week after they were placed in the sampling sites, and weekly thereafter. Because of differences in snail densities at different sites, each sample was expressed as a % of the sample after one week.

After sampling snails were returned to the trap so that, assuming that snails remained attached to the traps, colony levels should immediately have been as high as pre-sampling levels.

3.2.2. Intersample time

In previous projects a variety of different time intervals between samples have been used. A great deal depends on the practical necessities of the area to be covered, manpower available, duration of the project and the required resolution of the measurements. Chu and Vanderburg (1976) sampled every two days during a two month project, mainly designed to test sampling methods. Weekly sampling intervals were used by Webbe and Msangi (1958), Eisenberg (1966) and Boerger (1975). Fortnightly intervals were used by Pringle and Msangi (1961), Webbe (1962a) and Sturrock (1973a). Monthly intervals were used by Shiff (1966), Dazo et al (1966) and Klumpp and Chu (1977).

Obviously, more detailed information can be obtained by more frequent sampling but the level of interference with the population also increases. Gross changes in aquatic snail populations can be followed monthly but more frequent sampling is required to be sure of recording sudden declines and bursts of egg laying. One objective was to measure detailed changes at a small number of sites and thus weekly

sampling was adopted. The samples can then be lumped together providing larger degrees of freedom for parameters which need only be measured monthly.

3.2.3. Sample uniformity

Although the traps were designed to maximise the uniformity of samples, there were obvious differences both within traps and between trap positions which needed quantifying.

3.2.3.1. Trap underside v. upperside: Where (as in the majority of cases) traps were laid in water < 50cm deep, the traps were at a slant (Fig. 3.2), and it quickly became obvious that, due to differences in light and sedimentation, algal growth on the upperside of the traps was quite different from that on the underside. It was also obvious that for this and/or other reasons (exposure to predators, excessive light, etc.) snails were colonising the underside far more heavily than the upperside. (See Table 3.1.)

3.2.3.2. Top v. bottom traps: It was considered possible that the position of a trap relative to the position of other traps in a site might make a difference to its suitability for snails:

The ratio of the snails on the top trap to those on the bottom trap should be unity provided trap positions are equally attractive. In fact, using data from pairs of

Table 3.1 Comparison of snail densities on each side of the traps.

(Data from two weeks during 1980 when snails were recorded separately from each side of each trap. Means and their 95% confidence limits are given.)

	Nguni dam		Benes dam	
	Week 1	Week 2	Week 1	Week 2
Mean snails/upper side	2.4 ± 1.0	1.5 ± 1.2	2.7 ± 1.5	0.8 ± 1.2
Mean snails/under side	16.4 ± 4.0	16.9 ± 3.7	10.6 ± 2.0	6.3 ± 2.5

i.e. from 4 to 11 times as many snails were found on the under side of traps as on the upper side.

traps during 1980 at Nguni dam, the mean ratio was 0.91 ± 0.11 ($n = 129$). A χ^2 test showed that this is not significantly different from 1 ($P < 0.05$).

At multiple trap sites, the preference ratio for each position is the number of snails at a trap position divided by the mean sample per trap. At seven-trap sites in Nguni dam the results were:

Top trap	0.86 ± 0.17	($n = 30$)
Trap 2	0.91 ± 0.15	"
Trap 3	1.01 ± 0.12	"
Trap 4	1.05 ± 0.14	"
Trap 5	1.01 ± 0.15	"
Trap 6	1.00 ± 0.16	"
Bottom trap	1.16 ± 0.20	"

i.e. the bottom position was marginally more attractive than the top two positions, with intermediate positions more or less equally attractive. (At all trap sites, individual traps were alternated in different positions in case of any preference for the trap rather than its position.)

3.2.3.3. Trap aging: The build-up of algae and sediment on traps throughout their sampling life may have changed their relative attraction for snails.

Randomly selected traps were replaced at sixteen trap sites when the remaining traps of each pair had been in the water for at least three and a half months. The replacement traps were unweathered. The relative sampling efficiency of new versus old traps is shown in Fig. 3.4. At one week, the mean sample size is significantly less on the new traps than on the old, but from two weeks on, if there is any difference it is not significant. Following these tests, a stock of replacement traps was kept in the water so that damaged or lost traps could be replaced immediately by weathered traps.

3.2.4. Trap calibration

Since the trap samples provided only relative density estimates, attempts were made to relate these measurements to absolute B. globosus density in the dams, and to compare them with estimates obtained from other commonly used sampling methods.

3.2.4.1. Absolute density: Since preliminary searches showed that B. globosus were almost exclusively associated with emergent vegetation and allochthonous material, the measurement of absolute snail density required counts of the number of snails per unit area of these substrates. At Nguni dam the dominant vegetation is a large sedge Cyperus exaltatus, whilst at Benes dam it is Typha latifolia. As both the plants have linear leaves, the surface area of the leaves is easily calculated as length x mean width x 2.

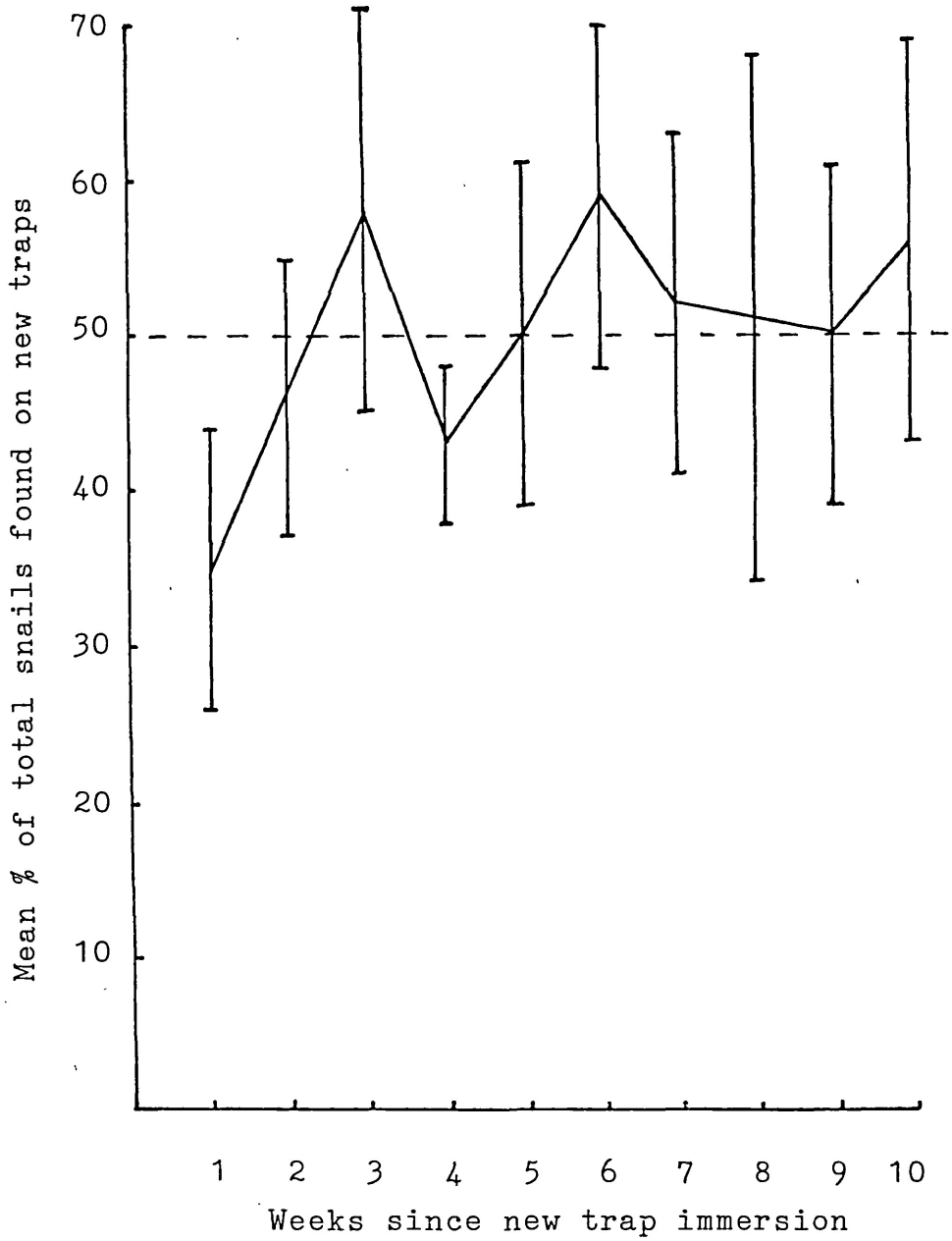


Fig. 3.4 Comparison of the relative attraction of new v. old traps. Samples from 16 new traps in Nguni dam, expressed as a percentage of the total site sample. Each new trap was paired with a trap which had been in the water for at least three months. (e.g. 50% indicates equal samples from each trap of the pair.)

It appears that new traps are less attractive, at least until they have been in the water for two weeks, than old traps.

By collecting lengths of leaf in the water, removing and counting any attached snails and measuring the surface area searched, a density estimate is obtained which is directly comparable with snail density on the traps. This was done regularly throughout the sampling programme at Nguni for C. exaltatus and during 1980 at Benes for T. latifolia.

Vegetation samples were taken from within 1m of a trap site and the observed density was then compared with the trap density at that site for that week. (See Table 3.2). In general, densities on vegetation appear to be 2 - 3 times those on the traps. Fig. 3.5 shows density trends in Nguni dam as measured by vegetation samples versus trap samples.

Two traps were constructed of Typha leaf and one of palm leaf (see Fig. 3.6). These were added to trap sites and used over six weeks after which they began to decay (see Table 3.3). Once again the vegetation appears to be more attractive, although in these tests the ratio is between 1 - 2 times.

Except on the Typha trap at Benes dam, the number of egg masses is also greater on vegetation. However, in terms of egg masses/snail, reproduction is virtually the same on plastic traps as on vegetation. The average ratios from all the above tests are:

Snails : 2.0 times as dense on vegetation.

Egg masses : 2.2 times as dense on vegetation.

Table 3.2 *B. globosus* densities on traps compared to those on natural vegetation.

(95% confidence limits shown.)

		Mean no. of snails /$\frac{1}{2}m^2$ vegetation	Mean no. of snails/trap
1980/81	Nguni	72 $\pm$ 29 (n = 11)	31 $\pm$ 4 (n = 51)
1981/82	Nguni	12 $\pm$ 5 (n = 23)	6 $\pm$ 1 (n = 76)
1980	Benes	30 $\pm$ 18 (n = 8)	11 $\pm$ 2 (n = 40)

		Mean no. of egg masses/$\frac{1}{2}m^2$ vegetation	Mean no. of egg masses/trap
1980/81	Nguni	3.0 $\pm$ 2.7	3.0 $\pm$ 1.0
1981/82	Nguni	2.6 $\pm$ 2.2	1.2 $\pm$ 0.7
1980	Benes	2.1 $\pm$ 2.9	0.4 $\pm$ 0.2

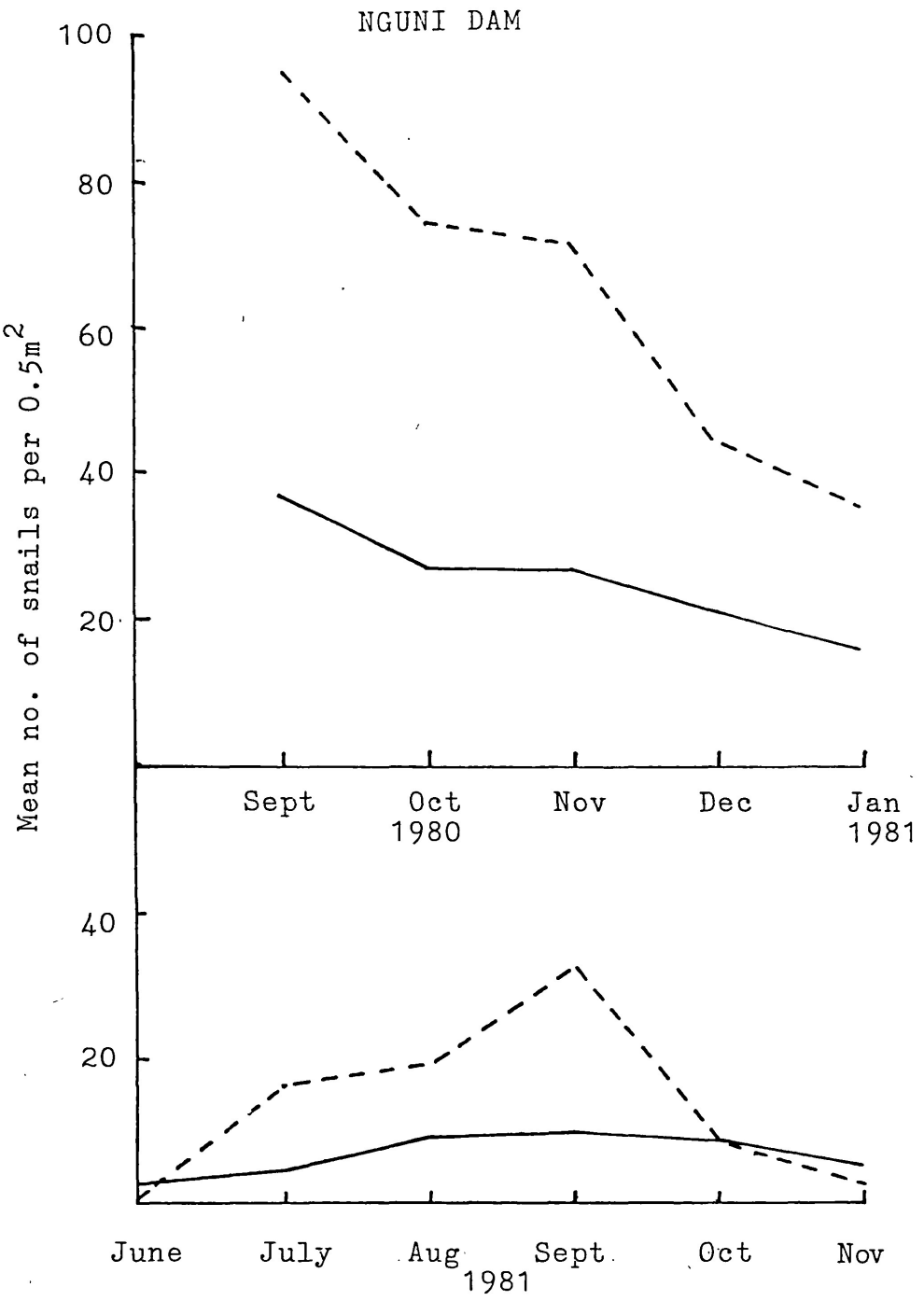


Fig. 3.5 Comparison of B. globosus densities on vegetation (- - -) and trap plastic (——).

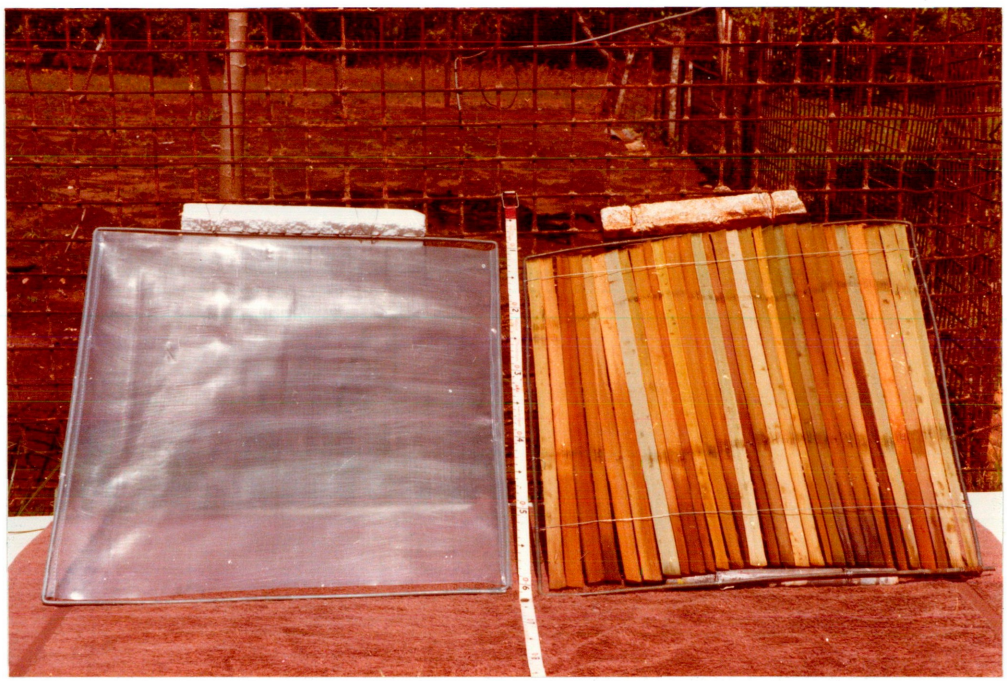


Fig. 3.6 Snail trap constructed of Typha latifolia leaf to compare the relative attractions of vegetation and trap plastic.

Table 3.3 Comparison of numbers of B. globosus on vegetation traps and plastic traps over six weeks.

NGUNI	No. on *Typha* trap	No. on plastic trap	Ratio *Typha*:plastic
B. globosus	106	49	2.2
Egg masses	42	26	1.6

NGUNI	No. on palm trap	No. on plastic trap	Ratio palm:plastic
B. globosus	249	167	1.5
Egg masses	12	5	2.4

BENES	No. on *Typha* trap	No. on plastic trap	Ratio *Typha*:plastic
B. globosus	71	56	1.3
Egg masses	10	8	1·3

This is an important result as it indicates that eggs/snail recorded from traps provide a realistic estimate of the overall reproduction of snails in the dams.

3.2.4.2. Man-time samples: This sampling method was used principally to collect snails outside trap site areas, for shedding tests. These collections were arranged to provide some measure of density changes and also as a comparison with trap samples. Since they were always taken in different areas from trap sites in order to avoid habitat disturbance, they are not strictly comparable with trap samples but nevertheless give an overall idea of the relative efficiency of the two methods.

Collections were confined to $4m^2$ areas within which as many snails as possible were gathered during a 15 minute period, using a long handled sieve and forceps. During trials, great difficulty was experienced in finding small snails among the vegetation, especially once the sediment was stirred up in the sample area. Since the collections were primarily for shedding tests, it was decided to ignore snails <3mm long. The results (given in Table 3.4) are therefore for snails larger than 3mm.

Removing a trap from its position and searching it for snails and egg masses took on average five minutes. The timed searches were therefore more efficient in terms of snails collected/minute. In addition, the traps required

Table 3.4 Comparison of numbers of B. globosus (>3mm) collected per 15 minute search and per plastic trap.

(95% confidence limits are given.)

	Mean no. of snails/15 mins.	Mean no. of snails/trap	Ratio Search:trap
1980 Benes	34 ± 11 (n =20)	5.4	6.2
Nguni	67 ± 38 (n = 7)	9.4	7.1
1981 Benes	40 ± 6 (n =34)	4.0	10.0
Nguni	27 ± 8 (n =19)	4.3	6.3

i.e. Between 6 - 10 traps were needed to provide the same numbers of snails as one 15 minute search.

considerable initial investment in construction. However, small snails and egg masses are much easier to see on traps and the size-specific accuracy of samples is therefore much greater.

These results are in accordance with the finding of Chu and Vanderburg (1976), that palm leaf mats provided more objective and sensitive results, but were less economical in terms of time spent sampling than man-time searches.

3.2.4.3. Small snail sampling: The average hatch size of B. globosus in Nguni and Benes dams was 0.8mm. At this size, they appear as little more than a light brown speck which requires some practice before they can be confidently recognised among the algae, sediment and other organisms found on leaves or traps. By the time the snails reach 4 - 5mm they are very obvious. Several workers have remarked on the difficulties of ensuring unbiased sampling at different sizes (e.g. Klumpp and Chu, 1977). Pesigan et al (1958) notes that even exhaustive techniques are likely to give an underestimate of very small snails.

In order to test the investigator's efficiency in recognising newly hatched snails from traps the following test was devised: 16 snails were hatched from an egg mass in the laboratory. A trap had been weathered for one month in a garden pond known to be devoid of snails. A helper, consulting random number tables, placed from 0 to 16 of the

hatchlings on the trap which the investigator then searched in an identical manner to that employed in the field. After being searched, the trap was taken away and any snails which had been missed were removed. After ten replicates, the sample totals were compared with the actual numbers on the trap. 88 out of a possible 92 snails were found (mean % success 97 $\pm$ 3). These results may be slightly higher than field results since the investigator knew that he was being tested and knew the maximum possible number of snails. However, it can confidently be stated that any major discrepancy would not be caused by a failure to find the small snails. This is important in the light of the sampling results (see Chapter 5), which consistently show an insufficient number of small snails to account for later numbers of adult snails.

3.3. Snail Measuring

Apart from recording snail numbers, the other essential parameter in population studies of snails is a measure of age. Obviously the size of the snails increases with age and size would perhaps best be measured as weight. This should ideally be measured as the shell free dry weight, the biomass of the animal, or the shell weight (Madsen, 1979). Such measures are only possible, however, when the snails are not being returned to the habitat. Thomas (1973) used wet weight measures of growth for laboratory

populations of Biomphalaria glabrata, but this is not a practical method for large numbers of snails in the field.

Almost all studies to date have used some linear measure of the shell as a measure of snail size, (e.g. the longest-axis shell length in the case of B. globosus). Stopped rules, vernier calipers and ocular calipers have routinely been used for measurements down to 0.1 or even 0.05mm. The accuracy of measurements has varied considerably in different studies. The snails are usually sorted into mm size classes (e.g. Shiff, 1964; Dazo et al, 1966; Boerger, 1975). Some workers have found that two or three different size classes (e.g. adult/juvenile or 0-10mm, 10-15mm, 15mm+) are sufficient (e.g. Webbe and Msangi, 1958; Pringle and Msangi, 1961; Otieno, 1969). For accurate age readings, measurements to 0.1mm (e.g. Eisenberg, 1966; Sturrock, 1973a) or at least 0.5mm (e.g. Webbe, 1962a) have been used.

It was decided initially to use a ruler to measure snails into mm size classes, mainly because of the difficulty of measuring more accurately in the field. It soon became apparent, however, that for mark-recapture growth estimates and for the examination of cohorts in snail boxes (see below), more accurate measurements were necessary. Vernier calipers were found to be very unsatisfactory because the lack of symmetry of B. globosus shells made orientation in the caliper jaws very difficult. It required up to ten measurements before two consecutive readings to the same 0.1mm were obtained. In contrast, as more experience was

gained, it was found that two or three readings were normally sufficient to obtain the same measurement to 0.1mm using a ruler. Since the snails were returned to the water immediately after measuring, in order to minimise disturbance, the use of a microscope graticule was not possible without taking the microscope into the field and setting it up at each site. This was impractical in terms of time and the amount of equipment to be carried. Furthermore in laboratory tests it provided only marginally more uniform results than measures using a ruler. It was therefore finally decided to return to the simpler method employing a ruler. Snails were placed on a slightly damp cloth to await measurement. This removed excess moisture and caused the snails to retract whilst preventing total dessication. They were removed one at a time from the cloth, placed on the rule, and measured by eye. A number of measurements were taken until two consecutive measurements tallied. Fig. 3.7 shows the level of consistency achieved.

3.4. Estimation of Snail Maturity

Size, and therefore age, of snails at adult recruitment is important in the investigation of age dependent reproduction.

Previous studies have normally allocated a single size, above which all snails are considered to be adult (e.g. 6.1mm+ for *Bulinus truncatus* (Paperna, 1972); 16mm+ for

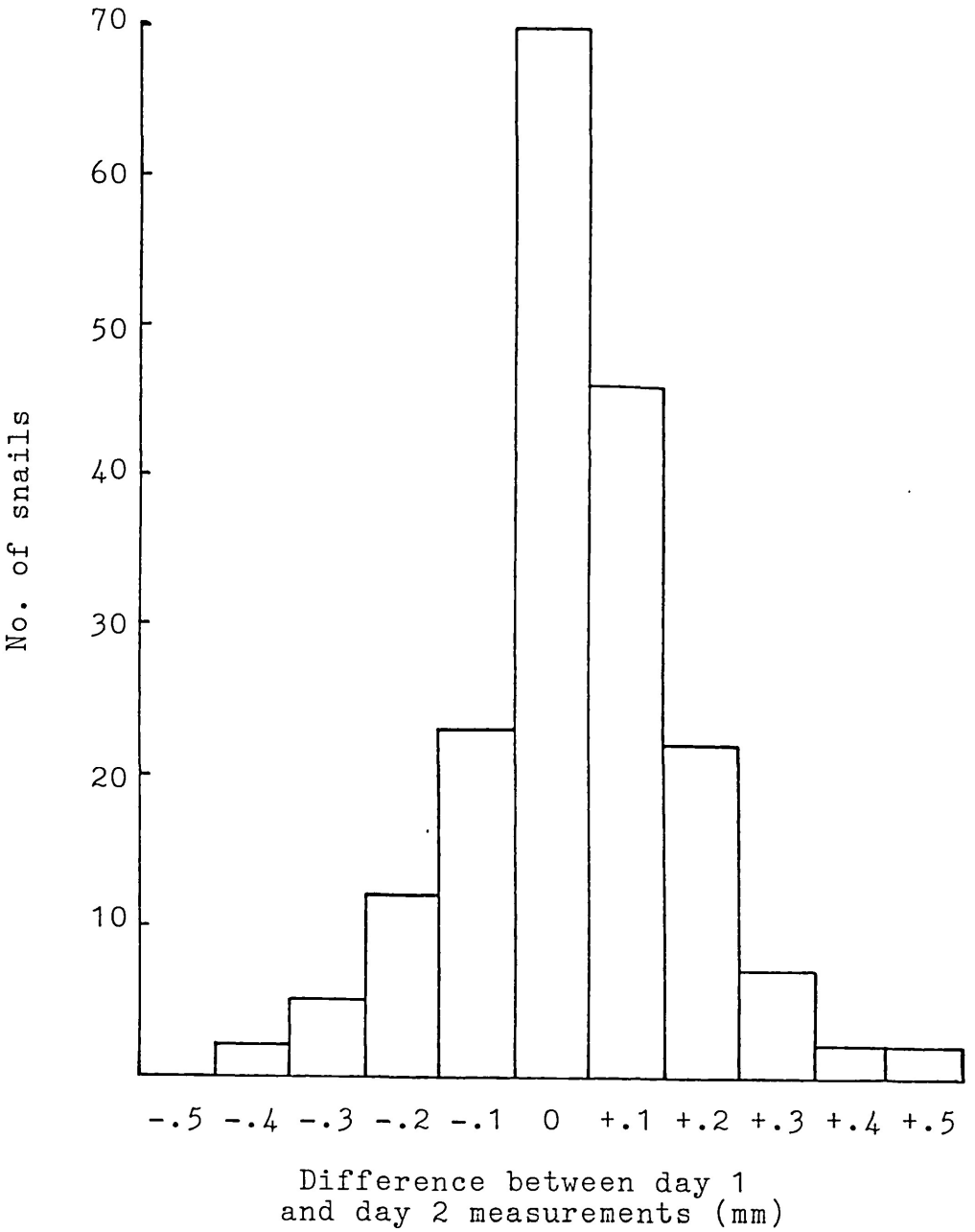


Fig. 3.7 Field measurement of B. globosus.

Marked snails 2.0 → 10.0mm were measured if they were recaptured on consecutive days.

Measurements should be the same or slightly larger (0.1mm or 0.2mm) if the measurements are accurate.

Helisoma trivolvis, (Boerger, 1975); 5mm+ for B. globosus, (Pringle and Msangi, 1960); 14mm+ for B. globosus, (Hira and Muller, 1966), or attempted to resolve an average age or size from laboratory data (e.g. Shiff, 1964, found that, at 25°C, B. globosus commenced egg-laying during the 4th fortnight). Pesigan et al (1958) recorded the sizes of all snails found copulating in the field and concluded that Oncomelania quadrasi males did not reach maturity until at least 3mm. Females appeared to be mature at 3.7mm, but in many cases egg production did not start until some weeks after copulation was observed. Both Pesigan (1958) and Shiff (1964) noted that environmental conditions could significantly affect the age at maturity of their snails. Sodeman and Dowda (1973) found that mean age at maturity in different laboratory-kept colonies of B. globosus varied between 20 and 39 days, whilst size varied between 5.1 and 6.9mm. Wright (1957a) suggested a comparatively simple method of recognising maturity in Bulinus jousseaumii (Dautzenberg), based on changes in the shell geometry. He concluded that, at the onset of maturity the accessory genital glands increase in size very rapidly necessitating an increase in shell volume to accommodate them. This is achieved by the body-whorl moving downward in relation to its predecessor, giving an increase in aperture length. The result is that maturity appears to be signalled by the exsertion of the spire. Fig. 3.8 shows the resulting difference in shell morph.

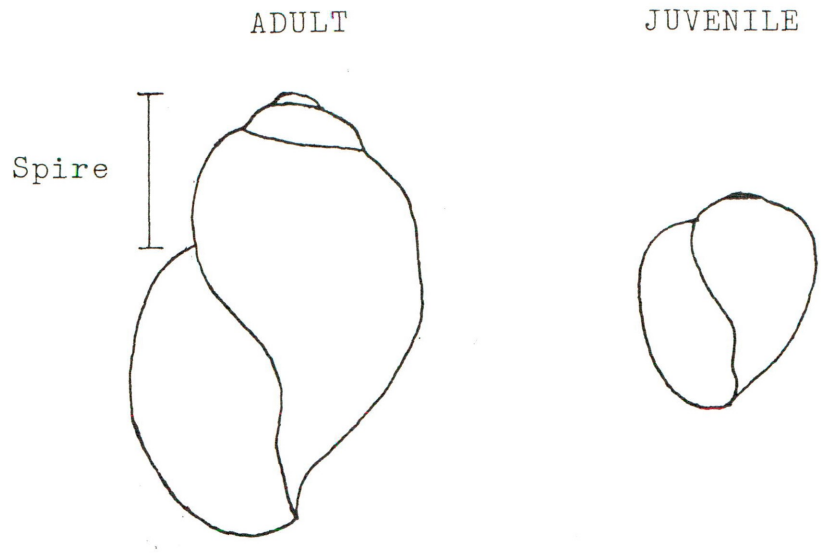




Fig. 3.8 Field recognition of maturity in B. globosus.

Adult spire exsertion caused by the growth of the accessory genital glands (Wright, 1957a).

Since Wright (1957a) proposed B. jousseaumei as a sub-species of B. globosus it is reasonable to expect that the same growth pattern would apply to both. During the preliminary survey differences in spire exsertion were recorded, and on this basis, shell length at maturity in different parts of the dam varied from 5 to 8.5mm. (O'Keeffe, 1979).

In order to test this method of adult identification, a number of B. globosus from different dams were collected and preserved in the way described by Wright (1957b). The snails were identified as juvenile or adult, according to the exsertion of the spire, in the same way as they would be in the field. The shells and their aperture lengths were then measured to the nearest 0.1mm after which an assistant removed the snails and coded each one. A partial dissection of each snail was then performed to determine maturity in terms of the relative size of the accessory reproductive glands, and in particular the albumen gland, the muciparous gland and the prostate (see Fig. 3.9). The englargement of these glands is considered to be the best available criterion of maturity other than egg-laying. The results from dissections were then matched up with the original estimates of maturity to provide a measure of the accuracy of estimates on field samples. Of the 128 snails examined 19 were assigned to the wrong class by the shell measurement method. Assuming the dissection method to be

JUVENILE ADULT

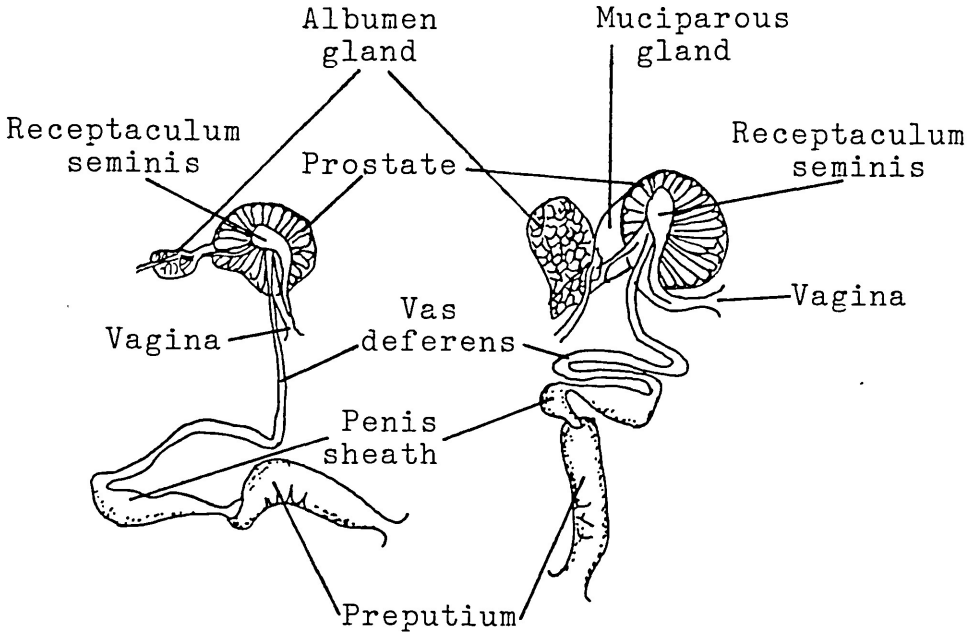


Fig. 3.9 The development of the accessory reproductive glands in Bulinus globosus.

(from Wright, 1957a.)

100% accurate, the field estimates of maturity would then have had an accuracy level of 85%. Since the attainment of maturity is a gradual process, there were obviously cases where even by dissection the snail appeared to be intermediate between adult and juvenile. In these cases a decision was made one way or the other since field samples had to be recorded either as adult or juvenile. These intermediate cases were largely responsible for the discrepancies in the results.

The shell length:aperture length ratios are plotted against shell length in Fig. 3.10. Juveniles and adults are identified by dissection results. The increase in the ratio (indicative of spire exsertion), is marked but gradual, offering no sudden increase with the onset of maturity, and therefore leaving an uncertain area at 6 to 7mm shell length.

A 'live' check on the recognition of maturity by spire exsertion was possible using the snails from the box experiments (see Section 3.6.1.). For each cohort (inspected weekly), the time of first adult recognition by spire exsertion was recorded. The observations in Table 3.5 were made on 28 cohorts which regularly laid eggs. The results suggest that the recognition of spire exsertion provided a consistently good estimate of the imminent onset of reproduction for those snails which were sufficiently healthy to reproduce.

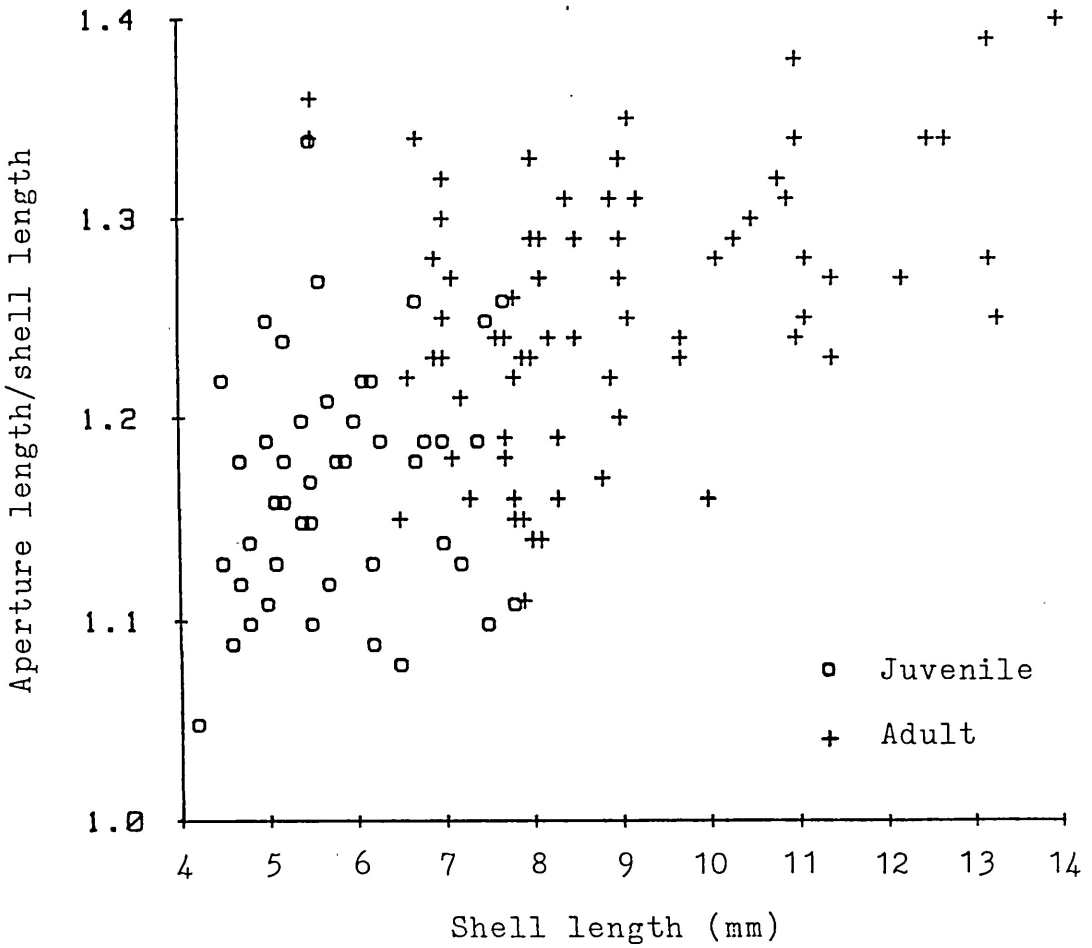


Fig. 3.10 The assessment of maturity in B. globosus, showing an increase in the aperture:shell length ratio with increasing size and maturity. (The maturity of the snails was assessed by dissection.)

Table 3.5 The onset of reproduction compared to time of adult recognition in box snails.

Delay between first adult recognition and first egg masses found	No. of cohorts
0 weeks	6
1 week	15
2 weeks	6
3 weeks	1

3.5. The Mark-Recapture Programme

The marking, release and subsequent recapture of animals can provide very detailed information about population numbers, losses and gains, growth rates and dispersal. The various methods of analysis of such data, however, make a number of assumptions which may not be valid in given field situations. These problems prompted Hairston et al (1958) to conclude that the techniques of mark-recapture are of little value (for aquatic snails) under most field conditions. It is important to note, however, that very few attempts have been made to measure population parameters for aquatic snails using mark-recapture techniques. Pringle and Msangi (1961) attempted to study B. globosus populations in a pond using single recapture techniques, but low recapture rates precluded much confidence in the data obtained. Most other mark-recapture programmes have been aimed at measuring snail dispersal. Table 3.6 summarises the duration and recapture levels of previous studies. In addition to these studies, Webbe (1962a) marked Bulinus nasutus with the radioactive isotope cobalt-60 in order to test whether they could survive when their habitat dried out. He recovered two radioactive snails after 130 days.

Leveque and Pointier (1976) and Stiven and Walton (1967) used marked snails in enclosures to measure growth increments at different sizes. During their study Stiven

Table 3.6 Summary of previous studies on aquatic snails using mark-recapture techniques.

Author	Species	Purpose	No. marked	% Recaptures at different intervals (days) after release												
				1	2	3	4	5	6	7	8	9	14	21	28	> 28
Bovbjerg (1952)	*Campeloma decisum*	Dispersal estimates	500	5	5	5	6	5	6							
			120	100	100	100										
Pringle & Msangi (1957)	*Bulinus globosus*	Population estimates	86							4					0	
			218							5				0		
			143				0									0
Radke & Ritchie (1961)	*Australorbis glabrata*	Mark tests & dispersal	10 to 600							7				4		5
Paulini (1963)	*Australorbis glabrata*	Dispersal estimates	100	68	69	49	53	56								
Berrie (1968)	*Biomphalaria sudanica*	Growth measurements	53												26	
Dazo et al (1966)	*Bulinus truncatus*	Dispersal estimates	428					0.7								
			580	0												
	Biomphalaria alexandrina		2526	3.2				0.04								
			1044					6.1								
Boerger (1975)	*Helisoma trivolvis*	Dispersal estimates	120		65					45			55	20	10	

and Walton found snails (Goniobasis proxima), which had been marked by a colleague over two years previously. In spite of Hairston and his colleagues' pessimism, the above projects show that it is possible to gain substantial information from the marking, release and recapture of aquatic snails.

Quick-drying enamel paint has been the preferred method of marking in the above studies, although Pringle and Msangi (1961) also tried BOSTIK glue and silver paper, and Dazo et al (1966) used white nail polish. Paints (or nail varnish) obviously offer the greatest flexibility in terms of individual or group codes, while the use of a radioactive isotope can only provide one single type of mark.

In this project, the aim was to use marking techniques to measure growth and survival rates in the field. It was also hoped that some information on dispersal rates would be gathered. No measures of absolute population numbers were attempted.

Since individual marks are necessary for accurate growth measurements, the marking medium had to provide a wide range of unique combinations. The final choice was a quick-drying waterproof paint. International Paint Marine Coatings Ltd. very kindly donated a chlor-rubber based paint which proved ideal. This paint is normally used for industrial marine applications and is normally available in a single colour. The company made up five different colours

specially for this project. Using numbers and letters, a total of 170 individual marks was available (the letters I and O were not used to prevent confusion with the numbers 1 and 0). With practise it was possible to apply two marks to snails > 5mm long, giving a very large number of combinations of symbols and colours.

Only snails with a shell length > 2mm could realistically be marked individually. Below 2mm it was possible to apply a dot of paint but only at the risk of unbalancing the snail or getting paint into the aperture. This was therefore not attempted.

Recaptures of snails at sites other than those at which they were marked were very scarce, and therefore each trap site was treated as a separate marking site. Marking was carried out in the field and it was found that up to 200 snails could be marked during one session. With more snails than this the risks of stress or mortality through dessication or overheating/crowding in the collecting bowls was considered too great. Consequently, samples from one or several sites were marked at any one time, depending on the density of snails at the chosen site(s).

Snails were kept in a collecting bowl whilst awaiting marks. Up to 30 at a time were placed on a damp cloth to allow the top of the shell to dry. After ten minutes an individual mark was applied and allowed to dry for at least thirty

minutes. The snails were then measured to the nearest 0.1mm and returned to the collecting bowl for at least thirty minutes recovery time. Each snail was inspected for movement (indicating that it was still alive) before being returned to its original trap site. Snails were returned to the water within two hours of collection at the most. On several occasions, samples had to be returned to the laboratory to be marked (usually because of bad weather preventing the shells from drying). On these occasions the snails, after marking, were kept in aquaria filled with dam water. Only three snails (out of more than 2,500 marked) died before they could be returned to the water.

3.5.1. The underlying assumptions of mark-recapture estimates

Although the aim was not to estimate population numbers, the general assumptions underlying recapture population estimation models have to be satisfied when they are employed to gain information for survival and mortality. The assumptions listed below are taken from Southwood (1978).

3.5.1.1. The marked animals are not affected by being marked and the marks will not be lost. This assumption has three components:

The process of marking the snails must not affect mortality or behaviour.
There must be no loss of marks and marks must all be noted.
Bearing a mark must not affect the behaviour or mortality of the animals.

Marks were tried out on laboratory kept animals and seemed not to affect the snails, nor to come off. As an initial test in March 1980, a cohort of 39 snails was split into 20 and 19 and placed in two snail boxes in Nguni dam. When the cohort was 66 days old, the snails in one box (randomly chosen) were marked. The subsequent demographic performance of the snails is shown in Table 3.7.

This limited test shows no mortality caused by the marking, growth rates were slightly faster for marked snails, and the reproduction rate was considerably higher among marked snails. Furthermore no marks were lost before the snails died. As there appeared to be no ill effects from marking, the programme was continued.

During 1980, 93 snails in boxes were individually marked, to further extend the testing of marking effects and mark durability, and to identify individual growth increments. All snails marked were >3mm long. In the event of marking causing increased mortality, given a general increase in mortality with snail age (see Chapter 5), there would be a disproportionate increase in % mortality immediately

Table 3.7 Comparison of marked v. unmarked snails kept in boxes in Nguni dam. Snails were hatched in the laboratory from 3 egg masses and were randomly assigned to each box.

	MARKED SNAILS		UNMARKED SNAILS	
	Mark date (age 66 days)	Mark date + 55 days (age 121 days)	Mark date (age 66 days)	Mark date + 55 days (age 121 days)
Mean size	7.2	8.5	7.4	8.5
No. of snails	13	13	14	14
Egg masses/snail	0	4.85	0	0.93

following the mark application. Fig. 3.11 shows no such anomaly and this observation is taken as further evidence that marking does not influence snail survival.

During 1981/82 the adoption of a multiple marking programme allowed a further test of whether marking had an effect on the snails. Again the assumption is that any effect caused by marking will be an immediate rather than a long term one. The following test checks only for direct mortality caused by or during the marking event. It does not test for increased mortality caused by bearing a mark, due to such factors as predation.

The test was devised by Manly (1971) and basically compares the survival of previously marked animals with that of newly marked animals. The test estimates y, the difference between newly marked and previously marked snails. A statistic g is then calculated by dividing y by its variance. A value $g < 1.64$ indicates that y is not significantly different from zero (at $P < 0.05$), and therefore suggests that there is no mortality effect from marking. Table 3.8 gives results for all daily marking events during 1981/82. The final three marking sequences indicate highly significant increases in survival of old marks. However, 6 of the 9 tests failed to show a significant increase in mortality due to marking. With the evidence described earlier from marked snails kept in boxes, it is considered that on average, marking has a minimal impact on the survival of the snails.

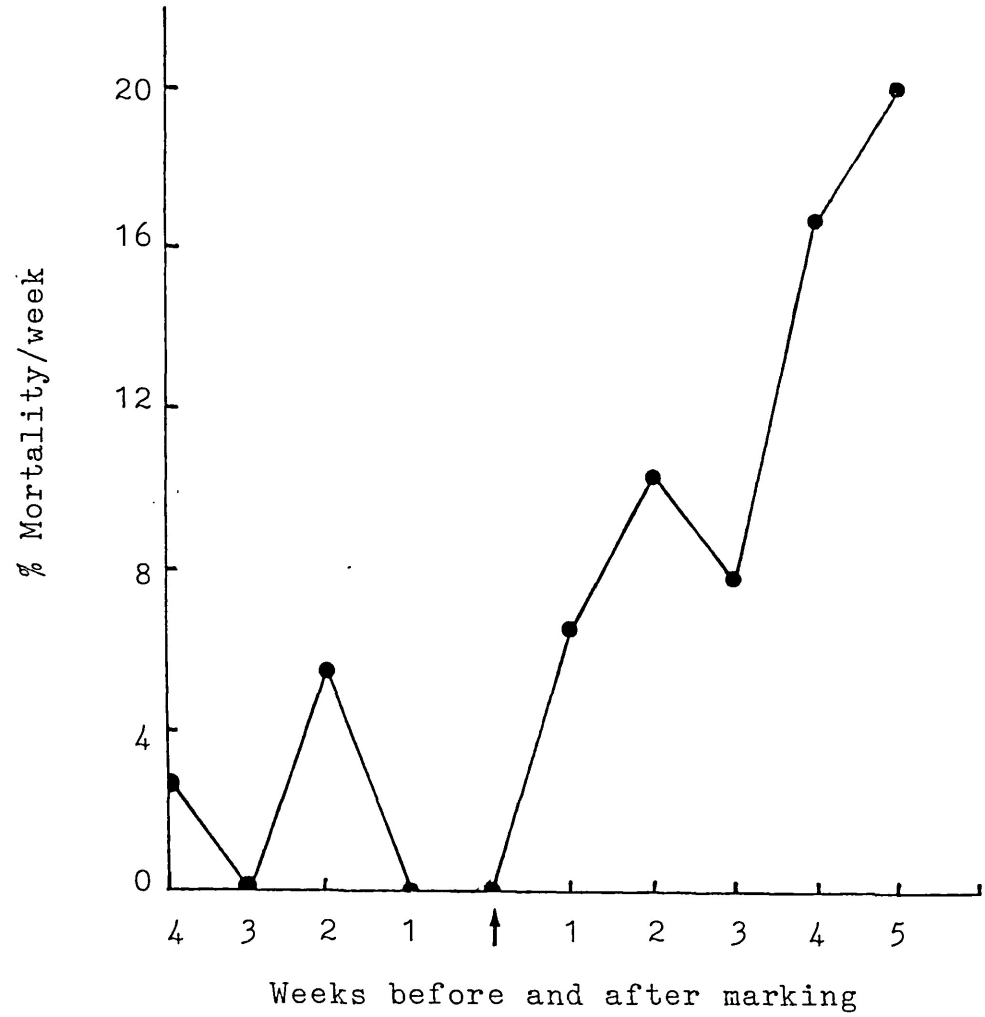


Fig. 3.11 The effect of marking on snail mortality.

93 snails were marked at some time during their lives in boxes. The graph shows an increase in mortality rate with age, but no increase in mortality immediately after marking, which would be expected if marking had an adverse effect.

Table 3.8 The effect of the marking process on snail mortality. Results from Manly's (1971) test.

y is a measure of the difference between the probability of recapture of a newly marked snail and that of a previously marked snail (which has therefore survived the marking process). y will be zero if marking does not cause mortality.

The statistic g determines the significance of the difference between y and zero.

Data from all daily mark sequences during 1981/82 at Nguni dam.

Start date	Site(s)	y	g	Significance(> zero)
8. 6.81	39-48	-0.15	-0.66	P >0.05
6. 7.81	39/40	0.27	1.12	P >0.05
6. 7.81	47/48	0.05	0.20	P >0.05
10. 8.81	7/8	-0.40	-1.64	P >0.05
7. 9.81	15/16	0.11	0.64	P >0.05
5.10.81	29/30	-0.20	-1.22	P >0.05
10.11.81	15/16	0.35	2.37	P <0.05
16.11.81	47/48	0.25	2.41	P <0.05
11. 1.82	All sites	0.59	3.71	P <0.05

Mark durability was measured from marked snails in boxes. Altogether 148 snails in boxes were marked and 10 of these lost their marks completely before they died, either because of the paint peeling off or being rubbed off or grazed off by other snails. In addition, 13 of the marks were sufficiently damaged to be unrecognisable. In mark-recapture experiments in Nguni dam, 12 marks out of 538 recaptures at weekly intervals were sufficiently damaged to be unrecognisable. Table 3.9 shows the rate of mark damage in boxes and in wild snails, and estimates the average mark loss rate from wild snails as 0.7% per week.

Both mark loss and mark induced mortality lead to an overestimate of population size and an underestimate of survival rate. The tests above, however, show that in both cases, if there is an effect, the bias is sufficiently small to be considered insignificant.

The third aspect of assumption one is the most difficult to test. The most likely effect of bearing a mark would be an increase in predation due to increased visibility to the predator. This could only have been tested by extensive investigations into predation and these were not undertaken. Marked snails in boxes survived as well as unmarked snails, but the boxes excluded all macro-predators. No differences in behaviour or physiology were noticed between marked and unmarked snails. In the absence of any evidence to the contrary, the working assumption must be that marks make no difference to mortality or behaviour.

Table 3.9 Mark durability.

The rate at which marks were lost or became unrecognisable in box-kept snails compared with the rate at which marks became unrecognisable in wild snails. This provides a measure of mark loss in the field, assuming that the proportion of marks damaged:lost is similar in the field and in boxes.

		Weeks since marking						
		1	2	3	4	5	6	7
Box snails (initial total 148)	% loss/week	0	1.5	1.3	0.8	0	1.1	0.9
	% newly unrecognisable/week	1.0	2.5	2.8	3.2	2.0	3.3	1.4
Wild snails	Total recaptured	295	132	56	28	11	7	5
	% unrecognisable/week	1.0	1.5	1·8	3·6	0	0	0

If $\frac{D}{L} = \frac{D'}{L'}$ where D = damage to marks on box snails
L = loss of marks on box snails
D′ = damage to marks on wild snails
L′ = loss of marks on wild snails

then $\hat{L}' = \frac{LD'}{D}$

Ignoring weeks 5 - 7, for which the recapture data is too sparse:

L (mean box snail mark loss/week) = 0.9%
D (mean box snail mark damage/week) = 2.4%
D′ (mean wild snail mark damage/week) = 1·8 %

$\therefore \hat{L}' = \frac{0.9 \times 1.8}{2.4} = 0.75$

i.e. the best estimate of mark loss from wild snails is 0.75%/week.

3.5.1.2. Equal catchability: Southwood's (1978) assumption two, (complete mixing), is essentially part of assumption three, (equal catchability). If animals are not equally catchable, population size will be underestimated, since marked snails will be more prone to recapture. Estimates of survival rates, however, will not necessarily be affected since they are based on data from marked snails only. Begon (1979) gives a test for the independence of mark status which measures the change in probability of recapture with successive captures. Table 3.10 shows the results of this test applied to daily mark-recapture data from Nguni dam. Since daily mark sequences were continued for six days, data from days three and four have been tested. This allows for a sufficient number of capture opportunities before and after the test date. Grouped results from all daily marking occasions show a very significant increase in the likelihood of recapture with a number of previous recaptures. Both Begon (1979) and Southwood (1978) cast doubts on the validity and interpretation of the above test and other tests for equal catchability. The fact that three of the subset tests in Table 3.10 show no significant difference in catchability may indicate that the effect is small. However, there would be serious doubt about the accuracy of any estimates of population size from these data. As mentioned above, the data was collected primarily for survival rate estimation and is not used for obtaining population estimates.

Table 3.10 Test for independence of mark status. (Begon, 1979.)

Essentially a test for equal catchability, it examines the probability of an animal being recaptured in the light of previous recaptures. If previously captured animals become more prone to recapture, the assumption of equal catchability is violated.

Data from day 3 and day 4 captures, Nguni dam, 1981/82. Results had to be grouped to provide sufficient data.

Day 3 samples (2 degrees of freedom as 0, 1 or 2 previous captures were possible. Critical χ^2 = 5.99 at $P < 0.05$).

Dates	No. of snails	Observed χ^2	Significance
8/ 6/81 - 2/11/81	118	5.1	$P > 0.05$
16/11/81 - 11/ 1/81	57	18.3	$P < 0.05$
All dates	175	18.2	$P < 0.05$

Day 4 samples (3 degrees of freedom as 0 to 3 previous captures were possible. Critical χ^2 = 7.81 at $P < 0.05$).

Dates	No. of snails	Observed χ^2	Significance
8/ 6/81 - 2/11/81	123	5.3	$P > 0.05$
16/11/81 - 11/ 1/81	83	4.6	$P > 0.05$
All dates	206	8.8	$P < 0.05$

3.5.1.3. Time intervals between samples: Sampling must be at discrete time intervals and the time involved in marking should be small in relation to total time.

For daily marking sequences, the maximum number of snails marked at one time was 60, and these were returned to the water within 60 minutes of their removal. Sampling was carried out at the same time each day and snails were removed from and returned to their sites in the same order each day. The time in the water between samples therefore varied at most between 23 and 24 hours.

For weekly samples, larger numbers of snails were marked at one time, but the maximum length of time out of the water was still less than 2 hours.

3.5.1.4. Every marked animal must have the same probability of surviving the sampling period.

Violation of this assumption does not affect population estimates but will affect the interpretation of survival estimates. For B. globosus mortality is age-dependent (see Chapter 5), the probability of survival being lowest in the very young and very old snails. At first sight the assumption would therefore seem to be violated. However, mark-recapture survival rate estimates cannot distinguish between mortality and emigration. It appears that small snails are much more prone to disperse than large ones (see

Chapter 5). In addition, snails less than 2mm shell-length could not be marked, so that the youngest size classes (those most prone to high mortality) are not included in the analysis. The net result is shown in Fig. 3.12. Any increase in mortality among old snails is offset by increased emigration among young snails, so that the survival rate as estimated by Jolly's stochastic method, is not significantly different at different ages.

In conclusion, the above tests suggest that the mark-recapture data collected is adequate for use in estimates of the survival rates of B. globosus in Nguni dam, bearing in mind that the estimates include mortality and emigration effects. In order to use the data for population estimates, more knowledge would be needed about sampling effects and the impact of mark status and factors such as susceptibility to predation.

3.6. Snail Boxes

3.6.1. Design and Purpose

Some of the applications of snail boxes have been mentioned above. The following is an account of the purposes, methods of construction and use of these boxes.

The aim was to produce a simple, cheap, robust enclosure which would allow snails to be kept in as near natural

Fig. 3.12 Mean survival by size from mark recapture data, using Jolly's stochastic method.

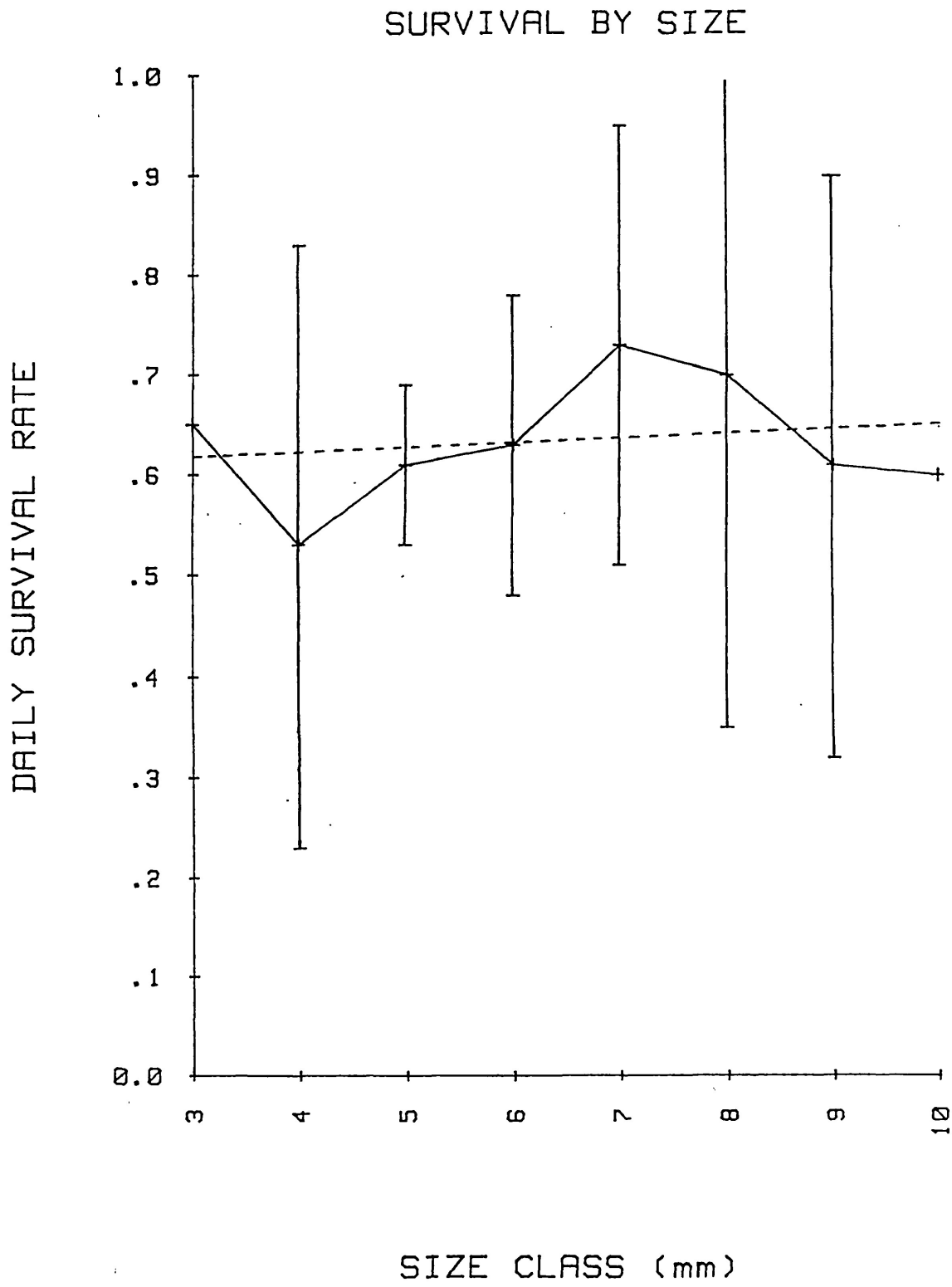
All data from daily marking sequences (649 snails) for Nguni dam 1981/82 were used.

"Survival" estimates make no distinction between mortality and emigration and are therefore measures of the proportion of animals still available for capture after each day.

The regression (- - -) of survival rate on size is: $y = 0.006x + 0.601$

$r^2 = 0.007$

i.e. there is no significant relationship between survival rate and size.


SURVIVAL BY SIZE
DAILY SURVIVAL RATE
1.0
.9
.8
.7
.6
.5
.4
.3
.2
.1
0.0
3
4
5
6
7
8
9
10
SIZE CLASS (mm)

conditions as possible, but with the capability of allowing measurements to be taken of various parameters of the snail's life-cycle. In this way it was hoped to complement field measurements in natural free-living snail populations, of factors such as absolute life-span, age-specific fecundity and duration of infections. At the same time, by manipulating densities and food supply, the aim was to establish the influence of these factors on growth rates, survival and fecundity. As the snails would be living in the same temperature and water chemistry conditions as natural populations, it was hoped that the relative effects of environmental change over time would reflect the changes occurring in the natural habitat.

To achieve close control of the captive snails, it was necessary to compromise the natural conditions to some extent. Two major differences between conditions in any type of enclosure and those in natural surroundings are immediately evident. In order to enclose the study populations, the surrounding barrier acted to keep certain other macro organisms out (predators in particular). Furthermore, by enclosing the snails, movement or dispersal was necessarily curtailed. The effect was to create artificial densities which could only be controlled by mortality other than by macro predation, and to provide a limited (and mostly artificial) substrate choice for the snails. Snail enclosures have been used for many years for

the purpose of measuring miracidial transmission rates (e.g. Chu et al, 1981). However, these enclosures have been designed purely for the containment of adult snails for short periods of time. Effects on the snails' behaviour, and the recovery of eggs and small snails are not a consideration in these studies. To allow for the aims of this present study, a more elaborate form of enclosure was needed than that described by Upatham (1972).

Several experimental enclosures were constructed before an ideal design was reached. It was obviously necessary to incorporate some form of netting to allow a free flow of water through the enclosures. An enclosure constructed of netting on a frame was rejected because of the difficulty of accurate sampling (there were too many corners in which very small snails could be hidden among detritus). A container which stretched from the water surface to the dam bottom at 60cm was also rejected for sampling reasons, since the whole enclosure could not be searched effectively to recover the entire population. The eventual choice is shown in Fig. 3.13. Plastic sealable boxes (locally made but similar to TUPPERWARE-type containers) were bought in bulk for approximately 40p each. Windows were cut in the sides of the boxes (to allow a flow of water through) and in the lid of the box (to allow a choice of sunlit or shady environment). The bottom of the box was not pierced, so as to allow some build up of mud to resemble the natural bottom of a water body. For newly hatched snails, 0.3mm nylon mesh was used

Fig. 3.13 Snail boxes.

Two designs were used: Photo (i) and drawing for snails ≥3mm. Photo (ii) for newly hatched snails.

The nylon mesh (0.3mm) in the boxes for newly hatched snails prevented the escape of even the smallest snails, but became choked with aufwuchs within a month. Snails were transferred to the larger mesh netting when all inhabitants of a box were ≥3mm.

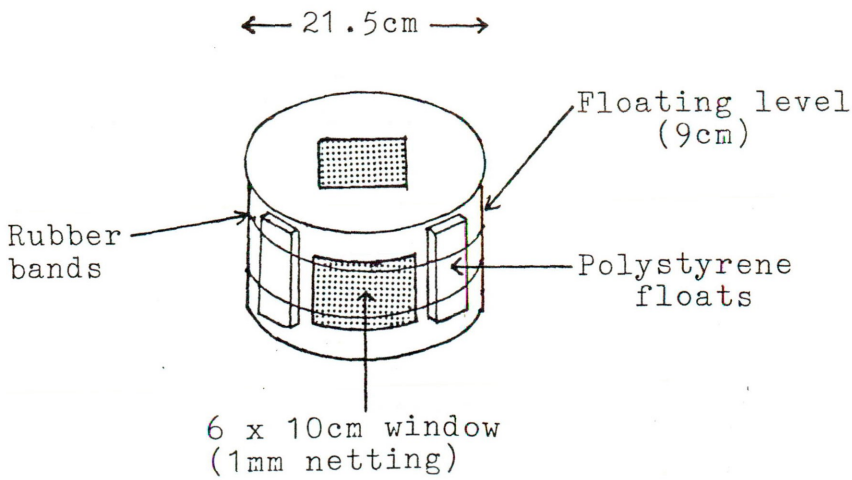
The polystyrene floats were held on by rubber bands, allowing the buoyancy of the boxes to be adjusted to maintain a 9cm depth (i.e. a constant volume of water) in the box.

(i)



(ii)




21.5cm
Floating level
(9cm)
Rubber
bands
Polystyrene
floats
6 x 10cm window
(1mm netting)

to cover the underwater windows. This prevented any escapes but became clogged with algae and detritus to such an extent within a month as to be waterproof. It had then to be cleaned by drying and the removal of the attached material. To counter this, the snails were transferred, when they had grown to 3mm+, into boxes in which the windows were covered with more robust 1mm nylon mesh. This type of covering took considerably longer to clog, and being stronger, could be cleared whilst wet, allowing continuous use of the boxes. Both types of window were attached using EVO-STIK glue which proved reliable and waterproof. Frayed edges of mesh were melted onto the box plastic using a welding iron. Snail proof windows were achieved without corners or flaps in which small snails could hide themselves.

Four polystyrene floats were attached with rubber bands round the outside of each box so as to allow the boxes to float 9cm deep, allowing snails to come to the surface in the box. The floats could be adjusted to maintain an equal volume of water in each box (3.3 litres).

The immersed surface area inside each box formed by the sides and bottom of the container was 850cm^2. This served as one type of substrate for the box-kept snails. To provide a removeable substrate for egg collection and to equalise the area of substrate available per snail, 10 x 10cm squares of plastic sheet were added to the boxes. These were weighted at one end by a small piece of metal to ensure

that they remained under the water. Further substrate was provided by measured areas of vegetation (Cyperus exaltatus, Nymphaea caerulea, or Typha latifolia) which was added to provide a natural food choice.

3.6.2. Initial tests of snail boxes

During 1980 the boxes were developed and tested. It was necessary to establish what density levels could realistically be maintained in the boxes, how best to manipulate feeding and how long snails were likely to live in the boxes.

Cohorts of between 5 and 100 newly hatched snails were placed in the boxes and subsequently inspected once a week. Snails were removed and measured, dead shells discarded, food replenished if necessary and egg masses and eggs per mass counted and removed. Periodically, snails were removed to the laboratory for shedding tests. Any snails found to be shedding cercariae were individually marked and returned to the box except if the cercariae were suspected of being schistosomes. In this case, the snail was maintained in the laboratory and processed as described below. It was discovered that not more than 20 snails could be maintained in a box for any length of time. The ideal density appeared to be approximately five snails per box, at which level snails achieved good growth and reproduction rates, given an adequate food supply.

The food sources in the boxes were free living algae, epiphytic algae attached either to plant or plastic surfaces, and the plant material itself. The addition of lily (Nymphaea) leaf resulted in a considerable increase in growth and reproduction among the snails, and was consumed at a rate of up to 30cm^2 per snail per week. The other leaves (Cyperus and Typha) were not eaten but were used as substrate for grazing algal covering, as were the plastic surfaces. Reproduction and growth among snails with Cyperus and Typha leaf added to their boxes was not noticeably better than among those with no added leaf.

3.6.3. 1981/82 box treatments

From the experience gained during 1980, it was possible to construct boxes for the following year which would provide quantitative information about the effects of density, different feeding regimes, and seasonal changes throughout the year.

Nine boxes were set up each month in Nguni dam, starting in June. The experimental design was to have three different initial density treatments of 5, 10 and 20 snails in three boxes each, making a total of 105 snails. Within each density treatment there were three different feeding regimes. The type 1 feeding regime was planned as a high quality high quantity diet. 10cm^2 of Nymphaea leaf per snail per week was provided. In addition, a 20cm length of Cyperus leaf

per snail was kept in the box and replaced when it rotted. 10 x 10cm plastic squares (described above) were added until the surface area of plastic per snail (including box plastic) was equal in all boxes, irrespective of snail density. (e.g. for a box containing 20 snails, 16 plastic squares were added, giving 16 x 200 = 3,200cm^2 extra surface area, + 850cm^2 box surface area giving 202.5cm^2 per snail. For a box containing 10 snails, 6 plastic squares were added, giving 1,200 + 850cm^2 or 205cm^2 per snail).

The type 2 feeding regime consisted of the same diet as for type 1, except that no Nymphaea leaf was added. The diet can be described as a low quality, high quantity diet.

The type 3 regime was low quality, moderate quantity. Irrespective of snail density, 4 x 20cm lengths of Cyperus leaf and two plastic squares were added to each box, so that the surface area of substrate per snail was lower at high densities and higher at low densities than for type 1 and 2 boxes.

In the case of type 1 and 2 boxes, plants and plastic squares were adjusted to retain a constant area per snail as mortality decreased the density. For all three regimes, nothing was added for the first two weeks, and from week two to week five only half the allotted amounts were added, in order to provide an increasing food supply as the snails grew.

For C. exaltatus and T. latifolia leaf, the extent of decay of the leaves must make a difference to the algal growth on their surface, and to their general attractiveness and palatability to snails. To standardise (as far as possible) the quality of leaf put into the boxes, the following treatment was devised. 20cm lengths of leaf were cut from living plants (the average leaf width for C. exaltatus was found to be 1.7cm and for T. latifolia 1.5cm, so that a standard length of Cyperus leaf provided on average 68cm^2 of substrate and 60cm^2 for Typha leaf). Unusually wide or narrow lengths of leaf were discarded. The rest were kept in the water in a spare snail box until needed. A stock was kept which ensured that there were leaf lengths at least two and not more than four weeks old at all times. From this stock the oldest leaves were used to replace rotted leaves in boxes or to stock new boxes. After two weeks in the water, the leaves resembled natural leaf material in the water on which the great majority of free snails were found. It was usually approximately eight weeks before Cyperus leaves began to disintegrate, although Typha leaves were liable to do so after four weeks.

The plastic squares were also weathered in the water for at least two weeks before they were used in boxes.

Cyperus leaves were used in boxes in Nguni dam since the species C. exaltatus was the only emergent plant in the dam apart from some isolated clumps of Nymphaea caerulea. In

Benes dam, Typha latifolia is the dominant emergent and was used in most boxes, but C. exaltatus is also abundant and was used in some boxes.

One week before a set of boxes was due to be used for experimentation, the empty boxes were placed in the water to weather. A collection of egg masses was made from around the dam. The 105 snails to be reared in the boxes ideally had to hatch within a day of each other and therefore about 100 egg masses were collected to cater for this constraint. During some months natural reproduction was so low that eggs from existing box snails had to be used to augment those collected from the dam.

The eggs were hatched in petri dishes in the laboratory. Those hatching prior to the appointed date were cleared out each day so as to keep a check on the exact age of snails used. If an insufficient number hatched on the appointed day some boxes were left empty until a later date. All snails in the same box were always the same age. The snails were carefully counted into the boxes at no more than one day old. Snails were not hatched in the boxes because of the difficulty of knowing how many would hatch from each egg mass, and of checking on the hatch date. Before closing the box, a recount was made and all snails were checked for movement indicating that the trauma of the transfer to the box had not affected their viability.

After the first week the snails were counted and measured. Due to their small size (0.8 - 1.0mm), they were sometimes very difficult to find and the shells of those which had died during the initial week were even more difficult to locate. It had to be assumed that those which were found alive constituted the entire population of survivors. Boxes were never cleaned out during the first two weeks, so that if live snails were not located at the time of sampling, they would nevertheless stay in the box until the following sampling date. On four occasions one extra live snail was found at the second weekly sample, indicating that in a few cases, previous counts were in error.

The average initial density of snails in type 2 boxes was one snail for each 205cm^2 of substrate. This amounts to 24 snails per $\frac{1}{2}$m^2 of substrate, which compares with an average of 5.5 snails per trap (= $\frac{1}{2}$m^2) in weekly samples during 1981/82. This comparatively high density in the boxes was necessary in order to maintain a sufficient number of snails for measurement. Juvenile mortality usually reduced the densities of box snails considerably, and mean snail biomass density was therefore probably comparable to the natural population. A comparison of growth rates, reproduction and survival between box-kept snails and wild snails (see Chapters 4 to 7) indicated that any disadvantages of increased substrate density were not marked.

3.6.4. Hatching boxes

The snail boxes were not used to hatch eggs for the reasons given above. A series of smaller plastic containers, designated hatching boxes, were adapted for this purpose. (See Fig. 3.14.) Two windows, each $4cm^2$, were cut in the lid and bottom of the containers and covered with 0.3mm nylon gauze. In use, the containers were secured in the end of a nylon stocking (which protected the windows, kept the lid in place and allowed a tether to be attached).

Several traps were placed in the dam, away from the weekly sampling sites, purely for the purpose of egg collection. When egg masses were required for hatching, these traps were inspected, all egg masses removed and the time noted. The traps were subsequently inspected at least once a day, the time being noted on each occasion. If any egg masses were found, a section of plastic sheet bearing the egg mass was cut out, the number of eggs counted and then put into a hatching box. After four days, the hatching box was inspected at least daily, the time being noted on each occasion. When all the eggs had hatched (a process lasting several hours), the hatch time was measured as:



Fig. 3.14 Hatching boxes. (7cm diameter x 6cm deep)

Egg masses laid at a known time were placed in these containers which were kept in the dam and inspected daily until the eggs hatched. The container was then carefully searched to find all live snails. This provided measures of hatch time and hatch success.

$$T_3 - T_2 + \frac{T_2 - T_1}{2} + \frac{T_4 - T_3}{2}$$

Where: T_1 is the last time at which eggs were not found on the trap.

T_2 is the time when the eggs were found.

T_3 is the last inspection time at which the egg mass had not hatched.

T_4 is the inspection time after the last egg had hatched.

Hatch success is defined as the number of snails found after hatching divided by the number of eggs originally counted.

After use the hatching box was left in the water for a further week and then carefully searched again, in case any newly hatched snails had been missed. On three occasions (out of 118 egg masses hatched) one extra snail was found. If snails were missed on other occasions but did not survive for the extra week, the hatch success percentage would have been an underestimate.

A further minor source of error resulted from the counting of eggs in the egg masses. This was done by eye and, as the eggs are <1mm long, mistakes during counting were possible. A test was carried out in the laboratory to examine the accuracy of egg counts in the field. Table 3.11 gives the results. Assuming that microscope counts

Table 3.11 Egg count accuracy.

To test counts by eye of the number of eggs per egg mass. Egg masses found in the dams were counted by eye and then taken back to the laboratory and recounted using a dissecting microscope.

Substrate	No. of egg masses	Total eggs		Difference	% Difference
		Eye count	Microscope count		
Trap plastic	36	589	599	+10	1.7
Vegetation	16	151	150	- 1	0.7
Total	52	740	749	+ 9	1.2

36 egg masses gave equal counts by both methods.

13 egg masses gave a discrepancy of 1 egg.

3 egg masses gave a discrepancy of 2 eggs.

were completely accurate, field counts by eye gave a 1.2% underestimate of the actual number of eggs. This effect would tend to overestimate slightly the percentage hatch success.

3.7. Laboratory Aquaria

Since most of the demographic parameters which are usually obtained in the laboratory could be measured in the snail boxes under more realistic field conditions, the need for snail maintenance in the laboratory was considerably reduced.

Aquaria were used initially for growth rate and size specific fecundity measurements, for testing mark durability and as holding tanks during shedding tests. 10 litre plastic aquaria were used, filled with water from Nguni dam which was kept for at least one week before being put in the aquaria. Snails were fed on dried, boiled lettuce or fresh lily leaf, and the water was changed at least once a week. No temperature control or aeration was used.

Although snails were easily maintained for indefinite periods and could be coaxed to comparatively high growth and reproductive rates by keeping them at low densities and by careful feeding, standardisation of aquaria was not achieved.

Measurements of pH, oxygen levels and total conductivity were all found to vary considerably within days of starting with apparently uniform tanks. Sudden mass mortality in an individual tank was frequently experienced, especially when snails were kept at more than 5 per litre. In some aquaria, snails would persistently crawl out of the water and remain attached to the aquarium sides. Shiff and Garnett (1967) noticed this phenomenon with Biomphalaria pfeifferi and described it as a migratory phase. Since no feeding, growth or reproduction takes place during this phase, it creates difficulties for life-table construction.

For all the above reasons data from aquarium-kept snails was difficult to equate with field conditions and rather than use resources to try to develop a more controlled laboratory based system, efforts were directed to obtaining field measurements by means of marked snails and snail boxes.

3.8. Testing For Infections

Snails were tested for patent infections using the method described by Olivier (1973), by which snails are isolated in 10ml water in sunlight for a day. The water was then inspected under a low power microscope for cercariae. This process was repeated for two days. A small square of dried, boiled lettuce was added to the water, since it was noted that snails sometimes failed to produce cercariae after a time, but could be induced to continue shedding

after feeding. When large numbers of snails had to be screened, up to five snails were kept in one petri dish. After the first day inspection, snails from dishes containing cercariae were separated into individual containers.

Some stress was inevitably involved in these tests and snails died on several occasions. This mortality may have been more pronounced among infected snails. Where possible, snails which died during testing were dissected, the presence of fully formed cercariae being taken as evidence of a patent infection. On several occasions decomposition rendered this procedure impossible. On two occasions more than 5% of a sample died during testing and on these occasions the entire sample was discarded.

No attempt was made to identify cercariae to the species level in Kenya. Cercariae were inspected at up to x40 magnification and assigned a letter as a species designation. Samples of all different types of cercariae encountered were concentrated by pipetting off excess water and were then killed and fixed in 5% formalin. Some idea of the family to which a cercaria might belong was obtained from Frandsen (1980). If the host snail(s) could be kept alive, they were packed in damp cotton wool and sent to the British Museum (Natural History) for inspection and identification of the parasite by Dr. C.A. Wright and his colleagues.

Criteria for identifying mammalian schistosome-type cercariae were taken from Stirewalt (1973). These are slightly less than 1mm long, with a bifurcated tail in which the bifurcations are shorter than the rest of the tail; oral and ventral suckers present; no eyespots. Any cercariae fitting this description were assumed to be Schistosoma haematobium, since S. mansoni and other mammalian schistosomes have not been found on the Kenya coast. No schistosome shedding snails were returned to their original habitats and all surviving snails were sent to the British Museum (Natural History) for investigation as described above.

Snails from sample sites in the two main dams were only individually tested at the end of sampling programmes, since the disruption to the populations would have been too great. Snails from searches and vegetation samples away from the weekly sample sites were taken to the laboratory for testing. A mass screening method was used to check the presence or absence of patent infections at weekly sample sites. During sampling, snails from the traps were placed in a small ($\sim$ 100ml) pool of water in a bowl. Snails $>$ 3mm (i.e. those which might be shedding) were in the bowl for a minimum of ten minutes while the traps were searched for small snails and eggs, and while other snails were being measured and recorded. After the traps had been returned to the water, a 20ml aliquot was taken from the collecting bowl and inspected for cercariae on returning to the

laboratory. Tests in the laboratory in which a single shedding snail was placed in 100ml water for ten minutes between 10.00a.m. and 2.00p.m. (when field samples were collected), gave the results shown (as laboratory tests) in Table 3.12. Later tests were conducted with water samples collected from the field, during snail box processing where the number of snails shedding in each box was known.

Laboratory tests with schistosome shedding snails indicated a fair probability of registering cercariae even from a single snail. Tests on other infections were less promising. The field tests, using water in which on average 8 shedding snails had been maintained for at least ten minutes, gave very poor prospects of picking up a single patent infection. The method is therefore considered to be of very little practical value but it can give an indication of the presence of infections in different places. Its chief merit was that it could be done extremely quickly and easily, with little disturbance to the snails.

Box-kept snails were tested periodically by returning them to the laboratory and isolating them, as for other snails, except that they were tested only for one day each time, to minimise disturbance to the boxed populations. Snails found to be shedding were individually marked for future observation.

Table 3.12 Testing the efficiency of the mass screening method used for detecting patent infections. (See text for explanation.)

Type of test	Cercariae type	No. of snails	No. of snails/test	No. of tests	% Positive	Mean no. of cercariae /snail/test
Lab.	Schistosome	3	1	26	77	5.4
Lab.	Others*	4	1	22	55	1.1
Field	Others*	8	8	15	47	0.4

*"Others" means all other than schistosome type cercariae.

3.9. Environmental Measurements

3.9.1. Temperature and basic water chemistry measurements in the dams

A set of portable electronic instruments known as an "Environmental Multi Probe" (manufactured by Walden Precision Apparatus Ltd., Saffron Walden, Essex, CB11 3BD) was used for field measurements of spot temperatures, pH, water conductivity and water oxygen content. The system is battery operated, and portable in its own briefcase sized carrying case (see Fig. 3.15). In general, it proved very convenient and robust for field use. Some problems arose, however, as a result of the effects of humidity on the pH and oxygen meters. These measurements had to be discontinued from midway through 1981 because the readout meter began to give wildly fluctuating readings, and sometimes failed to register at all. According to the manufacturers, both of these instruments require a high impedance at their connections to function uniformly and any moisture will introduce electrical leakage resulting in fluctuating readings. The very high levels of humidity on the Kenya coast provided enough atmospheric moisture to upset the instruments. The temperature and conductivity meters by contrast are low impedance instruments which are more immune to moisture effects. The only way to overcome the effects of excessive humidity would be to seal the instruments hermetically.



Fig. 3.15 The portable system used for measuring spot temperatures, pH, conductivity and oxygen content at Benes and Nguni dams.

Weekly maximum and minimum water temperature readings were taken using a Gallenkamp Zecol Mercury Maximum/Minimum thermometer.

3.9.2. Rainfall and atmospheric temperature readings

Two private weather stations are maintained in the vicinity of the main sampling sites, and both kindly provided daily measurements of rainfall and atmospheric temperature.

Data for Benes dam came from the Vipingo Sisal Estate weather station (03°49'N 39°48'E, altitude 75ft), 4km from the dam which is at an altitude of 275ft. Data for Nguni dam came from the Bamburi airfield weather station (03°58'N 39°44'E, altitude 50ft), 5km from Nguni which is at 130ft.

3.9.3. Detailed water chemistry

Two sets of complete water analysis for Benes dam, for 1978 and 1979, had been commissioned by Vipingo Sisal Estates and the results of these were kindly made available for use in this project.

A series of water samples from Nguni dam was collected during 1981/82 and these were analysed for nitrate nitrogen and calcium by Moir and Palgrave (Public analysts), 73 - 77 Bermondsey Street, London SE1 3XZ.

CHAPTER 4 GROWTH RATES

4.1. Introduction

For animals whose generations overlap significantly, the grouping of sampled individuals into age class facilitates population study (Southwood, 1978).

Bulinus globosus exhibits completely overlapping generations. Unlike insects, aquatic snails have no distinct developmental stages on which to base age groups. In addition, growth rates are dramatically affected by the environment so that not only are laboratory based growth rates usually unrepresentative of field rates, but it is unreasonable to expect a single average field growth curve to yield reliable information in all conditions (Shiff, 1964). The logical conclusion is that a separate average growth curve is necessary to distinguish the members of each cohort that is being followed through its life span. This is often not practical and in most previous studies a single growth curve (constructed either from laboratory and field data combined or from laboratory data alone) has been used. Pesigan et al (1958) and Webbe (1962a) both used single growth curves based on mode-following in successive field samples, augmented by laboratory data. Dazo et al (1966) and Sturrock (1973a) found little variation in a number of mode-following curves from different field sites, and therefore opted for a single average growth rate. Shiff (1964) and Demian and

Kamel (1972) found considerable differences in growth curves measured from snail populations in a single pond at different times of the year. Stiven and Walton (1967) and Leveque and Pointier (1976) both used marked snails in enclosures to measure growth increments at different snail sizes. These can then be converted to continuous growth curves using a growth rate against snail size regression and Brody's sigmoid growth equation (Stiven and Walton, 1967) or a Walford plot and von Bertalanffy's growth equation (Leveque and Pointier, 1976).

Both mode-following and mark-recapture estimates of growth rates have drawbacks. To be recognisable as a dominant cohort over its lifespan, a cohort used for growth rate measurement must comprise much larger numbers of animals than the preceding or succeeding generations, and is therefore subject to the attendant density effects which are difficult to quantify. Thus even a succession of growth curves may only be a reflection of growth rates at unusually high densities. Using unconstrained marked snails this problem does not arise, as long as the conditions in which the marking sequences are conducted are representative of the unmarked population. The major drawbacks with this method are that the resulting growth rate is time-specific (or vertical) in that it is representative of snails of different sizes during one time period rather than over the life-span of a cohort. The remedy, when a number of sequential growth curves have been measured, is to apply the

appropriate part of each growth curve to a cohort as it grows through the relevant time period. Fig. 4.1 shows a simplified hypothetical example of this conversion of time-specific to cohort growth rates.

In formal terms, using monthly time-specific von Bertalanffy (1938) growth equations, cohort growth curves can be estimated as follows:

$$l_t = L_i(1 - e^{-K_i t}) \qquad (4.1)$$

$$t = \text{Log}_e\left(\frac{(1 - l_t \div L_{i+1})}{-K_{i+1}}\right) \qquad (4.2)$$

Where l_t = shell length at time t.

L_i = asymptotic shell length for month i.

K_i = a growth constant for month i, whose value is calculated from Walford plots. (e^{-K} being the slope of the regression.)

Shell length by the end of the first month is found by substituting t = one month. t in equation (4.2) is then found using l_t from equation (4.1), and the process is repeated, incrementing i by one each time equation (4.1) is used.

There is a further problem with growth rate estimates from marked snail data. Using von Bertalanffy's equation, the

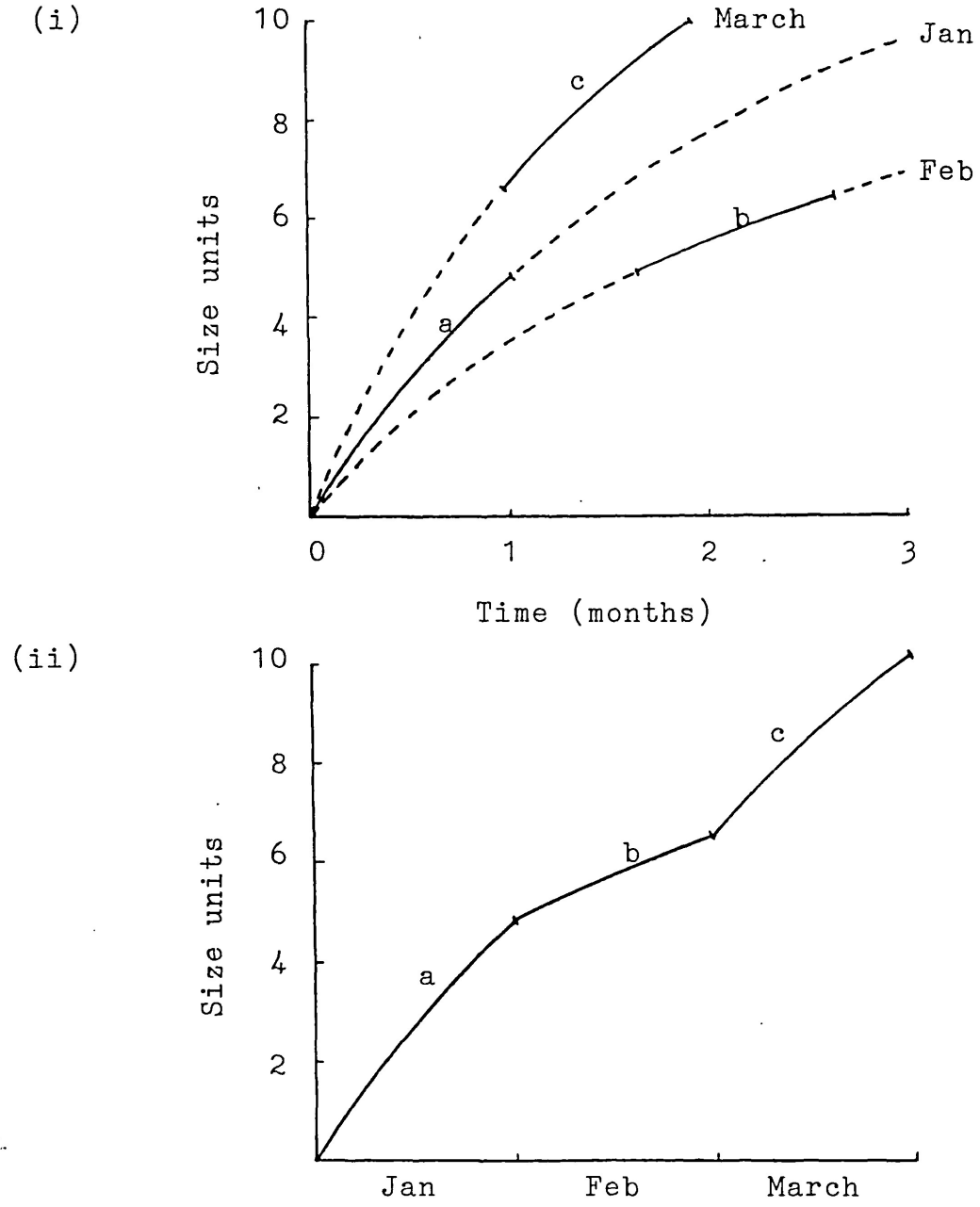


Fig. 4.1 Estimation of a cohort growth curve from time-specific von Bertalanffy growth curves. (Hypothetical data.)

(i) Growth rates declined after January but increased considerably during March. Solid lines show the actual rates applying to animals born at the beginning of January.

(ii) Best estimates of the actual growth of animals born at the beginning of January, through January, February and March.

(See text for further explanation.)

calculated growth curve is valid only for the range of sizes observed and should not be extrapolated because the growth function may change outside the observed range. The von Bertalanffy equation assumes an exponential rate of increase which asymptotically attains a zero growth rate as t approaches infinity. In fact the growth function for Bulinus globosus was found to be sigmoid (see Section 4.3) and therefore the von Bertalanffy curve is inappropriate for the early stages of growth. Since it was impossible to mark very small snails (< 2mm shell length) effectively, growth data for wild snails up to this size could not be collected and therefore data from snail boxes has been used. The exponential equation fits the early growth data very well, and is therefore used in the following form for growth to 2mm:

$$l_t = 0.8\ e^{rt} \qquad (4.3)$$

Where l_t = shell length at time t.

r = a monthly growth constant.

This further complicates the cohort growth curve estimates which have to switch from equation (4.3) to equation (4.1) when $l_t > 2$. The resulting calculations are extremely tedious but can easily be programmed. Appendix B shows a BASIC program which calculates weekly cohort sizes given monthly values for K and L (from equation 4.1), and r (from equation 4.3).

Growth rate measures were obtained from marked snail growth increments; by following modes in successive samples; and from box-kept snails during this project. The results are presented and compared below.

4.2. Growth Curves from Marked Snails

Snail marking operations were undertaken in Nguni dam during 1980, 1981 and 1982. In Benes dam snails were only marked during 1980. As the project progressed, larger numbers of snails were marked and more accurate measurements were made, allowing finer resolution in growth rate estimates. Only captures more than four days apart were used in growth calculations.

Table 4.1 shows the numbers of recaptures used for each time-specific growth curve. The criterion for subdividing the data was not merely numbers of recaptures, but the distribution of recaptures at different size classes.

Fig. 4.2 shows mean growth rates/day in each size class for snails from Nguni dam 1981/82. The variation is indicated by the 95% confidence limit bars, and at first sight does not appear excessive. However, the variance is cumulative and the implications of different growth rates are shown in Fig. 4.3 for different months. It should be emphasized that these are average rather than extreme growth curves.

Table 4.1 Summary of time-specific data from growth increments of marked snails recaptured at least four days after the previous capture.

Dam	Date	No. of recaptures	*Early growth parameter r	von Bertalanffy parameters **L_∞	K
Nguni	May-Sept 1980	76	0.574	11.346	0.110
	Oct-Nov	83		10.092	0.128
	Dec	50		9.336	0.140
	June 1981	17	0.592	9.27	0.254
	July	27	0.377	10.41	0.136
	August	40	0.299	16.76	0.046
	Sept	63	0.312	10.06	0.054
	Oct	60	0.323	9.32	0.150
	Nov	92	0.575	9.76	0.223
	Dec	58	0.360	9.89	0.139
	Jan/Feb 1982	43		9.72	0.082
Benes	Mar-Aug 1980	55	0.637	6.58	0.627
	Sept-Dec	31		7.88	0.168

* Data from snail boxes (see equation 4.3)

** L_∞ = L in equation 4.1.

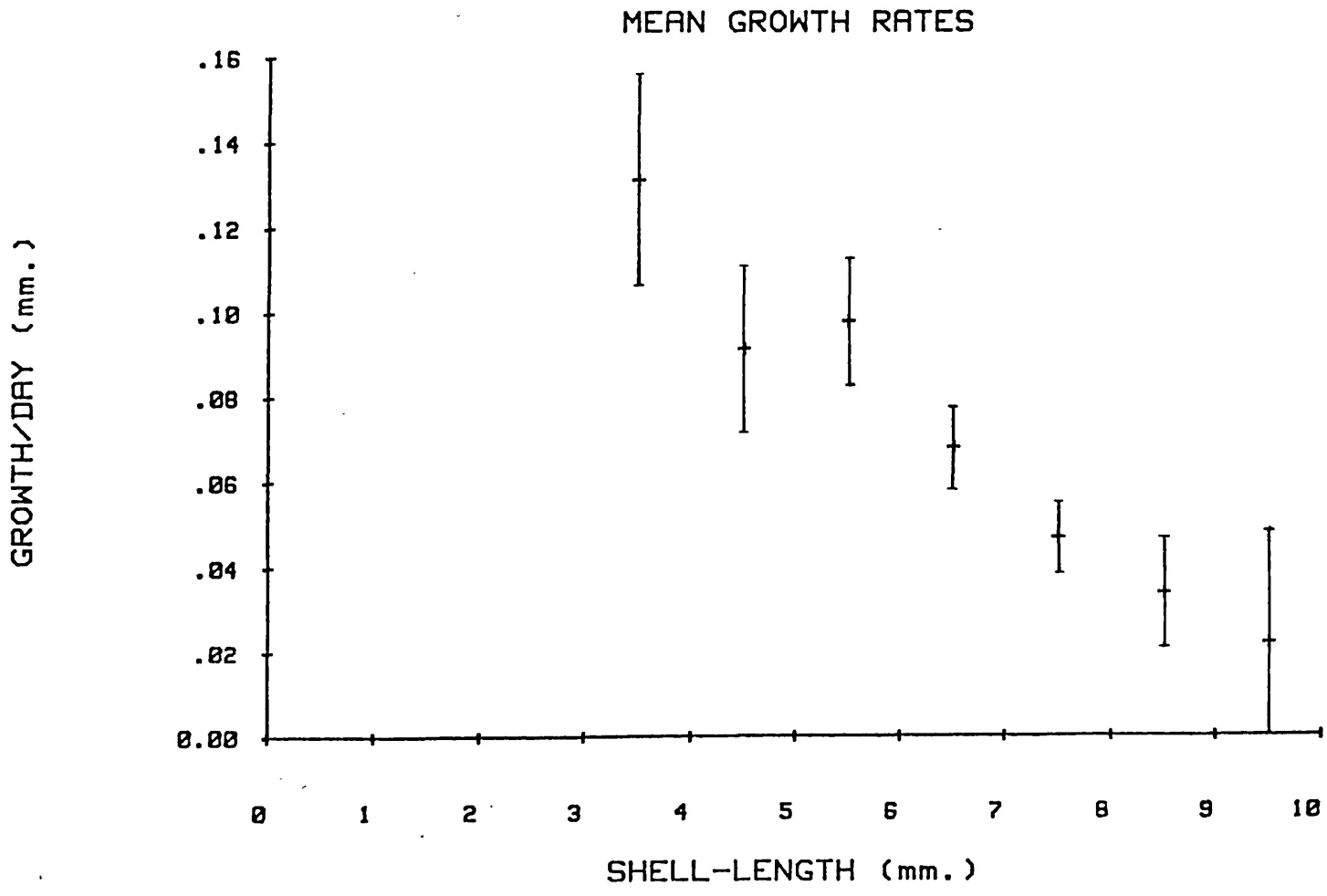


Fig. 4.2 Mean growth rates at different mm size classes, from 385 snails recaptured after at least four days in Nguni dam during 1981/82. Vertical bars show 95% confidence limits.

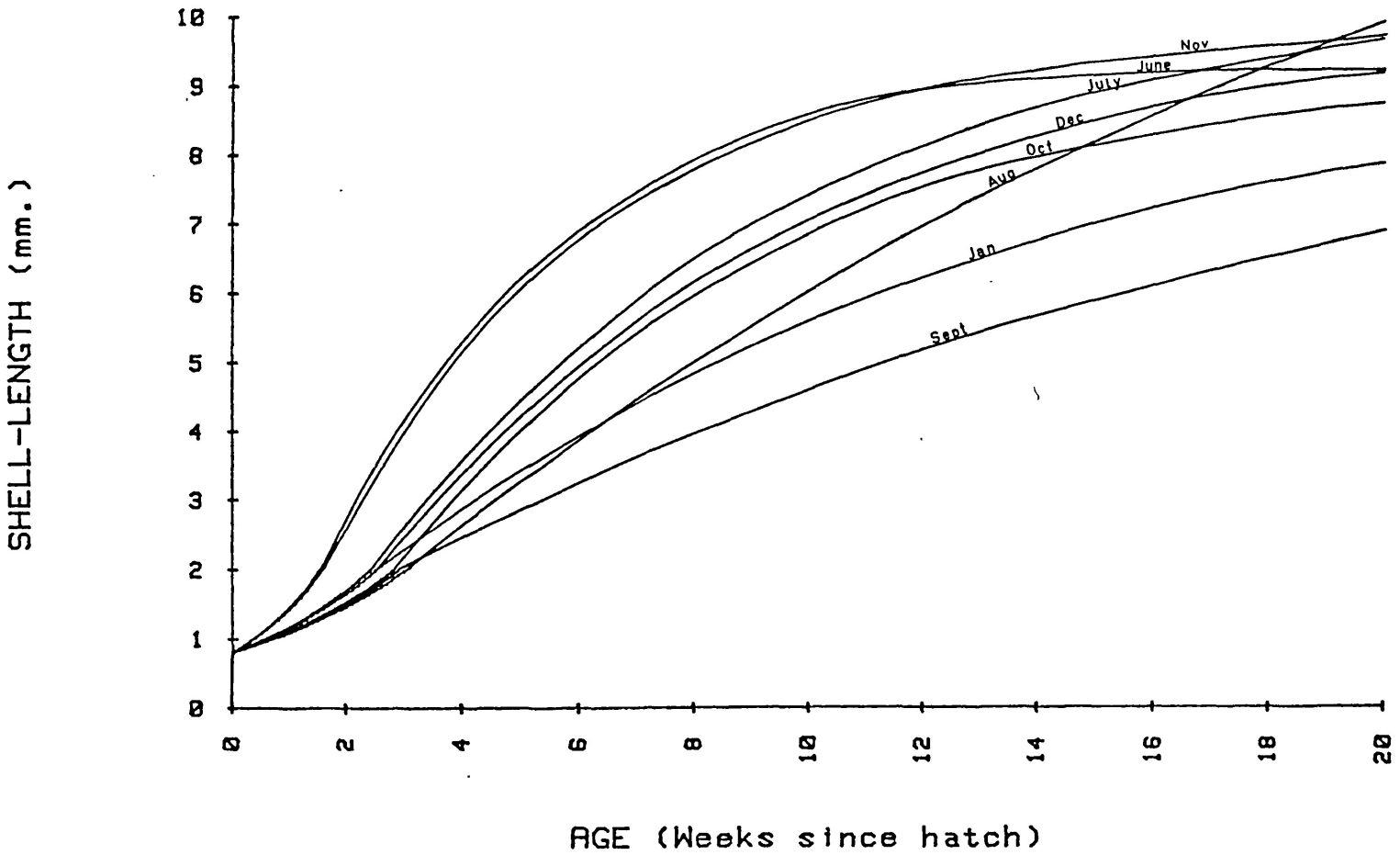


Fig. 4.3 Average time-specific growth curves for B. globosus in Nguni dam during 1981/82. (Growth to 2mm from box-snail data, from 2mm on curves from von Bertalanffy equations fitted to recapture data using Walford growth increment plots Walford, 1946).

Figs. 4.4 and 4.5 show growth rates for different periods during 1980 at Nguni and Benes dams. Lower resolution measurements and less recaptures allow fewer individual curves to be calculated.

Once the time-specific growth equations were solved, cohort growth curves were calculated as explained above (Section 4.1). Fig. 4.6 shows monthly cohort growth curves from Nguni dam during 1980. They are irregular because of the changes in conditions for growth throughout the snails' lives. Growth curves are not extrapolated beyond the twentieth week because the asymptotic nature of the curve and the inherent variation between snails preclude any confidence in predictions once the asymptote is approached.

The curves shown in Fig. 4.6 are a complex combination of different functions. Since they are a product of a number of fitted functions, it was not considered justified to simplify them again by further curve-fitting for predictive purposes. However, they have been fitted by a modified von Bertalanffy function (see Section 4.5) in order to obtain a parameter for comparison with growth curves from other sources. For predictive purposes, individual weekly cohort growth curves were calculated using the programme in Appendix B.

The time-specific growth curves shown in Figs. 4.4 and 4.5 for 1980 have been used as cohort curves for life-table construction, without further modification. This is because

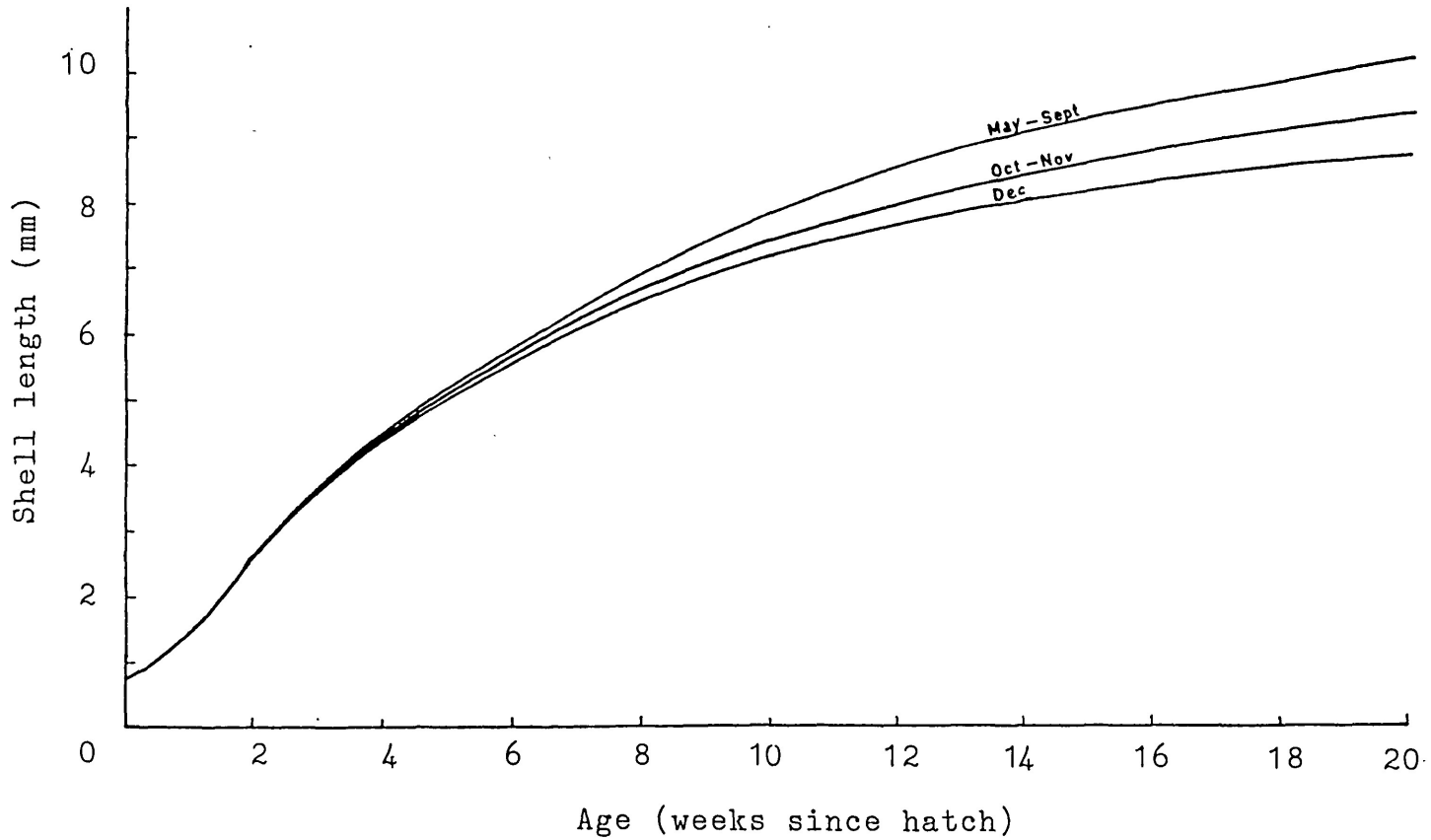


Fig. 4.4 Average time-specific growth curves for B. globosus in Nguni dam during 1980.

(Growth to 3mm from box snails, from 3mm+ curves from von Bertalanffy equations fitted to recapture data using Walford growth increment plots.)

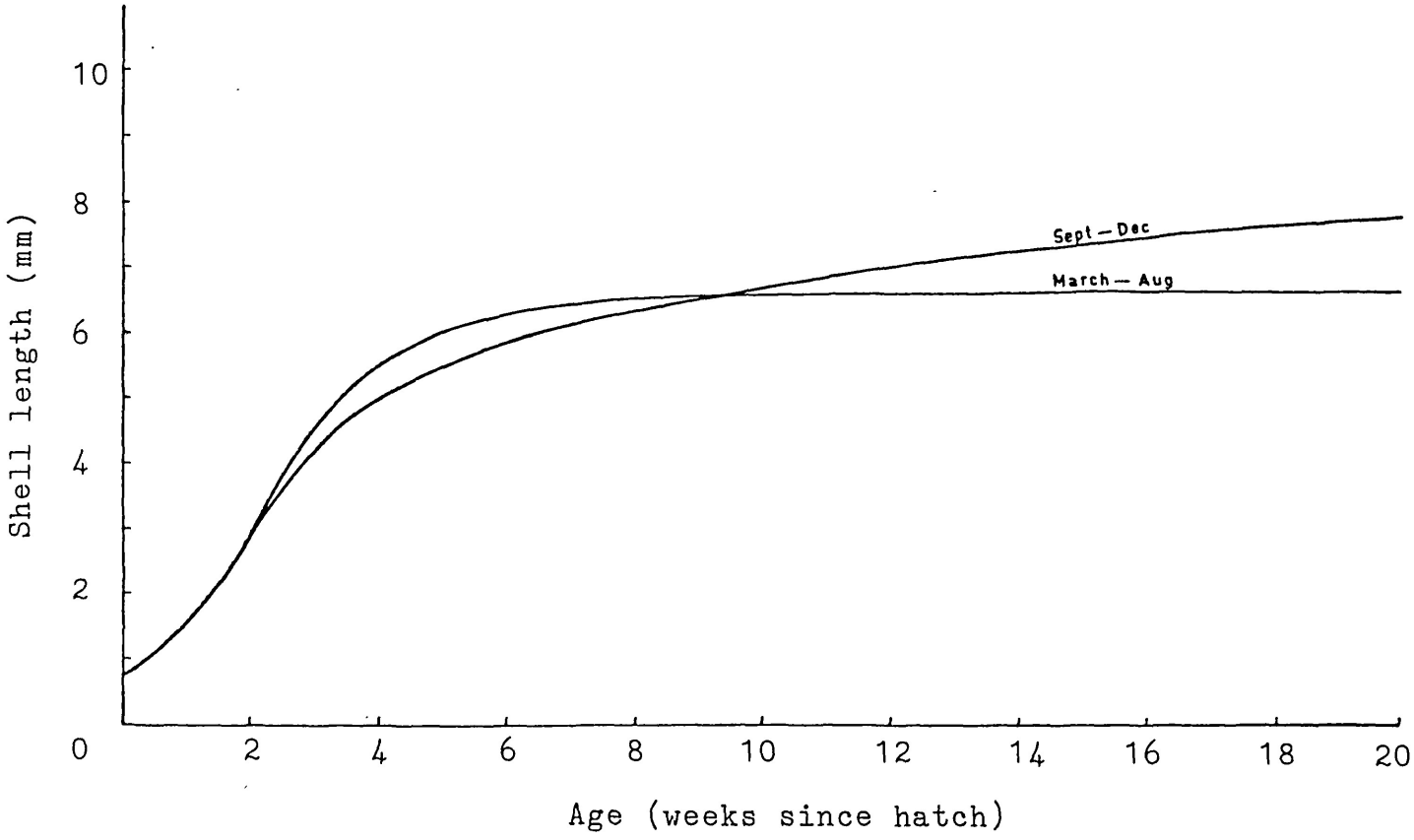


Fig. 4.5 Average time-specific growth curves for B. globosus in Benes dam during 1980.

(Growth to 4mm from box-snails, from 4mm+ from von Bertalanffy equations fitted to recapture data using Walford growth increment plots.)

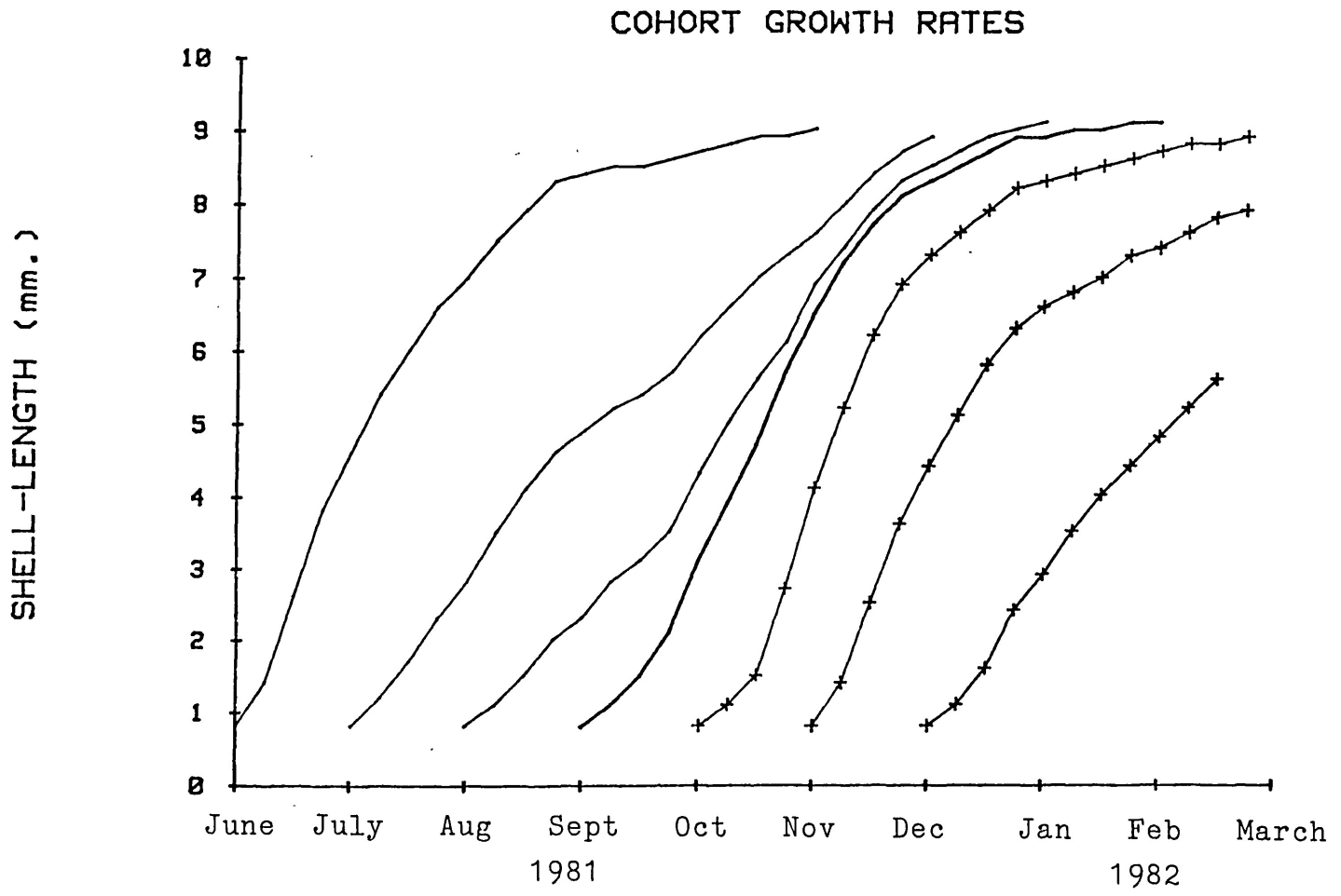


Fig. 4.6 Cohort growth curves for B. globosus during 1981 in Nguni dam.
(Curves are for monthly cohorts hatched in the middle of the month indicated.)

each curve is calculated from a number of months' data and is therefore already an average for some cohorts' lifespans. In addition, the variation in the curves is much less than for those shown in Fig. 4.3. For these reasons, the gain in precision from conversion to cohort curves is negligible. The time-specific curves remain the best available measures of growth rate history from marked snails.

4.3. Growth Curves from Box Snails

B. globosus kept in boxes were measured weekly and therefore provide a direct history of cohort growth rates. The purpose of these measures was to provide a comparison of growth in different feeding and density regimes within the boxes, and to calibrate the conditions in the boxes with those outside by comparing growth performance from marked snail data. Ideally it is necessary to have growth parameters which encapsulate growth success for comparative purposes. The von Bertalanffy equation provides two parameters: L_∞ and K, which can be estimated from Walford plots (Madsen, 1979). L_∞ , the asymptote, is an average measure of final linear size, while K is a measure of the speed of approach to the asymptote. Both incorporate some measure of growth success. As has been mentioned above, the von Bertalanffy equation describes an asymptotic exponential growth form, in which K is the slope of the curve at time 0. The actual growth curve for B. globosus as has previously been noted (e.g. Shiff, 1964), incorporates an initial lag phase and

is therefore sigmoid. Von Bertalanffy's equation can accommodate this initial lag by a cubic modification:

$$L_t = L\infty\,(1 - e^{-K_t})^3 \qquad (4.4)$$

Since the hatch length of B. globosus was found to be 0.8mm, the relevant growth function from the time of hatching would be:

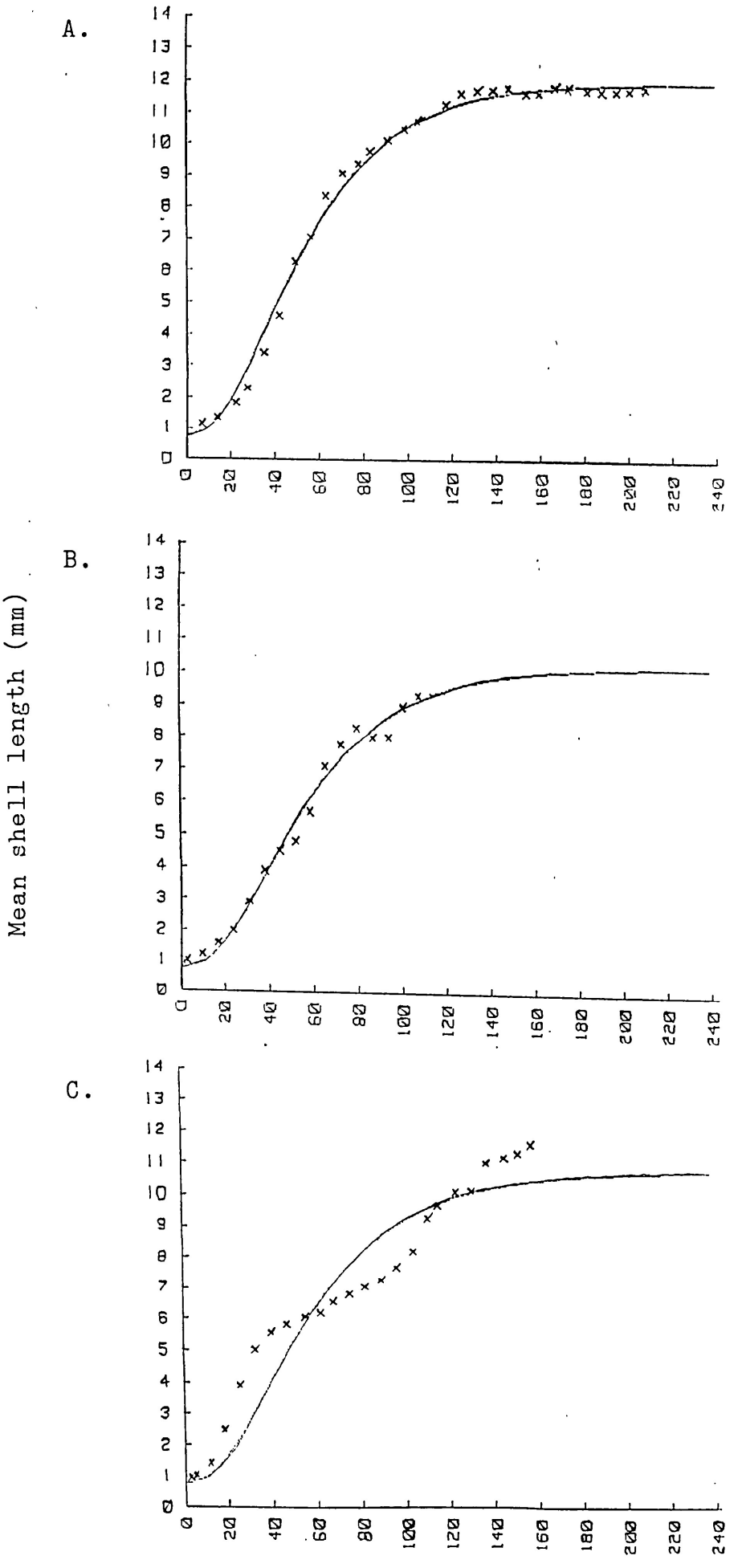
$$L_t = L\infty(i - e^{-K_t})^3 + 0.8 \qquad (4.5)$$

This modified von Bertalanffy equation provides a very good empirical fit to growth data from box snails in most cases. Fig. 4.7 shows three examples. The data in A and B is very well approximated by the function, but C is not. Sudden mortality lowering the density in a box, or sub-optimal feeding tended to cause growth irregularities. This is dramatically illustrated by Fig. 4.8 which shows a two-stage growth curve caused by a diet change mid-way through the life of a cohort. The modified von Bertalanffy equation is therefore considered to be a good approximation of the regular linear growth form of B. globosus, and is used for comparative purposes to characterise the various growth curves measured in this project. (It is not, however, used for predictive purposes, because of the irregularities in growth rates which are caused by environmental changes over time).

Fig. 4.7 Modified von Bertalanffy curves fitted to growth data from box snails.

$$L_t = L_\infty (1 - e^{-K_t})^3 + 0.8$$

(See text for explanation.)


A.
B.
C.
Mean shell length (mm)
AGE (DAYS)

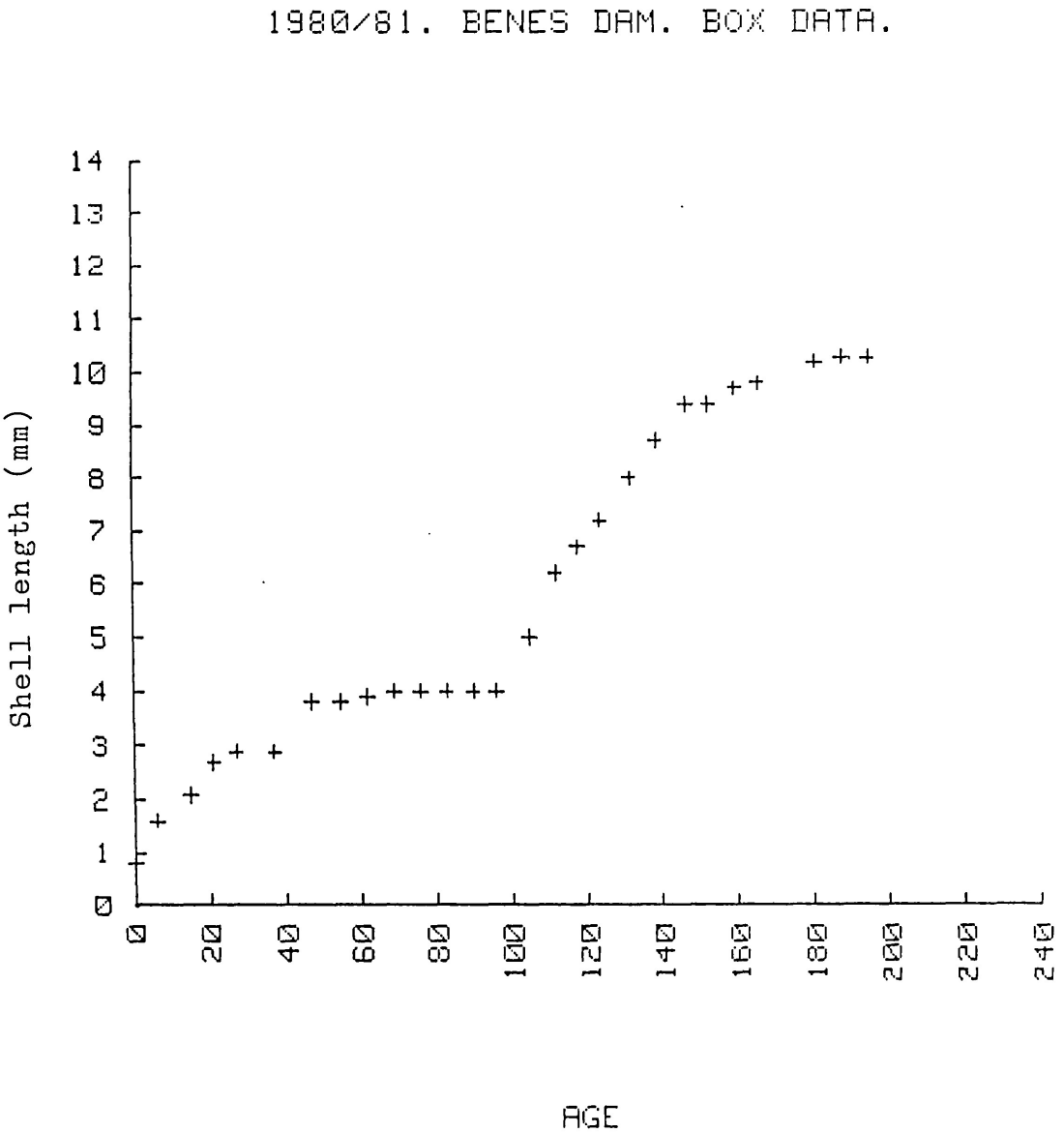


Fig. 4.8 Feeding effect on growth rate.

The graph shows weekly mean growth increments of a cohort of 15 snails whose diet was augmented by approximately 200cm^2 Nymphaea caerulea leaf per week after day 96.

Equation 4.5 was used to obtain measures for $L\infty$ and K. K is now a measure, not of the slope at time 0 (which is zero), but of the slope at a point early in the curve which varies according to the height of the asymptote ($L\infty$). Neither $L\infty$ nor K on their own provide a complete measure of growth performance, but the product of the two combines the ultimate linear size of the snails and the rate at which they reach it, and has therefore been used as the comparative parameter of growth success. Using the product $L\infty$ x K can obviously give the same result for a fast growing snail with a small final size as for a slower growing, finally larger snail. This seems a reasonable result since both contain different components of "good" and "bad" growth.

Table 4.2 summarises the results of B. globosus growth in boxes. Once again, data is most abundant for Nguni dam during 1981 and has been split by month. Data has only been used for boxes which contained snails of a single age.

Fig. 4.9 shows growth curves from monthly cohorts in Nguni dam from June 1981 to January 1982, over the first twenty weeks. The top of the growth curves are difficult to interpret since density decreases caused by mortality often led to increased growth rates.

A factorial analysis of variance was used to test the significance of the difference between mean growth

Table 4.2 Summary of growth parameters from modified von Bertalanffy equations fitted to snail growth in boxes. (95% confidence limits are shown for $L_\infty \times K$).

Dam	Year	Month	No. of snails	No. of boxes	Mean L_∞	Mean K	Mean $L_\infty \times K$
Benes	1980/81	All	171	7	7.89	0.078	0.568 ± 0.233
Benes	1981/82	All	50	5	7.91	0.048	0.365 ± 0.195
Nguni	1980/81	All	69	5	8.08	0.057	0.455 ± 0.181
Nguni	1981	June	70	6	8.61	0.050	0.403 ± 0.086
Nguni	1981	July	105	9	9.30	0.037	0.343 ± 0.042
Nguni	1981	August	105	9	10.54	0.027	0.285 ± 0.051
Nguni	1981	Sept.	105	9	10.76	0.032	0.336 ± 0.078
Nguni	1981	Oct.	105	9	7.90	0.046	0.348 ± 0.048
Nguni	1981	Nov.	105	9	6.43	0.077	0.483 ± 0.099
Nguni	1981	Jan.	105	9	7.19	0.047	0.322 ± 0.086

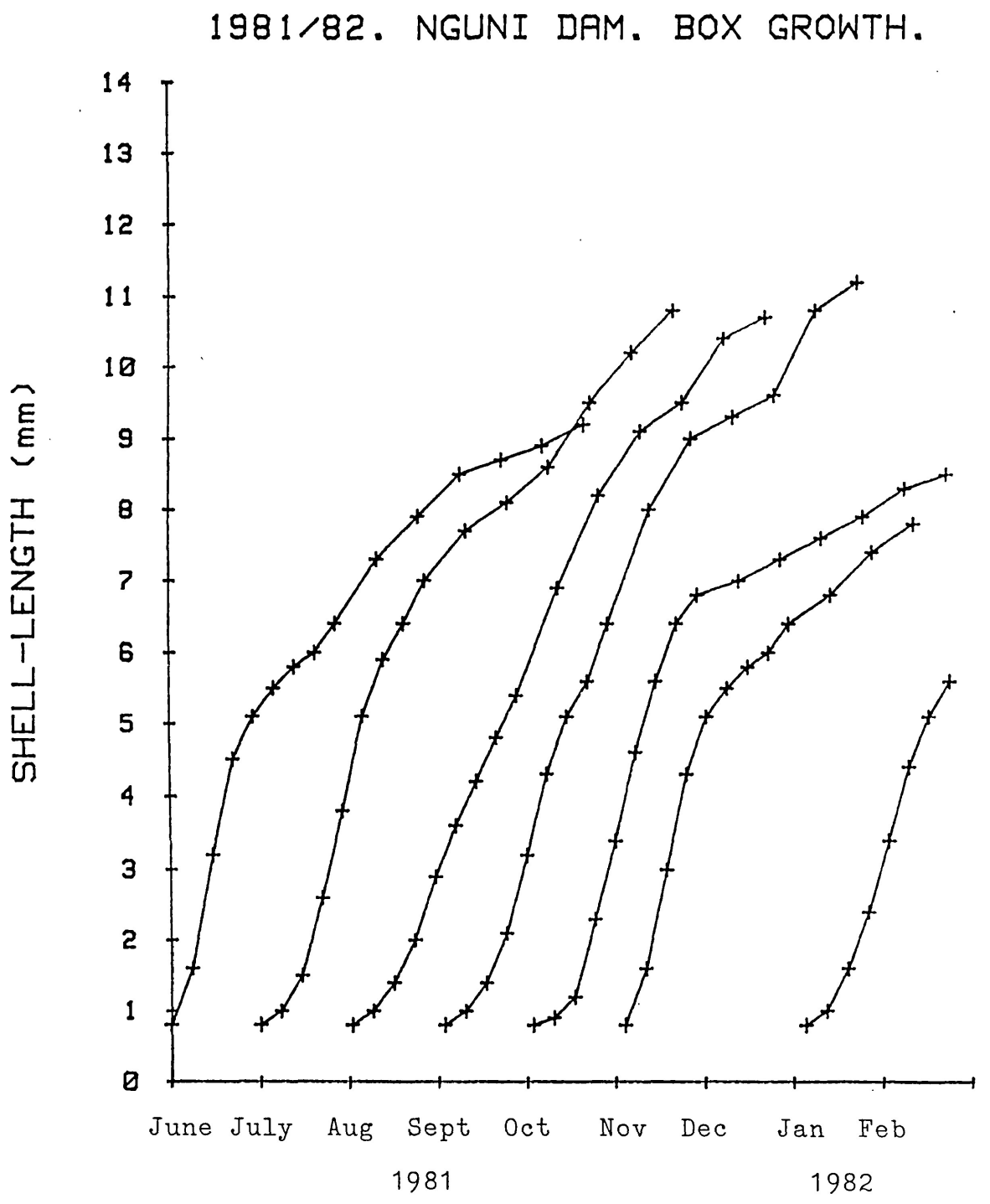


Fig. 4.9 Mean cohort growth rates from box-kept snails. June 1981 - January 1982.

(Cohorts were hatched at the beginning of the month indicated.)

performance in different months. (Data for June were not included, since fewer boxes were started then and the ratios of different treatments were not the same as for other months). For the modified von Bertalanffy growth parameter $L_\infty \times K$, the mean value for November box snails was significantly higher than for the other months, and the mean for August was significantly lower.

4.3.1. Feeding and density effects on box snail growth

Factorial analysis of variance was also used to test the different effects of the feeding and initial density regimes described in section 3.6.3. Since densities were not manipulated after the boxes were started, the test is for the effect of initial density differences.

Not surprisingly, in view of Fig. 4.8, feeding with lily leaf produced a very significant improvement in growth. Low initial densities also led to significantly better growth rates. Table 4.3 summarises the mean growth parameters. Lily leaf feeding produced the highest mean growth parameter values irrespective of initial density.

4.4. Growth Curves from Sample Modes

Reproduction in both Nguni and Benes was virtually continuous throughout 1980 - 1982. Although there were population peaks, they were not caused by large numbers of

Table 4.3 The results of factorial analysis of variance for mean growth performance (L_∞ x K) of B. globosus in boxes, July 1981 - January 1982, Nguni dam.

Density treatments 1 to 3 indicate low to high initial density.

Feeding treatments 1 to 3 indicate high quality to low quality diet (see section 3.6.3 for explanation).

(Data from 54 boxes containing 630 snails)

A. MAIN EFFECT MEANS:

	Treatment		
	1	2	3
Feeding	0.438*	0.325	0.295
Initial density	0.397*	0.342	0.319

B. TWO WAY INTERACTION MEANS:

		Initial Density		
		1	2	3
Feeding	1	0.467	0.427	0.419
	2	0.397	0.302	0.277
	3	0.328	0.297	0.260

The analysis indicated significant differences in mean growth (at $P < 0.05$) both from different feeding and initial density regimes.

* Indicates significant ($P < 0.05$) differences from multiple comparisons using the least significant difference method.

B. globosus of a single generation, and the identification of size class modes from which to construct growth curves is not straightforward.

Since growth rate changes with size, samples in different size classes from the same date do not accurately reflect the relative dominance of cohorts. Thus the smaller size class samples reflect survival from a few days' reproduction, whilst the large size class samples reflect survivorship from several weeks' reproduction. In addition, mortality continually reduces the relative dominance of old cohorts (e.g. no weekly sample of 10 - 11mm B. globosus comprised more snails than the 9 - 10mm sample for the same week). This problem can be overcome by comparing weekly samples of the same size class and identifying the week when that size class was most abundant relative to other weeks. The fluctuations of weekly sample size, due to environmental effects, obscures the results from this comparison, but can be overcome by expressing the sample for each size class in each week as a percentage of the total sample for that week.

To sum up, in order to identify dominant cohorts and to follow their average size increases through time, weekly sample results were treated as follows:

The number of snails in each size class for each week was expressed as a percentage of that week's total sample. A

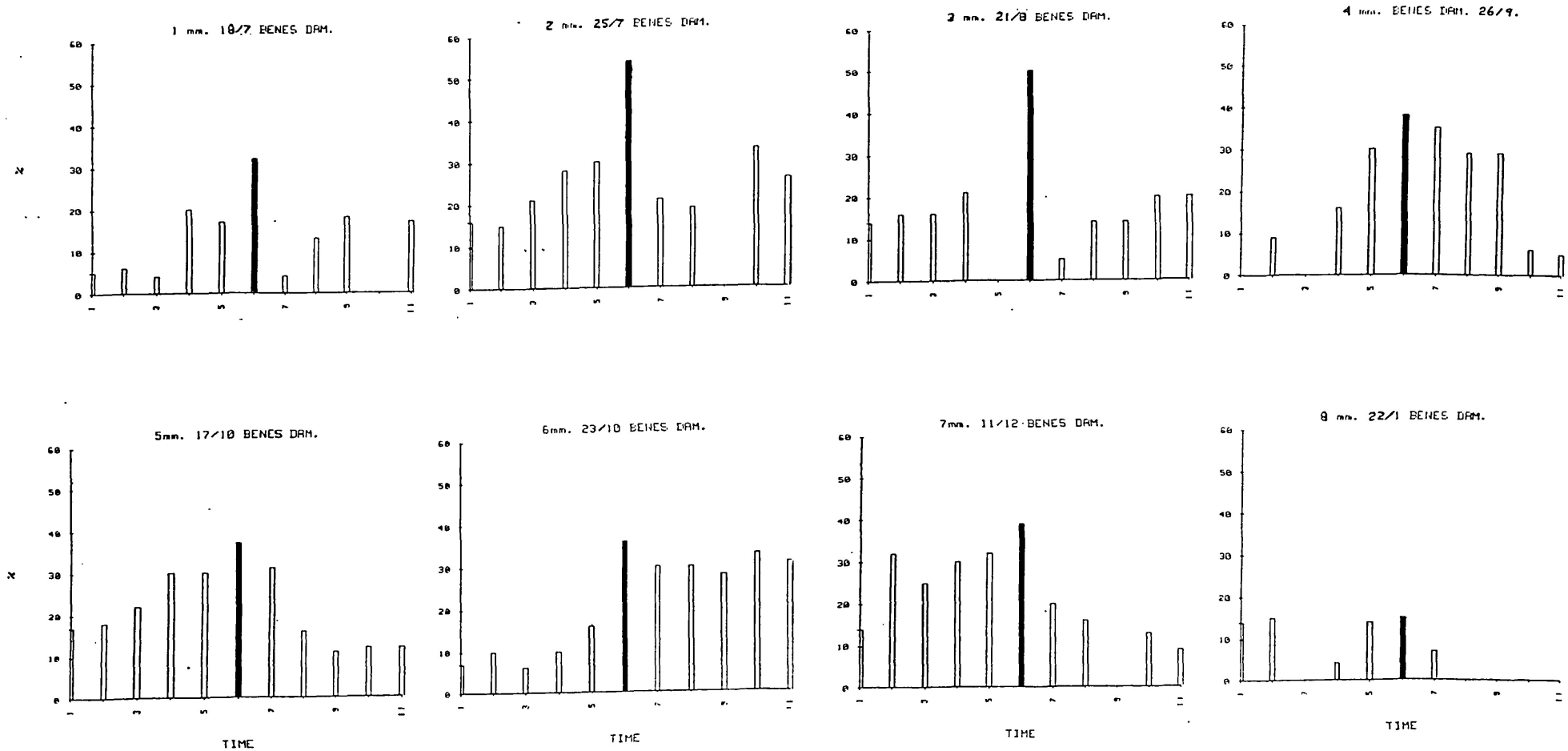
comparison within each size class shows the week on which that size class comprised the largest proportion of all snails collected, which indicates a dominant cohort. Following these relative modes in successive size classes over succeeding weeks provides a series of size-at-age estimates.

Only cohorts which can be identified early and followed throughout their lives are of use for growth curve construction. Figs. 4.10 to 4.13 show four cohorts, (one for each year in each dam), growing through successive size classes. The modified von Bertalanffy equation was fitted to the size-at-age results (see Table 4.4).

4.5. Discussion

Of the three methods used for growth measurement, data from box-kept snails provides completely accurate measurements but in conditions which may vary from those of natural populations. Data from marked snails and from sample modes represents genuine field data, but the growth rates are derived indirectly and may therefore be suspect.

Table 4.5 summarises growth parameters from all three sources. Box snails grew faster and larger, on average, than free snails. From the results in Table 4.3, it is obvious that the lily leaf feeding regime was responsible for increasing overall growth performance. Relative changes from box-kept



Figs. 4.10 Benes dam 1980/81. Growth rates from successive size class modes.

Each graph shows weekly samples for one size class, expressed as a % of the total weekly sample. The dominant week's class (■) is shown at each size, compared with the % for that size class on the five preceding and succeeding weeks. The dates shown are dates for the dominant cohort samples.

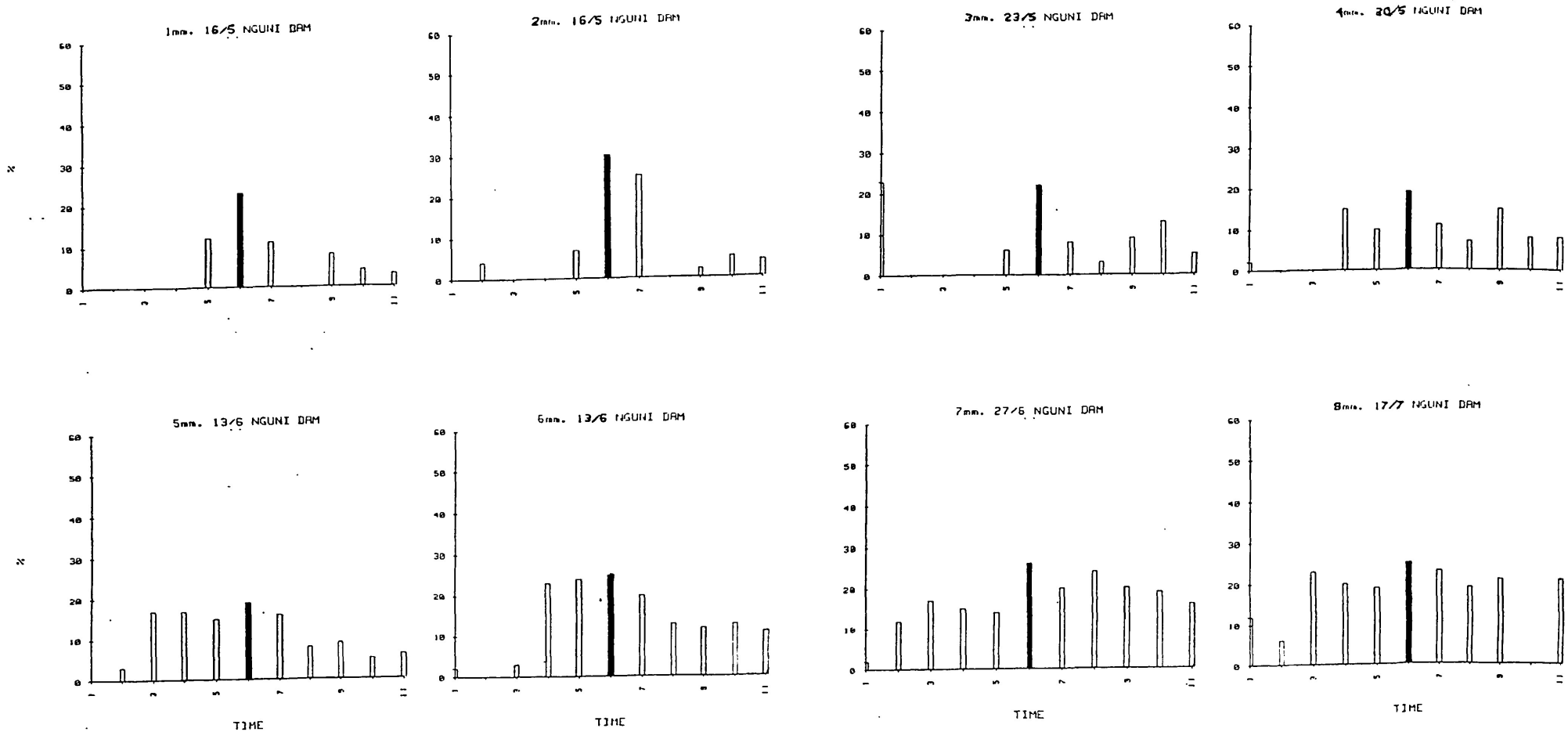


Fig. 4.11 Dominant cohort growth in Nguni dam 16/5/80 to 17/7/80.

(See Fig. 4.10 for explanation.)

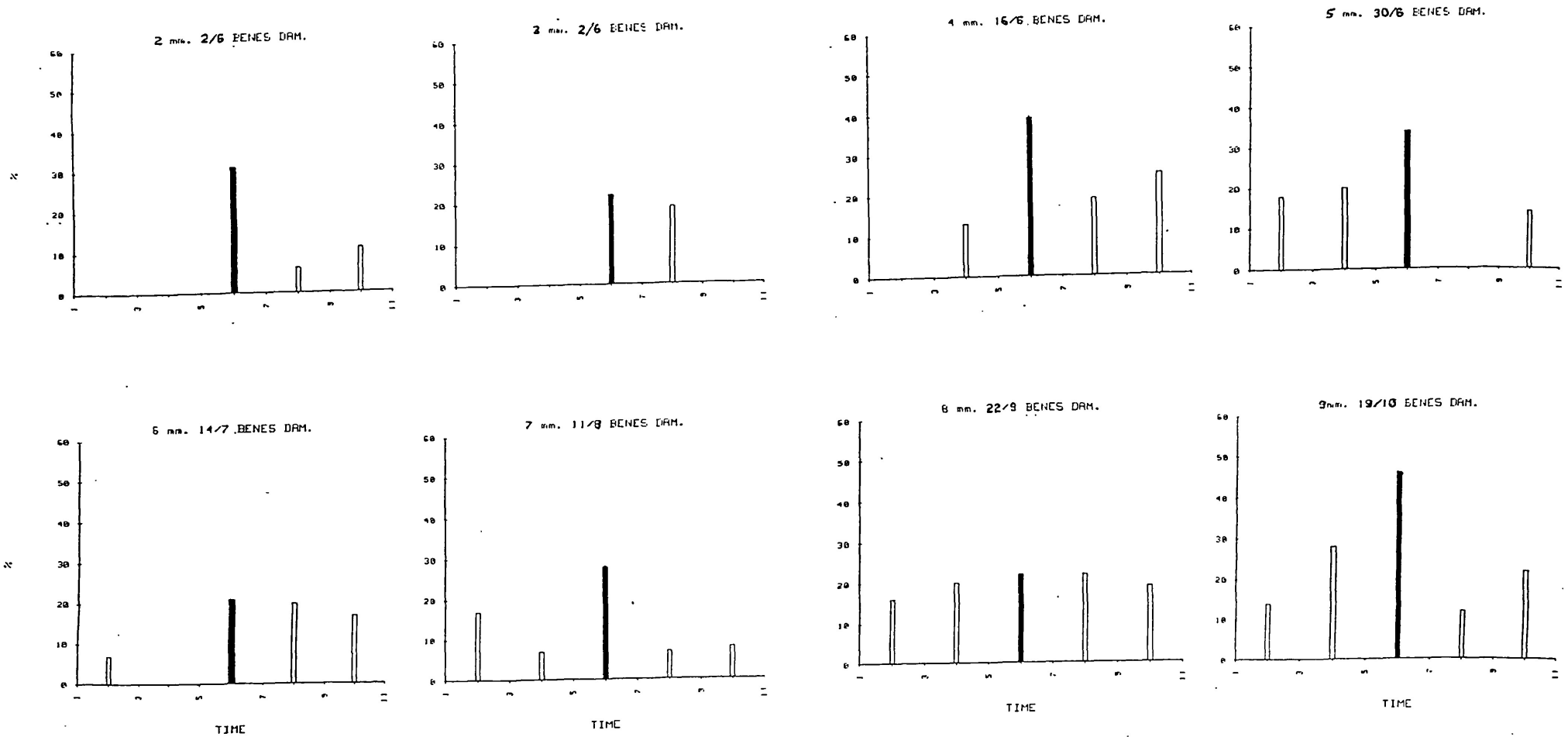


Fig. 4.12 Dominant cohort growth in Benes dam 2/6/81 to 19/10/81.

(See Fig. 4.10 for explanation.)

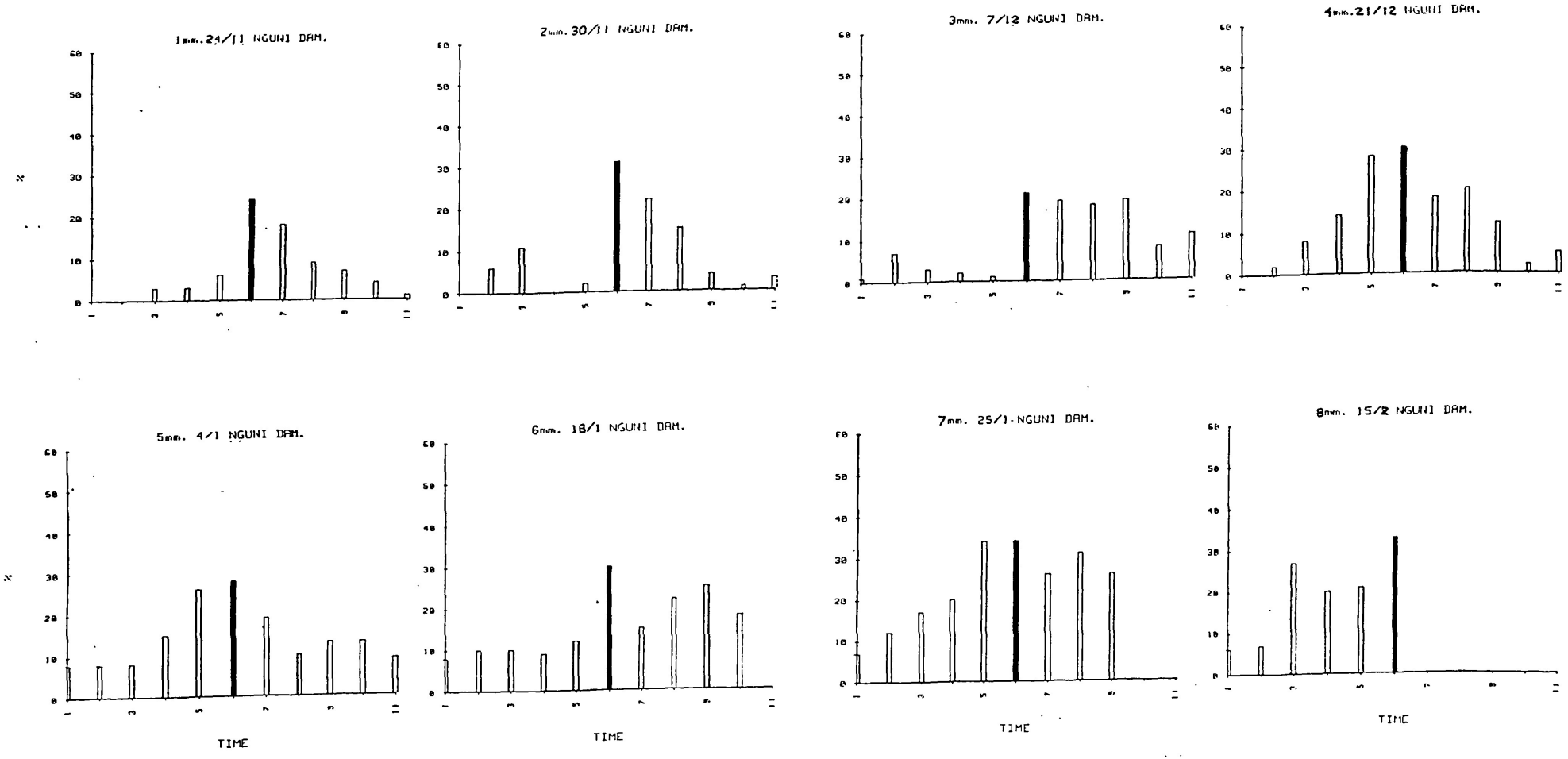


Fig. 4.13 Dominant cohort growth in Nguni dam 24/11/81 to 15/2/82.

(See Fig. 4.10 for explanation.)

Table 4.4 Growth parameters using the modified von Bertalanffy equation to fit data from field sample mode sizes.

Hatch date	Dam	L_∞	K	L_∞ x K
May 1980	Nguni	7.36	0.055	0.402
July 1980	Benes	6.83	0.020	0.139
May 1981	Benes	7.01	0.040	0.280
Dec. 1981	Nguni	6.73	0.045	0.301

Table 4.5 $L\infty$ x K growth parameters for two dams during two years. The table shows mean values from different data sources.

	Box snails	Marked snails	Mode following
1980/81 Benes dam	0.568	0.498	0.139
1980/81 Nguni dam	0.455	0.378	0.402
1981/82 Benes dam	0.365	-	0.280
1981/82 Nguni dam	0.358	0.313	0.301

snails should reflect environmental changes which affected free snails. Fig. 4.14 compares fluctuations in growth performance from box snails and marked snails. Apart from one month, values for marked snails are uniformly lower than for box snails, and track their fluctuations very closely. Parameter values derived from mode following are generally lower than from marked snails, perhaps because of the density effects implicit in measurements from dominant cohorts. Because of this, and because more separate growth curve measurements are available from marked snails, mode-following growth curves have not been used predictively in this project.

Section 4.3.1. showed that significant density effects were influencing growth rates in boxes as well as the type of food available. Crowding effects in aquarium-kept snails have often been observed (e.g. Wright, 1960; Shiff, 1964), and Berrie (1968) reported inhibited growth in a natural population of Biomphalaria sudanica due to crowding. Jobin and Michelson (1967) concluded that crowding could adversely affect a natural population of Bulinus globosus at a density of one snail per 100 litres of water.

Growth performance measures from the different box treatments straddled the values obtained from marked snails, as they were designed to do. Since lily leaf was relatively scarce in both dams, it was expected that the type 2 or 3

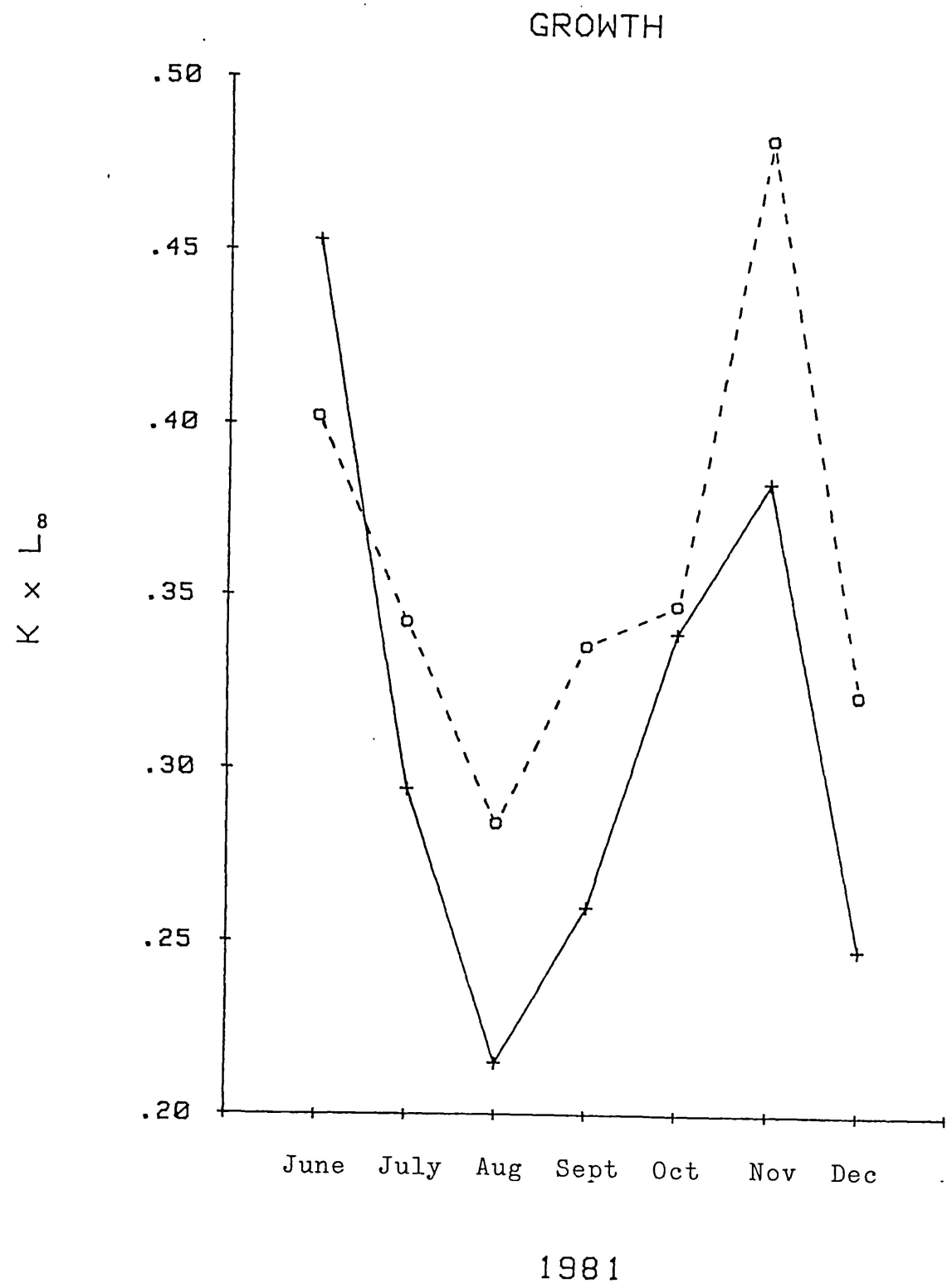


Fig. 4.14 Comparison of growth performance from box-snails (o---o) and marked snails (+——+) in Nguni dam.

The ordinate axis shows values of a compound parameter from the modified von Bertalanffy equation:

$$L_t = L\infty\ (1 - e^{-Kt})^3 + 0.8$$

(See text for explanation.) (The data points are for cohorts of snails hatched at the beginning of the months indicated.)

feeding (Cyperus/Typha leaf) would be more likely to approximate on average the real conditions. Table 4.3 gave growth results for the various treatments. For comparable months (July 1981 - January 1982) in Nguni dam, the growth parameter L_∞ x K is 0.290 $\pm$ 0.062. This is closest to type 32 boxes (initial density 10 snails, fed on 270cm^2 surface area Cyperus exaltatus leaf per box) at 0.297 $\pm$ 0.079; type 23 boxes (initial density 20 snails, fed on 70cm^2 C. exaltatus per snail) at 0.277 $\pm$ 0.041; and type 22 boxes (initial density 10 snails, fed on 70cm^2 surface area C. exaltatus per snail) at 0.302 $\pm$ 0.067.. On average therefore, snails in Nguni dam appeared to be living in relatively poor conditions, on a low grade diet.

Comparison of growth measured during this study with those from other studies indicates that snails in both Nguni and Benes dams were not fulfilling their entire growth potential. Field growth rates obtained in Foyle pond, Rhodesia by Shiff (1964) are compared with those from this study in Fig. 4.15. Initially, growth rates compare favourably with those from Rhodesia, but the asymptote is reached at a much smaller size. Webbe and Msangi (1958), though giving no growth rates, recorded large numbers of B. globosus of 15mm+ shell-length from sites on the coast of Tanzania. In a previous project, the author found B. globosus up to 18mm long from sites in and around Benes dam (O'Keeffe, 1979). During this project only one B. globosus > 14mm was found during weekly sampling. The W.H.O. identification booklet (1973)

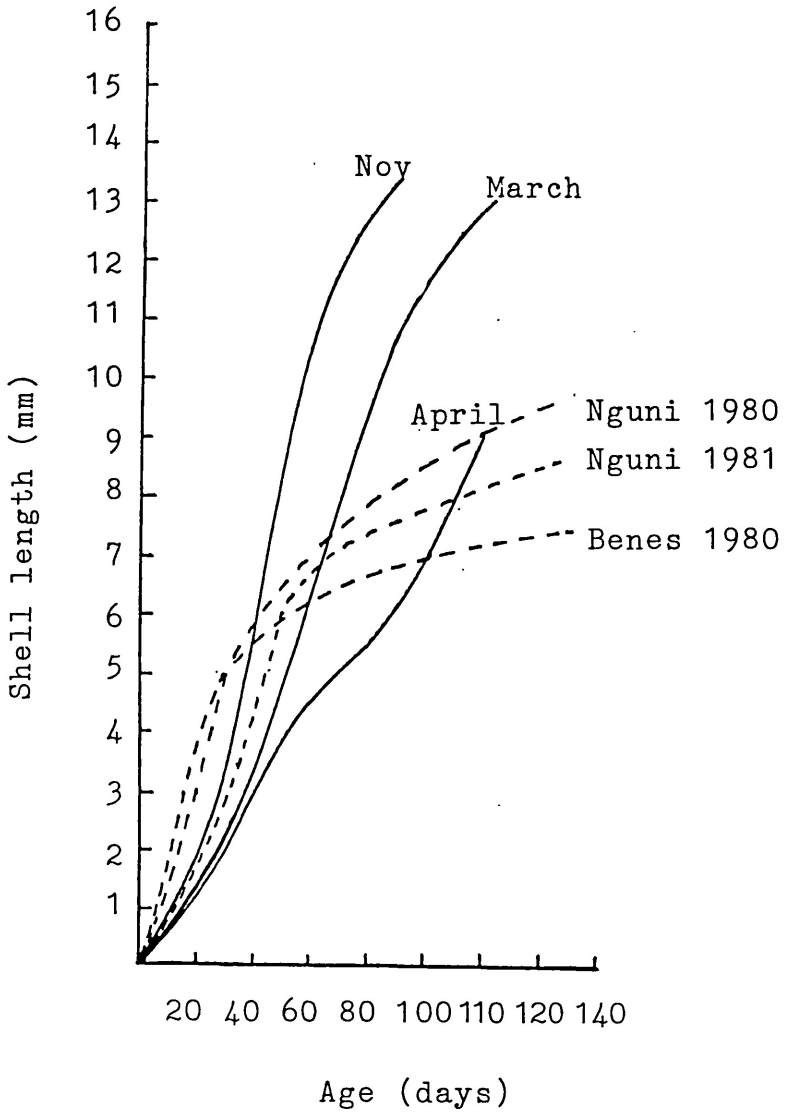


Fig. 4.15 Comparison of growth rates for B. globosus from Rhodesia (——) (Shiff, 1964), and this project (- - -).

gives 15 - 16mm as a typical size for B. globosus and both W.H.O. (1973) and Brown (1980) indicate sizes up to 22.5mm It would therefore appear that B. globosus in Nguni and Benes dams were smaller than average from 1980 - 1982, though not necessarily during other years.

4.5.1. Factors influencing growth

External physical and chemical factors influencing growth in aquatic snails are discussed, along with their effects on other population parameters, in Chapter 9. Intrinsic effects are obviously mitigated by these external factors, and have created difficulties in their interpretation.

Thomas and his colleagues have carried out extensive laboratory investigations of density effects on the growth of Biomphalaria glabrata. Thomas and Benjamin (1974) found that, whilst small snail growth was inhibited at increasing densities, large snail growth could be enhanced. Thomas, Goldsworthy and Aram (1975) found that growth rates correlated strongly with decrements of calcium and conductivity values in the water. Thomas, Powles and Lodge (1976) caused slower growth in juvenile snails by the addition of ammonia, but Thomas, Lough and Lodge (1975) could find no good evidence that snails produced the growth inhibiting substances themselves, contrary to previous findings by Wright (1960), Berrie (1969) and Levy et al (1973). Thomas (1973) reviews much of the above work and concludes that there is no

evidence of inhibitory pheromones but that the causes of growth inhibition may be food shortage, depletion of other resources (such as calcium or oxygen), or inhibitory factors produced by plants.

In field studies, where densities are not being experimentally manipulated, density effects on growth are still more difficult to show. High densities presumably occur as a result of optimum conditions which may tend to counteract to some extent adverse density effects. In this project there is no inverse correlation between growth parameters and sample densities. Growth parameters for 1980 are higher than for 1981 in Nguni dam (see Table 4.4) although sample densities were 1.5 - 2 times as high. Despite this, results from box snails indicate that density effects can be important even when the volume of water per snail is not constrained.

CHAPTER 5 SURVIVAL

5.1. Introduction

The life-span of the host snails of schistosome species is of crucial importance to the transmission dynamics of the parasite. Anderson and May (1979) have reviewed studies of the latent period (the time period from the point of infection to cercarial release) of the three major schistosome species of man. For Schistosoma haematobium the latent period is primarily affected by temperature and varies between 25 days (at a temperature of 32 - 33°C) and 119 days (at a temperature of 18 - 20°C). Mean yearly temperatures on the Kenya coast are 26°C, and both Shiff et al (1975) and Gordon et al (1934) indicate latent periods of around 35 days for this temperature in Bulinus globosus. Factors other than temperature, such as food of the snail host and the age of the host at infection, may also affect the latent period (Anderson and May, 1979). The obvious conclusion is that the snails must live for at least a month in order to have a chance of contributing to the transmission of bilharzia.

As with growth rates, survival rates were measured by independent methods for box-kept snails, marked snails and snails gathered in weekly samples. The aim was to estimate a single parameter which could be used to compare survival at different times and in different circumstances, as well as allowing the results to be related to other studies.

Barlow and Muench (1951) found that mortality in Bulinus truncatus was very high during early and late life, and the resulting survivorship curve is an amalgamation of Pearl's type III and type I (Pearl, 1928). Observed survivorship in box-kept snails provides the same result for B. globosus. Because survival is of a complex age dependent form, it is difficult to characterize mortality by means of a single parameter for each cohort. Anderson and May (1979) used an average death rate (obtained from a log regression for combined age classes) to characterize mortality in different studies. This method has been used here for relative comparisons of box-kept snails during different months and in different conditions. For field estimates a different parameter had to be found because discrepancies in the sampling of small snails, especially in Nguni dam, would have affected regressions, and because many of the cohorts could not be followed to extinction. An alternative parameter was chosen for comparative purposes, namely; average mortality over a ten week period. By the time snails were ten weeks old the initial sampling discrepancies were not apparent, the snails were mature and in mid-reproductive phase, and many more cohort mortalities could be estimated than for a more advanced age. From the average mortality rates, mean expected life spans were calculated. For all survival and mortality calculations in this chapter, $x = 0$ at the hatch date, and l_x at $x = 0$ is the number of successfully hatched snails expressed as a cohort of 1000.

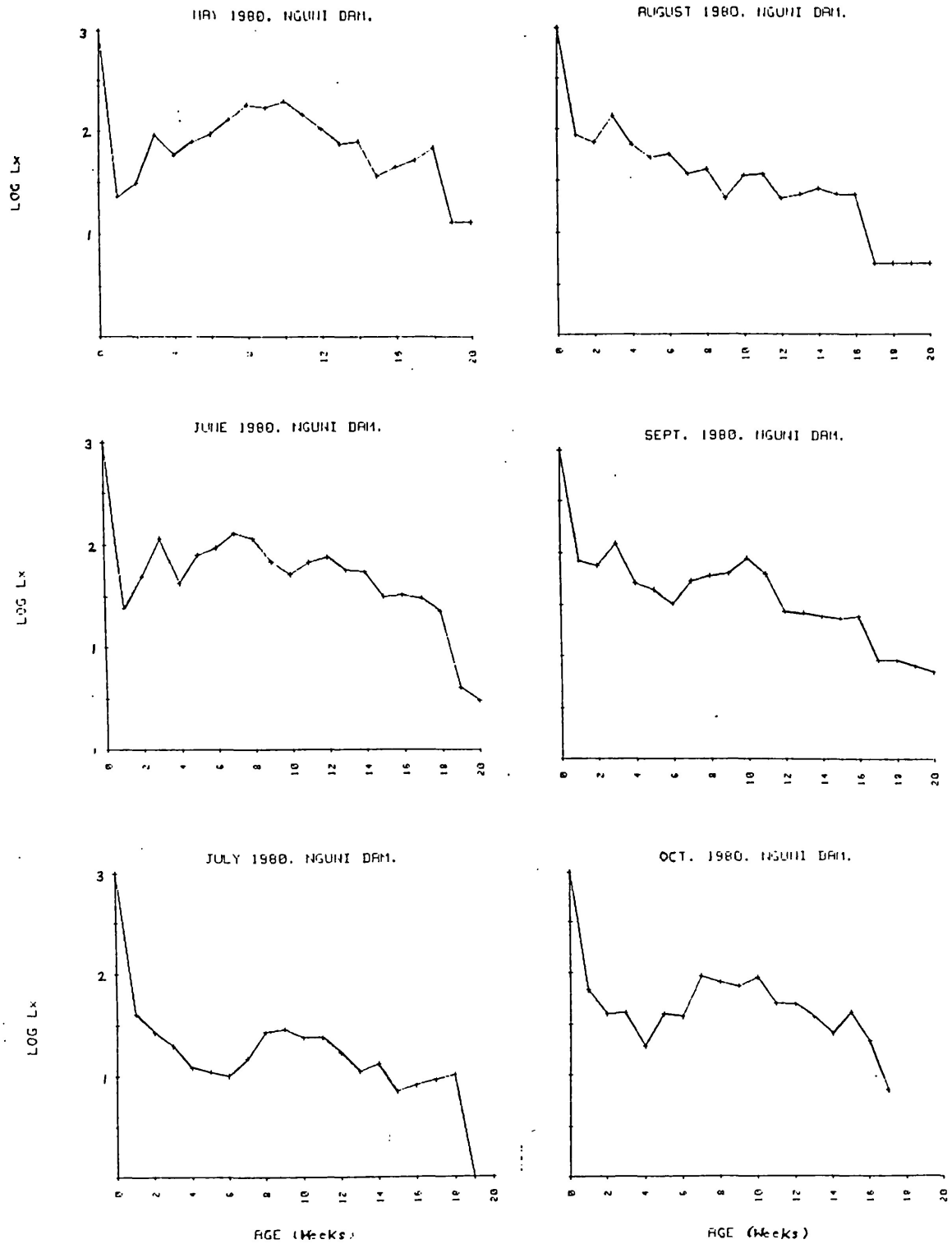
5.2. Field Survival

5.2.1. Survival from trap samples

Numbers of snails surviving each week were calculated from weekly trap samples using the cohort growth curves shown in Figs. 4.4, 4.5 and 4.6, (for Nguni dam during 1981, weekly growth curves were calculated and used). Appendix C shows a computer program, written in BASIC language, to derive the initial number of snails (from observed egg masses) and survivors throughout succeeding weeks. The asymptotic nature of the growth curve makes extrapolation beyond 20 weeks unreliable. Weekly cohorts (either 4 or 5) have been grouped and averaged for each month and l_x curves are plotted for Benes and Nguni dams during 1980 and 1981 in Figs. 5.1 to 5.3. Monthly survival for Benes dam during 1981 has not been calculated, since the intensity of sampling did not provide sufficient data. Because the sampling variation and other sources of error lead to inconsistencies even in snails aged ten weeks, the mean number of survivors at weeks nine, ten and eleven has been used to calculate average ten week mortality. Table 5.1 gives a summary of mortality parameters for 1980 and 1981.

The obvious undersampling of small snails in Nguni dam survival estimates requires an explanation.

For practical purposes, since the discrepancies are predominantly among juvenile snails, they make very little


MAY 1980. NGUNI DAM.
AUGUST 1980. NGUNI DAM.
JUNE 1980. NGUNI DAM.
SEPT. 1980. NGUNI DAM.
JULY 1980. NGUNI DAM.
OCT. 1980. NGUNI DAM.
LOG Lx
AGE (Weeks)

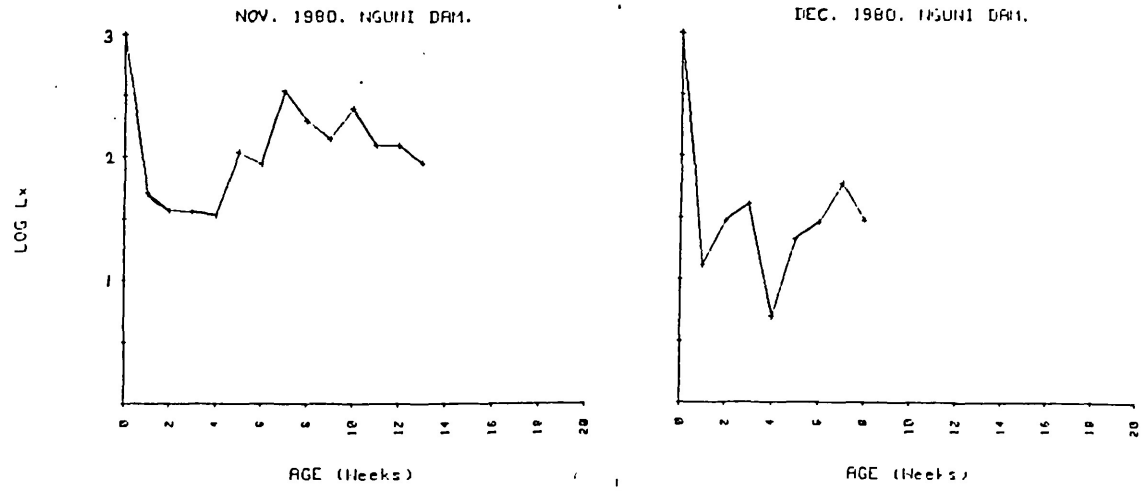
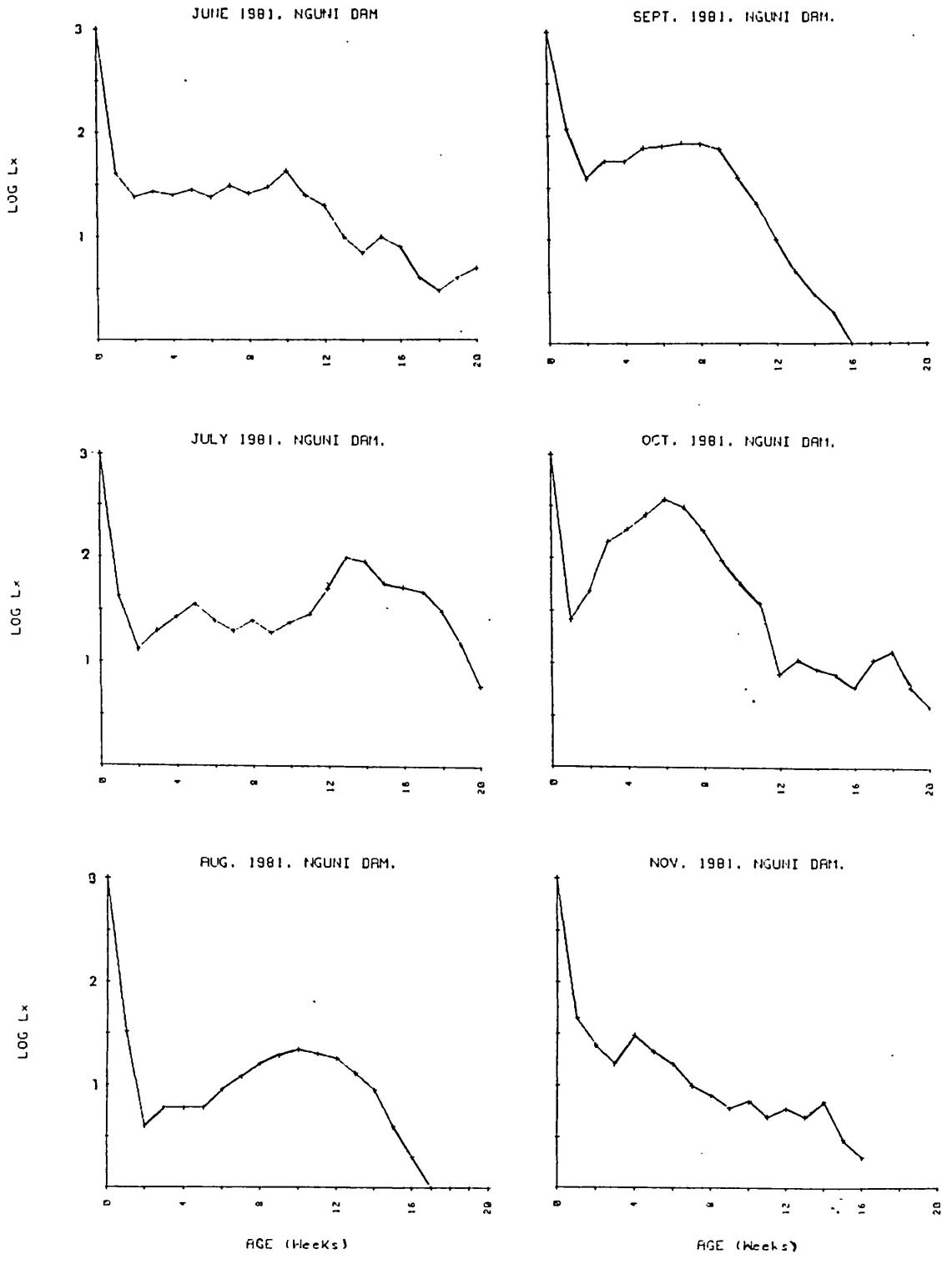


Fig. 5.1 Mean survivorship curves ($\log_{10} l_x$) for cohorts of B. globosus in Nguni dam hatched during the month specified.

(Each l_x value is the mean of 4 or 5 weekly values.)


JUNE 1981. NGUNI DAM
SEPT. 1981. NGUNI DAM.
JULY 1981. NGUNI DAM.
OCT. 1981. NGUNI DAM.
AUG. 1981. NGUNI DAM.
NOV. 1981. NGUNI DAM.
LOG Lx
AGE (Weeks)

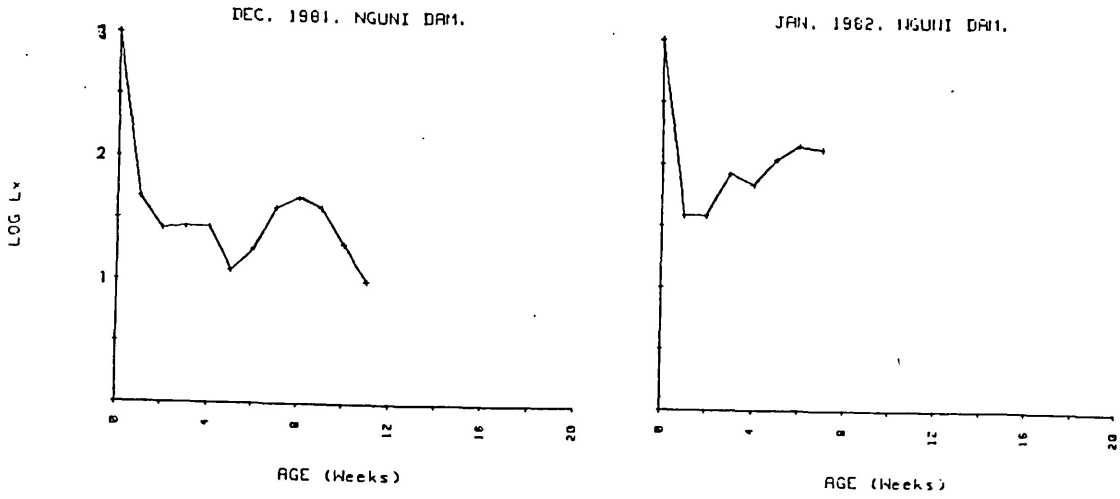
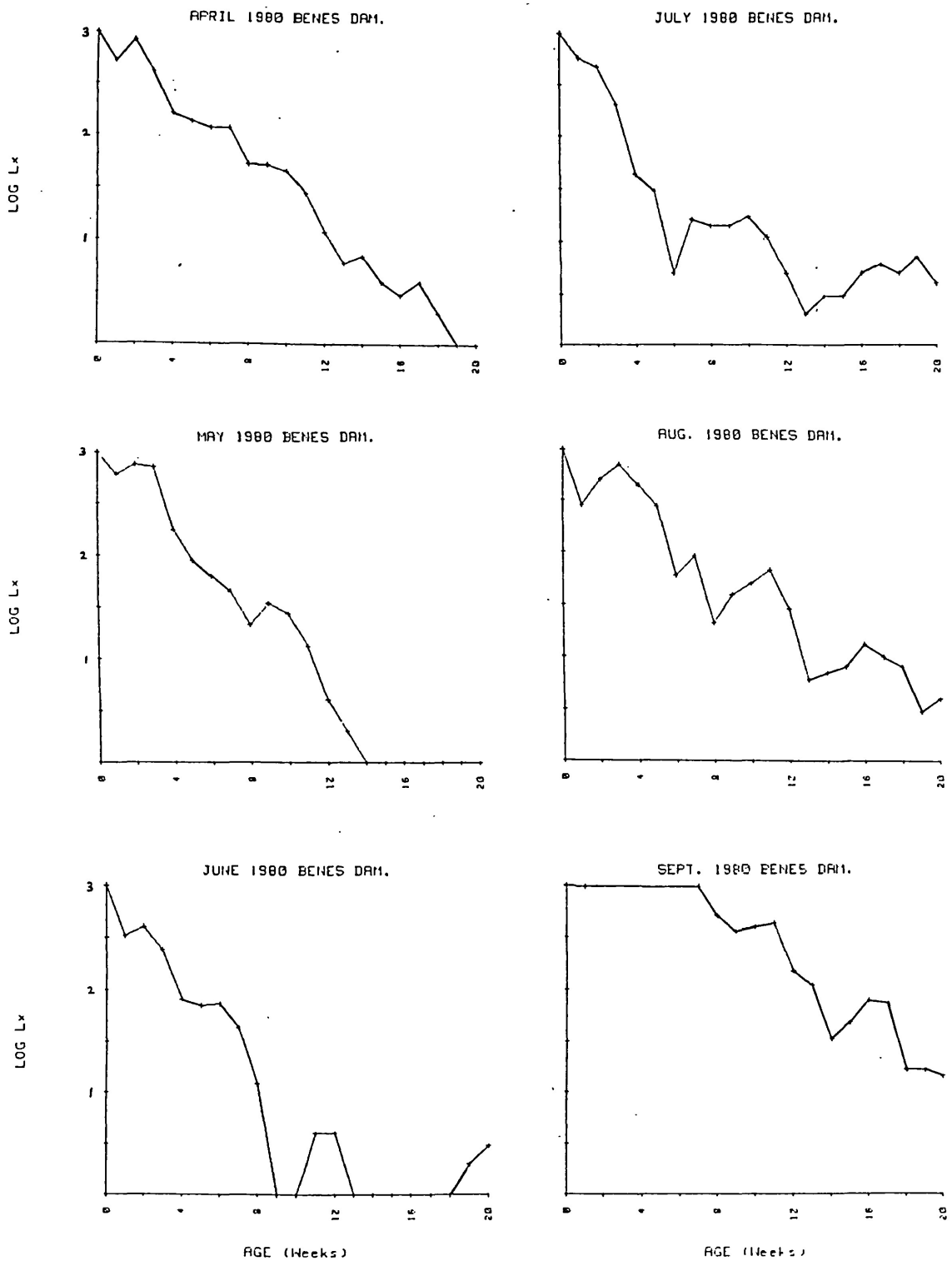


Fig. 5.2 Mean survivorship curves ($\log_{10} l_x$) for cohorts of B. globosus in Nguni dam, hatched during the month specified.

(Each l_x value is the mean of 4 or 5 weekly values.)


APRIL 1980 BENES DAM.
JULY 1980 BENES DAM.
MAY 1980 BENES DAM.
AUG. 1980 BENES DAM.
JUNE 1980 BENES DAM.
SEPT. 1980 BENES DAM.
LOG Lx
AGE (Weeks)

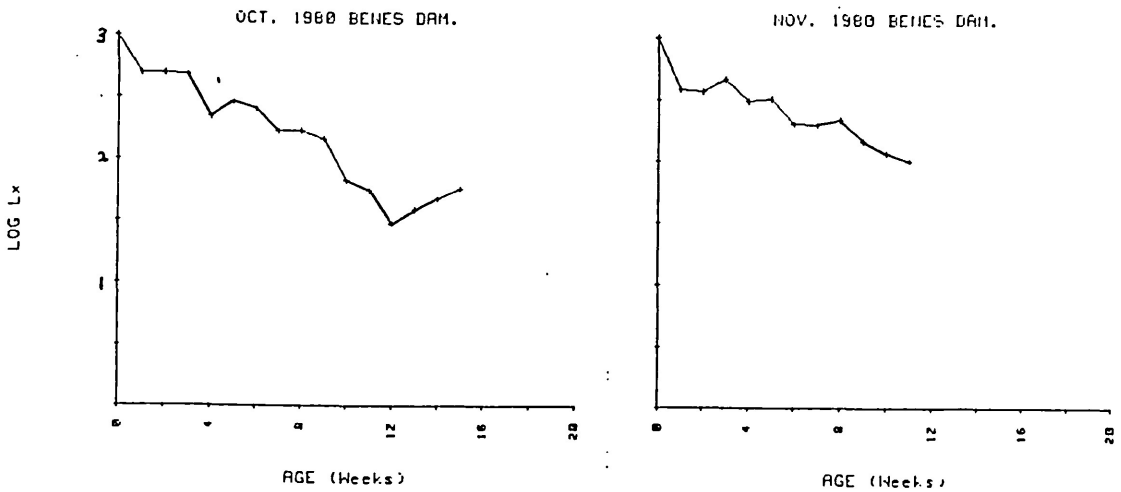


Fig. 5.3 Mean survivorship curves ($\log_{10} l_x$) for cohorts of B. globosus in Benes dam, hatched during the month specified.

(Each l_x value is the mean of 4 or 5 weekly values.)

Table 5.1 Summary of average weekly mortality estimates (over 10 weeks) from trap sample data.

The parameter K is defined as the weekly instantaneous mortality rate and is estimated from the 10 week mortality rate μ where $K = -\mu/10$, $\mu = l_{10} - l_0$ and l_{10} is $\log_e$ number of survivors, after 10 weeks, starting with 1000 newly hatched snails at week 0.

	NGUNI DAM			BENES DAM		
1980	l_{10}	k/week	Mean life expectancy (weeks)	l_{10}	k/week	Mean life expectancy (weeks)
April	-	-	-	3.737	.317	3.2
May	5.156	.175	5.7	3.205	.370	2.7
June	4.126	.278	3.6	0.511	.640	1.6
July	3.244	.366	2.7	2.639	.427	2.3
August	3.424	.348	2.9	3.951	.296	3.4
September	4.262	.265	3.8	5.971	.094	10.7
October	4.248	.266	3.8	4.511	.240	4.2
November	5.146	.176	5.7	4.803	.210	4.8
Mean		$.268 \pm .066$	4.0 ± 1.1		$.324 \pm .133$	4.1 ± 2.3
1981						
June	3.486	.342	2.9			
July	3.178	.373	2.7			
August	3.012	.390	2.6			
September	3.822	.309	3.2			
October	4.163	.274	3.6			
November	1.791	.512	2.0			
December	3.136	.377	2.7			
Mean		$.368 \pm .068$	2.8 ± 0.4			

difference to population projections, nor to the calculation of demographic parameters, but the implications for the methods of estimation are serious. There are three possible sources of error in the underestimation of small snails:

i. That small snails were being overlooked on traps.
ii. That growth rates were either underestimated for large snails or overestimated for small snails.
iii. That trap sampling in Nguni dam provides size biased samples.

The first possibility was tested (see Section 3.2.4.3.) and rejected since the rate of capture of the smallest snails precludes the possibility that large numbers of 3 and 4mm snails could have been missed. Growth rate inaccuracies (ii) are a possible source of error since box snails were used for early growth rate estimates, and in larger snails these were relatively higher than field estimates. But, the survivorship estimates require an adjustment of between x2 and x8 the number of small snails to account for the numbers of larger snails later on. This obviously cannot be achieved by minor adjustments in the growth rate, which is therefore not considered a reasonable explanation for the observed errors. The most likely explanation is that small snails undergo a free-floating dispersal phase during which they would not have been recorded on traps. This would explain the progressive nature of the discrepancy (since one week old snails are often more numerous than subsequent

young age groups). It is also interesting that in Benes dam, where these discrepancies were not observed, the sample sites were closed in by vegetation, allowing much less scope for dispersal.

Although attempts were made to sweep the water surface with a fine mesh sieve, no small snails were found by this method and therefore no direct evidence can be given for the above hypothesis.

5.2.2. Survival from marked snails

Jolly's stochastic method of treating recapture data (Begon, 1979) provides a finite rate $\emptyset$ which for convenience is referred to as survival rate, but in fact incorporates both mortality and emigration. Table 5.2 summarises survival and mortality estimates for Nguni dam 1981/82. Survival is very low and mortality rates from daily marks are approaching an order of magnitude higher than those from trap samples (see Table 5.1). Mortality rates from weekly marks are much lower than from daily marks because of the exponential decay nature of the relationship of snail loss with time. Comparisons with trap sample results should therefore be made with weekly mark data.

Because snails were not marked on multiple occasions during 1980/81, no estimates of $\emptyset$ are possible. However, figures 5.4 and 5.5 contrast recapture rates during 1980/81 and 1981/82 to give a relative measure of survival with time

Table 5.2 Survival estimates for Nguni dam 1981/82 from marked snails.

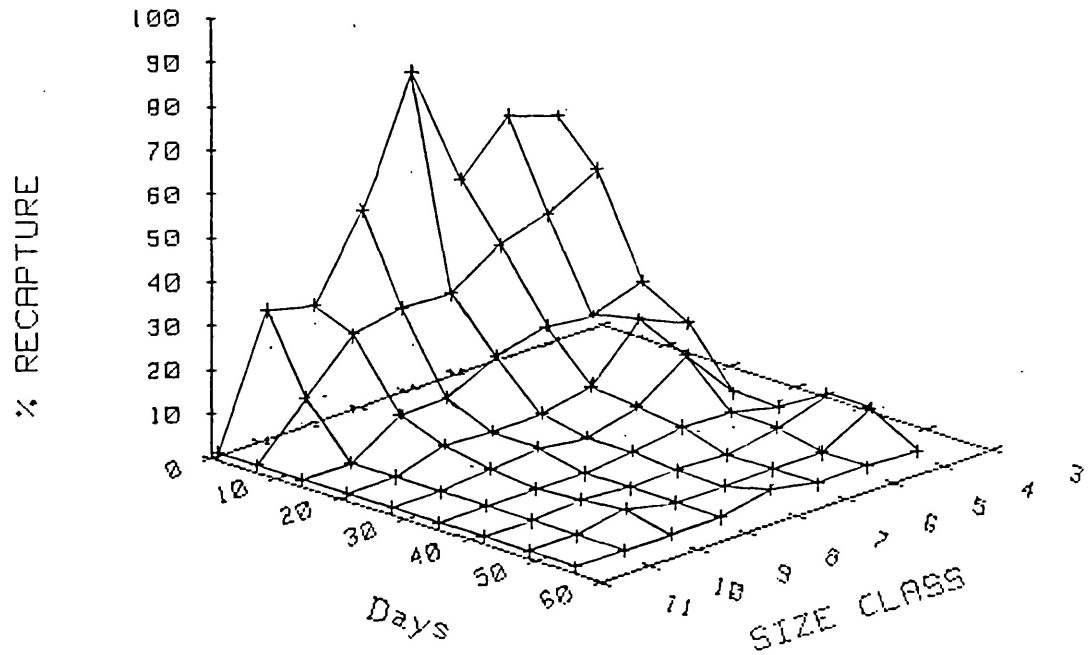
$\emptyset = l_x/l_0$, $K = -\text{Log}_e\emptyset$. N.B. $\emptyset$ (and therefore K) incorporates mortality and emigration losses and therefore no calculation of mean life expectancy is possible.

	Daily Marks*			Weekly Marks*		
Month	No. of marks	Mean $\emptyset$ / day	Mean K / week	No. of marks	Mean $\emptyset$ / week	Mean K / week
June	35	0.73	2.61	-	-	-
July	72	0.62	3.47	-	-	-
August	65	0.58	4.34	-	-	-
September	109	0.57	4.03	368	0.59	0.61
October	66	0.78	1.92			
November	124	0.78	1.78	525	0.44	0.87
December	-	-	-			
January	167	0.55	4.55	220	0.14	2.60
February	-	-	-			
All	638	0.65	3.12	1113	0.31	1.21

* Daily marks were samples marked daily over six days; weekly marks were marked weekly for five weeks.

Fig. 5.4 % recaptures of marked snails in Nguni dam by size and by time. (From one day to eight weeks after marking.)

1980/81. NGUNI DAM. % RECAPTURES.



1981/82. NGUNI DAM. % RECAPTURES.

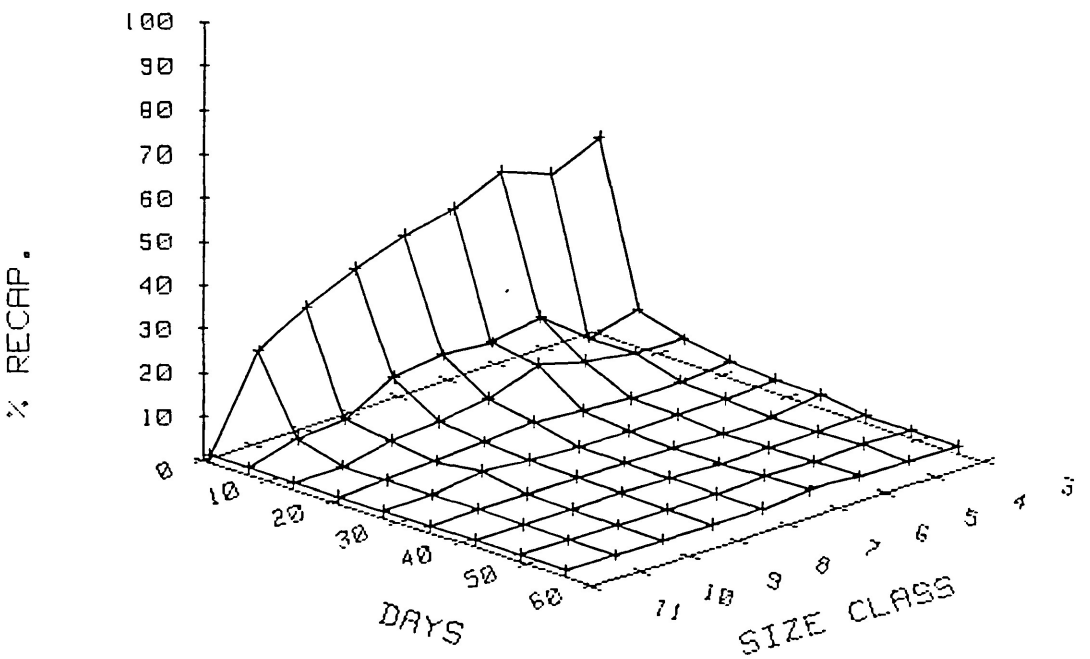
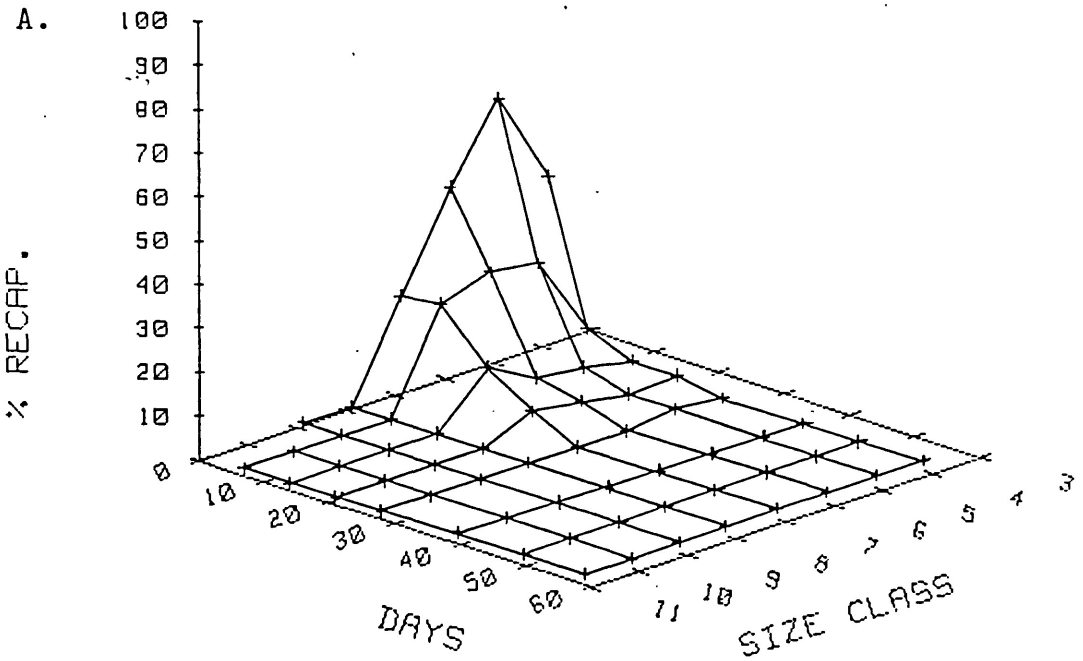


Fig. 5.5 % recaptures of marked snails.

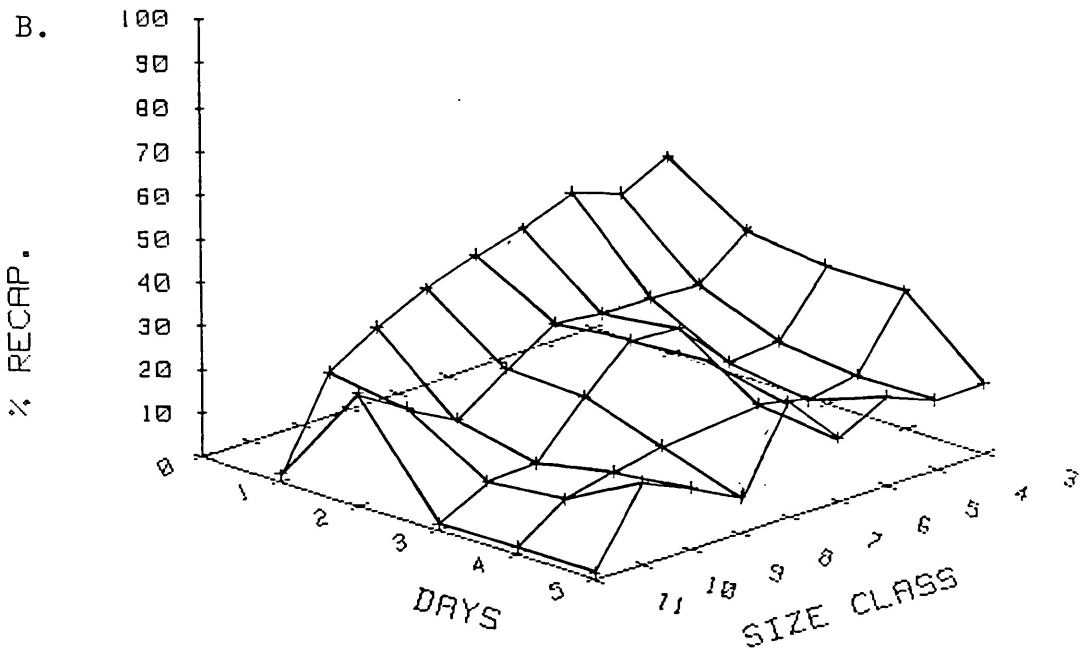
A. From one day to eight weeks after marking in Benes dam.

B. From one to five days after marking in Nguni dam.

1980/81. BENES DAM. % RECAPTURES.



1981/82. NGUNI DAM. DAILY % RECAP



in different size classes. The figures in Table 5.3 indicate that survival rates were highest in Nguni dam during 1980/81 and that those for Benes dam during 1980/81 were slightly higher than for Nguni during 1981/82. On average, survival decreases with size, but in Benes dam the mortality rate was lowest at 5 to 7mm shell length.

5.3. Survival from Box-kept Snails

Two separate measures of survival have been used for box-kept snail survival estimates. Because there are no sampling errors, a log regression has been used to provide parameters to compare survival between boxes. Estimates of l_x at ten weeks have been used to provide parameters which can be compared with field data.

Table 5.4 summarises the results of a factorial analysis of variance on snail boxes and shows that both feeding and initial density have a significant effect on survival. Table 5.5 summarises survival and mortality rates at ten weeks after hatch.

Since snails in boxes were regularly tested for infections, it is possible to compare the survival of shedding snails with those which were not shedding: 29 snails which were shedding a heterophyid cercaria were identified and marked in Nguni dam boxes during 1981. All continued to shed until at least a few days prior to death. Mean life span for

Table 5.3 Summary of % recapture rates over different time periods for all sizes of B. globosus

	Days since marking													
	1	2	3	4	5	7	14	21	28	35	42	49	56	Total marked
1980/81 Nguni dam	43.3	-	-	-	-	25.0	9.9	4.8	2.5	0.9	0.6	0.6	0.5	472
1981/82 Nguni dam	35.1	22.3	20.2	17.5	15.8	8.8	4.6	1.7	0.7	0.3	0.1	0.1	0.1	1617
1980/81 Benes dam	39.6	-	-	-	-	17.2	4.7	2.5	0.3	0	0	0	0	361

Table 5.4. The results of factorial analysis of variance for survival of B. globosus in boxes, July 1981 to January 1982, Nguni dam.

The survival parameter is a in the expression:

$$\log l_x = ax + l_o$$

Density and feeding treatments as for Table 4.3. (Described in Section 3.6.3.).

A. MAIN EFFECT MEANS:

	Treatment		
	1	2	3
Feeding	- .00625*	- .01091	- .01186
Initial density	- .00555*	- .00821	- .01527

B. TWO WAY INTERACTION MEANS:

		Initial density		
		1	2	3
	1	- .00444	- .00450	- .00982
Feeding	2	- .00436	- .01158	- .01679
	3	- .00784	- .00854	- .01921

The analysis indicated significant differences in mean survival (at $P < 0.05$) both from different feeding and different initial densities.

*Indicates significant ($P < 0.05$) differences between type 1 and type 3 (but not type 2) from multiple comparisons using the least significant difference method.

Table 5.5. Survival and mortality in box-kept snails after 10 weeks.

Year	Dam	Month	l_0	l_{10}	K/week	Mean life expectancy (weeks)
1981	Nguni	June	70	44	0.046	21.5
		July	105	68	0.043	23.0
		Aug.	105	56	0.063	15.9
		Sept.	105	42	0.092	10.9
		Oct.	105	31	0.122	8.2
		Nov.	105	63	0.051	19.6
		*Jan.	105	64	0.050	20.2
		Mean			0.067 ± 0.027	17.0 ± 5.0
1980	Nguni	All	69	49	0.034	29.2
1981	Benes	All	50	24	0.073	13.6
1980	Benes	All	171	49	0.125	8.0**

* January boxes had to be discontinued at 50 days, so a mean proportional 50 to 70 day loss has been subtracted.

** Mean initial densities were higher than for other data sets.

these snails was 21.1 $\pm$ 2.6 weeks. Since infected snails were not identified before they began shedding, any mortality caused by prepatent infections cannot be quantified. For comparison therefore, weekly mortality from four weeks to ten weeks after hatch was calculated for all boxes in Nguni dam during 1981/82. From this a mean expected life-span of 23.3 weeks was derived. This indicates that no significant mortality was caused by the heterophyid infection.

Only two snails in boxes were identified as shedding schistosome cercariae. These were immediately removed from the boxes to prevent them from transmitting to local people, and therefore no estimate of the effect of schistosome infection on mortality is possible.

5.4. Discussion

5.4.1. Factors causing mortality

Of all the aspects of aquatic snail ecology, the least quantitative information is available about the causes of mortality. Michelson (1957) and Malek (1958) reviewed the then current knowledge of mortality factors, and included lists of known snail predators. Malek mentions the probable implication of micro-organisms in snail mortality, and the earlier death in laboratory aquaria of trematode infected snails. Since 1958, very little has been added to this knowledge (see Madsen, 1979 and Brown, 1980).

Some other predatory species have been observed to kill snails, but only one quantitative estimate of the effects of predation in the field is available (Voelker, 1968, quoted in Brown, 1980).

In both Nguni and Benes dams, several snail predator species were present. Only two (leeches and a larval glow-worm (lampyridae) were actually observed feeding on snails. Catfish (Clarius lazera), monitor lizards (Varanus niloticus) ducks, geese, herons, crabs and dytiscid beetles were also present - all known snail predators. None of these animals had access to box-kept snails which were therefore protected from the effects of macro-predation.

Two other possible major causes of snail mortality do not apply to box-kept snails: dispersal loss caused by flooding and dispersal loss caused by the failure to find a suitable substrate.

Flood loss (usually followed by an upsurge in reproduction by the survivors) has frequently been noted as a feature of annual snail life-cycles (e.g. Hira and Muller, 1966; Appleton, 1974). Flooding in Nguni and Benes dams was followed initially by much lower numbers of snails in the samples. The evidence for snail mortality caused by the failure to find a suitable substrate is more speculative. Aquatic vegetation and allochthonous material undoubtedly formed the exclusive habitat of B. globosus in Nguni and

Benes. Despite repeated sieve searches of bottom mud, only single live B. globosus were ever found. (Melanoides tuberculata, however, was found on the bottom in great numbers.)

A great deal of work has been done on snail/plant associations, particularly in the Volta Lake by Paperna (1969), Odei (1973) and Klumpp and Chu (1980), who stated that they could confirm that, because of Bulinus rohlfsi's preference for the plant, Ceratophyllum is the main ecological factor determining the duration of cercarial transmission. Plants are therefore of considerable importance to the snails. However, in other water bodies on the Kenya coast, where rocks or gravel rather than mud constituted part of the bottom, B. globosus were frequently found on these more solid surfaces. The implication is that disadvantages of a muddy substrate, as much as the positive features of the plants, may be dictating the distribution of B. globosus. In view of the abundance of M. tuberculata on mud, the lack of an operculum may be the factor limiting the presence of B. globosus.

Since B. globosus has only a limited ability to direct its final destination during a floating phase, the number arriving on mud compared to plants should be proportional to their respective availability. Large numbers of snails could be lost in this way.

The purpose of this speculative discussion is to emphasize that different factors affected box-kept snails and free-living snails. Snail boxes prevented the dispersal of snails onto unsuitable substrates.

5.4.2. Differences between field and box snail mortality

B. globosus mortality from hatch to ten weeks is compared for free-living and box snails in Fig. 5.6.

Because of the differences in predation and dispersal, mortality rates for free-living snails measured from trap samples are between 2 and 10 times higher than for box snails. In addition, mortality trends over seven months show very little agreement between box and free-living snails. This strengthens the conclusion that different mortality factors are at work.

Loss rates (including emigration) as measured from marked snails are almost an order of magnitude greater than mortality rates from trap samples (for reasons explained in Section 5.2.2.). The trend, however, is very similar except for November 1981, when mortality measured from trap samples was very high. On November 11th 1981 heavy rainfall caused Nguni dam to overflow and the trap samples the following week reflect a considerable decline in snail numbers. Daily mark sequences were conducted from November 2nd to 8th and from November 16th to 22nd, so that the catastrophic

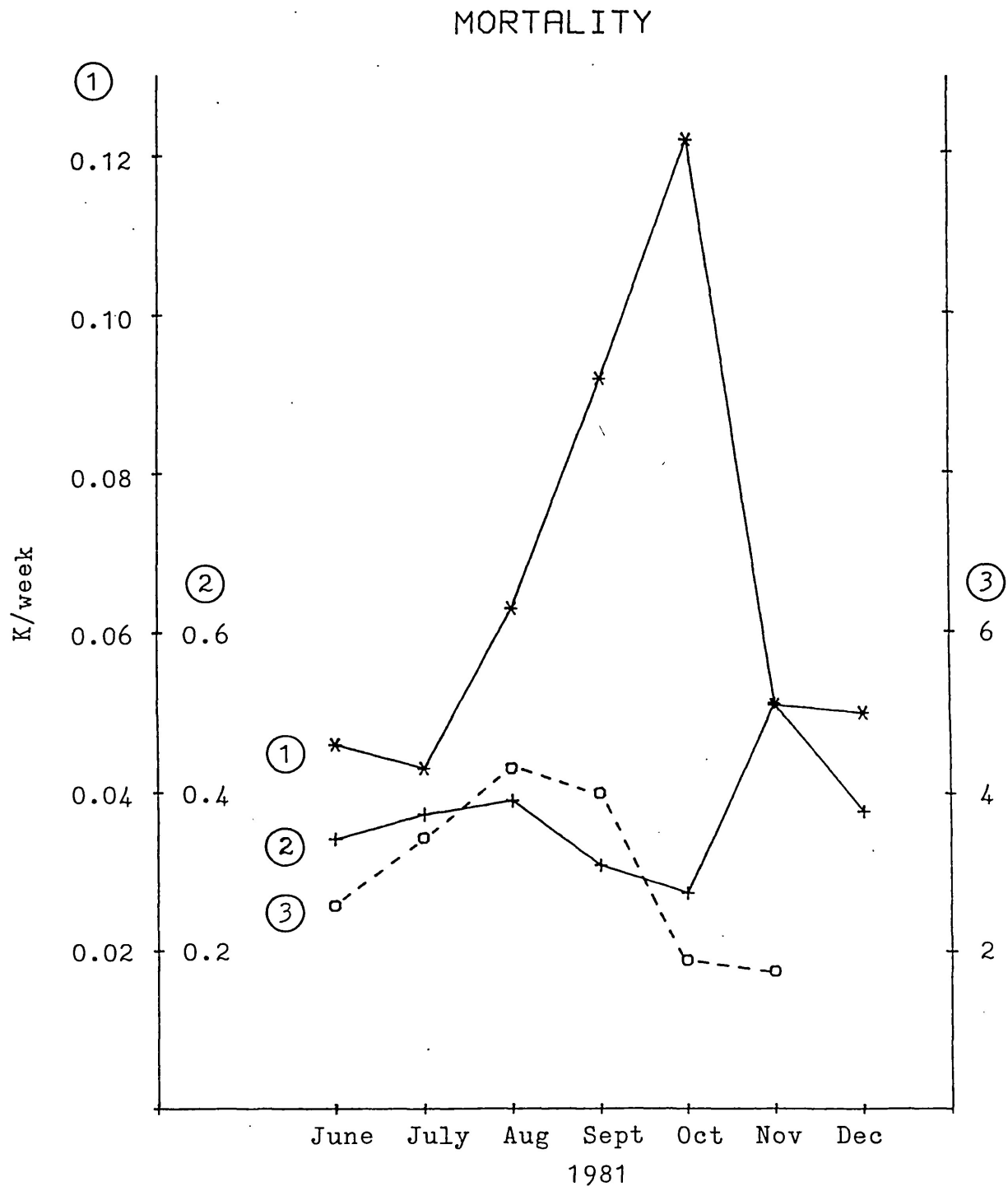


Fig. 5.6 Mortality rates from recaptures of marked snails (3), from trap samples (2), and from boxes (1), for cohorts hatched during the months on the x axis.

(N.B. K values on the y axis represent a different order of magnitude for each data set.)

(Data from Nguni dam.)

snail loss due to flooding was not recorded by survival estimates from daily marks. Thirty-six snails were marked as part of a weekly sequence on November 9th, and none of these were ever recaptured. Forty-five snails were marked between November 2nd and 8th, and 11 of these were recaptured on November 10th, but none were ever recaptured subsequently. Therefore, the discrepancy in mortality rate measures for November is caused by an unfortunate choice of marking dates.

Table 5.6 shows a summary of average weekly mortality rates calculated by the different methods. Taking into account 1980/81 recapture data (see Table 5.3), the survival rate was highest in Nguni dam during 1980/81.

5.4.3. Comparisons of results with those from previous studies

Since marked snail loss estimates contain a large element of emigration loss, values measured from trap samples are the most suitable for comparison with mortality rates from previous studies. The use of the hatch to ten week average weekly mortality rate is not a true average but is a good approximation as Table 5.7 shows.

Mean death rates from previous studies are summarized in Table 6 of Anderson and May (1979). These range from 0.175 to 0.280 for bulinid snails in the field, (laboratory rates are much lower) and give mean life expectancies from 3.6 to 5.7 weeks. One major study not included in the above table

Table 5.6. Summary of average weekly mortality rates from hatch to ten weeks, measured by different methods.

		Data Source			
		Boxes	Trap samples	Weekly mark recaptures	Daily mark recaptures
1980/81	Benes dam	0.125	0.324	-	-
	Nguni dam	0.034	0.268	-	-
1981/82	Benes dam	0.073	-	-	-
	Nguni dam	0.067	0.368	1.21	3.12

Table 5.7. To test whether an average weekly mortality rate from hatch to 10 weeks is a good reflection of mortality rates over the whole life of a cohort:

17 boxes in which snails survived until at least 20 weeks were used to compare weekly mortality rates over 10 and 20 weeks.

	Average weekly mortality rate	
	10 weeks	20 weeks
	0.022	0.011
	0.069	0.035
	0	0.046
	0	0.110
	0.105	0.095
	0.161	0.080
	0	0.001
	0.051	0.026
	0.051	0.115
	0.036	0.026
	0	0.011
	0.060	0.040
	0.092	0.046
	0.012	0.095
	0.092	0.115
	0.016	0.080
	0.051	0.060
Mean	0.051 ± 0.023	0.058 ± 0.020

Observed t = 0.67

Critical t = 2.04 (at $P < 0.05$, for 32 degrees of freedom).

There is no significant difference between average weekly mortality rates measured at 10 or 20 weeks after hatch.

is that by Shiff (1964) on Bulinus globosus. Average weekly mortality rates for five monthly cohorts have been calculated from hatch to 10 weeks from Shiff's data, and range from 0.214 (mean expected lifespan 4.7 weeks) to 0.512 (mean expected lifespan 2.0 weeks). The mean from the five cohorts is 0.325 (expected lifespan 3.4 weeks).

Estimates from this project are extremely close to Shiff's figures, ranging from 0.268 (mean expected lifespan 3.7 weeks) for B. globosus in Nguni dam during 1980/81 to 0.368 (mean expected lifespan 2.7 weeks) for the same dam during 1981/82. These mortality rates are among the highest for all the studies quoted by Anderson and May (1979) for all schistosome host snails. As for growth rates, these results indicate that on average, conditions for B. globosus in Benes and Nguni dams are sub-optimal.

A lifespan of under four weeks is only just long enough to permit the development of cercarial shedding even when conditions allow the shortest prepatent period (25 days) and miracidial penetration occurs on the hatch date. Obviously, heavy early mortality contributes significantly to the short average lifespan and snails living beyond the first week have a much longer life expectancy. Nevertheless, only exceptionally long-lived and robust snails will be able to make a significant contribution to the transmission of bilharzia. Although numbers of snails found to be shedding schistosome cercariae were too low to generalise,

it may be significant that the only snail found to be shedding at the main weekly sampling sites at Benes dam was found in one of the snail boxes, where the mean mortality rate was less than half that for free-living snails.

CHAPTER 6 REPRODUCTION

6.1. Introduction

Two different methods have previously been employed to produce reproduction data for demographic studies of snails with overlapping generations. Pesigan et al (1958) found that they could not accurately measure egg-laying nor young snail survival in the field, and therefore used an index, M of the combination of the two (designated the mean daily reproduction index), namely:

$$M = Y_{t+1}/A_t \qquad (6.1)$$

Where A_t is the number of adults at time t.

Y_{t+1} is the number of young at time t+1 who are assumed to have been produced by the A_t adults one time unit ago.

The number of young is determined by reference to the growth curve which gives the maximum size that a young snail could have reached if the egg was laid on the day that the adults were counted. This method requires an accurate estimate of age at maturity and of growth rates, but age specific reproduction need not be measured since snails from maturity on are treated as a single age class. This method was also used by Webbe (1962a,1965), Demian and Kamel (1972) and Sturrock (1973a).

If the number of eggs and reasonable measures of age-specific fecundity can be measured in field conditions, values of l_x and m_x can then be used to calculate the intrinsic rate of natural increase under field conditions. The major problem is that direct allocation of field reproduction to age classes is impossible and therefore approximations have to be made. Shiff (1964) and Dazo et al (1966) used laboratory-kept snails to allocate proportional reproduction to field samples. Shiff noted the critical effect of temperature on reproduction, and used fecundity data from laboratory tanks kept as near to field temperatures as possible.

In this project, measures of several aspects of reproduction have been made in order to arrive at m_x values which accurately reflect changing environmental conditions.

Trap samples provide basic measures of the total numbers of egg masses and the mean number of eggs per mass for which the number of adult snails in the sample are responsible. From this information the aim was to calculate the proportion of young snails hatching for which each adult in each age class is responsible each week. It was therefore necessary to examine the hatch time, hatch success and proportion of eggs laid by snails in each size class, and how these various parameters might vary in different conditions.

Snail boxes provided the nearest possible approximation to field conditions for the above measurements. Whereas

survival patterns were fundamentally altered by the enclosures, reproductive performance per snail was substantially similar as measured from trap samples and boxes (see Fig. 6.1), bearing in mind the differences in age structure of the populations. (e.g. because boxes were first set up in June, no box snails were older than 8 weeks during July,)

6.2. Results

6.2.1. The relationship of size and age to maturity and reproduction

Although the eventual aim is age specific measurements of reproduction, most of the previous studies quoted above have initially allocated reproduction to size classes of snails. This follows the implicit assumption that reproduction is more closely correlated with size than with age.

B. globosus kept in boxes provided comparative data since both the age and size of snails was known. Table 6.1 demonstrates that the onset of reproduction is clearly more closely related to size than it is to age and that therefore reproduction should initially be allocated to size classes of snails. (Anderson et al, 1982, have demonstrated a similar relationship between size, rather than age, of Biomphalaria glabrata and declining susceptibility to schistosome infections.)

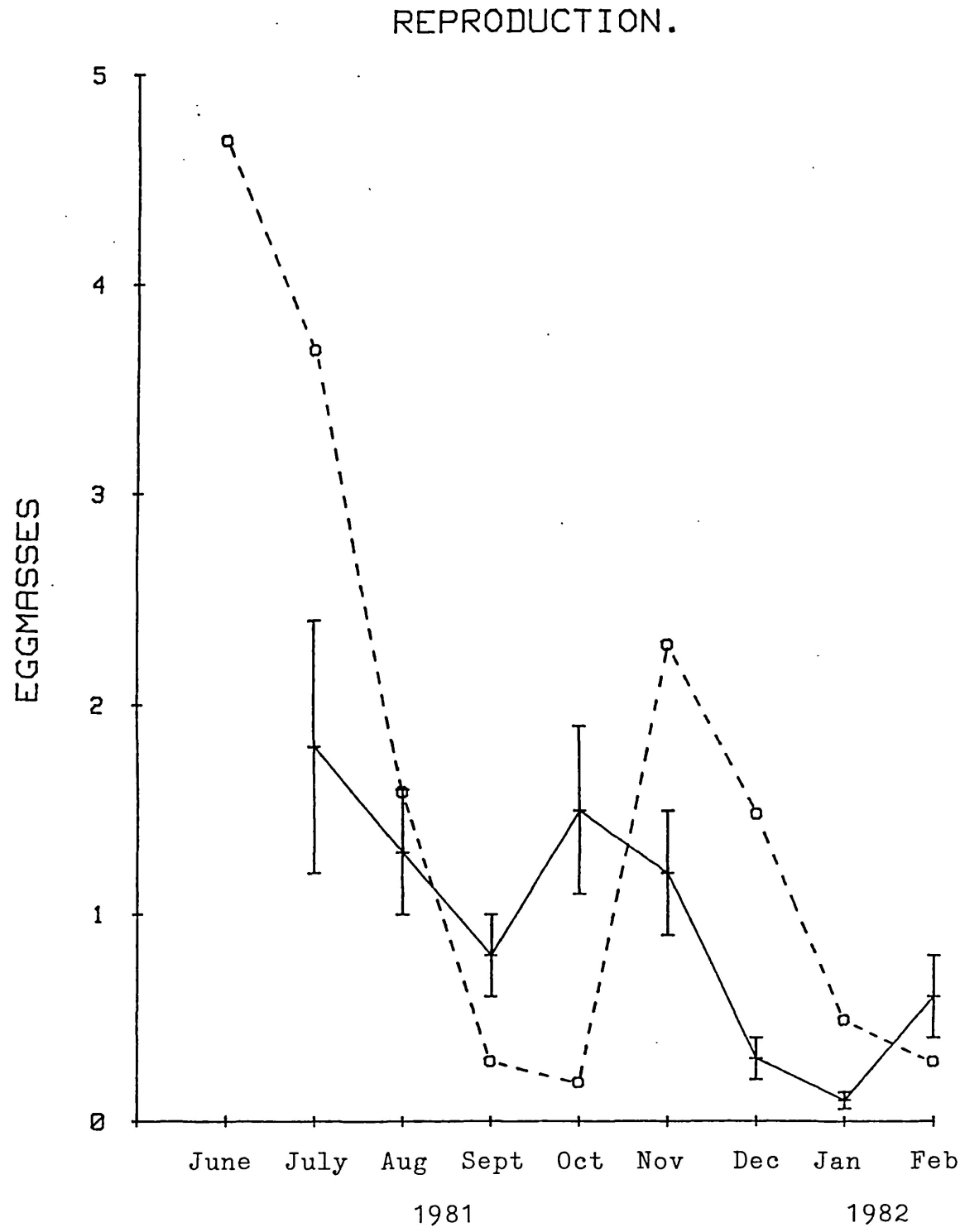


Fig. 6.1 Comparison of reproductive performance (egg masses/adult/week) of free-living snails from trap samples (o- - -o) and box-kept snails (+——+).

Means and 95% confidence limits are shown for box-kept snails.

(Data from Nguni dam.)

Table 6.1 Comparison of age and size at maturity and initial reproduction.

(Data from box-kept B. globosus in Nguni and Benes dams, 1980-82)

	Adult recruitment	First eggs laid
Mean age (σ_{n-1}) (days)	39.5 (13.0)	55.1 (24.7)
Coefficient of variation	0.329	0.448
Mean size (σ_{n-1}) (mm)	6.00 (0.77)	6.60 (0.94)
Coefficient of variation	0.128	0.142

6.2.2. Hatch time

Initially hatch time was measured using isolated egg masses laid at known times in laboratory dishes. However, when egg masses were hatched in the field (as described in Section 3.6.4.) it was found that laboratory-hatched egg masses generally took longer to hatch, even in ostensibly similar ambient temperatures.

Table 6.2 summarises monthly and yearly hatch times measured in the field. Since there are significant differences in the mean days to hatch for different months, monthly values have been used where possible in life-table calculations. For Benes and Nguni dams in 1980/81 the scarcity of field data necessitates the use of a yearly mean.

Since traps were sampled weekly, the conversion of observed egg masses, EM, to total egg masses, T, per week is obtained by:

$$T = EM \times \frac{7}{HT} \qquad (6.2)$$

Where HT = hatch time in days.

Table 6.2 Summary of mean hatch times for egg masses laid by snails in the field at known times, and hatched in hatching boxes (see Section 3.6.4.).

Dam	Year	Month	No. of Egg masses	Mean hatch time (days)
Nguni	1981	June	6	5.79 ± 0.72
		July	17	7.01 ± 0.34
		August	18	6.44 ± 0.18
		Sept.	13	6.42 ± 0.45
		Oct.	8	6.40 ± 0.44
		Nov.	19	5.63 ± 0.37
	1982	Dec. / Jan.	3	5.46 ± 0.64
Nguni	1981/82	All	84	6.30 ± 0.17
Nguni	1980/81	All	9	5.80 ± 1.04
Benes	1980/81	All	10	7.28 ± 0.70

6.2.3. Hatch success

Hatch success was also measured using egg masses laid by free-living snails and kept in hatching boxes. As for hatch time, significant differences are apparent in hatching rates at different times and these are shown in Table 6.3.

Egg masses hatched in boxes are, of course, not subject to mortality caused by macro predation and damage, either by large snails or other organisms. Traps should be sampling egg masses that are on average half way to hatching (ranging from just laid to just about to hatch). Assuming that any egg mass loss is constant during incubation, trap samples are therefore reflecting a population of eggs which have suffered half their eventual loss.

Attempts were made to quantify this source of loss by making indelible marks around egg masses on traps. These were seldom successful due to loss of marks and because constant checking was needed to be sure of observing the egg mass in the process of hatching. However, on six occasions egg masses were observed for more than five days before disappearance, indicating a high probability of successful hatching, and on no occasion were egg masses known to have been lost before hatching.

The net result is that no measure of pre-hatching predation/ damage loss was obtained. A search of the literature fails

Table 6.3 Mean % hatch success from field laid and box hatched egg masses.

Dam	Year	Month	No. of Egg masses	Mean hatch success (%)
Nguni	1981	June	6	84 ± 16
		July	20	78 ± 8
		August	18	87 ± 9
		Sept.	14	62 ± 15
		Oct.	10	51 ± 25
		Nov.	17	68 ± 10
	1982	Dec. / Jan.	6	71 ± 20
Nguni	1981/82	All	91	72 ± 5
Nguni	1980/81	All	13	63 ± 25
Benes	1980/81	All	39	73 ± 15

to reveal any estimates (or indeed mention) of this source of loss. Therefore the hatch success estimates from boxes remain the best available.

6.2.4. Numbers of eggs per egg mass

Numbers of eggs per egg mass were counted from trap samples. The change in mean numbers over time at Nguni and Benes dams is shown in Fig. 6.2. Weekly means (which are available for all samples except those from Benes dam in 1981/82) are used to calculate initial cohort numbers for life-tables.

Fig. 6.3 relates the number of eggs per mass to snail size. The laboratory-kept snails were maintained at low densities (<1 per litre) and were fed lily leaf and lettuce to excess with the result that they laid consistently larger egg masses than box-kept snails. The comparison between egg mass sizes in the laboratory and in boxes is interesting both because it reinforces the point made by Shiff (1964) that using laboratory data to calculate field reproduction rates is problematical, and because it indicates that in general the snails in the dams are failing to fulfil their full reproductive potential.

6.2.5. Adult recruitment size

Adult snails were recognised from trap samples by spire exsertion of the shell. There was considerable overlap of

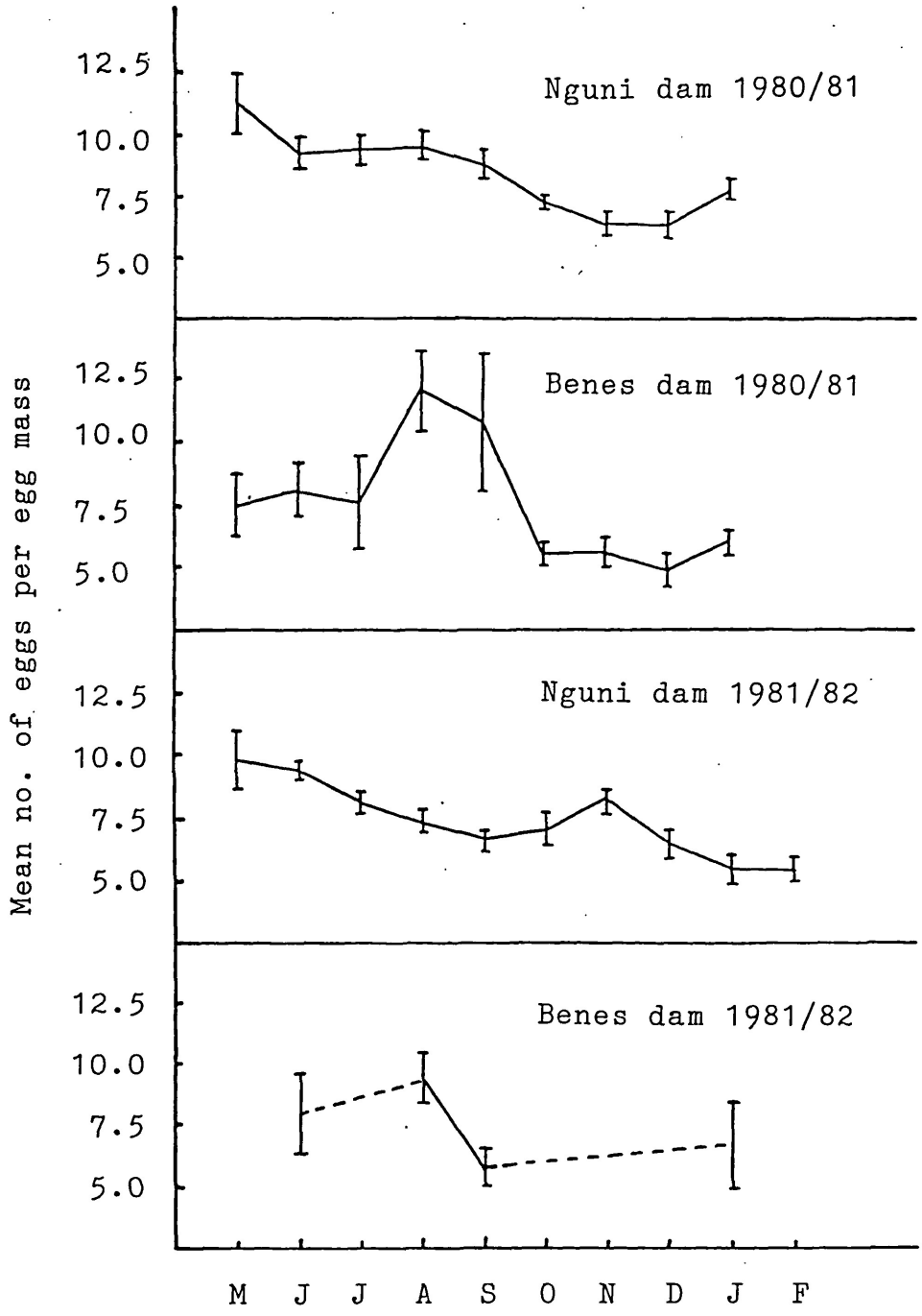


Fig. 6.2 Changes in egg mass sizes with time.

Yearly means for each dam:

		Egg/egg mass	N
1980/81	Nguni dam	7.96 ± 0.16	992
	Benes dam	6.88 ± 0.41	255
1981/82	Nguni dam	7.84 ± 0.15	1095
	Benes dam	8.11 ± 0.75	52

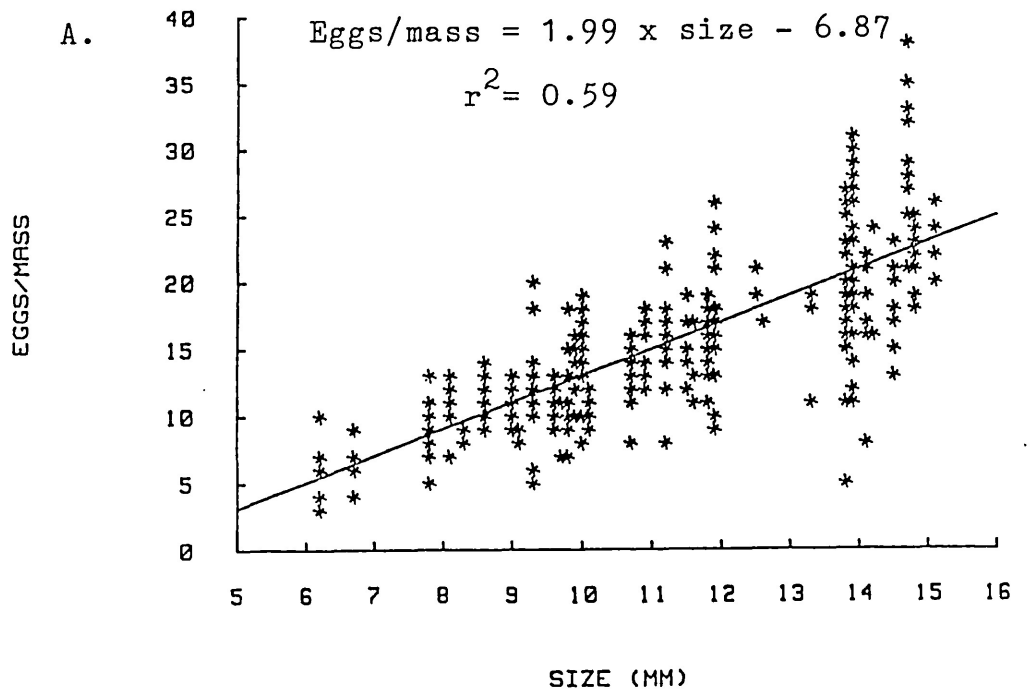
(Data from trap samples.)

Fig. 6.3 The relationship between egg mass size and snail size from:

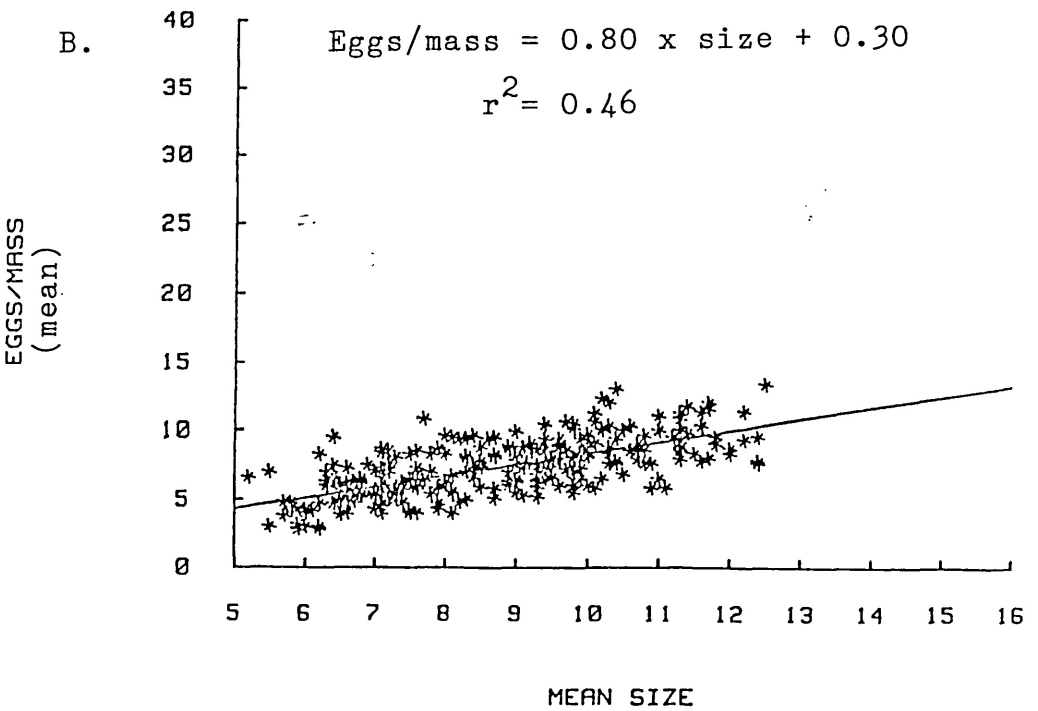
A. Laboratory-kept snails.

B. Box-kept snails.

SIZE-SPECIFIC EGG-LAYING BY LABORATORY-KEPT B. GLOBOSUS.



1981/82. NGUNI DAM. SIZE-SPECIFIC EGG-LAYING BY B.GLOBOSUS IN BOXES.



adults and juveniles in the same size classes, and mean size at adult recruitment was therefore recognised as the size where the proportion of adults and juveniles would be 0.5. Fig. 6.4 shows the method and average sizes at recruitment in each year. Recruitment size varied considerably for different months and the change in average size with time is shown in Fig. 6.5.

6.2.6. Feeding and density effects on reproduction

Table 6.4 summarises the results of relative reproductive performance in boxes with different feeding and density regimes. Initial densities appeared to have little effect on reproduction which was uniformly low in all boxes except those which were fed added lily leaf.

For all boxes, the mean number of eggs per adult per week was 5.46, compared to the mean of 7.73 eggs per adult per week for a similar period from trap samples.

6.2.7. Size specific reproduction in snail boxes

Since reproduction in boxes provides a fair quantitative reflection of reproduction in the field, it seems reasonable to assume that proportional egg-laying by different sized snails will be the same for box-kept and free-living snails. Table 6.5 shows the relative reproductive performance per snail for each size class of box-kept snails. Results from Nguni dam during 1981/82 indicate an increase with size

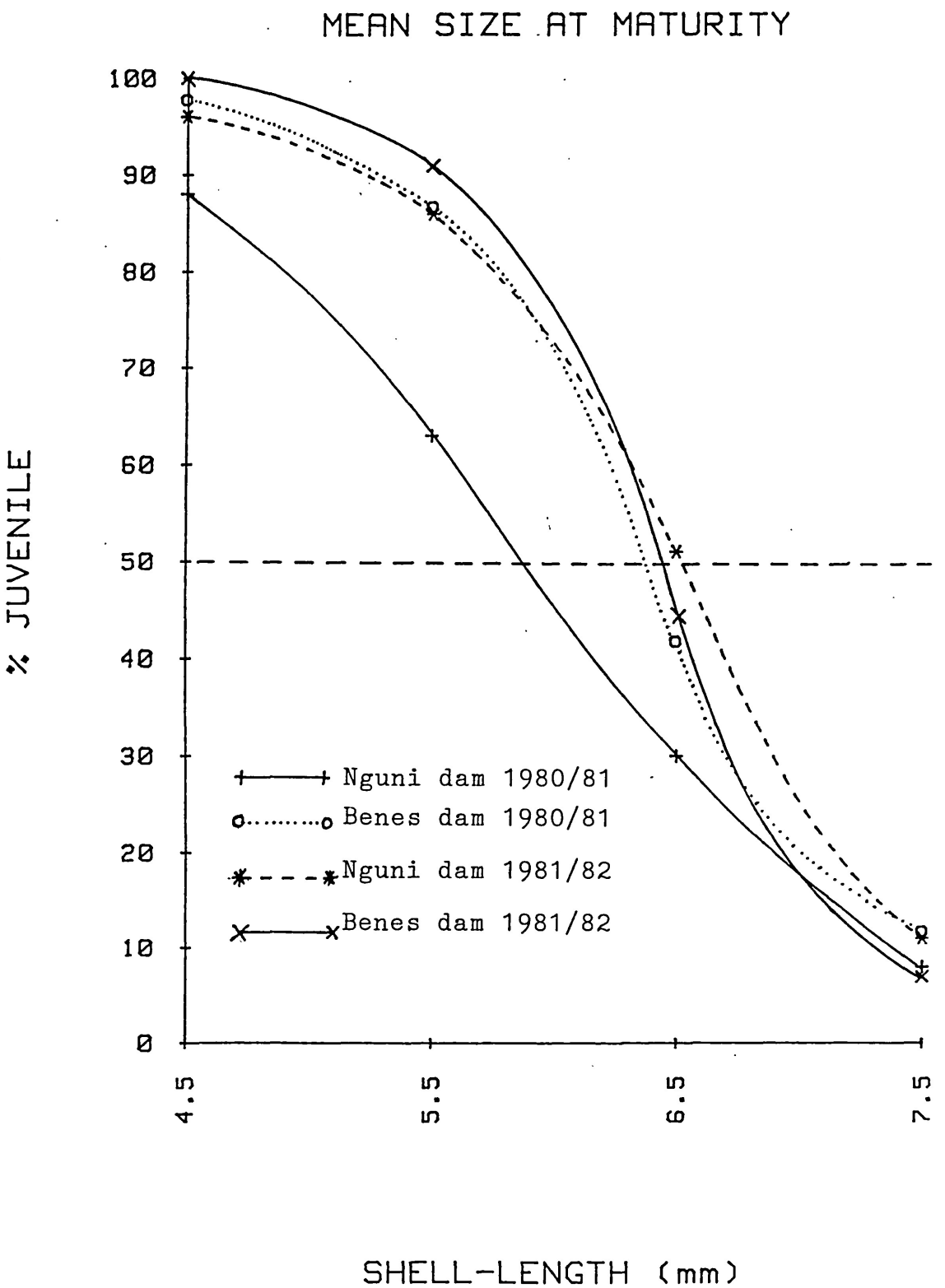


Fig. 6.4 Mean adult recruitment size was taken as the size at which the number of juveniles equals the number of adults:

1980/81 Nguni dam 5.9mm Benes dam 6.4mm
1981/82 Nguni dam 6.5mm Benes dam 6.4mm

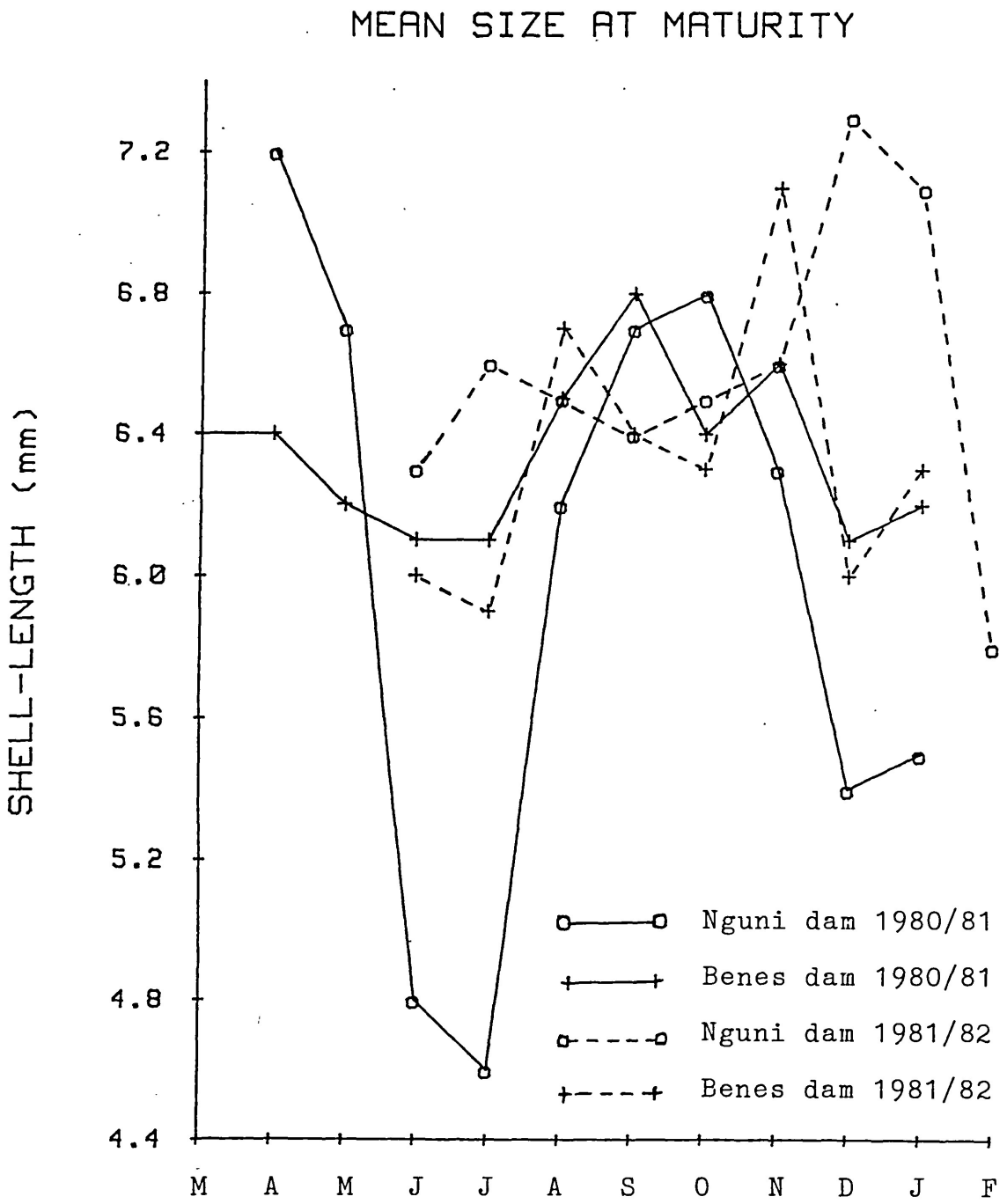


Fig. 6.5 The change in average size at adult recruitment with time.

Table 6.4 The results of factorial analysis of variance for mean reproductive performance (eggs/adult/week) of B. globosus in boxes, July 1981 - January 1982, Nguni dam.

Density treatments 1 to 3 indicate low to high initial density.

Feeding treatments 1 to 3 indicate high quality to low quality diet (see Section 3.6.3. for explanation.
(Data from 54 boxes containing 630 snails).

A. MAIN EFFECT MEANS:

	Treatment		
	1	2	3
Feeding	11.72*	2.16	2.50
Initial density	5.53	6.64	4.21

B. TWO WAY INTERACTION MEANS:

		Initial density		
		1	2	3
	1	12.08	11.63	11.44
Feeding	2	2.35	3.56	0.56
	3	2.16	4.72	0.62

The analysis indicated significant differences in mean number of eggs (at $P < 0.05$) between different feeding regimes but not between different initial densities.

* Indicates significant ($P < 0.05$) difference from multiple comparisons using the least significant difference method.

Table 6.5 Proportional reproduction by snails of different size classes in boxes.

(Expressed as eggs/adult/week ÷ ∑ eggs/adult/week for all size classes.)

	1980/81		1981/82	
Size class (mm)	Nguni dam	Benes dam	*Nguni dam	Benes dam
4 - 5	0	0	0	0
5 - 6	.0	.03	.02 ± .02	0
6 - 7	.20	.05	.07 ± .07	.12
7 - 8	.21	.21	.13 ± .07	.34
8 - 9	.24	.34	.19 ± .11	.19
9 -10	.24	.35	.29 ± .07	.14
10+	.11	. 1	.30 ± .08	.21
No. of adult snails	45	41	302	21

* Mean and ± 95% confidence limits from monthly results.

(shown graphically in Fig. 6.6). In fact there was a reduction in reproductive performance after 11mm, but these larger size classes have been pooled for convenience. (Snails >10mm in the field comprised only 0.5% of the population.)

Results for 1980/81 and from Benes dam in 1981/82 are less consistent. However, all the observations suggest that the onset of reproduction occurs at 6mm.

6.3. Discussion

Although egg-laying in both Nguni and Benes dams was continuous throughout the periods of the study, there were considerable fluctuations in total reproduction and in most of the reproductive parameters measured. These are summarised in Table 6.6. In general, large numbers of egg masses observed correlated with high hatch success and more eggs per egg mass, all tending to increase reproduction during favourable months.

Fig. 6.7 shows the relationship of individual snail reproduction to overall snail density. The data shows a wide scatter under maximum values which show a severe decrease with increasing density. The implication is that individual reproductive potential is greatest only when snail density is low and when other environmental conditions are favourable.

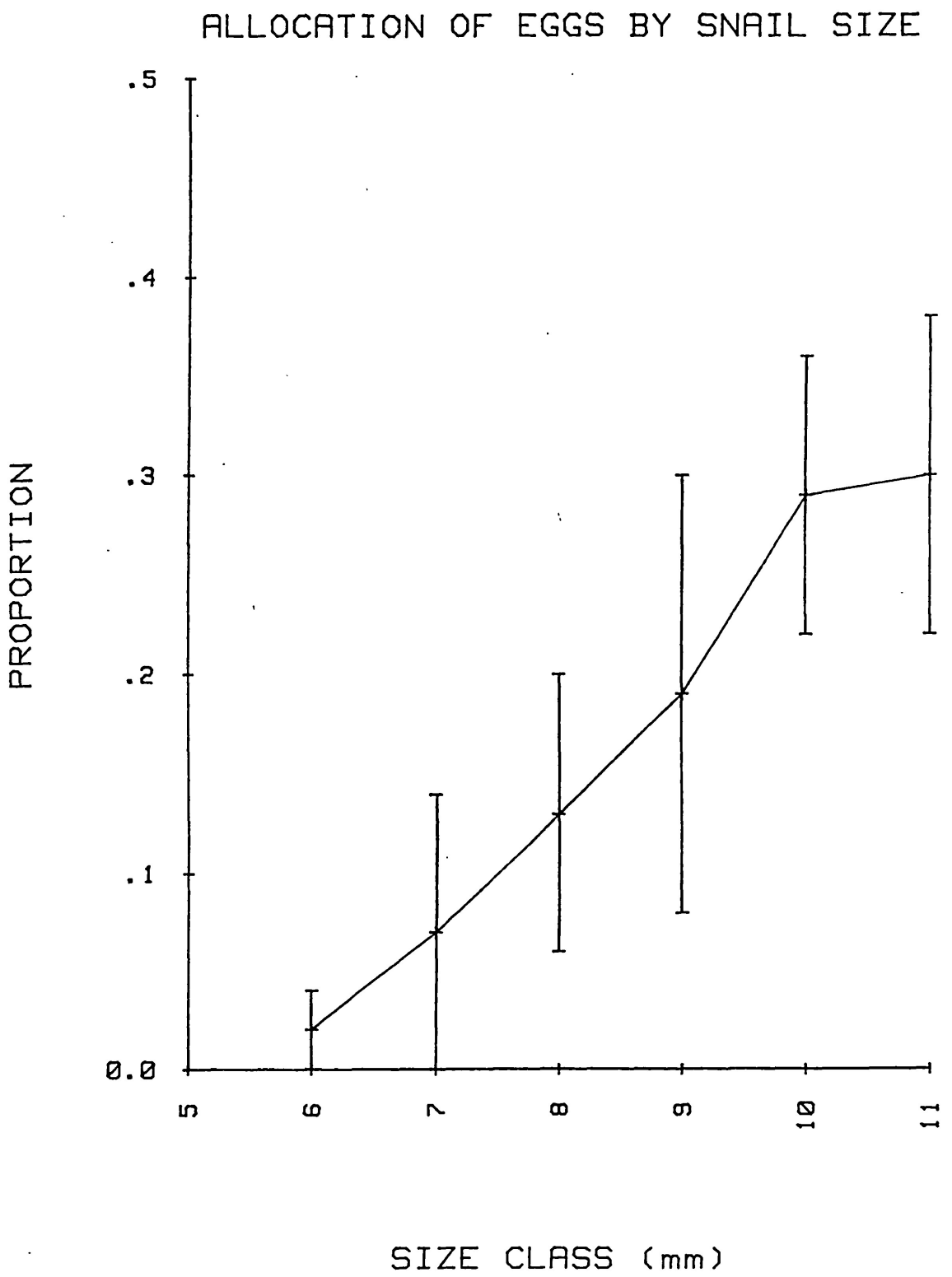


Fig. 6.6 Mean proportions of total reproduction allocated to each size class from box-snails in Nguni dam June - November hatched cohorts, 1981.

Table 6.6 Comparison of different aspects of reproduction from June 1981 to January 1982 in Nguni dam, and for yearly averages.

	Nguni Dam 1981/82							
	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.
Egg masses/trap/week	2.1	4.8	5.9	1.4	0.9	3.1	0.7	0.2
Egg masses/adult/week	4.7	3.7	1.6	0.3	0.2	2.3	1.5	0.5
Hatch time (days)	5.8	7.0	6.4	6.4	6.4	5.6	5.5	
Hatch success (%)	84	78	87	62	51	68	71	
Eggs per mass	9.4	8.2	7.3	6.6	7.2	8.2	6.5	5.5
Size at maturity (mm.)	6.3	6.6	6.5	6.4	6.5	6.6	7.3	7.1

	1980/81		1981/82	
	Nguni	Benes	Nguni	Benes
Egg masses/trap/week	3.0	0.6	2.1	0.7
Egg masses/adult/week	0.5	1.5	1.0	1.5
Hatch time (days)	5.8	7.3	6.3	-
Hatch success (%)	63	73	72	-
Eggs per mass	8.0	6.9	7.8	8.1
Size at maturity (mm.)	5.9	6.4	6.5	6.4

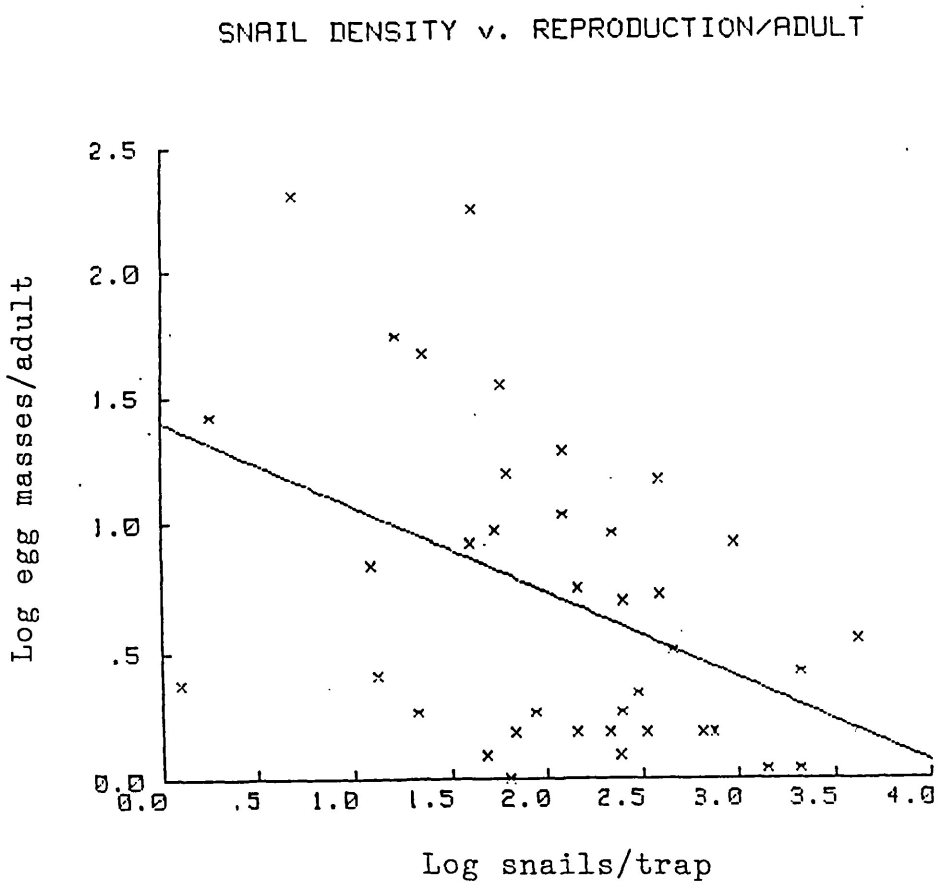


Fig. 6.7 Snail density effects on reproduction. The graph shows a severe reduction in the maximum number of egg masses per adult at increasing snail density.

(N.B. The regression line is included to demonstrate the trend, but is not quantitatively suitable due to the non-uniformity in the distribution of the variance of y in relation to the variance of x.)

Teesdale (1962), working at Chonyi, 20km north of the sites in this study, also found that the reproduction of Bulinus globosus continued throughout the year. Webbe and Msangi (1958) found that B. globosus on the Tanzanian coast exhibited breeding seasons in April/May and November/December to coincide with the rainy seasons.

From previous studies it is obvious that size at initial egg-laying for B. globosus varied considerably. Shiff (1964), sampling monthly, used size classes from 5.8 to 8.0mm, 10.00 to 11.7mm, and 12.7 to 13.6mm as the smallest to reproduce in different cohorts. Pringle and Msangi (1961) designated all B. globosus over 5mm as adults. Otieno (1969) shows a new generation hatching ten weeks after the hatch of eggs placed in cages in a pond, indicating an age of nine weeks at first egg-laying, (and a shell-length of approximately 8mm). Hira and Muller (1966) found that no B. globosus below 8mm shell-length laid eggs. They also measured the time to hatch as 12 to 15 days (in water temperatures of 24° to 29°C, very similar to those in Nguni and Benes dams). Shiff (1964) measured a 12 day incubation period for eggs kept at 22.5°C in the laboratory. These measures are very much longer than those from this project which rarely exceeded one week. Shiff also measured the hatch success of field laid eggs as 75%, slightly more than in this project. Reproduction levels in Shiff's pond in Rhodesia varied considerably, (regulated in his view primarily by the water temperature), reaching a peak breeding level of 23.9 eggs/

snail/day. The highest levels during this project were for June 1981 in Nguni dam, when adults laid 4.7 egg masses at an average of 9.4 eggs per mass each week - 6.3 eggs per adult per day, but only 1.3 eggs per snail per day. This confirms the earlier conclusion that reproduction in Nguni and Benes dams was always below the maximum potential for B. globosus.

6.3.1. The calculation of m_x values

The initial calculation of the number of eggs laid per week (N) to be allocated to adult snails was made by combining observed egg masses (EM), mean number of eggs per mass (E), mean proportion hatching successfully (S) and mean hatch time (H):

$$N = \frac{EM \times E \times S \times 7}{H} \qquad (6.3)$$

The number of adults per week was available from trap sample records, but results from snail boxes indicate that age at maturity only correlates well with the onset of reproduction in good conditions (i.e. type 1 feeding boxes). Overall there were considerable delays between the time at which snails were recognised as being mature and the time at which the first eggs appeared (see Table 6.1). In contrast, proportional reproduction by snails of different sizes in boxes showed negligible differences in the

reproductive start point (see Table 6.5), indicating that differences in size at maturity are irrelevant to overall fecundity. Because they form the most extensive and coherent database, the proportional reproduction results from Nguni dam during 1981/82 have been used for the allocation of eggs to size classes. Table 6.7 uses these proportions to calculate a hypothetical example for a week's trap samples.

Results from Nguni and Benes dams from 1980 - 1982 were calculated using the computer program in Appendix C.

Table 6.7 A hypothetical example of the calculation method used to allocate eggs to size classes in field samples. (Adapted from Madsen, 1979.)

Assume a weekly trap sample of 50 x 6mm, 60 x 7mm, 70 x 8mm, 60 x 9mm and 50 x 10mm snails, responsible for 230 egg masses.

Assume mean 8.98 eggs/mass, 83% hatch success, 6.0 day hatch.

$\therefore$ viable eggs/week = $\frac{230 \times 8.98 \times 0.83 \times 7}{6}$ = 2000

Size class (mm)	Relative egg-laying A	Snails in the sample B	Relative snail abundance C(=B÷ΣB)	Proportional egg-laying in the field D(=A x C)	No. of eggs laid/week E(=D÷ΣD x 2000)
6	0.02	50	0.17	0.003	43
7	0.07	60	0.21	0.015	217
8	0.13	70	0.24	0.031	449
9	0.19	60	0.21	0.041	580
10	0.29	50	0.17	0.049	711
11+	0.30	0	0	0	0
	1.00	290	1.00	0.138	2000

CHAPTER 7 LIFE TABLES AND THE INTRINSIC RATE OF NATURAL INCREASE

7.1. Introduction

Deevey (1947) listed three types of information from which life tables could be constructed: age at death can be used if enduring remains can be sampled and aged; cohorts sampled throughout their lifespan provide the basis for horizontal life tables (≡ cohort life tables, Krebs, 1972); the age structure from one sample can provide the basis for a vertical (≡ static, Krebs, 1972) life table.

Vertical life tables are of very limited use since there may be no relationship between the observed proportion of animals in each age class and the proportions that they represent of their original cohorts. Survivorship data from this kind of information may not therefore reflect any real situation. The life tables and derived statistics presented here are all developed from the best estimates of cohort survivorship.

7.1.1. The intrinsic rate of natural increase

Lotka (1925) derived a function r_m which he entitled "The intrinsic rate of natural increase":

$$\frac{dN_t}{dt} = bN_t - dN_t \qquad (7.1)$$

where N_t = the population size at time t,

b = instantaneous birth rate/individual and

d = instantaneous death rate/individual.

If r_m is defined as b - d, then $\frac{dN}{d_t} = r_m N$ (7.2)

of which the integral form is:

$$N_t = N_0 \, e^{r_m t} \qquad (7.3)$$

The parameter r_m depends on the fecundity, longevity and speed of development of an organism and is just as characteristic of a species as its size and shape. For this reason it is also known as the innate capacity for increase (Krebs, 1972).

Andrewartha and Birch (1954) provide a lucid account of the biological meaning of r_m. Basically, a population expanding in an unlimited environment with constant per capita age dependent birth and death rates will reach a stable age distribution, at which point the rate of increase will approach a constant:- r_m. Therefore:

"By definition, the innate capacity for increase, r_m, is the actual rate of increase of a population with a stable age distribution". Andrewartha and Birch (1954).

Krebs (1972) has pointed out that there are only two sets of

conditions in which a stable age distribution can pertain:

(a) If a population is increasing in an unlimited environment.

(b) In a population of constant size where b = d.

Since these conditions rarely occur in natural populations, r_m is of little use as a predictive statistic. As a result, r_m has mainly been used to measure the potential response of an organism (if (a) and (b) above were operative) in specified laboratory conditions (e.g. Harrison and Shiff, 1966). If this is a reasonable use of r_m, then it follows that r_m is a measure of the suitability of a habitat for the population growth of a particular animal. In other words, it is a collective statistic summarising the potential fecundity, longevity and speed of development of a population in a particular environment. Since r_m is a species characteristic it is comparable for that species over any set of conditions, and therefore provides a standardised habitat measure in terms of its suitability for the species. Smith (1954) concluded that r_m is a measure of the expected harshness of an animal's environment.

7.1.2. Estimating r

Any values calculated for r_m can only be estimates since the underlying assumptions cannot be shown to pertain exactly in any given habitat. Southwood (1978) has described several different rates of increase:

r_m is the maximum value of r under natural conditions.

r_p is the theoretical maximum fertility under conditions of zero mortality.

r_s is the rate at which a population would change if the age distribution was stable. (As density effects decrease, r_s approaches r_m.)

r_c is known as the capacity for increase (an approximate r_m), defined as:

$$r_c = \log_e R_0/T_c \qquad (7.4)$$

where $R_0 = \sum l_x m_x$

and $T_c = \sum l_x m_x x / \sum l_x m_x$ (the cohort generation time)

l_x and m_x are the life table parameters denoting proportion surviving at x and number of offspring produced per snail from time x - 1 to x.

In addition to the above, there is the actual rate of increase (designated plain r by Shiff, 1964) which is found by substituting totals at successive samples for N_0 and N_t in equation 7.3.

$$\therefore \quad r = \frac{\log (N_t \div N_0)}{t} \qquad (7.5)$$

This is of limited use as it merely describes the empirical dynamics embodied in the numbers of animals sampled.

Of these various definitions r_m is the statistic which has been calculated for this project. The method of calculation used is the well known Euler equation:

$$\sum l_x m_x e^{-r_m x} = 1 \qquad (7.6)$$

which can easily be solved iteratively using a computer.

Slobodkin (1962) and Roughgarden (1979) both provide particularly clear explanations of the above relationship. It derives from the assumption of the Lotka model that the number of births now is related to the number of births at any time in the past (as a consequence of the stable age distribution, which is itself a consequence of exponential population growth). If l_0 at time t (the number of animals born at time t) is set at 1, then at time t - x there were e^{-rx} individuals born. By time t they are represented by $l_x e^{-rx}$ survivors. The number of offspring born to animals alive at time t is therefore $\sum l_x m_x e^{-rx}$. This is equivalent to l_0 at time t which was initially set at 1.

May (1976a, 1976b) discusses the relationship between r_m (solved as above) and r_c (solved as in equation 7.4) and concludes that the biological meaning of r_m is not at all transparent. Presumably this is because of the interdependence of the assumptions and the circular nature of the argument used in equation 7.6.

However, r_c is not immune from circular arguments and is only an approximation of r_m because, for the exact calculation of T_c (the generation time), the value of r_m must be previously known (Andrewartha and Birch, 1954).

7.2. Life Tables and r_m from Boxes

Since survivorship, age and reproduction could all be measured directly for box-kept snails, the results form a ready-made life table from which r_m could be estimated.

Table 7.1 summarizes r_m values from all boxes. As for survival and reproduction, data for 1980/81 and for Benes dam during 1981/82 has been grouped for the whole year because r_m values could only be calculated for a few boxes.

The effects of different feeding and density regimes were tested for cohorts hatched in Nguni dam from July to October 1981. (Cohorts hatched after October still survived in large numbers by the end of the project.) Table 7.2 summarizes the results of a factorial analysis of variance. Lily leaf feeding made a large (nearly 4-fold) difference to the mean rate of increase. The highest initial density had a significant effect on depressing r_m, but only snails at the highest density and on the low quality feeding regimes failed to exhibit some potential for increase.

Table 7.1 r_m values calculated from cohorts of box-kept *B. globosus*.

Dam	Year	Hatch month	No. of snails	No. of boxes	Mean r_m/week
Nguni	1980/81	All	60	4	0.447 ± 0.383
Benes	1980/81	All	157	6	0.440 ± 0.333
Nguni	1981/82	June	70	6	0.383 ± 0.128
		July	105	9	0.321 ± 0.142
		August	105	9	0.232 *
		Sept.	105	9	0.131 *
		Oct.	105	9	0.165 *
		Nov.	105	9	0.151 *
		All	595	51	0.222
Benes	1981/82	All	50	5	0.094 *

* For some cohorts no reproduction occurred. r_m is therefore $-\infty$, but for purposes of calculating means, one egg mass was allocated during week 10 and the consequent r_m value was used. (No confidence limits are given for data sets which include these manufactured r_m values).

Table 7.2 The results of a factorial analysis of variance for the mean intrinsic rate of natural increase (r_m) of B. globosus kept in boxes in Nguni dam, July 1981 to January 1982.

Density treatments 1 to 3 indicate low to high initial density.

Feeding treatments 1 to 3 indicate high quality to low quality diet (see Section 3.6.3. for explanation).

(Data from 36 boxes containing 420 snails.)

A. MAIN EFFECT MEANS

	Treatment		
	1	2	3
Feeding	0.461*	0.121	0.055
Initial density	0.256	0.259	0.123*

B. TWO WAY INTERACTION MEANS

		Initial density		
		1	2	3
	1	0.482	0.483	0.416
Feeding	2	0.282	0.102	-0.020
	3	0.003	0.191	-0.028

The analysis indicated significant ($P < 0.05$) differences in mean r_m from different feeding and initial density regimes.

* Indicates significant ($P < 0.05$) differences from multiple comparisons using the least significant difference method.

These r_m values were calculated from data covering the whole life-span of box snails. For free-living cohorts, survival data was only calculated to 20 weeks of age. In order to determine what difference this might make to the calculated values of r_m, box results were used to investigate the addition to the estimated r_m of survival and reproduction after 20 weeks. Out of 42 cohorts, 20 did not survive beyond 20 weeks, 13 survived but did not reproduce, and 9 produced eggs after 20 weeks. In none of these 9 cases did the added reproduction after 20 weeks make any difference to the estimate of r_m to three decimal places. This is in spite of the fact that up to 11% of reproduction occurred after 20 weeks. In a "compound interest" model of this kind, speed of development and early reproduction is of paramount importance in determining the final value of r_m. Indeed, the highest r_m values calculated from box cohorts were 0.726 and 0.946, both from cohorts which survived for only 7 weeks.

The conclusion is that the failure to extend measurements beyond 20 weeks for field cohorts had no effect on the estimation of r_m.

7.3. Life Tables and r_m from Trap Samples

Survival and reproduction schedules have been presented for free-living B. globosus populations in Chapters 5 and 6. The results were combined to find values for R_0 (the net reproductive rate) and r_m. The life tables for weekly

cohorts are shown in Appendix D.

r_m values for weekly cohorts are plotted in Figs. 7.1 to 7.3. Estimates were only made for cohorts hatched at least fifteen weeks before sampling stopped. For February and March 1980, snail densities in Nguni dam were too low to allow reasonable life table construction. Sample data from Benes dam during 1981/82 was too scarce to permit detailed analysis.

Each r_m value provides a measure of the potential cohort performance in environmental conditions averaged over the twenty weeks following the hatch date, but strongly influenced by the initial weeks following adult recruitment. When $r_m>0$ the population could potentially have increased during the 20 weeks, but may not have done due to extrinsic factors (e.g. Nguni cohorts hatched during September and October 1981 indicate a potential to increase, due to rapid development and heavy egg-laying, which is not subsequently realised as a result of very low survival rates during November and December). When $r_m<0$ there can be no population increase as a result of that cohort's reproduction, (although the population may initially increase as a result of a previous cohort's reproduction).

In order to compare the difference between r_m and r_c, values for both have been calculated for Nguni dam during 1981/82. Table 7.3 shows that r_m is often slightly higher than r_c

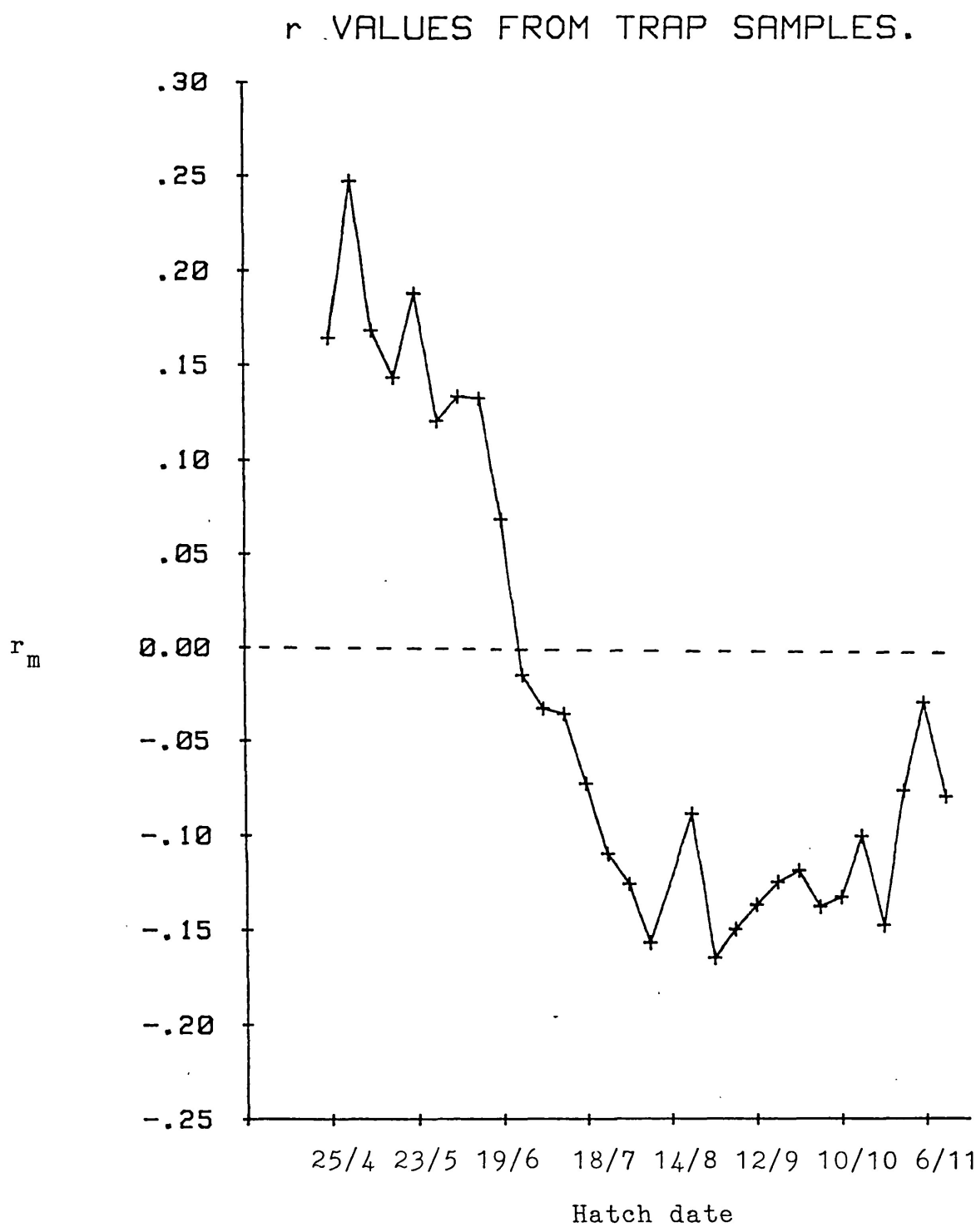


Fig. 7.1 r_m values for cohorts hatched on the date indicated on the x axis.

(Data from weekly trap samples, Nguni dam, 1980.)

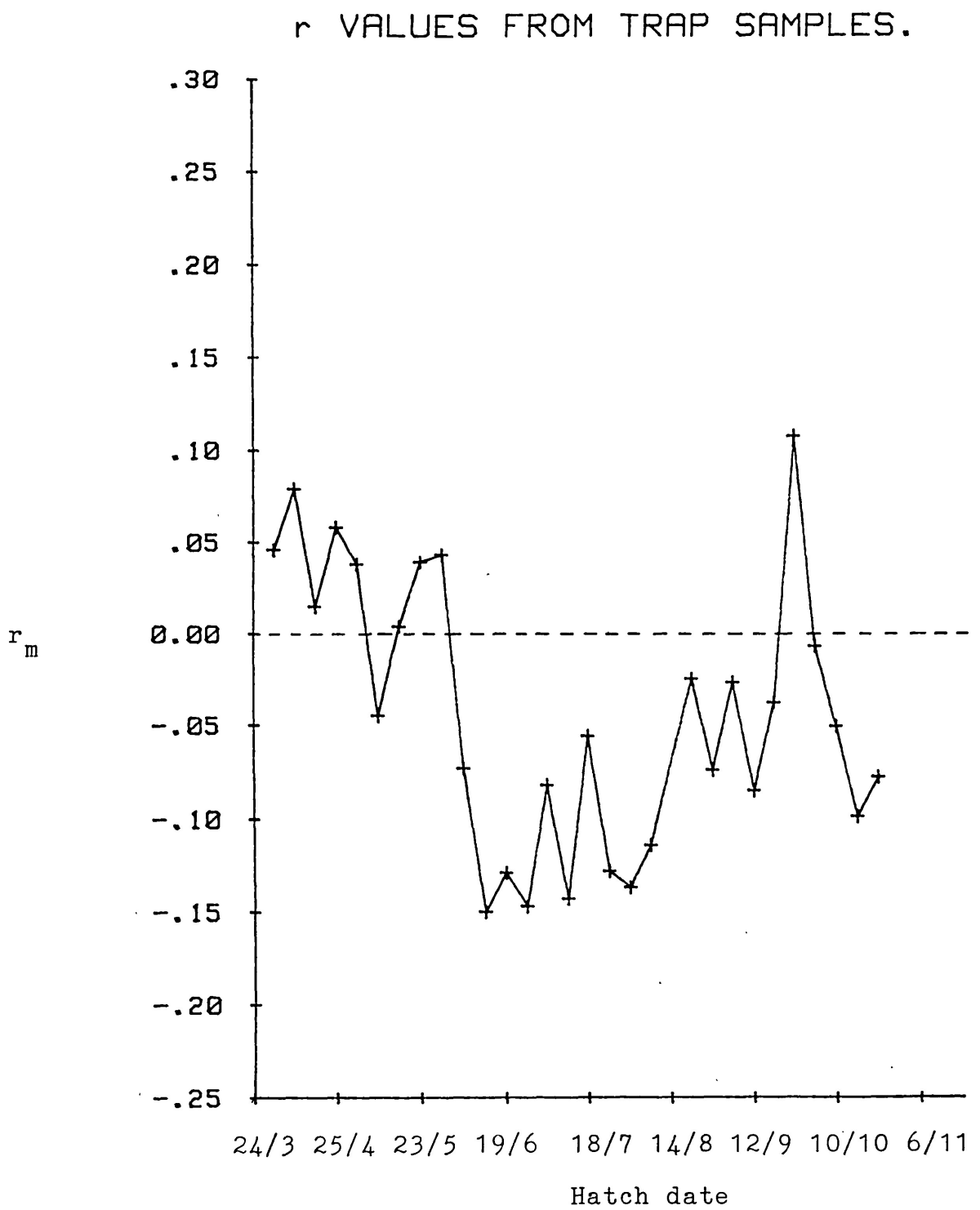


Fig. 7.2 r_m values for cohorts hatched on the date indicated on the x axis.

(Data from weekly trap samples, Benes dam, 1980.)

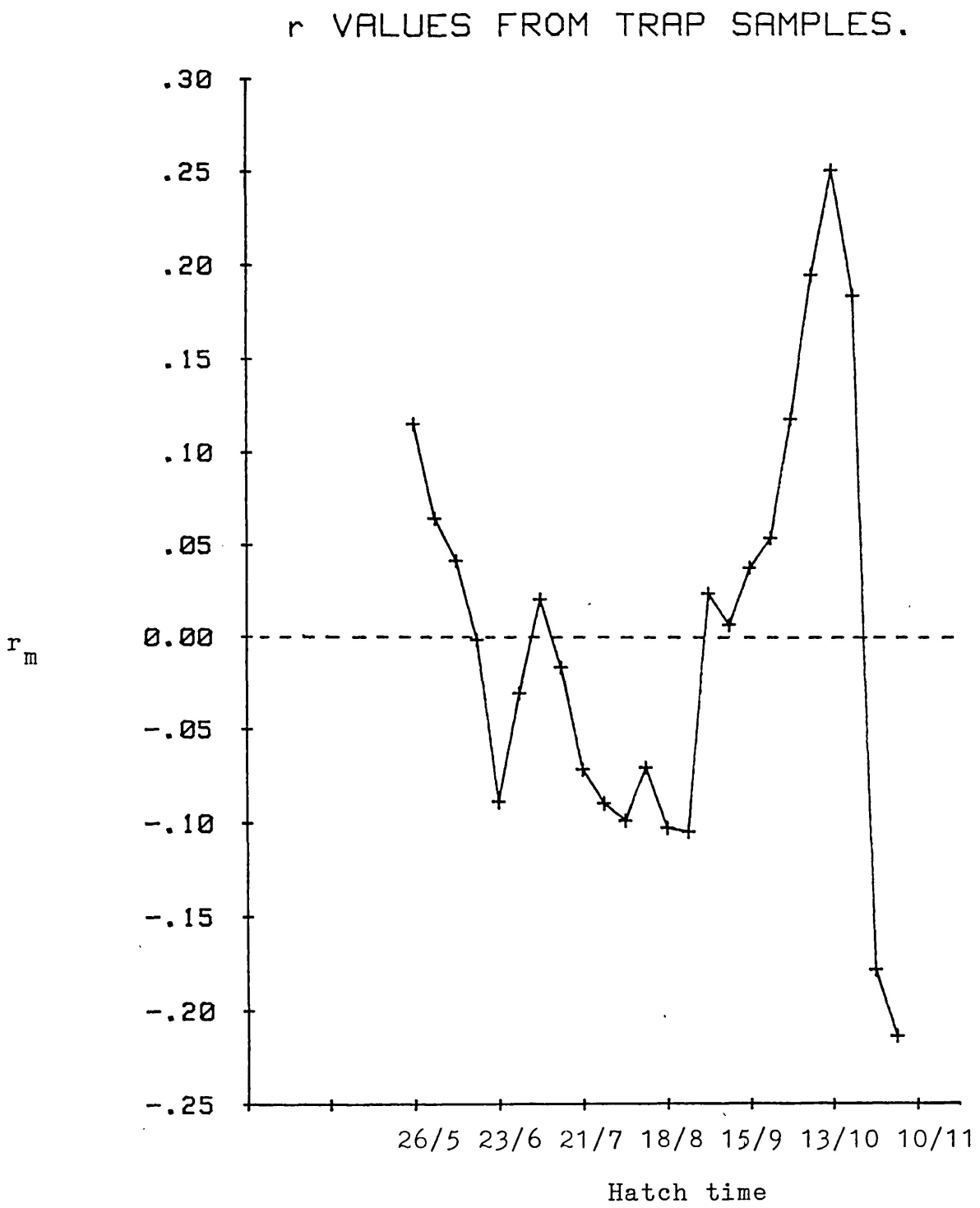


Fig. 7.3 Nguni dam 1981/82. r_m values for cohorts hatched on the date indicated on the x axis.

(Data from weekly trap samples.)

Table 7.3 Comparison of r_m and r_c for Nguni trap samples 1981/82.

r_m as in $\sum l_x m_x e^{-r_m x} = 1$

r_c as in $r_c = \frac{\log R_0}{T_c}$

$$T_c = \frac{\sum l_x m_x x}{R_0}$$

Week	r_m	r_c	Difference (+ indicates r_m is larger)
1	.115	.113	+ .002
2	.064	.063	+ .001
3	.041	.041	-
4	- .002	- .002	-
5	- .095	- .095	-
6	- .031	- .031	-
7	.020	.020	-
8	- .017	- .017	-
9	- .072	- .073	+ .001
10	- .090	- .091	+ .001
11	- .099	- .100	+ .001
12	- .071	- .072	+ .001
13	- .103	- .103	-
14	- .105	- .105	-
15	- .023	- .023	-
16	.006	.006	-
17	.037	.037	-
18	.053	.053	-
19	.117	.117	-
20	.194	.192	+ .002
21	.250	.245	+ .005
22	.183	.180	+ .003
23	- .179	- .188	+ .009
24	- .214	- .229	+ .015

(i.e. that T_c is slightly overestimated), but that the difference is insignificant, except possibly for extreme r values.

7.4. Discussion

Generally, there appear to be two times during the year when B. globosus in Nguni and Benes dams are able to exhibit population growth. The first, for snails hatched from March or April to June, was exploited in both dams during 1980 and resulted in peak populations during September. The second (for snails hatched in September/October/November) may be inversely dependent on the densities achieved after the first period of increase. Thus snails that were hatched in Nguni dam during November, although they exhibited a relative improvement in r_m, failed to achieve a level at which they could increase.

The pronounced peak in r_m values for September/October cohorts in Nguni dam during 1981 (see Fig. 7.3) cannot be relied on as they result from a sequence of events not taken into account by the sampling methods. The prevailing south-east wind swept large numbers of free-floating snails to the extreme west end of the dam inlet (see Fig. 2.5), beyond the last sampling site. These snails were not included in sample estimates and therefore reflect a mass emigration. (When these concentrations were noticed, some traps were added to the dam inlet to monitor this concentration. During October an average of 52.6 snails/trap were found, higher

than the highest densities found during the project at the weekly sampling sites). On November 11th 1981 heavy rain caused the dam to flood. Water rushing into the dam inlet dispersed the above concentrations of snails back into the main body of the dam, and catalysed a reproductive boom (see Fig. 2.8).

Standard weekly sampling results, from which r_m is calculated, show low reproduction in September and October. Original cohort numbers at $x = 0$ are therefore very low during this time (see Appendix D). These cohorts were in their early reproductive stage when the flood occurred. Although sample numbers continue to decline, enough adult snails are reintroduced from the dam inlet concentrations to show very high survival levels in the September/October cohort life tables (in Appendix D). These, combined with the reproductive boom, lead to artificially high r_m values.

Unfortunately, there is no reasonable way of disentangling these effects in order to identify migration-free survival, and therefore the r_m values for Nguni dam cohorts hatched during September and October 1981 are left out of subsequent analysis.

Table 7.4 gives a summary of the means and ranges of values estimated for B. globosus in Nguni and Benes dams. As expected, mean values from box-kept snails are higher and the ranges are wider than for free-living snails. Eisenberg

Table 7.4 Summary of r_m values measured for box-kept and free-living B. globosus.

		Data Source			
		Trap samples		Boxes	
		Mean	Range	Mean	Range
1980/81	Nguni dam	-0.023	-0.165 to 0.247	0.447	0.134 to 0.710
	Benes dam	-0.051	-0.150 to 0.107	0.440	0.126 to 0.946
1981/82	Nguni dam	0.014	-0.214 to 0.250*	0.222	- ∞ to 0.572
	Benes dam	-	-	0.094	- ∞ to 0.324

*The highest values for 1981/82 may be an overestimate, see text.

(1966) carried out feeding and density experiments on Lymnaea elodes in pens, and concluded that density regulation was achieved through an adjustment in adult fecundity as influenced by food supply. He felt that food limitation was a relative rather than an absolute control. In a later study (Eisenberg, 1970) he identified two distinct levels of feeding: The first he called "maintenance nutrition", at which level the snails do not die but are barely capable of reproduction. The second level, "positive nutrition" allows the organism to realise some portion of its potential for growth and reproduction. Type one (lily leaf) feeding of box-kept snails obviously corresponds to Eisenberg's second level feeding, and type two and three feeding to his first level. What is most interesting is the very clear cut differences between the two levels, so that the capacity to increase was nearly four times as high for lily-fed snails as for those fed on coarse vegetation only.

Superimposed on these differences are the changes in mean r_m from boxes during different months and different years. r_m during 1980/81 was very much higher in both dams than during 1981/82. Mean r_m values for monthly sets of boxes in Nguni dam during 1981/82 are plotted in Fig. 7.4. The general trends are similar to those from trap samples,with declining values from June to September, an increase in October, followed by a decline in November, indicating that similar environmental effects are operating, although the absolute values and scope of the changes is very different.

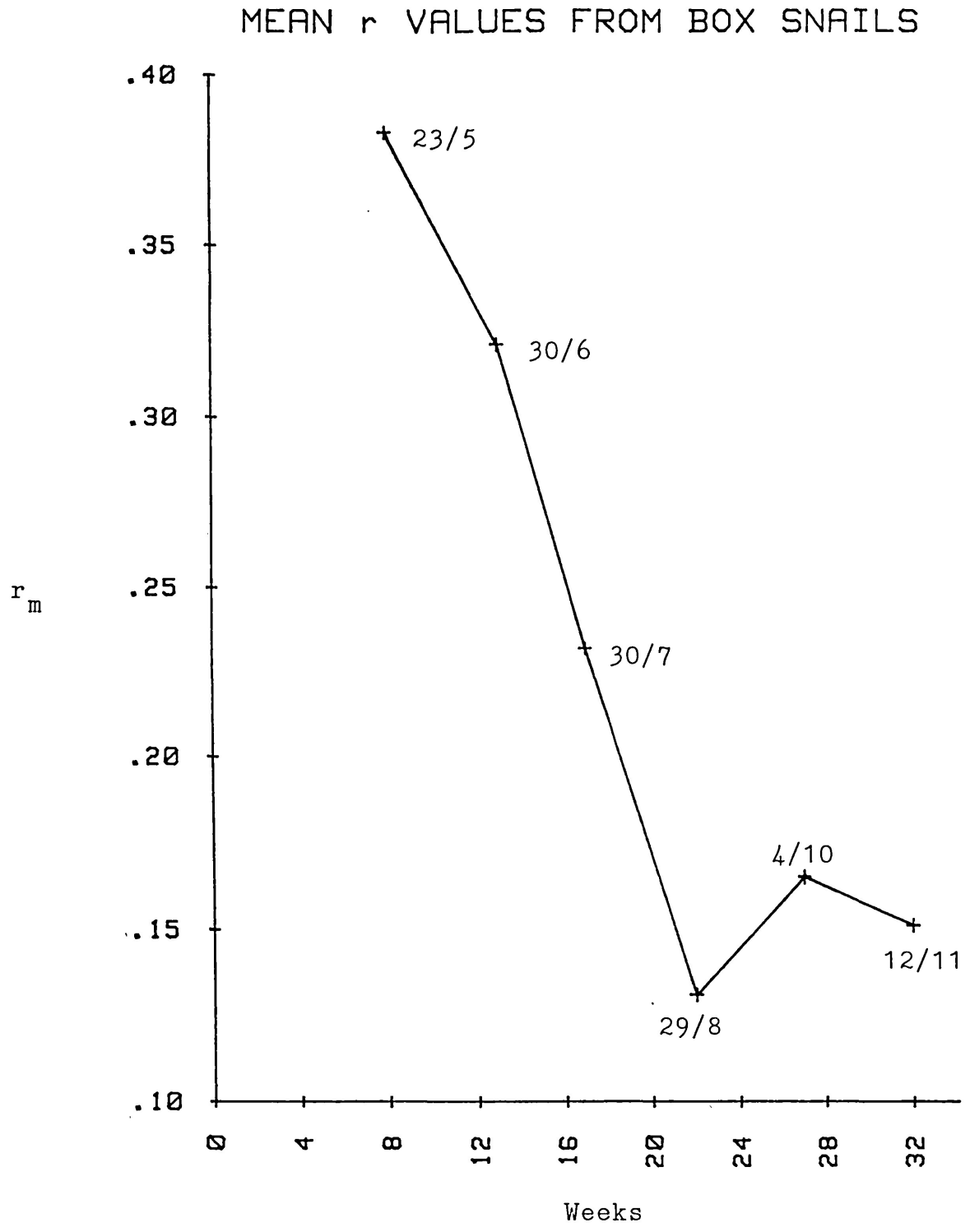


Fig. 7.4 Mean r_m values for box-kept snails hatched on the dates indicated.

(Data from boxes in Nguni dam, 1981.)

7.4.1. The interpretation of r_m and comparisons with previous studies

Estimates of r_m have previously been made for schistosome host snails for two different purposes. Dazo et al (1966) planned molluscicide operations in Egypt to coincide with times of lowest intrinsic rates of increase so as to delay the recovery of snail populations for as long as possible. Sturrock (1973a) calculated values of r_m in order to be able to predict rates of repopulation following molluscicide. In both these cases rates were measured in the field and r_m values were used predictively, on the assumption that molluscicide creates an underpopulated environment in which the snails' potential exponential increase will be realised, at least initially.

Several laboratory and semi-field studies have used r_m (or r_c) as a way of establishing the optimum level of a resource for the snails' requirements. Shiff and Garnett (1967) examined Biomphalaria pfeifferi in different temperatures in this way, Williams (1970) measured r_c for B. pfeifferi in different calcium carbonate concentrations, and Harrison and Shiff (1966) estimated r_m for B. pfeifferi and Bulinus globosus at different temperatures and in different bicarbonate concentrations. Combrinck and van Eeden (1975) measured r_c for Bulinus tropicus and Lymnaea natalensis in a semi-field river model to determine which type of substrate was most beneficial.

In all these cases it has been implicitly assumed that the populations studied approximate to a stable age distribution. Whilst this is almost always patently untrue for the population as a whole (as it is for the snails in this project), the actual cohorts for which the values of r_m are estimated will, over their lifetime, exhibit a population structure very similar to their theoretical stable age distributions. This can be calculated (Krebs, 1972) using the following formula:

$$C_x = \frac{\lambda^{-x} l_x}{\sum \lambda^{-x} l_x} \qquad (7.7)$$

Where C_x is the proportion of organisms in the age category x to x + 1 in a population increasing geometrically.

λ is e^{r_m} (the finite rate of increase).

l_x is the survivorship function from the life table.

Because of the sampling anomalies for small snails, this method cannot reasonably be used for free-living cohorts, but Fig. 7.5 compares a theoretical stable age distribution from a box-kept cohort with the actual age distribution of a free-living cohort with similar r_m. The distributions have dissimilarities, but are substantially the same at the peak reproductive period, from week 7 to week 13.

The estimation of r_m is influenced by the environment of the cohort for which it is measured, but not by the effects on

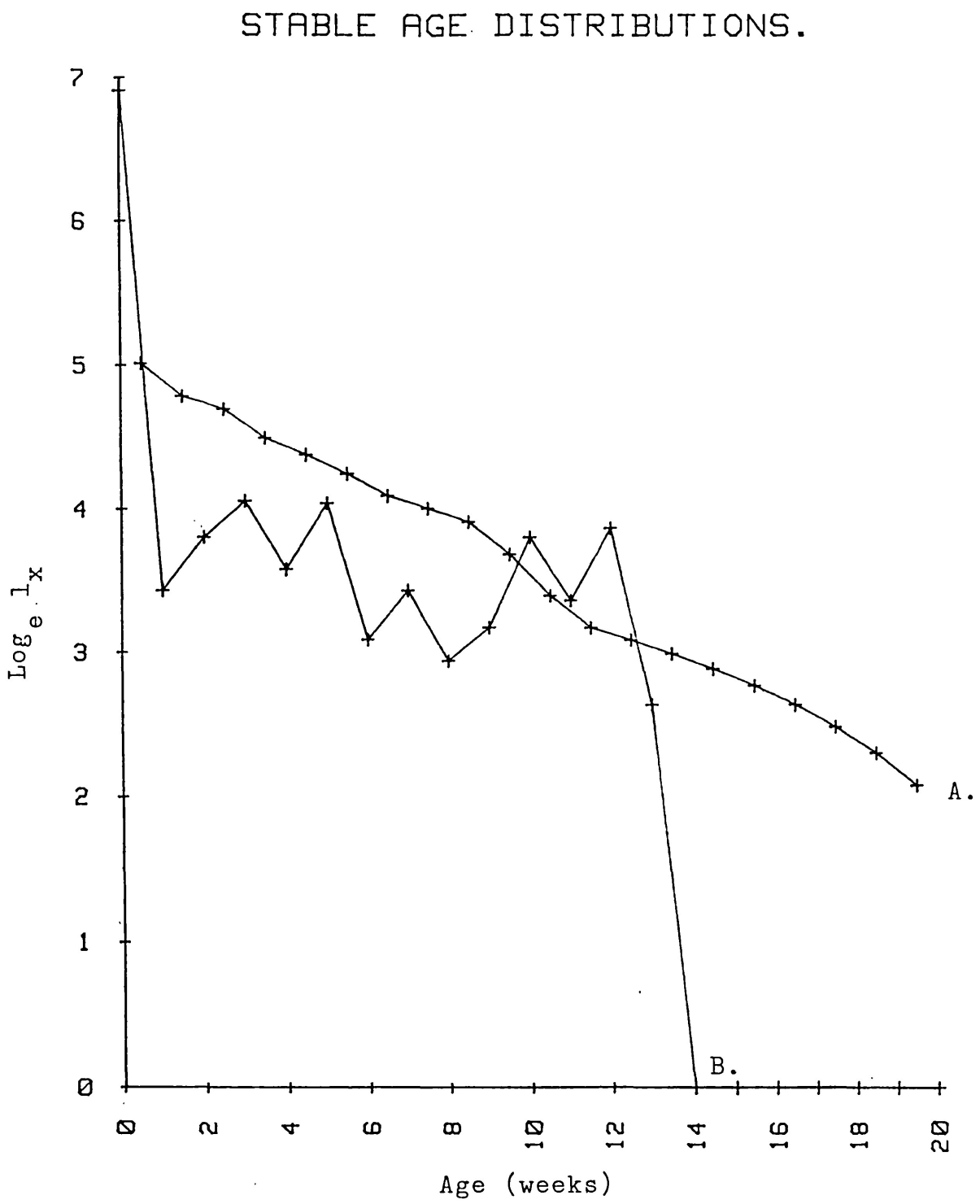


Fig. 7.5 Comparison of a theoretical stable age distribution (A) from a box cohort with r_m = 0.098, and the actual age distribution of a cohort from trap samples (B) with r_m = 0.115.

the future offspring to which it gives rise. It therefore carries the assumption that the average environmental conditions prevailing over the life of the cohort will continue over subsequent generations. Among these conditions are density effects, which are included in the estimate, and have therefore to be regarded as an external environmental factor. This is a drawback to the use of r_m as a measure of habitat suitability, since density effects are not an intrinsic part of a habitat. Unless a population is expanding in the long-term, density effects should be neutral over the whole year, and the mean value of R_0 should approach one and of r_m should approach 0. For useful comparisons of habitat suitability, a range of r_m values covering all seasonal changes should be measured, and the range of values, rather than the mean, is the most useful statistic.

Very few field studies to date provide measures of intrinsic rates, and of those that do some provide only one or two estimates. Table 7.5 summarises those who have estimated r_m (or r_c) or from whose data r_m has been calculated. Values for Bulinus and Biomphalaria are very similar in range to values for this project. For Oncomelania quadrasi (the intermediate host of Schistosoma japonicum) the values of r in exponential growth situations are considerably lower, probably because of the relatively long time to adult recruitment (90 - 94 days). Gillespie (1969) has estimated r_m values per week for four temperate climate aquatic snails:

Table 7.5 Values for r/week estimated for bulinid and other bilharzia intermediate host snails during previous field studies.

Snail (country)	Mean r (No. of estimates)	Range	Comments	Authors
Bulinus globosus (Zimbabwe)	0.096 (2)	-0.129 to 0.062	r_m	Shiff (1964)
Bulinus truncatus (Egypt)	0.336 (1)	0.336	Max. r_m for month of greatest increase.	Dazo et al (1966)
Bulinus tropicus (South Africa)	0.096 (5)	0.067 to 0.106	r_c from semi-field data.	Combrinck and van Eeden (1975)
Biomphalaria alexandrina (Egypt)	0.273 (1)	0.273	Max. r_m for month of greatest increase.	Dazo et al (1966)
Biomphalaria glabrata (St. Lucia)	-0.063 (12)	-0.604 to 0.295	Mean r_m values from 2 to 11 observations (total 52 estimates).	Sturrock (1973a)
Oncomelania quadrasi (Phillipines)	0.027 (3)	0.025 to 0.029	r calculated from predicted recovery rates.	Pesigan et al (1958)
Oncomelania quadrasi (Phillipines)	0.064 (1)	0.064	r calculated from observed recovery rate.	Pesigan et al (1958)

Physa gyrina (gastropod)	- 0.204 to 0.568
Gyraulus deflectus (gastropod)	- 0.062 to 0.253
Valvata humeralis (gastropod)	- 0.837 to 0.664
Pisidium compressum (pelecypod)	- 0.128 to 0.219

These values are of the same order as those for the tropical snails in Table 7.5, with some higher values probably due to the very favourable conditions for expansion usually associated with the temperate spring season.

Actual rates of increase can considerably exceed the maximum estimates of r_m. This occurs when the age distribution is significantly biased towards adults and conditions suddenly become favourable for reproduction. Shiff (1964) measured actual rates of increase of 3.630 per week in a pond which had been dry, immediately after refilling. In this project, during which neither dam dried out completely, actual rates in Nguni dam never exceeded 0.237, slightly below the maximum estimate for r_m, but in Benes dam a rate of 0.221 per week (twice the maximum r_m) was measured immediately following the flooding of the dam by heavy rain in 1980.

In summary, r_m is a useful measure of the potential increase of species in a particular habitat. Its major disadvantage is that it includes density effects which may obscure an evaluation of the extrinsic environment. Its main advantage is that it provides a universal relative measure of habitat

suitability which even takes account of the evolutionary adaptation of the population to its particular environment. The parameter r_m does not necessarily provide any measure of the schistosome transmission potential of a snail population (for which longevity is a crucial factor), since longevity of a cohort may not be the prime factor affecting its intrinsic rate of increase if maturity is reached quickly and early reproduction is high.

CHAPTER 8 INFECTIONS

8.1. Introduction

Schistosoma haematobium is the only schistosome at present known to occur on the Kenya coast. S. mansoni is absent because no suitable host snail (Biomphalaria spp) seems able to establish itself in the coastal region. The reasons for the absence of S. bovis are less obvious since two possible intermediate hosts (Bulinus nasutus and Bulinus globosus, Southgate and Knowles, 1975b) are present and S. bovis is known to occur further inland (Southgate and Knowles, 1975a).

B. nasutus is the main intermediate host for S. haematobium in N.W. Tanzania (Webbe, 1962a) and Brown (1980) considers that it is probably an important host in coastal Kenya. He also considers that B. globosus is a potential host for S. haematobium throughout its range. Teesdale (1962) found B. globosus shedding S. haematobium at Chonyi (approximately 20 km north of Benes dam). In a previous survey (O'Keeffe, 1979), four large B. globosus were found to be shedding an unidentified schistosome in a small pond near Benes dam. Apart from the above, there is very little information about the identity of schistosome intermediate hosts on the Kenya coast, and no certainty, at least on the coastal strip north of Mombasa, as to which species of snail is implicated in transmission.

In this project, parasite infections were of importance for two reasons; namely, the identification of bilharzia transmission foci and of the species of snail responsible, and the quantification of all parasite infections of the snails from the viewpoint of their effect on the population dynamics of their hosts.

With the first aim in mind, collections of B. globosus and B. nasutus were made from all habitats where they were found and these were tested for patent schistosome infections. Collections from the two main sampling sites (Nguni and Benes dams) were more frequent and all cases of cercarial shedding were recorded. Four recognisably different cercarial forms were encountered:

Schistosomes
Strigeids
Heterophyids
Monostomes

Strigeids were found in two B. globosus from Nguni dam and six from Benes. Monostome cercariae were shed by 19 B. globosus from Nguni dam. No attempt was made to identify either of these groups further. Heterophyid infections were abundant in Nguni and fairly common in Benes dam, and are discussed below.

8.2. Schistosome Infections

Benes dam provides the main water resource for the village of Gongoni, situated 0.5km away. Professor G. Kinoti from the University of Nairobi visited Gongoni Primary school in February 1981 in order to collect schistosome eggs for laboratory cultures. He kindly agreed to keep some of the individual urine samples separate in order to quantify the proportion of schoolchildren infected.

The results indicate that approximately 20 - 30% of the children from the age of 8 to 17 were suffering from Schistosoma haematobium infections (see Table 8.1). Inspection of a single urine sample does not provide an infallible method of diagnosis (Macdonald, 1973). In addition, the samples were taken from children (a) who go to school and (b) who were at school on the particular morning of the survey. These factors may tend to generate an underestimate of actual prevalence, (assuming some absence due to illness and a relationship between parental care and school attendance).

Nguni dam was unlikely to be a major transmission site because its use as a washing/drinking/fishing area is forbidden to the local population and it is guarded by a watchman. Other sites inspected were open to public use.

The habitats of the two potential schistosome host snails

Table 8.1 Results of a schistosome egg survey from single urine samples of primary school children at Gongoni village.

Only samples from children in standard 4 were individually inspected for eggs. The samples from other children were merely inspected for unusually dark colour, indicating haematuria.

Standard (= class)	Approximate age	No. of children	No. of samples containing *S. haematobium* eggs	No. of samples showing haematuria	%
3	8 - 10	45	N.D.	11	24
4	10 - 13	28	8	N.D.	29
5	13 - 17	27	N.D.	6	22

were mutually exclusive (see Chapter 2). Collections during 1980 were made from six B. globosus habitats and from two B. nasutus habitats (the quarry entrance pond and Utange pond). A total of 2,577 B. globosus were tested, of which thirteen were found to be shedding schistosomes (Table 8.2 shows the distribution from different sites). The surviving snails with patent infections were sent to the British Museum (Natural History) for further identification of the schistosomes. Only three stayed alive long enough for the infections to be passaged, (two from Benes dam and one from Bamburi old dam). All three carried single sex S. haematobium infections (R. Knowles, pers. comm.).

From the B. nasutus sites, 1,644 snails were tested during 1980 and none were found to be shedding schistosomes. Both Utange pond and the quarry entrance pond were temporary habitats and only contained water from April to November. During 1981 both sites were only intermittently full, and snail numbers were very low. A further 65 B. nasutus were tested but none were found to be shedding.

During 1981/82 a further 3,536 B. globosus from Benes and Nguni dams were tested, and four more snails were found to be positive for schistosomes (see Table 8.2). No B. globosus from other habitats were tested.

In summary, a total of 6,113 B. globosus were tested from March 1980 to February 1982, of which 17 were found to be shedding schistosomes (an overall prevalence of 0.28% for

Table 8.2 Numbers of *B. globosus* tested for cercarial shedding

1980/81

Site	No. tested	No. shedding schistosomes	%
Nguni dam	804	0	0
Bamburi old dam	503	1	0.2
Quarry dam west	135	0	0
Benes dam	891	10	1.2
Benes soak pond	134	0	0
Junju dam	110	2	1.8
	2577	13	0.5

1981/82

Site	No. tested	No. shedding schistosomes	%
Nguni dam	1507	3	0.2
Benes dam	2029	1	0.0
	3536	4	0.1

patent infections).

8.2.1. Seasonality and age distribution of schistosome infections

With so few infected individuals, any attempt at detailed analysis of transmission patterns should be cautious. There was however, a striking seasonal pattern to the infections (shown graphically in Fig. 8.1).

During 1980/81 mature infections were confined to December and January. These were found in three separate dams and the ten infected snails from Benes dam were found at four different sites, none of which were accessible from each other for a snail (due to screening by emergent vegetation). The results therefore represent the synchronous appearance of infected snails at six separate sites.

Infected snails ranged in size from 6.3mm to 14.5mm shell length, and averaged 8.8 $\pm$ 1.7mm. This is slightly (though not significantly at $P < 0.05$) larger than the mean size (7.8 $\pm$ .2mm) of all the snails in the samples in which they were found. Two of the infected snails were found in boxes and could therefore be aged exactly. One was 202 days old, but may have been shedding for some time before discovery. The other was 59 days old and could only have been shedding for a few weeks at most. Neither of these snails displayed

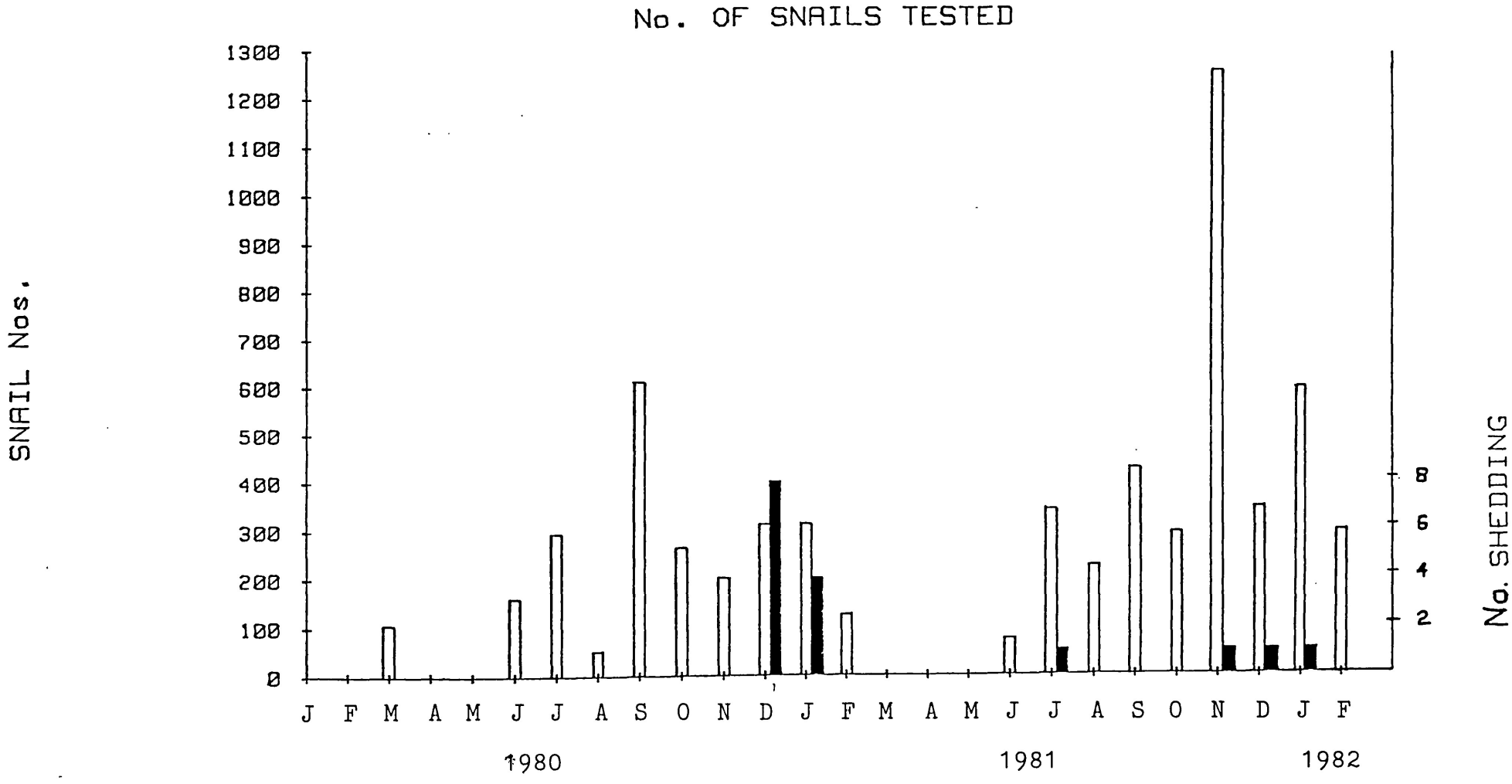


Fig. 8.1 Distribution of B. globosus shedding schistosome cercariae. The number of snails tested (□) from all sites is shown by month, and the number of snails found to be shedding (■) is shown on the y axis on the right.

any unusual growth. One was the smallest of three snails of identical age, and measured 6.3mm, the other two measuring 6.9 and 7.7mm. The other was 11.0mm, the fourth largest of 14 snails (of the same age) from 9.2 - 11.5mm. The other snails which could be aged (those from Nguni and Benes dams) varied from approximately 45 to more than 140 days old when found.

Three of the four infected snails found during 1981/82 came from Nguni dam. Since this dam is rarely approached by more than five to ten people per day, of whom only employees of the owners have any legitimate reason for water contact, the infections are most likely to be the result of casual urination which would not necessarily lead to any self-perpetuating transmission. It is unlikely that Nguni dam constitutes an important focus for schistosome transmission with the local population.

8.3. Heterophyid Infections

Very high levels of heterophyid infection were found, especially in Nguni dam during 1980. Specimens of infected snails were sent to the British Museum (Natural History) for identification, but to date no specific identification has been made. Attempts to infect quails, hamsters and mice have failed, so that there is as yet no evidence for the identity of the definitive host (R. Knowles, Pers. comm.).

Infection by this organism rendered the snails unable to reproduce, though whether this was a castratory or reversible effect is unknown. No eggs were ever found in boxes in which all snails were shedding, nor did any isolated snails lay eggs after cercariae were found. Dissection of infected snails showed the reproductive tracts to be filled with cercariae. Evidence has already been given from box snails that mortality of shedding snails was not significantly higher than for non-shedders. Growth patterns of shedding snails were no different than for non-shedding snails of the same age in boxes.

Once they had begun to shed cercariae, all box-kept infected snails continued to shed cercariae at subsequent tests, except for four snails which all died within a week of the negative tests.

Nutrition undoubtedly plays an important role in the rate of cercarial development and production (Wright, 1971; Kennedy, 1975). This is confirmed by the difference in observed rates of infection from snails in boxes with different feeding regimes (see Table 8.3). Since free-living snails most closely resemble type II and III box snails in terms of growth, survival and reproduction, it appears that substantial numbers of miracidial penetrations do not develop to cercarial production.

Table 8.3 Differences in observed prevalence of snails shedding heterophyid cercariae from B. globosus kept in boxes in Nguni dam during 1981/82.

Feeding regime	No. of adult snails tested	No. observed shedding	%
1	128	18	14
2	139	7	5
3	70	4	6

Successive tests of box-kept snails give an indication of the time when most patent infections began (see Table 8.4).. Assuming a latent period of approximately five to six weeks, miracidial activity was most pronounced during June and July. Fig. 8.2 shows the monthly differences in the proportion of box-kept snails shedding by feeding type. The figure also shows an apparent decrease in the force of infection through the year. A similar conclusion cannot be drawn from the results of testing samples of free-living (as opposed to box-kept) snails (see Fig. 8.3). These exhibited at least two peaks per year, with much higher prevalence during 1980/81 than during 1981/82. Data from Benes dam shows a similar two peak cycle during 1980, but levels are very much lower, reaching a maximum of 7.8% in August and 6.5% in December. During 1981/82 only two snails were found in Benes dam with mature heterophyid infections.

Levels of infection continued to rise with the size of the snails (see Fig. 8.4), but conversion of size to age (Fig. 8.5) indicates that the rate of increase of infections decreased with age.

8.4. Discussion

Bulinus globosus was responsible for all the schistosome transmission that was found. Although no infected B. nasutus were found, the possibility remains that they may be transmitting S. haematobium during other years when the

Table 8.4 The onset of heterophyid shedding in box-kept snails by month. (Nguni dam, 1981.)

Assuming a pre-patent period of at least five weeks, it was possible, by successive testing of box-snails monthly, to identify the month during which snails began to shed cercariae.

Month (1981)	No. starting to shed	Average no. available to start shedding	%
*July	0	52	0
August	11	148	7.4
September	5	190	2.6
October	6	167	3.6
November	2	173	1.2
December	1	149	0.7

*No box-kept snails were older than two months during July (because the first boxes were put in at the beginning of June, so the opportunity to start shedding per snail was perhaps not as high as for subsequent months.

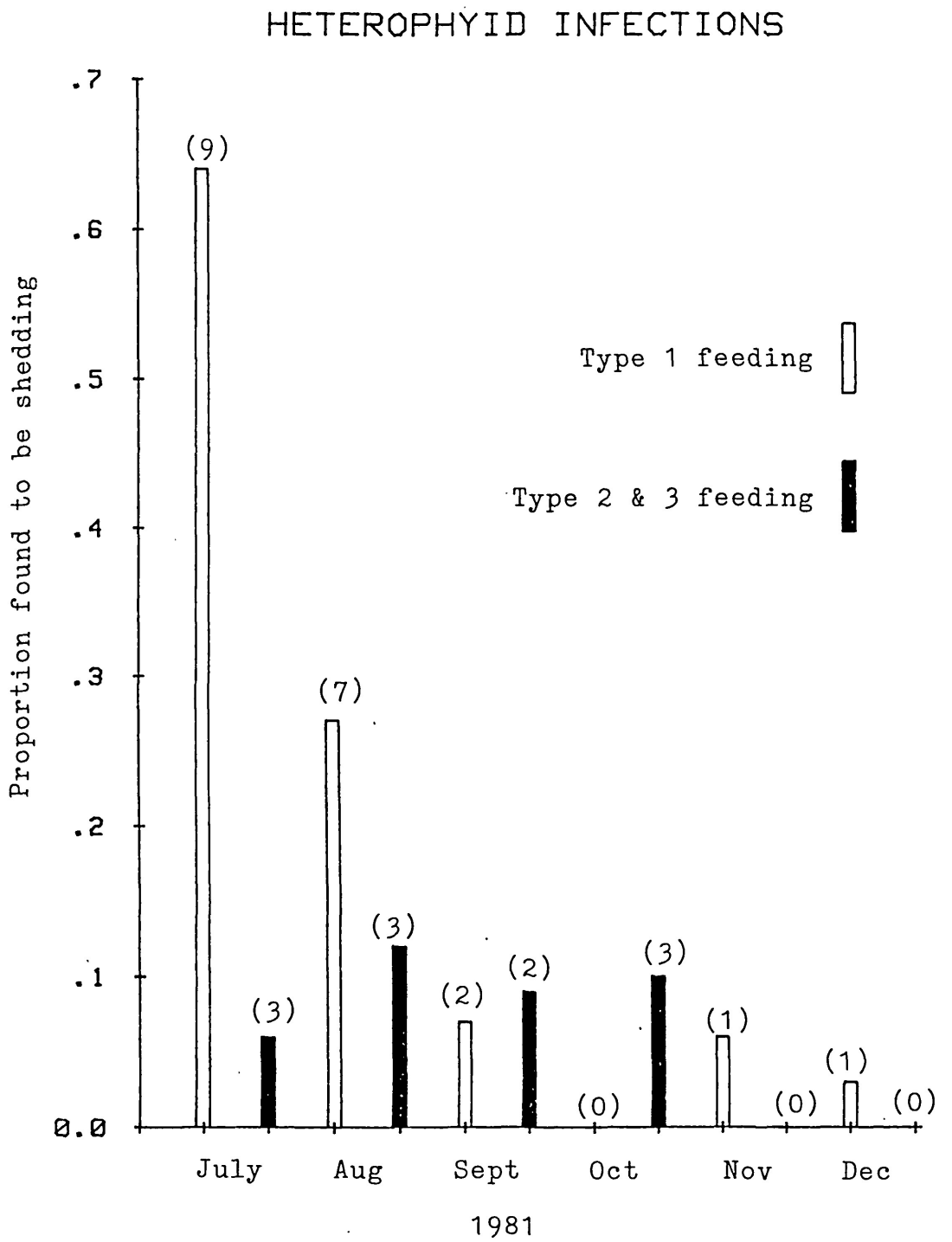


Fig. 8.2 Proportions of B. globosus in boxes shedding heterophyid cercariae. Nguni dam 1981/82. Showing the difference between different feeding regimes, and the diminution of the force of infection throughout the year.

(Numbers of snails shedding are shown in brackets.)

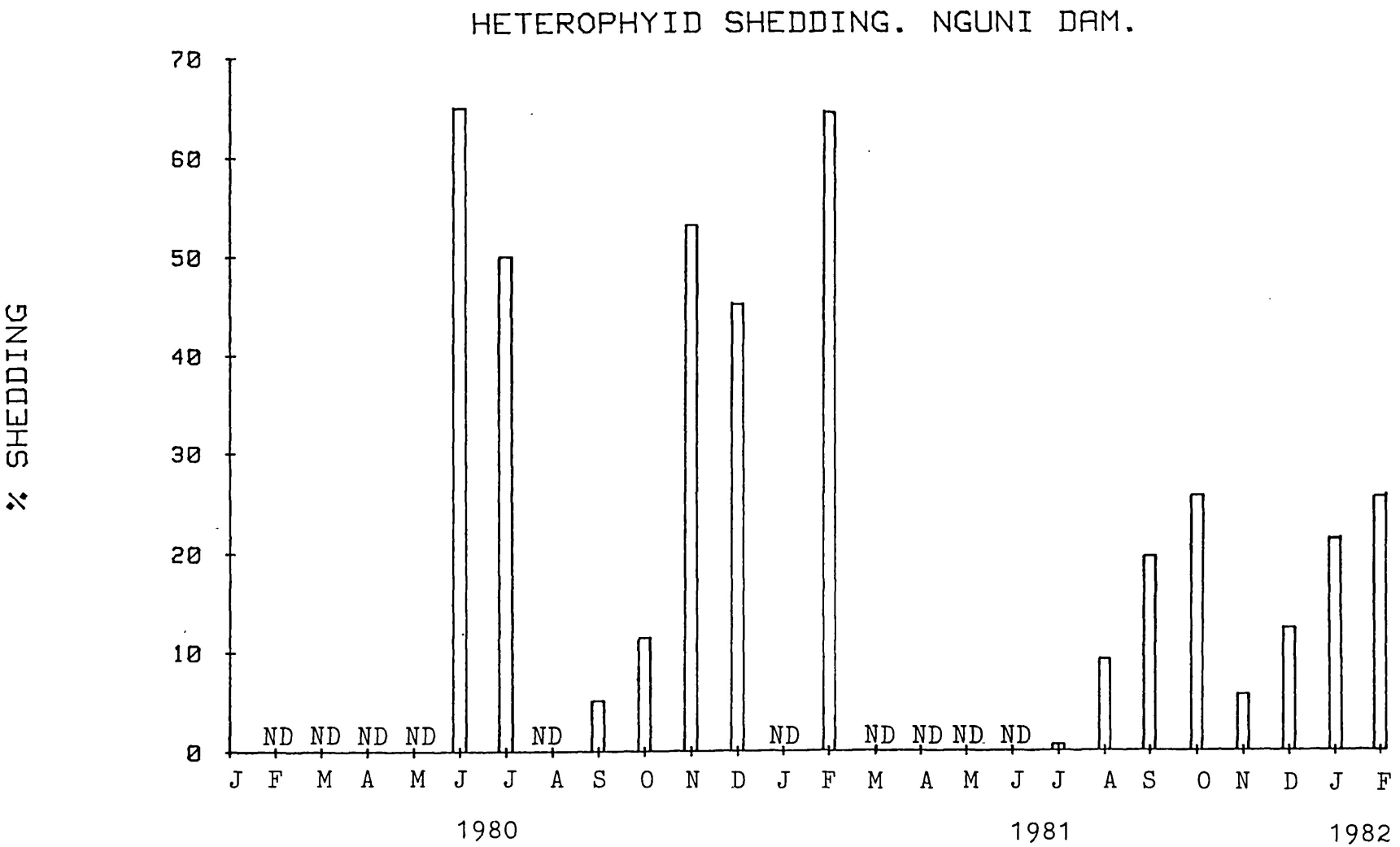


Fig. 8.3 Proportions of snails showing mature heterophyid infections by month. (ND indicates no snails tested.)

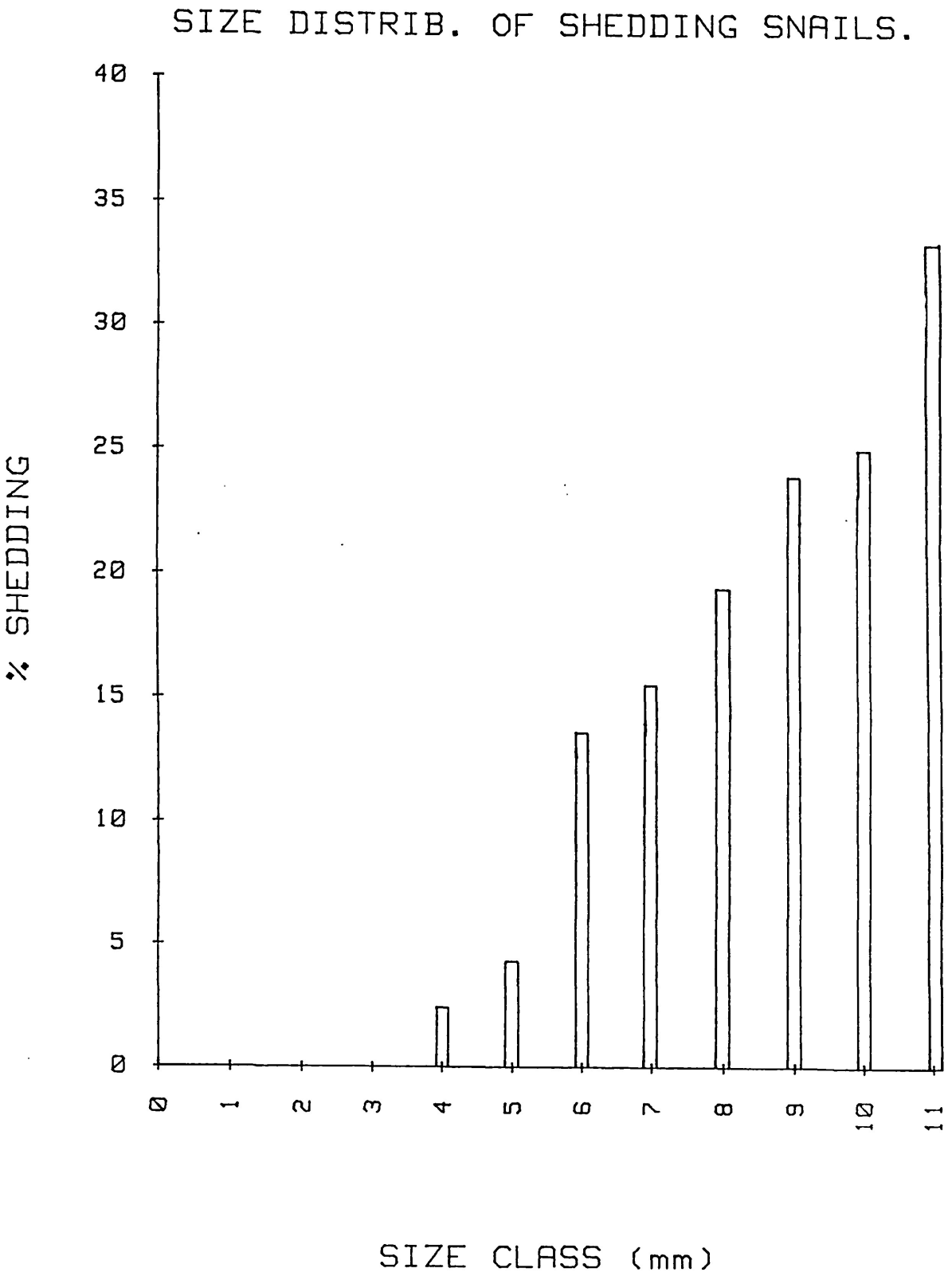


Fig. 8.4 Size-specific prevalence of heterophyid shedding B. globosus in Nguni dam during 1981/82.

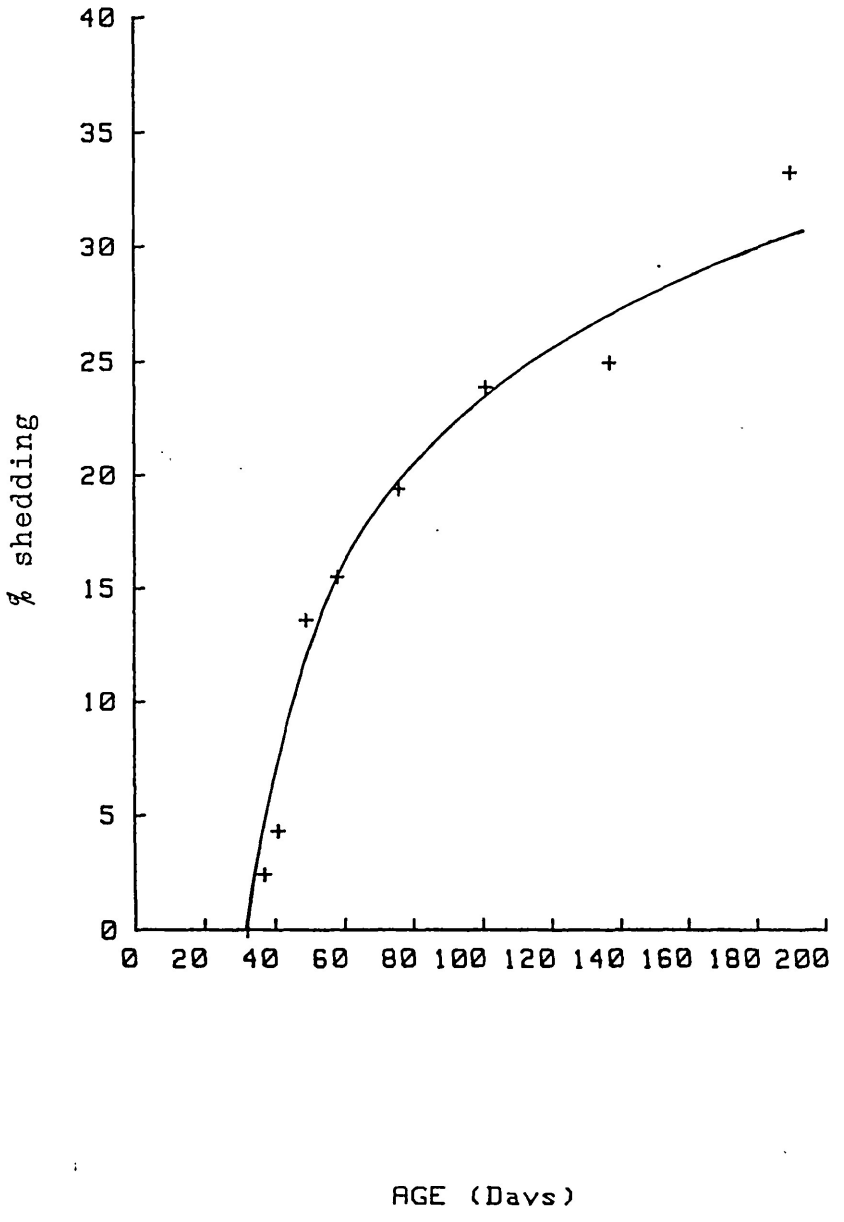


Fig. 8.5 Data from Fig. 8.4 transformed to show prevalence of heterophyid shedding snails by age. (Curve fitted by eye.)

pattern of filling and drying in temporary habitats is different. (Temporary habitats were dry during December 1980 and January 1981, when the majority of infected B. globosus were found.)

The synchronous appearance of patent infections in a number of places (spread over 25km) indicates a gross environmental influence. Many workers have recorded the highest patent infection prevalence during times of greatest population density (Webbe, 1962a, 1962b; Hira and Muller, 1966; Appleton, 1974), but there are instances of an inverse relationship between snail density and infections (e.g. Berrie, 1964; Onambiro, 1972). Webbe and Msangi (1958) and Sturrock (1973a) found a correlation between numbers of old snails and levels of infection.

During this project, infected snails appeared around three to four months after the major population peak in September 1980 (which was discernible in all water bodies sampled regularly). This would imply that snails which subsequently achieved patent infections were hatching during the time of maximum snail density. The proportions of old snails (>7mm shell-length) in Benes and Nguni dam during December/ January were considerably higher than the average for the whole year. (12.3% as opposed to 5.5% for Benes dam, and 79% as opposed to 46% for Nguni dam.)

Because infections appeared at different water bodies it is unlikely that any pattern of human behaviour is responsible

for the temporal distribution of infected snails. No obvious changes in water contact patterns were observed throughout the year, although people from further afield may have used the dams during the dry season (December to March). This would not explain the input of schistosome eggs responsible for the December/January patent infections which must have been initiated prior to November. Anderson and May (1979) concluded that environmental fluctuations affecting the duration of the latent period and snail mortality were more likely to determine infection prevalence in snails than changes in input of infective stages into snail habitats. Having said this, one of the effects of the field work in Benes dam was undoubtedly to reduce the total input of eggs to the dam through an increased awareness of the disease in the local population. (e.g. initial talks explaining the purpose of the fieldwork resulted in an unsolicited ban on children bathing in the dam.) If the input of infective stages was constant throughout the year, the extremely seasonal nature of mature infections in B. globosus can only be interpreted in terms of the changes in snail populations. The absence of infections during most of the year argues that the snail populations are not capable of maintaining year round transmission. Theory predicts that there will be a critical snail density below which transmission cannot be maintained (Anderson and May, 1979). This threshold density level is obviously affected by the longevity of the snails, and other factors (such as food) which affect the probability

of a snail achieving a mature infection. In view of the relatively low survival, reproduction and growth rates of B. globosus in Benes dam, it seems likely that they are existing at a level not far above the critical threshold for transmission. This has important implications for the level of control necessary to break the transmission cycle (discussed in Chapter 10).

Low levels of observed prevalence within snail populations are the rule in field investigations, and caused problems in early models of transmission dynamics which predicted much higher rates (Anderson and May, 1979). These authors suggested that high levels of infected snail mortality and the duration of the latent period may account for this anomaly. Sturrock et al (1979) and Barbour (1982) have also pointed out that the spatial heterogeneity of snails and transmission sites will also tend to dilute the final prevalence figure which may well hide much higher local levels. (e.g. Webbe, 1962a, found up to 50% of snails infected in individual colonies). Taking temporal as well as spatial heterogeneity into account, patent infections in Benes dam at individual sites for individual samples reached 11.8%, and the overall prevalence for December 1980 and January 1981 in all sites where infections were found was 2.4%.

Anderson and May (1978) have pointed out the inverse relationship between the pathogenicity of parasites and

their prevalence in host populations. On this basis it is not surprising to find that mature heterophyid infections were extremely common, since infected snails from boxes survived as well as uninfected snails. They do, however, have a profound effect on the reproductive capacity of their snail hosts. During 1981/82 in Nguni dam there was an almost perfect inverse correlation between mean reproductive performance and the level of mature infections (see Fig.8.6). The same relationship does not hold for the very much higher infection levels in Nguni dam during 1980/81. As Fig. 6.7 shows, there is a strong density dependent element to reproductive performance, and this may well have been the limiting factor during 1980/81, when snail densities were very high, while infection levels seem to have dictated reproductive levels in the less dense population during 1981/82. Cridland (1957a, 1957b), Sturrock and Webbe (1971), and Anderson and May (1978, 1979) have all commented on the likely role of parasites in constraining host population growth. In this case the constraint was in terms of reproduction rather than mortality, and probably did not greatly influence the ultimate population density, since gross reproductive peaks do not appear to lead inevitably to increases in total population (see Fig. 2.8).

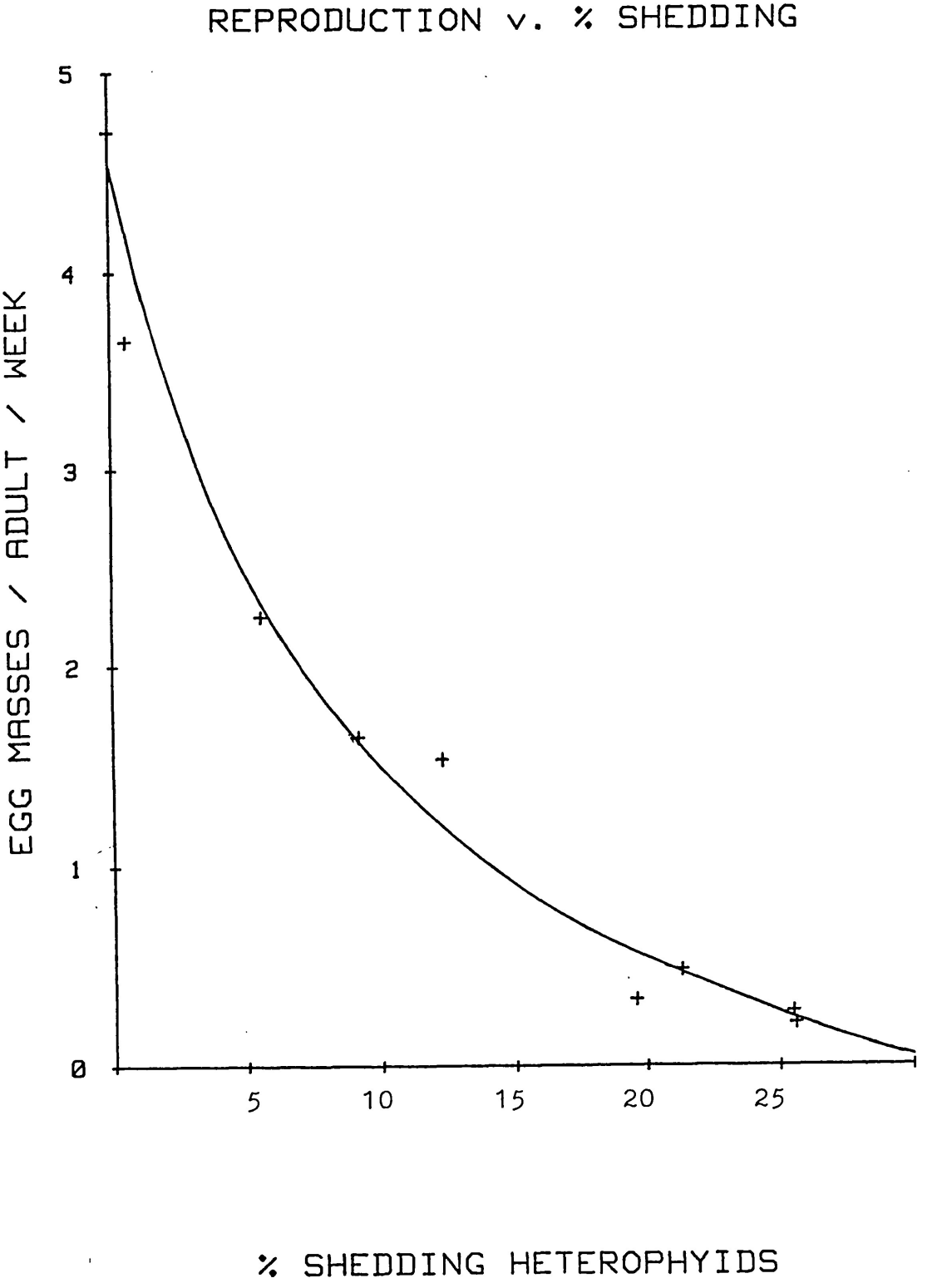
Fig. 8.6 The relationship between mature heterophyid infections and reproduction.

$$E = e^{-0.075H} + 4.51 \quad r^2 = 97\%$$

Where E = Monthly mean egg masses/adult /week.

and H = % of all snails >3mm tested that were found to be shedding heterophyid cercariae.

(Data from Nguni dam 1981/82.)


REPRODUCTION v. % SHEDDING
EGG MASSES / ADULT / WEEK
0
1
2
3
4
5
5
10
15
20
25
% SHEDDING HETEROPHYIDS

CHAPTER 9 THE ENVIRONMENT

9.1. Introduction

This chapter deals with the external influences that affect the populations of Bulinus globosus living in Benes and Nguni dams. Population density is unavoidably included in these environmental influences, although the aim is to disentangle density effects from those of extrinsic variables, rather than to consider them in their own right. Physical and chemical aspects of the environment are the primary concern. These can operate either to determine the distribution of a species, or to regulate the various population processes in a habitat.

Schutte and Frank (1964), Appleton (1978) and Thomas and Tait (1978) among others, have failed to find any simple correlation between water chemistry and the distribution of molluscs. However, many relationships between single factors and aspects of snail biology have been established. Shiff (1964), Demian and Kamel (1972), and Appleton (1977) conclude that temperature is a major factor limiting fecundity. Thomas, Goldsworthy and Aram (1975) found that growth rates in laboratory-kept Biomphalaria glabrata are strongly correlated with decrements in calcium and conductivity values. Webbe and Msangi (1958) and McCullough (1962) conclude that rainfall and temperature are the dominant influences on population trends. At the local level, Appleton has

established both current velocity (Appleton, 1976) and bedrock hardness (Appleton, 1975; Appleton and Stiles, 1976) as the limiting factors in mollusc distribution. Malek (1958), Schutte and Frank (1964), Appleton (1978) and Brown (1980) all provide extensive reviews of suggested and established environmental effects on aquatic snails.

Much of the difficulty in delimiting the effects of individual environmental aspects on snails is that many variables are interrelated. In addition, some factors (such as temperature and rainfall) may have two or more opposing effects. Low temperatures inhibit breeding by B. globosus in temperate regions (Shiff, 1964) but high temperatures in tropical climates also lower fecundity. Rainfall may stimulate breeding but at the same time may catastrophically reduce numbers of adult snails by sweeping them away in floods. This leads to population peaks at different times of the year (depending on the type of water body) which are principally affected by rainfall. In permanent streams, populations are often maximum during the late dry season because they are cut back by flooding during the rains (e.g. Appleton, 1974). In permanent ponds populations tend to be most dense during the early dry season after the rains provide a boost to reproduction (e.g. Hira and Muller, 1966). In temporary ponds the highest numbers are usually found late in the rainy season or in the early dry season before the water disappears (e.g. Webbe, 1962a; Hira and Muller, 1966). Since individual variables can have such diverse effects, the task of disentangling multivariate effects is

unlikely to be easy. Difficulties are further compounded by the broad ecological tolerance shown by schistosome host snails (described as "decidedly euryok" by Hubendick, 1958).

Perhaps the most useful contributions to date have been made by the type of laboratory-based studies mentioned in previous chapters which have used estimates of r_m in different conditions to establish the optimum level of a variable for a particular species and the relative effects of different levels. Using this method 25°C water temperature has been established as optimum for both B. globosus (Shiff, 1964) and Biomphalaria pfeifferi (Harrison and Shiff, 1966); calcium levels of 5 - 40mg/litre and bicarbonate levels of 20 - 200 mg/litre for B. globosus and Biomphalaria pfeifferi (Harrison and Shiff, 1966; Williams, 1970; Harrison et al, 1970), and total dissolved salts measuring 300 to 400 µmhos for B. pfeifferi (Jennings et al, 1973). These studies also indicate that, although the optimum requirements of both species tend to be very similar, B. globosus has a wider tolerance than B. pfeifferi and this may well explain its wider distribution (i.e. the absence of Biomphalaria from coastal East Africa). This supports Jordan and Webbe's (1969) opinion that the ecological requirements of bilharzia host snails are qualitatively similar but quantitatively different.

Malek (1958) listed the following factors as being principally responsible for conditioning the habitat of aquatic snails:

food, aquatic weeds, O_2 content, sunlight, current, type of substrate, ionic composition of the water, and predators and parasites. During this investigation, the O_2 content, pH and total conductivity of the water were measured weekly in two different places in each dam. During 1981/82 monthly water samples were taken from Nguni dam and these were subsequently analysed for nitrogen (as a measure of the fertility of the water) and calcium, which is of outstanding importance as a resource for molluscs because it is a major constituent of the shell (Brown, 1980). Food, aquatic weeds, substrate, predators and parasites have all been discussed in previous chapters.

9.2. Results

9.2.1. Chemical constituents of the water

Total chemical analyses of water from Benes dam were available for 1978 and 1979 from other sources (see Section 3.9.1.) and the results are given in Table 9.1. Not surprisingly, levels of phosphate and nitrates are very low and are probably the limiting nutrients for phytoplankton growth in the dams. Calcium and bicarbonate levels indicate a classification of soft water according to Schutte and Frank's (1964) criteria, but certainly not at limiting values for aquatic snails in Africa, which occur at concentrations below 1ppm (Brown, 1980). The sodium/calcium ratio in Benes dam (2.2 in 1979, 1.2 in 1978) is also within the limits which Schutte and Frank (1964) and Malek (1958)

Table 9.1 Chemical constituents of Benes dam water from samples taken during 1978 and 1979.

(Quantities are given as parts per million).

	1978 (August)	1979 (December)
Chloride	42.9	88.8
Nitrate	0.2	Not done
Sulphate	11.1	10.0
Total hardness (as $CaCO_3$)	64.7	Not done
Total alkalinity (as $CaCO_3$)	75.4	Not done
Calcium	24.6	26.4
Sodium	29.7	57.5
Potassium	3.6	2.7
Magnesium	0	24.0
Phosphate	0.1	Not done
Bicarbonates	Not done	120.0
pH	Not done	7.1
Conductivity ($\mu mhos/cm^2$)	Not done	400.0

have described. The absence of magnesium in the 1978 sample is difficult to explain, since the 1979 reading (24ppm) is quite high. Malek (1958) indicates that small quantities of magnesium are necessary for aquatic snails, so the 1978 measure must either have reflected a temporary absence or an incorrect analysis.

Calcium and nitrogen concentrations from Nguni dam during 1981/82 are shown in Table 9.2. On three occasions (January and June 1981, and February 1982), two water samples were taken within a short time interval. The variation in the nitrogen levels (an order of magnitude for the June samples, one day apart) precludes any detailed trend analysis, but levels remained low throughout the year. Calcium measures are more reliable and show a close correlation with total conductivity levels ($r = 0.79$) from June 1981 to February 1982, indicating that the other major ions are fluctuating in a similar manner. This relationship may not hold for the higher conductivities during 1980/81 since the low calcium reading for January 1981 (17ppm) corresponds to a relatively high conductivity level (470 µmhos).

9.2.2. Total dissolved salts

T.D.S. is a convenient measure of the salinity of water since it can be rapidly measured as electrical conductivity. It should be interpreted cautiously since it is only a

Table 9.2 Nitrogen (as nitrate) and calcium concentrations in Nguni dam during 1981/82.

Date		N (ppm)	Ca (ppm)
1981	January 29	0.92 0.47	17 17
	June 28	0.61	24
	June 29	0.06	20
	July 30	0.12	22
	August 20	0.10	27
	September 15	0.44	16
	October 16	0.39	17
	November 17	0.07	9
	December 14	0.03	20
1982	January 12	0.06	23
	February 8	0.41	22
	February 15	0.40	21

reflection of the changing levels of dominant ions, and is unaffected by changes in such minor constituents as phosphates and nitrates, which are usually of more importance (as limiting nutrients) to the ecology of a water body. Fig. 9.1 shows monthly mean fluctuations in T.D.S. throughout the project in Benes and Nguni dams. Very high levels accumulated in Nguni dam during the dry season as water evaporated, and the dramatic drop in concentration during April 1980 was caused by heavy rain which flooded Nguni dam. Overall, conductivity was significantly negatively correlated with rainfall ($r = -0.67$) in Nguni dam but not in Benes dam, where levels were generally very stable around 500 μmhos. In both dams, conductivity was significantly inversely correlated with water depth ($r = -0.76$ in Nguni dam, and $r = -0.58$ in Benes dam).

9.2.3. pH and oxygen

Figs. 9.2 and 9.3 shows pH and oxygen levels in both dams throughout 1980. Oxygen levels are very high throughout the year in both dams. The pH of Nguni dam water dropped sharply when the dam level rose in April and August, but within limits (6.5 to 8.5) which would not indicate necessarily adverse conditions for snails.

9.2.4. Water temperature

Spot temperature readings indicated no more than $0.5^{o}C$ difference in water temperature from the surface to a depth

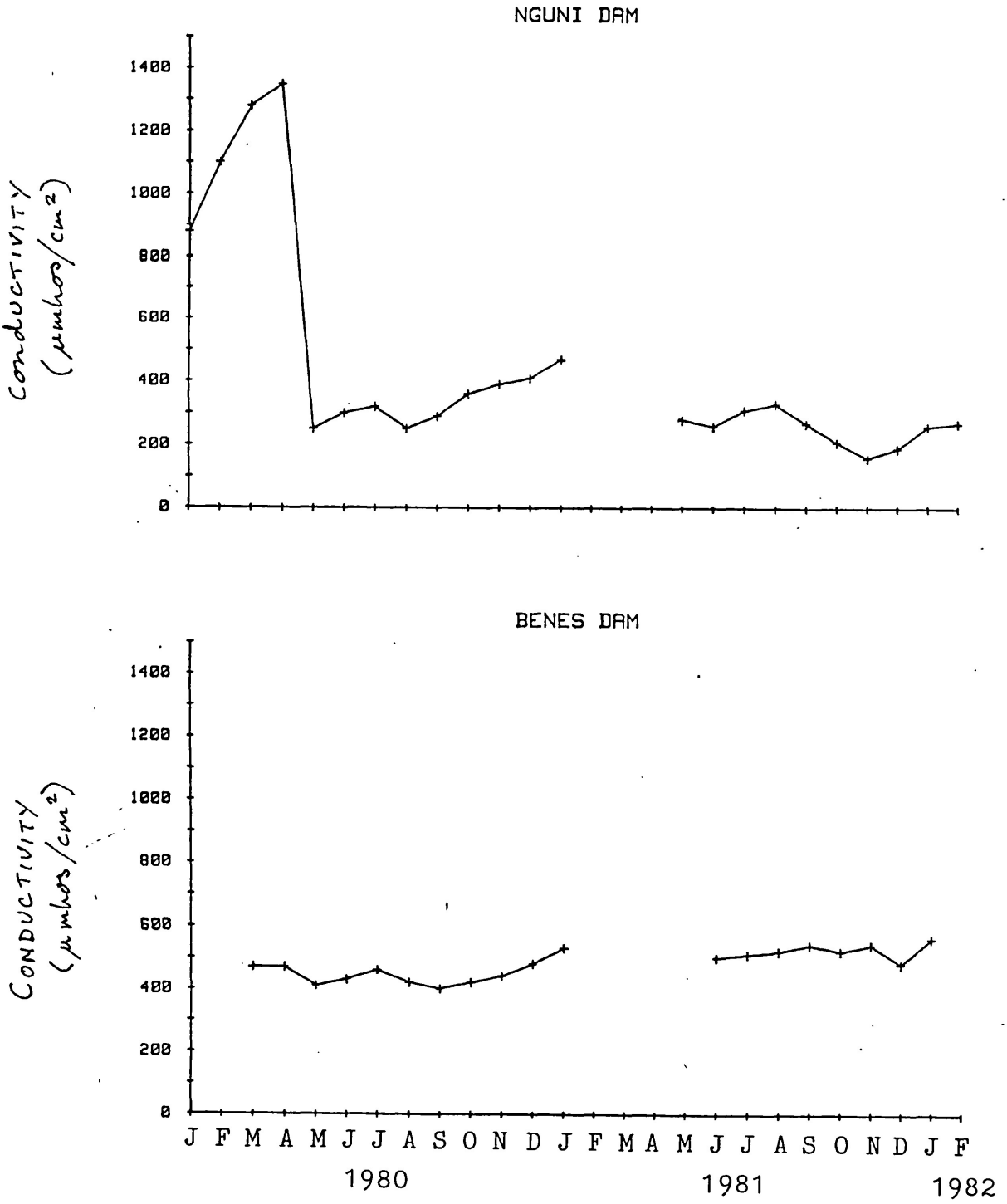


Fig. 9.1 Monthly mean total dissolved salts in the water (measured by electrical conductivity in µmhos).

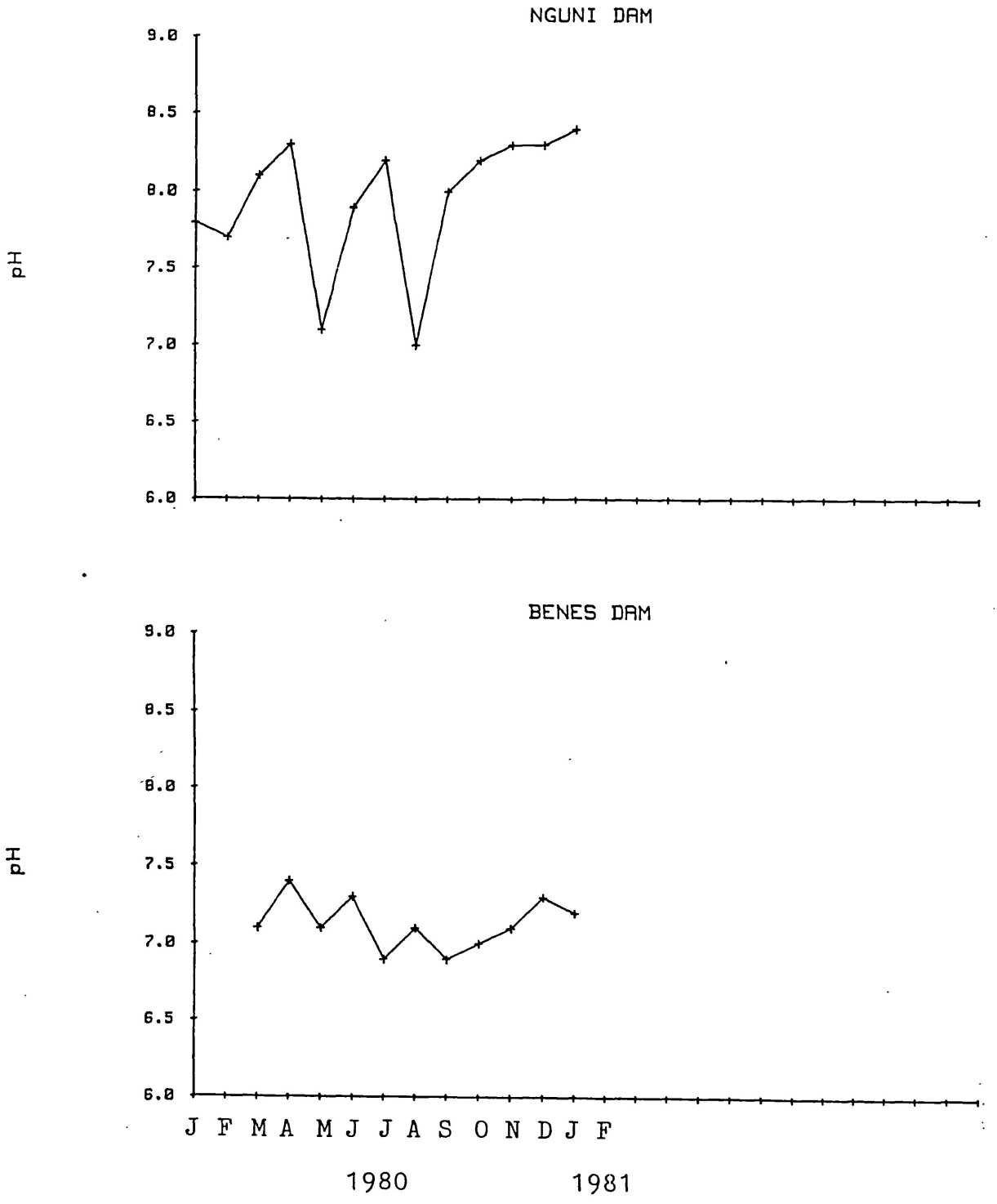


Fig. 9.2 Monthly mean pH fluctuations during 1980/81.

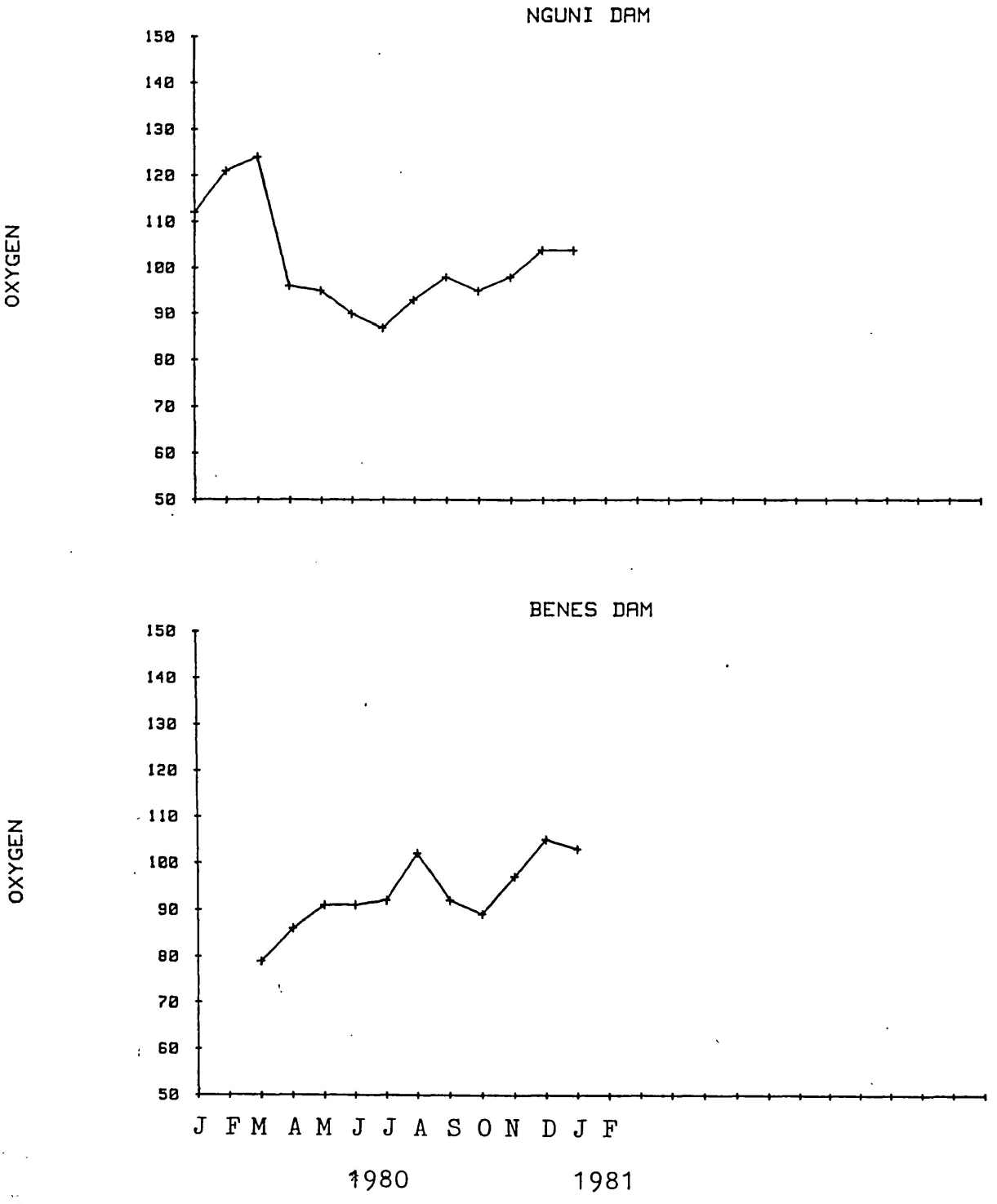


Fig. 9.3 Monthly mean % oxygen saturation in the water during 1980/81.

of one metre. Readings were therefore taken at between 10 and 20cm below the surface. Daily temperatures were maximum at 3.00p.m. and minimum at 6.00a.m. There was no obvious difference in snail distributions throughout the day in terms of depth or preference for shade, but rigorous tests for these effects were not done.

Fig. 9.4 shows temperature fluctuations for both dams during 1980/81 and for Nguni dam during 1981/82. (Patterns were the same for both dams.) Except during the coolest months, temperatures are always above the 25° optimum.

9.2.5. Rainfall

The general rainfall pattern for the Kenya coast (described in Chapter 2) is for two rainy seasons, a major one from April to June, and a lesser, and very variable season in October, November or December. Rainfall for 1980 and 1981/82 is shown in Fig. 9.5. 1980 was a year of quite low rainfall (878mm as opposed to a mean for 1964 to 1979 of 1279 $\pm$ 171mm at Nguni dam). The rainfall distribution was also unusual, with the highest monthly rainfall in August (222mm compared to a mean of 62.5 $\pm$ 17mm). It appears (see Fig. 2.8) that this rainfall was at least indirectly responsible for the very rapid population increase observed in both dams during August and September. Rainfall during 1981 (1139mm at Nguni dam) was very typical except that the long rains started earlier than usual, with very high rainfall in March. It seems likely therefore, that snail population sizes in

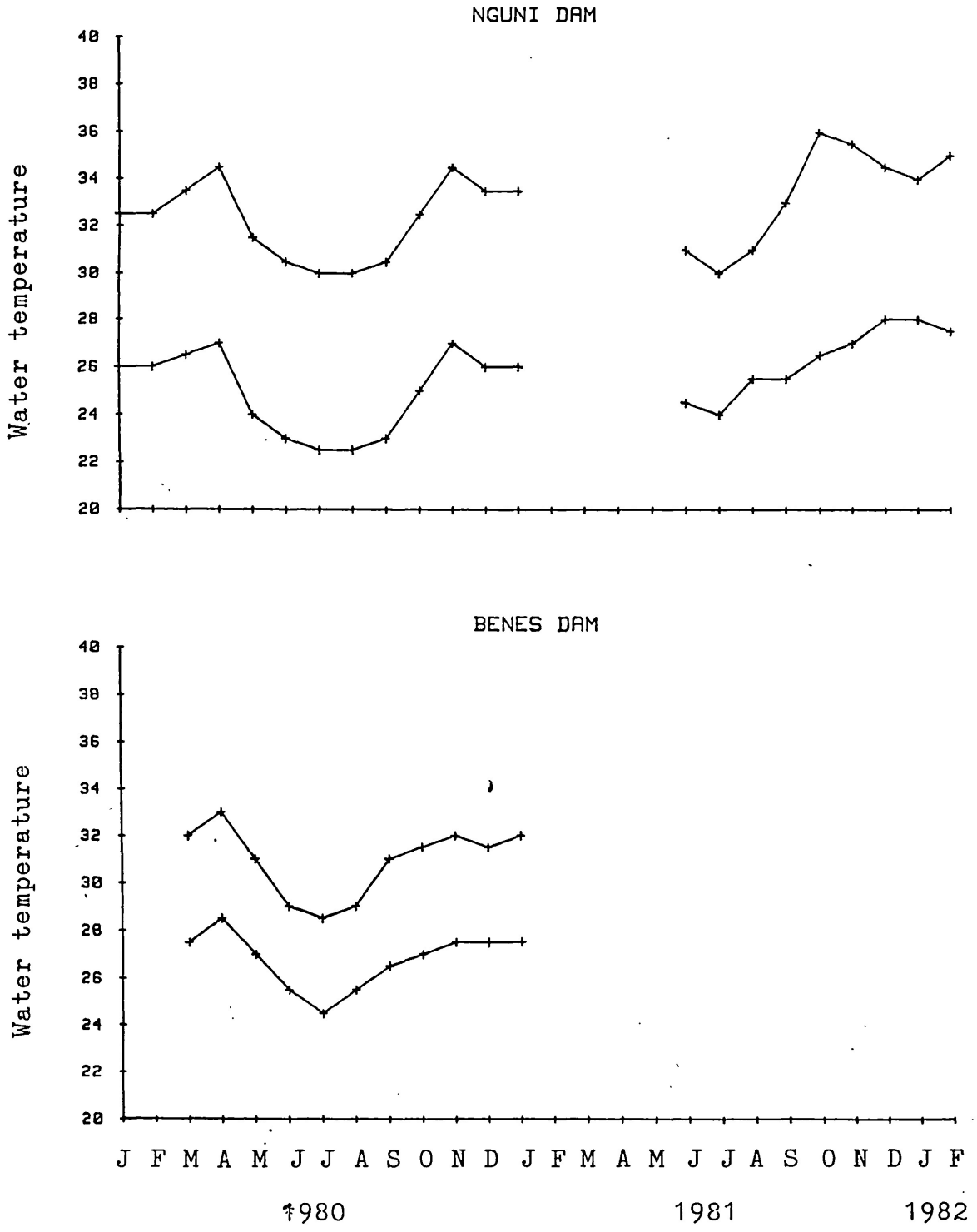


Fig. 9.4 Monthly mean maximum and minimum water temperatures (°C).

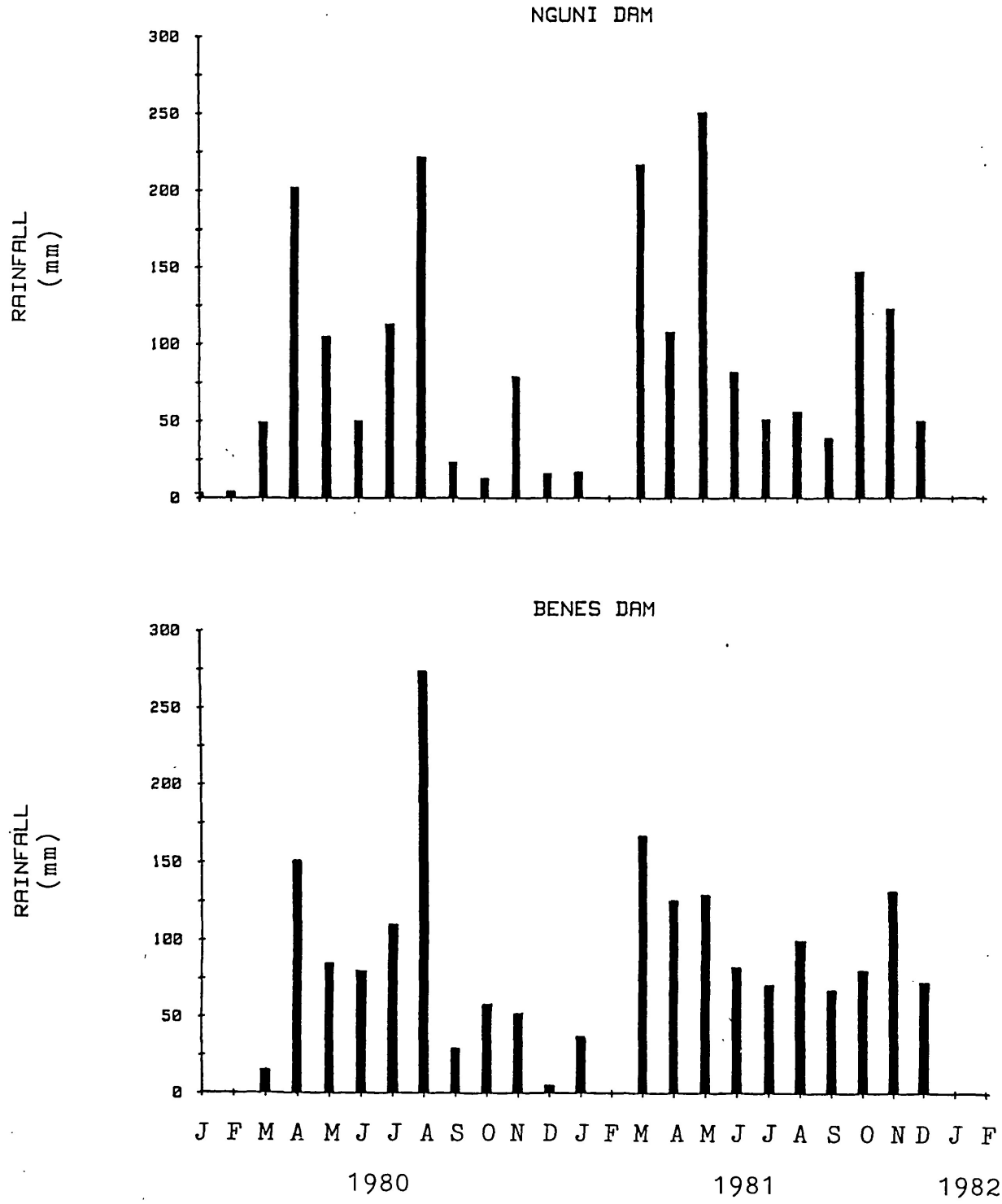


Fig. 9.5 Monthly rainfall measured at two stations 5 and 4km from Nguni and Benes dams respectively.

1981 were more typical than those in 1980. Further data from other years would be needed to substantiate this. The fluctuation in water level in the dams is shown in Fig. 9.6. Benes dam overflowed at a depth-pole reading of 140cm, while Nguni dam did so at 155cm.

9.2.6. Relationship between environmental variables and snail population parameters

Multiple linear regressions were used to examine the relationships between the intrinsic rate of natural increase (r_m) and the following variables:

Mean water temperature	Oxygen
Conductivity	pH
Snail density	Water depth
Rainfall	

Table 9.3 shows the significant autocorrelations between variables in Benes and Nguni dams. It is interesting to note that rainfall is not correlated with water depth (although rainfall is obviously responsible for the depth in the dam), because the water level remains high for some time after the rains. Some correlations obviously arose by chance; temperature and water depth are inversely correlated in Nguni dam and positively correlated in Benes dam. In general, there seems to be a group of variables (pH, oxygen and T.D.S.) which are related to water temperature and therefore interrelated. Apparent correlations of T.D.S. (in Nguni dam) and rainfall, pH and oxygen level

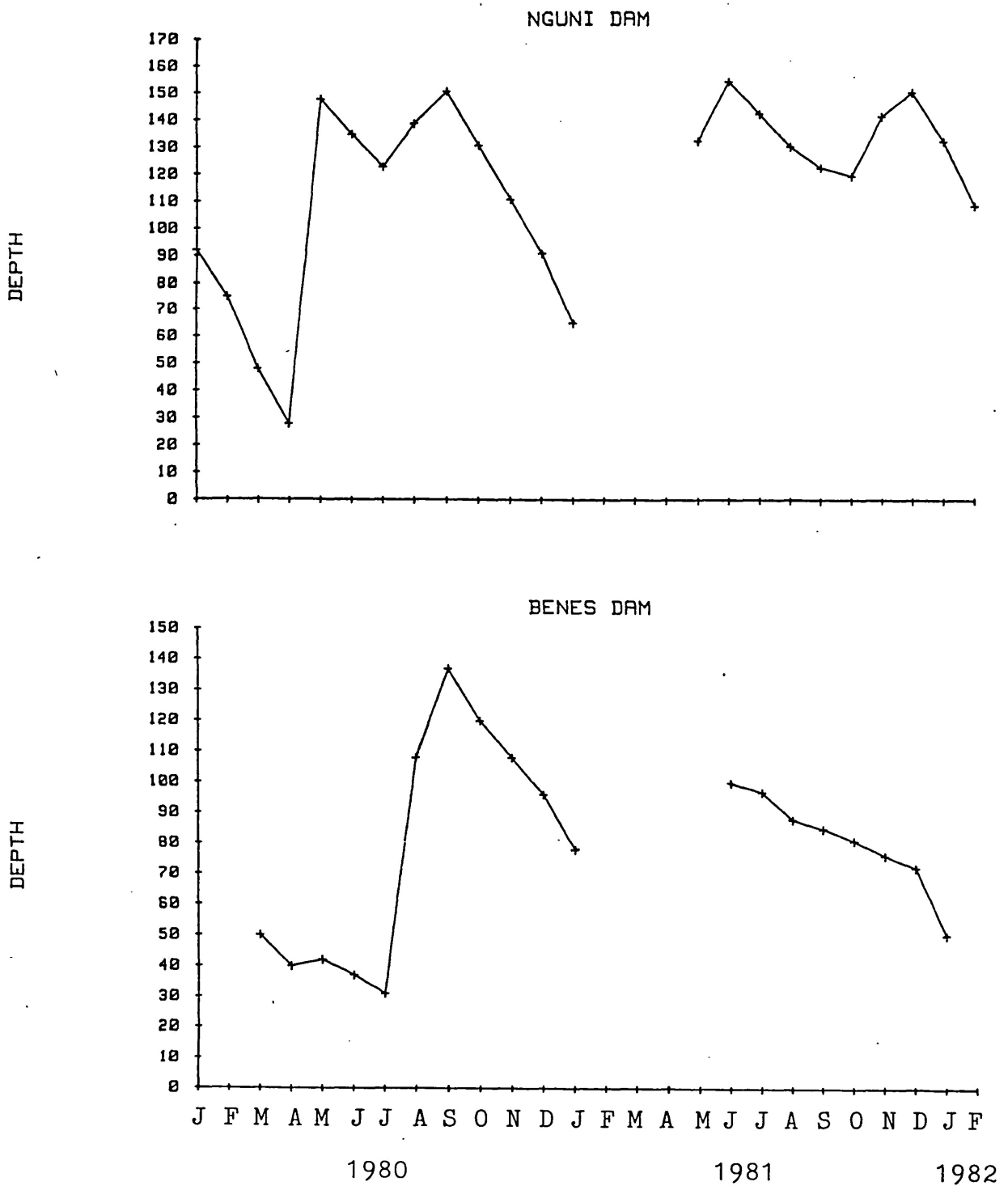


Fig. 9.6 Fluctuations in water levels measured in cm at arbitrary depth poles.

Table 9.3. Autocorrelations between environmental variables. Correlation coefficients significant at $P < 0.05$ for individual dams are given.

✓ indicates a significant correlation coefficient when data from both dams was tested.

NGUNI DAM

	Temperature	T.D.S.	Snail density	Rainfall	Depth	pH	Oxygen
Temperature		0.76 ✓		✓	-0.70		✓
T.D.S.	✓		0.55	-0.67	-0.76 ✓	0.79	✓
Snail density						✓	
Rainfall	✓		-0.66				
Depth	0.61	-0.58 ✓					
pH	0.55	0.63	0.71 ✓				
Oxygen	✓	0.61 ✓	-0.51			0.89	

BENES DAM

(in Benes dam) with snail density are not considered to be important because of the inevitable time lag between the environmental changes and the population changes for which they are responsible.

Values for r_m were measured over 20 weeks of cohorts' lifespans and are therefore a reflection of average environmental conditions over this time. However, r_m is very strongly influenced by the initial reproduction of the cohort and it was therefore decided to examine environmental measures at two and three months after cohorts' hatch dates, against their intrinsic rates of increase. Comparing results for two months after hatch ($r^2 = 0.52$) with those for three months after hatch ($r^2 = 0.77$) showed much higher correlations with the latter values which have therefore been used in the rest of this section.

Table 9.4 presents the significant correlation coefficients from a series of multiple regressions using data from Nguni dam during 1980/81 and 1981/82, and Benes dam during 1981/82. Oxygen and pH measures were discontinued after 1980/81 and nitrogen and calcium levels were only analysed for Nguni dam during 1981/82. So the choice of variables and the number of observations are limited by the available data.

No significant relationship was found for calcium or nitrogen levels with r_m. Snail density was used as a dependent variable in order to disentangle intrinsic and external influences. Temperature is obviously the major factor

Table 9.4 The results of multiple linear regressions and correlations on r_m of cohorts with environmental variables three months after the cohort hatched.

Dam	Year	Variables	Correlation (r^2) (significant at $P < 0.05$)	N
Nguni	1980	1,2,3	0.980	7
"	"	1,2,3,4	0.991	7
"	"	1,2,3,4,5	0.999	7
Benes	1980	1,2,3	0.947	7
"	"	1,2,3,4	0.987	7
"	"	1,2,3,4,5	0.999	7
Nguni	1980/81	1,2,3	0.871	12
Nguni & Benes	1980	1,2,3,4,6,7	0.853	14
"	"	1,2,3,4,5,6,7	0.870	14
Nguni & Benes	1980/81	1	0.671	19
"	"	1,2,3	0.767	19
"	"	1,2,3,4	0.768	19

Variables:

1 Water temperature
2 T.D.S.
3 Snail density
4 Rainfall
5 Oxygen
6 pH
7 Dam depth

ultimately determining the capacity to increase of the snails. Table 9.5 shows that water temperature and r_m were significantly inversely correlated in both dams and during both years of the project. A single variable linear regression of r_m and water temperature three months after hatching gives a correlation r of -0.819 (see Fig. 9.7). The only other variable which gave a significant partial correlation was snail density in Benes dam, which was inversely correlated with r_m ($r = -0.870$). However, the addition of extra variables makes little contribution to the explanatory power of the r_m to temperature relationship.

9.3. Discussion

The failure to find simple relationships with most aspects of the environment is not surprising in view of the points made in the introduction to this chapter. Measures of pH, oxygen, calcium and nitrogen in the water failed to add significantly to the explanation of snail population changes in the dams. However, they did show that all these variables stayed within values that were unlikely to place any limitations on the physiology of Bulinus globosus. Oxygen levels have to be very low to affect bulinids which are able to survive for long periods in anoxic conditions (Alberts, 1966). The measures of pH alone do not adequately explain the distribution of freshwater organisms (Macan, 1974), but values around or slightly above neutrality are not indicative of adverse conditions. Conductivity reached levels in Nguni dam which may have been disadvantageous to snails,

Table 9.5 Significant (at P <0.05) partial correlation coefficients between values for r_m and environmental measures three months after the cohort hatch date.

Dam	N	Variable	Correlation (r)
Nguni & Benes (2 year)	19	Temperature	-0.82
Nguni & Benes (1980)	14	"	-0.90
Nguni (1980)	7	"	-0.98
Nguni (2 year)	12	"	-0.88
Benes (1980)	7	"	-0.719
Benes (1980)	7	Density	-0.870

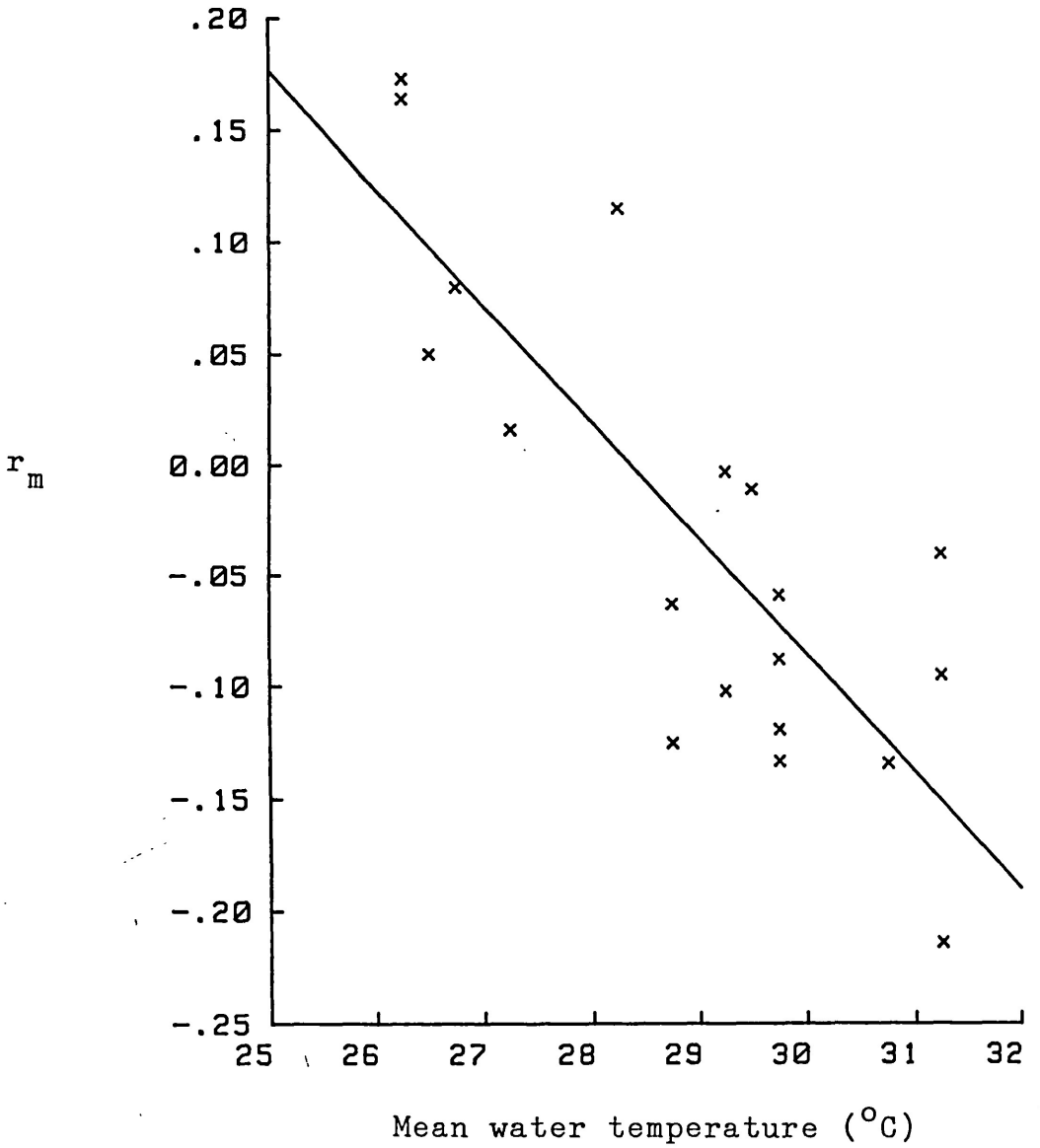


Fig. 9.7 The relationship of r_m to mean water temperature at a cohort age of three months.

$r_m = -0.052 \times \text{temperature} + 1.49$

correlation $r = -0.819$

$r^2 = 0.671$

(Data from Nguni and Benes dams 1980/81/82.)

but these conditions occurred during hot, dry months when snail populations were extremely low and were immediately diluted when the rains arrived in April 1980. The relative effects of these two variables on the snails are therefore difficult to disentangle because they are themselves interrelated.

The surprise is that a relatively simple linear relationship with water temperature should explain so much of the snails' potential for increase. This relationship, which holds across two different water bodies during one year, and for two different years in one water body, seems to have considerable predictive potential. Fig. 9.7 indicates that there was no possibility of population increases ($r_m < 0$) during months when the mean water temperature was above 28.5°C. The relationship is not simply explicable in terms of reproduction (as has been suggested by Malek, 1958, and others), since reproductive peaks occurred during hot as well as cool months (see Fig. 2.8), and reproductive performance is also strongly density dependent (see Chapter 7).

Other relationships are obvious but less easily quantifiable. The major population and/or reproductive peaks followed heavy rainfall and the flooding of the dams. It seems likely, therefore, that whilst the potential capacity to increase may largely be governed by water temperature, the realisation of that potential and the carrying capacity of a water body may be controlled by rainfall and the complex

of variables associated with it. The unusually heavy rainfall during the cool month of August 1980 may therefore have combined to cause the spectacular population increases observed in Benes and Nguni dams. The normal pattern of low rainfall during the coolest months in 1981 led to much more stable populations. Hairston (1973) reviewing previous studies on schistosome host snails, suggested the general conclusion that responsibility for population fluctuations in temperate and sub-tropical climates is usually ascribed to temperature (low temperatures controlling reproduction), whilst in tropical regions, rainfall is considered to be responsible. The results presented here indicate that high temperatures may be of fundamental importance in the control of tropical populations, as well as rainfall.

CHAPTER 10 CONCLUSIONS

10.1. The Distribution of Bulinus

Teesdale (1962) and Brown (1980) have noticed that freshwater habitats require some time to "mature" before they become suitable for colonisation by bulinid snails, although neither author has described the precise form of maturity that is necessary. The establishment of aquatic macrophytes is of considerable importance, since these form the preferred substrate for the snails.

The fourteen ponds and dams searched during this investigation lend support to this idea. Dams built during the project remained devoid of bulinids during their first year, although in some cases small numbers of snails (presumably residual populations from the marshy ground on which the dams were built), persisted for up to three months after the dams were flooded. The remaining habitats had all been in existence for over five years and all except one contained thriving populations of either Bulinus globosus or Bulinus nasutus at some time during the year. The exception (Chodari dam) contains abundant macrophytes and appears superficially to be entirely suitable for colonisation. That it has not been, may be a reflection of the poor dispersal powers of the snails, which depend on chance attachment to outside agencies (birds, animals, earthmoving equipment during the building of the dam, etc.) for transport across dry land.

10.2. The Sampling Methods

One of the major aims of the project was to develop a sampling system which could provide high resolution measurements of demographic parameters in natural populations with minimum disturbance. Relative sampling methods using plastic sheet snail traps provided a good reflection of *B. globosus* population changes throughout the year. Exhaustive sampling methods would have facilitated more accurate dispersal measurements and would have added to the usefulness of the mark-recapture programme. However, they would have severely reduced the number of samples taken and therefore the area covered. For example, the limited analysis of the data collected from Benes dam during 1981/82 is a direct consequence of the low number of samples collected. Weekly inspection of traps served to increase the total number of samples collected, but analysis of monthly changes is adequate for most purposes, serving to highlight general trends which may be obscured by variation between weekly samples.

Growth rate measurement is of crucial importance in the population study of animals with overlapping generations since the identification of cohorts (and therefore life table analyses) is based on the use of growth curves. Changes in mean growth rates over time were therefore of great significance, but measurement of these changes failed to explain all the variation observed, which remained considerable within monthly samples. Individual variability

in shell growth obviously limits the use of shell length as an indication of age, but this remains the only reasonable indicator for use with large samples. In order to make the best use of separate growth curve measurements, snails in the weekly samples should have been measured to 0.1mm, since 1.0mm size classes often represent several weeks of growth, especially for the larger snails. Once again a compromise had to be made between precision and the need to obtain adequate numbers of samples.

Snail boxes provided a useful adjunct to trap samples in determining population processes. Complementary results from the two sources have allowed the identification of many of the factors which affect growth and reproduction. Mortality in boxes was not closely related to that occurring in free-living populations, but this in itself narrows down the possible causes of mortality in natural populations (see Section 10.3.1.). The identification of density effects in box-kept snails does not necessarily have any direct bearing on field populations, because of the possible effect of the boxes themselves. Comparisons between totally closed boxes (without netting) and boxes with different proportions of netting might clarify box effects as distinct from any density effects in the surrounding free population.

10.3. Bulinus globosus in Nguni and Benes Dams

Brown (1980) commented on the increase in ecological stability of freshwater habitats with size. Environmental measurements

in Benes and Nguni dams (Chapter 9) reflect this relationship. Benes dam, one of the largest freshwater bodies on the Kenya coast, displays less fluctuation in conductivity, pH and oxygen level, and even the range of daily water temperatures is smaller. As a result, the fluctuations of the B. globosus population in Benes dam are less extreme than those in Nguni dam. Although population changes throughout the year were broadly similar in both dams, reproductive levels were considerably higher in Nguni dam (see Fig. 2.8). The range of values for r_m in Nguni was greater than for Benes, due to lower overall survival (see Table 5.6) and reproduction. Individual fecundity was actually higher in Benes dam (see Table 6.6), possibly because snail density was lower, but poor adult survival reduced total egg production. Snails larger than 6mm accounted for 59% of samples in Nguni dam during 1980/81 and 49% in 1981/82. By contrast, in Benes dam they formed only 15% of snails sampled in 1980/81 and 33% in 1981/82. More comprehensive sampling of juveniles in Benes dam (see Chapter 5) undoubtedly contributed to these results, but the relative absence of large snails in Benes dam is indicative of lower survival.

10.3.1. Population regulation

Bulinus globosus was investigated in terms of those aspects of its biology which affect population changes: reproduction, growth rate and mortality. The intrinsic rate of natural increase (r_m) is a convenient statistic which summarises

these three processes, and it was used to determine the environmental factors which have the greatest influence on snail numbers. Values of r_m reflect a cohort's ability to increase in the conditions prevailing during the lifetime of the cohort. Negative values indicate an inability of the cohort to increase, but do not necessarily imply that the population must decline, since previous and subsequent cohorts whose lifetimes overlap may have very different r_m values. Similarly a positive r_m value for a cohort does not automatically imply an increasing population.

The key environmental factors determining changes in population size have been shown to be water temperature and rainfall. The capacity of populations of B. globosus to increase in both dams is substantially reduced when the mean water temperature rises above 28.5°C. The rate of increase under such conditions often becomes negative, however, even when the temperature is below this "break even point". Population growth is also determined through rainfall by its action in "conditioning" the habitat (see Chapter 9).

While climate was the ultimate variable controlling population processes, feeding and density effects were found to be the most influential interactive factors. Results from boxes showed that positive r_m values could be maintained by B. globosus cohorts in all the conditions encountered during the project (see Table 7.4 and Fig. 7.4). One of the key factors in box-kept snails was the type of

feeding. The addition of a modest amount of lily leaf was sufficient to produce significant differences in reproductive, growth and survival performance, compared to snails fed on coarse vegetation. Growth, survival and reproduction indices for box-kept snails fed on lily leaf are all higher than for natural populations. Survival rates are not strictly comparable since box-kept snails are protected from certain predators and from dispersal losses. Growth rate indices for natural populations are closest to those for box-snails fed on coarse vegetation (see Section 4.5). Egg-laying performance by free-living snails was intermediate between box-snails fed on lily leaf and those fed on coarse vegetation (see Section 6.2.6). Mean field values for r_m are as low as the lowest obtained from box-kept snails (those kept as the highest densities and fed on coarse vegetation, see Tables 7.2 and 7.4), but the artificially high survival rates in boxes affect the calculation of r_m.

Overall, field populations most closely resemble the box-kept snails which were fed on coarse vegetation, suggesting that the quality of food in both dams is usually sub-optimal and is a significant factor in population regulation. The very clear distinction between lily leaf fed snails and others in boxes supports Eisenberg's hypothesis of two-level food regulation (Eisenberg, 1966, 1970). Food quality also appears to regulate the prevalence of mature infections (see Table 8.3). The relative food value of different plants to molluscs and the physiological effects of different feeding regimes are still poorly

understood and were not investigated during this project, but are obviously of considerable importance in view of the above results. The main source of food for adult snails is reputed to be epiphytic algae (Malek, 1958), and algal growth stimulated by increased nutrients washed in by rainfall may well prove to be the link between rainfall and food in snail population regulation.

Two factors were observed to have a major effect on reproductive rates. Individual egg-laying performance was severely curtailed at high snail densities in both dams (see Fig. 6.7). At lower densities in Nguni dam, the levels of mature heterophyid infections correlate closely with reproductive performance, and in view of the sterilising effect of the infections, the correlation is very likely to be causitive. In spite of this marked effect on reproduction, heterophyids have no apparent regulatory effect on the snail populations since they neither increased mortality (see Section 5.3) nor decreased growth rates significantly (see Section 8.3), and prevalence of heterophyid infections bore no relationship to r_m values. Increased snail densities did also have significant effects on growth rates and the survival of box-kept snails, but it is difficult to be certain that these effects also occur outside the boxes. Snail density is significantly inversely correlated with the value of r_m in Benes dam (see Fig. 9.5), suggesting that density effects are important in natural populations.

10.4. Further Research

Although this project has succeeded in explaining the main factors affecting population changes, and has identified, in many cases, the aspects of the snails' life cycle on which these factors operate, the precise mechanisms involved remain elusive. Description and quantification of feeding and types of food could provide the key to many of the effects observed here. Differences in mortality rates from box-kept snails and free-living snails indicate that predation and dispersal mortality are very significant, but precise information on predators and dispersal behaviour is very scarce.

Evidence presented in Chapter 5 suggests that a free-floating dispersal phase immediately after hatching may be responsible for the undersampling of small snails reported in almost all previous studies, but confirmation is needed.

The level of mature schistosome infections found in *B. globosus* in the project area did not allow detailed analysis of differences between infected and uninfected snails. However, values for the parameters suggested by Anderson and May (1979), relating to differences between infected and uninfected snails, could be resolved using the sampling system developed here, which has provided detailed data on heterophyid infections.

10.5. Schistosomiasis Transmission

Although Warren et al (1979) have shown that very high levels of endemic transmission of Schistosoma haematobium occur in the coast province of Kenya, the indications are that transmission in the area covered by this project is relatively low (see Section 8.2).

During the course of the project Bulinus globosus were found to be shedding schistosomes in Benes dam and Junju dam at Vipingo, and at Nguni dam and Bamburi old dam at Bamburi. Since only very small numbers of B. globosus were ever found in Junju dam, and Nguni dam is used by very few people, it must be concluded that any freshwater body in the project area where B. globosus is present represents a health hazard, irrespective of the snail density and level of human water contact.

There was no evidence of the type of temporary pool transmission by B. nasutus described from Tanzania by Webbe (1962a). The possibility remains, however, that seasonal changes are responsible for preventing the development of transmission in temporary sites (i.e. ponds are dry for long periods), but that mature infections could occur during years of exceptional rainfall.

10.5.1. Snail control measures

The higher maximum intrinsic rates of natural increase, and better survival of the snails indicate that, for an equal input of schistosome eggs, Nguni dam could become a more dangerous transmission site than the main washing site at Benes dam. Fortunately, Nguni dam remains under strict supervision and should not become a serious health hazard as long as this situation is maintained.

Benes dam contains a number of essentially separate populations of B. globosus, with thick emergent vegetation screening those in different parts of the dam from one another. (Even at the main water contact area, no marked snails were found outside the trap site at which they were marked, although sites were only 5m apart). Since the dam is large, blanket molluscicide would not be practical, and even focal molluscicide would be expensive and would require repeated treatments. However, comparisons of r_m, growth rates, reproduction rates, and survival with those from other studies and with those from box-kept snails indicate that B. globosus in Benes dam (at least in the main sampling area) are far from achieving their maximum biotic potential. The relatively low prevalence of schistosome infections in both the snails and the local people may well be a reflection of this. The use of "low-key" snail control measures might therefore be sufficient to create safe (transmission-free) zones at least at the main water contact sites. The simplest method, in view of the snails' preference for vegetation as

a substrate, would be to clear the fringing reedmace, sedges and water lilies from around these sites. A longer-term solution would be to attempt to introduce a biological control agent such as Marisa cornuarietis. Although density dependent effects and the spatial heterogeneity of the dam would make severe reductions of B. globosus by means of a competitor species unlikely, the circumstances listed above indicate that a modest reduction might be sufficient to reduce or eradicate transmission. In order to test the ability of M. cornuarietis to survive in Benes dam, and to control B. globosus, displacement series experiments (de Wit, 1971) should be conducted, using the boxes developed during this project. To safeguard against possible harmful effects of introduced species, initial introductions should be contained within pens of the type described by Eisenberg (1966).

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APPENDIX A

Numbers of Bulinus globosus from weekly trap sample results, by mm size class. A = adult, J = juvenile. During 1980/81 in Nguni dam, an intermediate class A/J was recorded, (see Appendix A ii), but dissections showed that these were, in fact, juveniles.

Appendix A(i). Benes dam 1980/81. Week 1 is 13/3/80, week 51 is 27/1/81. 20 traps were searched each week.

BENES DAM 1980/81 TRAP RESULTS

WEEK	SIZE (MM)	1 J	2 J	3 J	4 J	5 A	5 J	6 A	6 J	7 A	7 J	8 A	8 J	9 A	9 J	10 A	11 A	12 A	TOTAL
1		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5		0	0	3	4	1	2	0	4	3	5	6	0	3	0	1	0	0	32
6		10	0	1	6	0	8	4	18	6	1	7	2	3	0	0	0	0	66
7		3	9	0	4	0	5	2	12	15	8	5	2	3	0	1	0	0	69
8		0	19	5	5	0	18	0	15	4	12	7	0	4	1	2	0	0	92
9		1	2	13	9	0	16	1	25	5	11	10	6	1	0	3	0	0	103
10		13	35	24	16	0	21	3	19	14	20	20	4	9	0	8	1	0	207
11		5	18	12	21	1	36	3	18	22	3	11	1	5	0	3	1	0	160
12		1	0	3	7	0	8	1	7	3	2	3	0	1	0	0	1	0	37
13		28	22	8	5	0	10	2	6	6	6	4	2	3	0	3	0	0	105
14		35	82	11	1	0	3	1	4	7	4	4	0	3	0	2	0	0	157
15		36	53	37	7	1	6	1	4	5	1	1	0	3	0	0	0	0	155
16		18	49	62	35	2	16	0	7	5	0	4	0	1	0	2	0	0	201
17		6	32	49	61	1	30	1	10	7	0	4	0	1	0	0	0	0	202
18		7	21	21	36	1	35	0	20	9	0	2	0	1	0	0	0	0	153
19		7	12	24	28	0	23	3	15	3	3	1	0	0	0	0	0	0	119
20		5	15	19	19	1	10	3	7	2	2	1	0	1	0	1	0	0	86
21		45	23	19	9	1	8	2	6	7	2	2	1	1	0	0	0	0	126
22		39	47	16	11	0	15	0	12	4	1	2	0	1	0	0	0	0	148
23		35	57	21	15	4	7	4	6	3	1	0	0	1	0	0	0	0	154
24		7	67	17	13	0	8	0	7	2	3	0	0	1	0	0	0	0	125
25		17	26	27	20	0	13	4	14	18	2	3	0	1	0	0	0	0	145
26		34	26	17	16	0	17	2	12	1	1	5	0	1	0	0	0	0	132
27		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28		1	2	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	5
29		25	6	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	34
30		27	86	28	1	0	2	0	0	0	0	0	0	1	0	1	2	1	149
31		58	89	54	52	0	31	0	13	1	5	2	0	0	0	2	5	1	313
32		38	85	107	144	0	86	0	28	2	6	0	0	0	0	0	1	0	497
33		4	33	96	166	0	191	4	80	4	5	0	0	0	0	0	0	0	583
34		2	26	63	129	0	92	2	13	1	0	1	0	0	0	0	0	0	329
35		3	10	32	54	0	61	0	18	1	4	1	0	0	0	0	0	0	184
36		3	11	25	84	1	96	1	42	3	3	0	0	1	0	0	0	0	270
37		10	15	9	19	2	93	17	82	12	9	2	0	1	0	0	0	0	270
38		49	26	18	15	1	44	4	76	17	11	3	1	0	0	0	0	0	265
39		27	63	38	32	0	33	13	77	21	26	4	0	0	0	0	0	0	336
40		6	30	19	15	1	30	11	58	27	40	13	2	0	0	0	0	0	252
41		9	35	20	21	1	25	3	51	23	21	8	0	2	0	0	0	0	219
42		8	8	2	5	0	14	2	32	9	21	5	1	0	0	0	0	0	107
43		1	3	5	8	0	18	10	20	19	17	5	2	0	0	0	0	0	108
44		0	3	9	10	0	13	11	37	47	28	23	2	3	0	0	0	0	186
45		2	16	7	13	1	22	4	14	17	12	18	2	1	0	0	0	0	129
46		35	21	7	13	0	20	7	22	26	7	24	5	1	0	0	0	0	188
47		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
48		80	95	33	27	0	14	0	11	14	7	11	1	5	0	0	0	0	298
49		27	55	22	20	0	27	5	13	14	8	23	0	3	0	0	0	0	217
50		5	34	30	23	0	37	3	26	16	12	29	3	3	0	0	0	0	221
51		3	18	12	24	0	23	3	16	13	9	15	0	4	0	0	0	0	140
TOTAL		775	1385	1048	1224	20	1287	137	977	438	341	290	37	72	1	29	11	2	8074

	SIZE (MM)	1 J	2 J	3 J	4 J	5 A	5 J	6 A	6 J	7 A	7 J	8 A	8 J	9 A	9 J	10 A	11 A	12 A	TOTAL

Appendix A(ii). Nguni dam 1980/81. 65 traps/week until week 30, 36 traps/week thereafter. Week 1 is 14/3/80, week 51 is 29/1/81.

NGUNI DAM — 1980/81 TRAP RESULTS

WEEK	SIZE (MM)	1 J	2 J	3 J	4 J	A	5 AJ	J	A	6 AJ	J	A	7 AJ	J	A	8 AJ	J	A	9 AJ	J	A	10 AJ	J	11 A	12 A	13 A	14 A	15 A	TOTAL
1		0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3
2		0	1	3	3	0	1	2	2	1	1	2	1	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	20
3		0	1	2	0	0	0	0	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7
4		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	2
5		0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	3
6		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	2
7		0	0	0	0	0	0	2	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	6
8		0	0	0	1	0	0	2	0	0	2	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	7
9		0	0	0	0	0	0	3	0	0	1	0	2	5	1	0	1	1	0	0	1	0	0	0	0	0	0	0	15
10		0	2	6	0	0	0	2	0	0	1	2	3	1	8	2	2	5	0	0	3	0	0	0	1	0	0	0	36
11		0	0	0	1	0	0	1	0	3	0	0	1	4	6	1	0	4	0	0	1	0	0	0	0	0	0	0	24
12		0	0	0	0	0	0	1	0	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	3
13		4	1	0	0	0	0	0	0	1	0	0	0	2	0	5	1	0	0	3	0	0	0	0	1	0	0	0	18
14		15	16	4	4	0	0	2	0	0	0	0	0	0	2	0	0	1	0	0	1	0	0	0	0	0	0	0	45
15		10	31	21	13	0	3	16	0	3	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	101
16		0	0	11	16	0	4	9	4	6	6	5	4	1	8	1	0	1	0	0	2	0	0	0	2	0	0	0	80
17		8	4	6	10	2	11	7	17	6	3	10	5	2	6	0	0	2	0	0	2	0	0	0	1	2	0	0	104
18		16	7	17	37	5	24	11	15	12	6	14	0	0	9	0	0	2	0	0	0	0	0	0	0	0	0	0	169
19		4	17	38	56	24	19	5	33	8	2	34	4	0	14	0	0	7	0	0	4	0	0	0	0	0	0	0	269
20		16	47	67	115	35	34	7	63	17	1	142	4	2	93	0	0	24	0	0	7	0	0	0	1	0	0	0	675
21		37	43	23	54	31	26	7	69	12	2	137	0	0	121	0	0	67	0	0	26	0	0	0	8	0	0	1	664
22		54	52	37	43	30	14	3	100	2	0	168	0	2	152	0	0	74	0	0	27	0	0	0	5	1	0	0	764
23		56	54	12	24	24	20	6	109	3	2	182	0	3	218	0	0	114	0	0	51	0	0	0	7	0	1	0	886
24		109	50	23	20	17	34	11	96	24	2	188	5	0	231	0	0	145	0	0	54	0	0	0	12	1	0	1	1024
25		114	108	16	29	25	20	16	86	34	1	176	6	1	209	0	0	135	0	0	52	0	0	0	17	4	0	1	1050
26		148	197	43	27	20	26	14	73	23	7	195	0	0	238	0	0	161	1	0	54	0	0	0	17	5	0	0	1249
27		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28		43	6	1	0	1	1	4	1	7	1	27	3	0	43	1	0	31	0	0	14	0	0	0	4	1	0	0	189
29		111	140	36	13	0	1	6	9	9	5	65	6	0	178	0	0	150	0	0	75	0	0	0	20	3	2	0	829
30		307	325	104	187	1	5	112	6	18	23	54	27	8	279	4	0	286	0	0	129	0	0	0	44	14	2	1	1936
31		189	166	144	203	2	28	272	6	65	60	24	22	1	117	6	0	151	0	0	80	0	0	0	24	9	2	0	1571
32		69	131	198	245	1	55	215	9	129	62	23	40	7	66	14	0	115	1	0	70	0	0	0	32	16	3	2	1503
33		66	118	120	153	3	41	133	7	101	60	33	58	10	33	12	0	73	0	0	71	0	0	0	18	13	3	0	1126
34		71	75	88	114	0	32	134	11	80	106	54	122	21	68	36	1	99	1	0	102	0	0	0	39	15	1	1	1271
35		69	89	118	170	6	42	82	28	125	54	48	73	21	39	27	4	56	2	0	60	0	0	0	19	2	1	0	1134
36		61	99	57	72	5	46	42	42	74	24	74	53	9	96	21	1	88	0	0	56	0	0	0	23	6	0	0	949
37		37	76	76	74	2	39	59	27	72	27	50	60	13	64	27	5	58	1	1	49	0	0	0	11	4	1	0	833
38		4	10	12	17	2	18	22	10	45	12	57	73	11	104	57	3	89	5	0	56	0	0	0	18	3	1	0	629
39		4	11	6	23	1	11	25	16	63	25	73	60	6	164	50	1	110	2	0	43	0	0	0	10	1	0	0	725
40		1	1	1	10	1	6	11	14	39	25	130	90	18	286	60	1	212	7	0	87	0	0	0	10	1	1	0	1012
41		1	5	11	11	2	3	11	27	34	19	129	79	9	295	47	2	227	3	0	74	0	0	0	9	6	1	0	998
42		9	5	3	0	2	2	3	25	32	12	166	74	10	375	33	0	265	0	0	88	0	0	0	11	0	1	0	1116
43		7	5	1	4	2	2	3	29	18	6	149	36	5	308	16	0	219	0	0	64	0	0	0	9	1	0	0	884
44		1	4	1	0	1	2	1	14	12	5	129	23	2	289	8	0	206	0	0	70	0	0	0	2	0	0	0	770
45		0	2	6	2	0	1	1	12	11	5	135	19	4	274	2	0	217	0	0	65	0	0	0	7	1	0	0	764
46		0	0	0	0	0	1	2	3	2	0	28	8	0	46	0	0	32	0	0	8	0	0	0	0	0	0	0	130
47		0	2	0	1	0	0	0	5	0	0	37	1	1	83	0	0	65	0	0	40	0	0	0	6	2	0	0	243
48		4	6	3	5	1	0	0	3	2	1	28	4	0	117	0	1	192	0	0	110	0	0	0	20	4	0	0	501
49		27	16	6	3	0	0	1	1	1	0	21	3	0	139	1	0	219	0	0	129	0	0	0	39	1	0	0	607
50		18	30	10	3	0	0	0	5	1	1	9	2	1	75	0	0	202	0	0	165	0	0	0	65	10	1	0	598
51		3	28	14	12	0	1	2	1	3	1	10	2	1	52	1	0	165	0	0	109	0	0	0	41	6	0	0	452
TOTAL		1693	1981	1346	1775	246	573	1268	981	1098	565	2814	995	182	4916	429	224	276	23	22	103	0	0	552	129	19	7	1	27996

Appendix A(iii). Benes dam 1981/82. 6 traps were searched every fortnight.
Week 1 is 30/5/81, week 39 is 12/2/82.

BENES DAM 1981/82 TRAP RESULTS

WEEK	SIZE (MM)	1 J	2 J	3 J	4 J	5 A	5 J	6 A	6 J	7 A	7 J	8 A	8 J	9 A	9 J	10 A	11 A	12 A	TOTAL
1		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2		6	7	5	4	0	6	0	0	0	0	0	0	0	0	1	0	0	29
3		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4		1	1	3	8	0	4	0	2	1	0	0	0	0	0	0	0	0	20
5		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6		4	3	0	5	0	3	0	0	0	0	0	0	0	0	0	0	0	15
7		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8		3	0	0	1	0	0	1	1	2	0	0	0	0	0	0	0	0	8
9		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10		3	3	0	1	0	2	0	2	1	0	0	0	1	0	0	0	0	13
11		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12		0	2	0	2	0	1	0	7	4	9	7	0	1	0	0	0	0	33
13		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14		51	11	0	2	0	3	0	2	3	1	9	0	5	0	1	0	0	88
15		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16		16	6	2	4	0	1	0	5	6	3	18	1	16	0	0	0	0	78
17		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18		2	5	3	1	0	3	1	2	3	3	10	0	7	0	0	0	0	40
19		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20		1	2	0	0	0	2	0	2	2	1	6	0	4	0	0	0	0	20
21		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22		1	2	0	1	0	3	0	3	3	2	8	1	9	0	0	0	0	33
23		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24		0	1	0	2	0	3	0	2	0	0	5	1	2	0	0	0	0	16
25		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26		3	10	6	5	0	8	0	3	0	3	4	2	3	0	0	0	0	47
27		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29		3	4	6	4	0	3	0	2	1	0	1	0	2	0	1	0	0	27
30		0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
31		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33		4	16	6	4	0	1	1	1	2	2	3	0	2	0	0	0	0	42
34		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35		2	8	14	24	0	14	1	2	4	2	12	1	0	0	0	0	0	84
36		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
37		6	9	9	4	0	3	0	5	2	1	6	0	4	0	0	0	0	49
38		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
39		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TOTAL		106	92	54	72	0	60	4	41	34	27	89	6	56	0	3	0	0	644
	SIZE (MM)	1 J	2 J	3 J	4 J	5 A	5 J	6 A	6 J	7 A	7 J	8 A	8 J	9 A	9 J	10 A	11 A	12 A	TOTAL

Appendix A(iv). Nguni dam 1981/82. 30 traps were searched every week.
Week 1 is 26/5/81, week 39 is 15/2/82.

NGUNI DAM 1981/82 TRAP RESULTS

WEEK	SIZE (MM)	1 J	2 J	3 J	4 J	5 A	5 J	6 A	6 J	7 A	7 J	8 A	8 J	9 A	9 J	10 A	11 A	12 A	TOTAL
1		0	0	0	0	0	0	0	1	2	2	6	1	3	0	0	0	0	15
2		7	1	0	0	0	0	0	1	2	1	4	0	2	0	2	0	0	20
3		9	15	4	0	0	0	0	0	1	0	5	0	2	0	2	0	0	38
4		15	12	11	9	0	4	0	2	1	1	11	1	2	0	0	1	0	70
5		49	21	13	7	1	7	0	5	1	1	9	0	10	0	1	0	1	126
6		10	12	19	15	0	11	3	18	3	1	2	0	6	0	2	0	1	103
7		4	12	12	15	12	4	6	10	6	2	4	0	2	0	1	0	1	91
8		10	14	7	23	0	20	5	29	8	7	5	0	3	0	1	0	0	132
9		8	3	10	13	0	20	1	22	16	23	10	0	6	0	3	1	0	136
10		54	10	7	11	0	9	3	20	10	19	14	1	5	0	3	0	0	166
11		80	11	10	31	0	37	6	46	28	32	35	1	17	0	3	1	0	338
12		34	14	12	18	0	17	3	31	30	20	50	1	18	0	4	0	0	252
13		15	10	8	5	0	11	2	14	21	21	53	3	31	0	8	0	0	202
14		20	14	13	26	0	13	1	30	20	34	108	14	43	0	5	1	0	342
15		38	16	10	12	0	16	6	24	28	30	60	5	41	0	6	1	0	293
16		13	11	7	9	1	11	7	16	22	27	52	4	28	0	5	0	0	213
17		50	15	18	12	0	13	1	21	13	16	68	5	44	0	8	1	0	285
18		28	61	31	40	0	35	10	26	30	27	54	7	30	0	5	0	0	384
19		8	11	14	22	0	31	3	31	57	28	75	3	39	0	6	0	0	328
20		3	5	12	19	1	31	2	35	34	48	72	11	43	0	11	3	0	330
21		3	8	17	31	2	36	6	38	48	42	70	6	20	2	2	0	0	331
22		0	0	4	11	0	20	3	41	27	22	37	3	25	0	4	1	0	198
23		0	3	10	19	0	17	2	36	25	22	58	6	32	0	8	2	0	240
24		11	6	2	4	0	11	2	22	30	15	38	2	29	0	17	1	0	190
25		11	18	10	5	0	6	0	17	4	14	23	5	36	0	29	5	0	183
26		3	0	3	0	0	5	0	11	6	12	7	5	13	0	4	2	0	71
27		41	4	2	5	0	15	2	16	9	9	8	3	7	0	5	2	1	129
28		51	47	2	7	0	9	0	15	6	20	18	4	7	0	5	2	1	194
29		15	32	23	12	0	8	0	6	4	12	4	4	5	0	1	0	0	126
30		12	27	35	38	0	17	1	19	4	7	4	5	4	0	2	1	0	176
31		2	8	19	30	0	19	2	5	2	6	4	3	2	0	1	0	0	103
32		1	1	11	11	0	15	4	5	4	6	4	1	3	0	3	0	0	69
33		1	2	4	12	0	16	0	9	2	3	3	3	0	0	1	0	0	56
34		1	2	6	8	0	12	2	7	7	6	3	3	4	0	2	0	0	63
35		0	5	3	1	0	6	1	14	4	17	3	2	3	0	0	0	0	59
36		0	1	3	2	0	7	2	12	10	20	13	5	3	0	0	0	0	78
37		2	0	1	3	0	7	2	9	2	8	5	1	1	0	0	0	0	41
38		0	3	5	5	2	12	15	26	19	8	19	3	5	0	0	0	0	122
39		0	0	7	8	0	5	8	10	21	6	22	0	7	0	2	0	0	90
TOTAL		609	435	379	499	19	533	111	700	567	595	1040	121	581	2	162	25	5	6383
	SIZE (MM)	1 J	2 J	3 J	4 J	5 A	5 J	6 A	6 J	7 A	7 J	8 A	8 J	9 A	9 J	10 A	11 A	12 A	TOTAL

APPENDIX B

A computer program, written in BASIC language, for use on a Hewlett-Packard 9845B desktop computer.

```
10    REM                  PROGRAM NAME: AGEPR3
20    REM                  ---------------------
30    REM        THIS PROGRAM CALCULATES COHORT GROWTH RATES FROM TIME-SPECIFIC
40    REM        GROWTH INCREMENT DATA.
50    REM
60    REM        DATA REQUIREMENTS:
70    REM        EACH OBSERVATION REPRESENTS ONE MONTH.
80    REM        VARIABLE 1 TO N CONTAIN MODEL REFERENCE CODES (1 TO 5) FOR
90    REM        COHORTS HATCHED DURING MONTH1 TO N.
100   REM        CODES:     1 - USE r FROM EQ. 4.3 FOR MONTH I
110   REM                   2 - USE r FROM EQ. 4.3 FOR MONTH I+1
120   REM                   3 - USE K FROM EQ. 4.1 FOR MONTH I
130   REM                   4 - USE K FROM EQ. 4.1 FOR MONTH I+1
140   REM                   5 - USE K FROM EQ. 4.1 FOR MONTH I, AND DON'T
150   REM                       INCREMENT I.
160   REM        VARIABLE N+1 CONTAINS VALUES FOR r
170   REM        VARIABLE N+2 CONTAINS VALUES FOR K
180   REM        VARIABLE N+3 CONTAINS VALUES FOR L (EQ. 4.1)
190   REM        VARIABLE N+4 CONTAINS THE NUMBER OF DAYS IN EACH MONTH
200   REM        VARIABLE N+5 CONTAINS THE START DATE
210   REM        ------------------------------------------------------
220   PRINTER IS 0
230   OPTION BASE 1
240 Com:  COM D(1,1500),T$[80],Vn$(50)[10],Sn$(20)[10],Sc(20),L(50),M(50)
250   MAT D=ZER
260   MAT Sc=ZER
270   INPUT "FILE NAME FOR DATA",F$
280   ASSIGN #2 TO F$
290   READ #2,1;T$,No,Nv,Vn$(*),Ns,Sn$(*),Sc(*)
300   REDIM D(Nv,No)
310   READ #2,2
320   READ #2;D(*)
330   INPUT "START MONTH",M
340   H=M-1
350   FOR I=1 TO 8
360   H=H+1
370   IF H>8 THEN STOP
380   D=D(13,H)
390   M=H
400   PRINT "          "
410   PRINT "         "
420   FIXED 0
430   PRINT "MONTH No.";H;"   HATCH DATE";D
440   PRINT "      "
450   PRINT " AGE","MONTH";"  DATE"," SIZE"
460   W=0
470   T=0
480   L=.8                                    ! SIZE AT ONE WEEK
490   FIXED 2
500   PRINT T,M;D,L                           ! T IS AGE,M IS MONTH
510   N=D                                     ! D IS DATE,L IS SHELL LENGTH
520   FOR T=1 TO 20                           ! 20 WEEK'S GROWTH
530   N=N+7                                   ! INCREMENT BY ONE WEEK
540   IF N<=D(12,M) THEN 560                  ! NEW MONTH?
550   N=N-D(12,M)
560   R=D(9,M)                                ! R=r IN EQ. 4.3
570   IF R<0 THEN 860
580   K=D(10,M)                               ! K IN EQ. 4.1
590   Z=D(11,M)                               ! Z=Li IN EQ. 4.1
600   X=D(H,T)                                ! X IS THE CODE (1 TO 5)
610   IF X<0 THEN 860
620   IF X>2 THEN 720
```

```
630   IF X=1 THEN 670
640   M=M+1
650   R=D(9,M)
660   W=LOG(L/.8)/R
670   W=W+1
680   L=.8*EXP(R*W)
690   PRINT T,M;N,L
700   NEXT T
710   GOTO 520
720   IF X=3 THEN 820                          ! CALCULATIONS USING K
730   IF X=5 THEN 810
740   M=M+1
750   K=D(10,M)
760   IF K<0 THEN 860
770   Z=D(11,M)
780   IF L<Z THEN 810
790   PRINT "TERMINATED BECAUSE SIZE IS > NEXT L(Inf.)"
800   GOTO 860
810   W=LOG(1-L/Z)/-K
820   W=W+1
830   L=Z*(1-EXP(-K*W))
840   PRINT T,M;N,L
850   NEXT T
860   NEXT I
870   STOP
```

APPENDIX C

A computer program, written in BASIC language, for use on a Hewlett-Packard 9845B desktop computer.

```
10    REM                PROGRAM NAME: LxMxRm
20    REM                ---------------------
30    REM     THIS PROGRAM CALCULATES Mx FOR WEEKLY COHORTS FROM TRAP SAMPLE
40    REM     DATA, THEN CALCULATES LIFE TABLES AND THE SUM OF LxMx AND Rm.
50    REM     DATA REQUIREMENTS:
60    REM     EACH VARIABLE IS A WEEK
70    REM     OBS. 1 TO N : STANDARDISED NUMBER OF SNAILS PER SAMPLE FOR N SIZE
CLASSES
80    REM     OBS. N+1    : STANDARDISED NUMBER OF EGG MASSES PER SAMPLE
90    REM     OBS. N+2    : % HATCH SUCCESS
100   REM     OBS. N+3    : HATCH TIME (DAYS)
110   REM     OBS. N+4    : PROPORTION OF TOTAL REPRO. ALLOCATED TO EACH SIZE CL
ASS
120   REM     OBS. N+5 TO N+I : WEEKLY GROWTH INCREMENTS FOR I-5 GROWTH CURVES
130   REM     ------------------------------------------------------------------
140   PRINTER IS 0
150   OPTION BASE 1
160 Com:  COM D(1,1500),T$[80],Vn$(50)[10],Sn$(20)[10],Sc(20),L(50),M(50),Pr(50)
,Si(50),Re(50),Mx(6,500),X(50),U(50),G(50)
170   MAT D=ZER
180   MAT Sc=ZER
190   MAT Pr=ZER
200   MAT Si=ZER
210   MAT Re=ZER
220   MAT Mx=ZER
230   INPUT "FILE NAME FOR DATA",F$
240   ASSIGN #2 TO F$
250   READ #2,1;T$,No,Nv,Vn$(*),Ns,Sn$(*),Sc(*)
260   REDIM D(Nv,No)
270   READ #2,2
280   READ #2;D(*)
290   INPUT "START WEEK",V
300   INPUT "OBS. No. FOR GROWTH RATES",Gro
310   Gro=Gro-1
320   W=1
330   PRINT "      "
340   PRINT "      "
350   PRINT T$
360   PRINT "------------------------------"
370   PRINT
380   W=W+1
390   IF W>Nv THEN 790
400   FIXED 0
410   Tot=0
420   Pro=0
430   Sum=0
440   Lm=0
450   M=0
460   N=0
470   E=0
480   E=D(W,13)*D(W,14)*D(W,15)*7/D(W,16)     ! E IS TOTAL VIABLE EGGS/WEEK
490   D(W,11)=D(W,11)+D(W,12)                 ! ALLOCATE E TO SIZE CLASSES
500   FOR I=6 TO 11
510   Tot=Tot+D(W,I)
520   NEXT I
530   IF Tot=0 THEN 710
540   FOR I=6 TO 11
550   Re(I-5)=D(W,I)/Tot
560   NEXT I
570   FOR I=1 TO 6
580   Pr(I)=D(I,17)*Re(I)
590   Pro=Pro+Pr(I)
600   NEXT I
```

```
610   FOR I=1 TO 6
620   Si(I)=Pr(I)/Pro*E
630   IF Si(I)=0 THEN 680
640   IF D(W,I+5)>0 THEN 660
650   D(W,I+5)=1
660   Mx(I,W)=Si(I)/D(W,I+5)
670   GOTO 690
680   Mx(I,W)=0
690   NEXT I
700   GOTO 380
710   REM         IF THERE IS NO DATA, NO EGGS, OR NO ADULTS :
720   FOR J=1 TO 6
730   Mx(J,W)=0
740   NEXT J
750   GOTO 380
760   REM         A MATRIX Mx NOW CONTAINS Mx VALUES FOR EACH SIZE CLASS FOR EACH
770   REM         WEEK. THE NEXT SECTION OF THE PROGRAM CALCULATES Lx AND THE SUM
780   REM         OF LxMx.
790   W=V
800   FIXED 0
810   MAT X=ZER
820   MAT U=ZER
830   MAT G=ZER
840   MAT L=ZER
850   MAT M=ZER
860   PRINT "-------------------------------------------------------"
870   PRINT
880   PRINT "LIFE TABLE FOR A COHORT HATCHED IN WEEK ";V
890   PRINT
900   PRINT " X";"       WEEK";"    SIZE";"   No. SURV.","  Lx","  Mx"
910   PRINT "                 (mm.)                                          (*100)"
920   Lm=0
930   Gro=Gro+1
940   E=D(W,13)*D(W,14)*D(W,15)*7/D(W,16)  ! LIFE TABLE FOR X=0
950   X(1)=0                               ! X IS THE COHORT AGE
960   U(1)=.8                              ! U IS THE MEAN COHORT SHELL LENGTH
970   G(1)=E                               ! G IS THE NUMBER OF SURVIVORS
980   L(1)=1                               ! L IS Lx
990   M(1)=0                               ! M IS Mx
1000  FIXED 0
1010  W=W+1
1020  C=D(W,1)
1030  Z=D(2,Gro)
1040  D=D=Z-INT(Z)
1050  H=D*D(W,2)
1060  G(2)=C+H
1070  IF E>0 THEN 1130
1080  PRINT
1090  PRINT "NO DATA FOR WEEK ";V
1100  PRINT
1110  PRINT
1120  GOTO 1840
1130  L(2)=G(2)/E
1140  X(2)=1                               ! LIFE TABLE FOR X=1
1150  U(2)=.8+(Z-.8)/2
1160  M(2)=0
1170  Ct=2
1180  FOR I=W+1 TO W+19                    ! LIFE TABLE FOR X=2 TO 20
1190  IF I>Nv THEN 1470
1200  Ct=Ct+1
1210  J=Ct-1
1220  Z=D(Ct,Gro)
1230  Y=D(J,Gro)
1240  IF Z<0 THEN 1470
```

```
1250  F=INT(Z)+1
1260  IF INT(Z)=INT(Y) THEN 1360
1270  A=INT(Y)+1
1280  B=A-Y
1290  C=B*D(I,A)
1300  D=Z-INT(Z)
1310  H=D*D(I,F)
1320  IF INT(Z)-INT(Y)=1 THEN 1340
1330  H=H+D(I,INT(Z))
1340  G(Ct)=C+H
1350  GOTO 1370
1360  G(Ct)=(Z-Y)*D(I,F)
1370  L(Ct)=G(Ct)/E
1380  X(Ct)=I-(W-1)
1390  U(Ct)=Y+(Z-Y)/2
1400  Z=INT(U(Ct))-4
1410  IF Z<1 THEN 1440
1420  M(Ct)=Mx(Z,I)
1430  GOTO 1450
1440  M(Ct)=0
1450  Lm=Lm+L(Ct)*M(Ct)
1460  NEXT I
1470  FOR I=1 TO 21
1480  PRINT X(I);"      ";I+W-2;"      ";U(I)*10;"      .";G(I),L(I)*1000,M(I)*100
1490  NEXT I
1500  FIXED 3
1510  PRINT
1520  PRINT "THE SUM OF LxMx = ";Lm
1530  IF Lm>0 THEN 1550
1540  GOTO 1840
1550  R=LOG(Lm)                              ! CALCULATIONS FOR Rm
1560  K=R
1570  GOSUB 1790
1580  Step=.1
1590  A=SGN(S-1)
1600  R1=R
1610  R2=R1+A*100
1620  FOR R=R1 TO R2 STEP A*Step
1630  GOSUB 1790
1640  IF SGN(A)=SGN(S-1) THEN 1680
1650  IF DROUND(K*1000,3)=DROUND(R*1000,3) THEN 1740
1660  K=R
1670 'GOTO 1690
1680  NEXT R
1690  Step=Step*.1
1700  R1=K
1710  A=SGN(S-1)
1720  R2=R1+A*11*Step
1730  GOTO 1620
1740  FIXED 3
1750  PRINT
1760  PRINT "               r = ";R
1770  PRINT
1780  GOTO 1840
1790  S=0
1800  FOR X=2 TO 21
1810  S=S+EXP(-R*X)*L(X)*M(X)
1820  NEXT X
1830  RETURN
1840  V=V+1
1850  IF V>30 THEN STOP
1860  GOTO 800
```

APPENDIX D

Weekly cohort life tables for Bulinus globosus in Benes dam and Nguni dam . R_0 (the sum of $l_x m_x$) and r_m are also given for each cohort.

"x" is the cohort age in weeks.

"week" is the sampling week number, where week 1 for 1980/81 is the 25th April 1980, and week 41 is the 29th January 1981. Week 1 for 1981/82 is the 26th May 1981 and week 39 is the 15th February 1982.

"size" is the average shell-length (in mm x 10^{-1}) of the cohort during each week.

"no. surv." is the number of survivors as calculated from the trap samples using the relevant growth curve.

"Lx" is the number of survivors expressed as a proportion x 1000 of the original cohort number.

"Mx" is the number of eggs/adult x 100.

Life tables are given for Nguni dam during 1980/81 and 1981/82, and for Benes dam during 1980/81.

1980/81. BENES DAM. TRAP SAMPLES.

LIFE TABLE FOR A COHORT HATCHED IN WEEK 1

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	1	8	31	1000	0
1	2	12	2	64	0
2	3	22	39	1258	0
3	4	36	33	1071	0
4	5	46	4	142	0
5	6	51	4	131	0
6	7	55	2	64	0
7	8	59	2	55	0
8	9	62	1	45	268
9	10	65	2	54	914
10	11	67	2	61	648
11	12	69	1	33	609
12	13	70	0	9	988
13	14	72	0	12	448
14	15	73	0	7	1844
15	16	74	0	0	0
16	17	74	0	0	0
17	18	75	0	6	1046
18	19	76	0	8	2483
19	20	76	0	0	0
20	21	77	0	0	0

THE SUM OF LxMx = 1.744

r = .046

LIFE TABLE FOR A COHORT HATCHED IN WEEK 2

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	2	8	26	1000	0
1	3	12	31	1178	0
2	4	22	20	764	0
3	5	36	10	375	0
4	6	46	6	212	0
5	7	51	2	79	0
6	8	55	2	77	0
7	9	59	2	85	0
8	10	62	2	76	914
9	11	65	2	83	648
10	12	67	1	49	609
11	13	69	1	26	684
12	14	70	1	28	448
13	15	72	0	9	1844
14	16	73	0	0	0
15	17	74	0	0	0
16	18	74	0	9	1046
17	19	75	0	12	2483
18	20	76	0	0	0
19	21	76	0	0	0
20	22	77	0	1	13552

THE SUM OF LxMx = 2.545

r = .079

LIFE TABLE FOR A COHORT HATCHED IN WEEK 3

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	3	8	52	1000	0
1	4	12	14	270	0
2	5	22	3	52	0
3	6	36	9	170	0
4	7	46	2	32	0
5	8	51	3	51	0
6	9	55	3	54	0
7	10	59	3	66	0
8	11	62	3	49	648
9	12	65	1	28	609
10	13	67	1	16	684
11	14	69	2	30	310
12	15	70	0	8	1844
13	16	72	0	0	0
14	17	73	0	0	0
15	18	74	0	5	1046
16	19	74	0	8	2483
17	20	75	0	0	0
18	21	76	0	0	0
19	22	76	0	1	13552
20	23	77	0	0	0

THE SUM OF LxMx = 1.211

r = .015

1980/81 BENES DAM

LIFE TABLE FOR A COHORT HATCHED IN WEEK 4

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	4	8	26	1000	0
1	5	12	1	39	0
2	6	22	18	703	0
3	7	36	3	116	0
4	8	46	4	149	0
5	9	51	5	191	0
6	10	55	4	170	0
7	11	59	6	234	0
8	12	62	2	65	609
9	13	65	1	37	684
10	14	67	2	73	310
11	15	69	1	33	1277
12	16	70	0	8	0
13	17	72	0	0	0
14	18	73	0	13	1046
15	19	74	0	15	2483
16	20	74	0	0	0
17	21	75	0	0	0
18	22	76	0	2	13552
19	23	76	0	0	0
20	24	77	0	2	464

THE SUM OF LxMx = 2.083

r = .058

LIFE TABLE FOR A COHORT HATCHED IN WEEK 5

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	5	8	36	1000	0
1	6	12	39	1076	0
2	7	22	51	1404	0
3	8	36	13	353	0
4	9	46	10	273	0
5	10	51	8	229	0
6	11	55	8	221	0
7	12	59	5	147	0
8	13	62	1	31	684
9	14	65	2	60	310
10	15	67	1	29	1277
11	16	69	1	19	783
12	17	70	0	7	0
13	18	72	0	10	1046
14	19	73	1	15	2483
15	20	74	0	0	0
16	21	74	0	0	0
17	22	75	0	2	13552
18	23	76	0	0	0
19	24	76	0	3	464
20	25	77	0	0	0

THE SUM OF LxMx = 1.630

r = .038

LIFE TABLE FOR A COHORT HATCHED IN WEEK 6

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	6	8	145	1000	0
1	7	12	76	524	0
2	8	22	60	412	0
3	9	36	47	321	0
4	10	46	18	121	0
5	11	51	12	81	0
6	12	55	7	50	0
7	13	59	3	21	0
8	14	62	3	17	310
9	15	65	1	8	1277
10	16	67	1	6	783
11	17	69	1	6	1571
12	18	70	1	9	1046
13	19	72	1	4	2483
14	20	73	0	0	0
15	21	74	0	0	0
16	22	74	0	1	13552
17	23	75	0	0	0
18	24	76	0	1	464
19	25	76	0	0	0
20	26	77	0	0	0

THE SUM OF LxMx = .569

r = -.045

1980/81 BENES DAM

LIFE TABLE FOR A COHORT HATCHED IN WEEK 7

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	7	8	88	1000	0
1	8	12	63	710	0
2	9	22	80	912	0
3	10	36	78	881	0
4	11	46	20	225	0
5	12	51	9	105	0
6	13	55	4	45	0
7	14	59	3	31	0
8	15	62	1	16	1277
9	16	65	1	11	783
10	17	67	1	12	1571
11	18	69	3	39	724
12	19	70	1	6	2483
13	20	72	0	0	0
14	21	73	0	0	0
15	22	74	0	1	13552
16	23	74	0	0	0
17	24	75	0	1	464
18	25	76	0	0	0
19	26	76	0	0	0
20	27	77	0	0	1650

THE SUM OF LxMx = 1.045

r = .004

LIFE TABLE FOR A COHORT HATCHED IN WEEK 8

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	8	8	52	1000	0
1	9	12	43	820	0
2	10	22	60	1149	0
3	11	36	49	944	0
4	12	46	13	244	0
5	13	51	5	94	0
6	14	55	3	62	0
7	15	59	4	70	0
8	16	62	1	22	783
9	17	65	1	23	1571
10	18	67	4	81	724
11	19	69	0	7	1719
12	20	70	0	0	0
13	21	72	0	0	0
14	22	73	0	2	13552
15	23	74	0	0	0
16	24	74	0	3	464
17	25	75	0	0	0
18	26	76	0	0	0
19	27	76	0	1	1650
20	28	77	0	1	984

THE SUM OF LxMx = 1.557

r = .039

LIFE TABLE FOR A COHORT HATCHED IN WEEK 9

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	9	8	52	1000	0
1	10	12	20	376	0
2	11	22	29	568	0
3	12	36	37	720	0
4	13	46	6	117	0
5	14	51	4	75	0
6	15	55	5	93	0
7	16	59	3	58	0
8	17	62	1	27	1571
9	18	65	5	93	724
10	19	67	0	8	1719
11	20	69	0	0	0
12	21	70	0	0	0
13	22	72	0	2	13552
14	23	73	0	0	0
15	24	74	0	3	464
16	25	74	0	0	0
17	26	75	0	0	0
18	27	76	0	1	1650
19	28	76	0	1	984
20	29	77	0	0	0

THE SUM OF LxMx = 1.589

r = .043

1980/81 BENES DAM

LIFE TABLE FOR A COHORT HATCHED IN WEEK 10

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	10	8	136	1000	0
1	11	12	18	129	0
2	12	22	28	203	0
3	13	36	24	178	0
4	14	46	5	36	0
5	15	51	6	45	0
6	16	55	4	29	0
7	17	59	2	16	0
8	18	62	6	41	724
9	19	65	0	4	1719
10	20	67	0	0	0
11	21	69	0	0	0
12	22	70	0	1	13552
13	23	72	0	0	0
14	24	73	0	2	464
15	25	74	0	0	0
16	26	74	0	0	0
17	27	75	0	0	1650
18	28	76	0	0	984
19	29	76	0	0	0
20	30	77	0	0	434

THE SUM OF LxMx = .469

r = -.073

LIFE TABLE FOR A COHORT HATCHED IN WEEK 11

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	11	8	91	1000	0
1	12	12	13	143	0
2	13	22	25	271	0
3	14	36	14	150	0
4	15	46	8	91	0
5	16	51	5	53	0
6	17	55	3	31	0
7	18	59	6	67	0
8	19	62	1	6	1719
9	20	65	0	0	0
10	21	67	0	0	0
11	22	69	0	0	0
12	23	70	0	0	0
13	24	72	0	3	464
14	25	73	0	0	0
15	26	74	0	0	0
16	27	74	0	1	1650
17	28	75	0	1	984
18	29	76	0	0	0
19	30	76	0	1	434
20	31	77	0	1	341

THE SUM OF LxMx = .149

r = -.150

LIFE TABLE FOR A COHORT HATCHED IN WEEK 12

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	12	8	45	1000	0
1	13	12	13	276	0
2	14	22	29	631	0
3	15	36	17	377	0
4	16	46	6	133	0
5	17	51	4	79	0
6	18	55	7	159	0
7	19	59	4	89	0
8	20	62	0	0	0
9	21	65	0	0	0
10	22	67	0	0	0
11	23	69	0	0	0
12	24	70	0	11	464
13	25	72	0	0	0
14	26	73	0	0	0
15	27	74	0	2	1650
16	28	74	0	2	984
17	29	75	0	0	0
18	30	76	0	2	434
19	31	76	0	4	341
20	32	77	0	3	124

THE SUM OF LxMx = .123

r = -.129

1980/81 BENES DAM

LIFE TABLE FOR A COHORT HATCHED IN WEEK 13

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	13	8	74	1000	0
1	14	12	57	767	0
2	15	22	38	514	0
3	16	36	20	277	0
4	17	46	5	67	0
5	18	51	8	105	0
6	19	55	6	76	0
7	20	59	0	0	0
8	21	62	0	0	0
9	22	65	0	0	0
10	23	67	0	0	0
11	24	69	1	14	321
12	25	70	0	5	0
13	26	72	0	0	0
14	27	73	0	1	1650
15	28	74	0	1	984
16	29	74	0	0	0
17	30	75	0	2	434
18	31	76	0	3	341
19	32	76	0	3	124
20	33	77	0	6	70

THE SUM OF LxMx = .104

r = -.147

LIFE TABLE FOR A COHORT HATCHED IN WEEK 14

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	14	8	48	1000	0
1	15	12	63	1305	0
2	16	22	47	990	0
3	17	36	16	343	0
4	18	46	7	149	0
5	19	51	7	147	0
6	20	55	0	0	0
7	21	59	0	0	0
8	22	62	0	0	0
9	23	65	0	0	0
10	24	67	1	26	321
11	25	69	1	28	467
12	26	70	0	9	0
13	27	72	0	3	1650
14	28	73	0	2	984
15	29	74	0	0	0
16	30	74	0	3	434
17	31	75	0	5	341
18	32	76	0	4	124
19	33	76	1	16	70
20	34	77	0	5	76

THE SUM OF LxMx = .333

r = -.082

LIFE TABLE FOR A COHORT HATCHED IN WEEK 15

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	15	8	128	1000	0
1	16	12	64	497	0
2	17	22	49	382	0
3	18	36	27	208	0
4	19	46	9	73	0
5	20	51	0	0	0
6	21	55	0	0	0
7	22	59	0	0	0
8	23	62	0	0	0
9	24	65	1	11	321
10	25	67	2	13	467
11	26	69	2	12	84
12	27	70	0	1	1650
13	28	72	0	1	984
14	29	73	0	0	0
15	30	74	0	1	434
16	31	74	0	3	341
17	32	75	0	2	124
18	33	76	1	6	70
19	34	76	0	3	76
20	35	77	0	1	88

THE SUM OF LxMx = .159

r = -.143

1980/81 BENES DAM

LIFE TABLE FOR A COHORT HATCHED IN WEEK 16

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	16	8	48	1000	0
1	17	12	41	846	0
2	18	22	37	779	0
3	19	36	23	476	0
4	20	46	0	0	0
5	21	51	0	0	0
6	22	55	0	0	0
7	23	59	0	0	0
8	24	62	2	35	321
9	25	65	2	40	467
10	26	67	2	39	84
11	27	69	0	4	1143
12	28	70	0	7	984
13	29	72	0	0	0
14	30	73	0	5	434
15	31	74	0	7	341
16	32	74	0	7	124
17	33	75	1	19	70
18	34	76	0	8	76
19	35	76	0	6	88
20	36	77	0	4	11

THE SUM OF LxMx = .520

r = -.056

LIFE TABLE FOR A COHORT HATCHED IN WEEK 17

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	17	8	112	1000	0
1	18	12	30	269	0
2	19	22	28	253	0
3	20	36	0	0	0
4	21	46	0	0	0
5	22	51	0	0	0
6	23	55	0	0	0
7	24	59	4	35	0
8	25	62	2	20	467
9	26	65	2	19	84
10	27	67	0	2	1143
11	28	69	1	8	681
12	29	70	0	3	0
13	30	72	0	2	434
14	31	73	0	4	341
15	32	74	0	3	124
16	33	74	1	11	70
17	34	75	0	4	76
18	35	76	0	3	88
19	36	76	0	3	11
20	37	77	1	7	13

THE SUM OF LxMx = .224

r = -.128

LIFE TABLE FOR A COHORT HATCHED IN WEEK 18

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	18	8	192	1000	0
1	19	12	47	245	0
2	20	22	0	0	0
3	21	36	0	1	0
4	22	46	0	0	0
5	23	51	0	2	0
6	24	55	5	27	0
7	25	59	8	43	0
8	26	62	3	13	84
9	27	65	0	1	1143
10	28	67	1	5	681
11	29	69	1	5	1131
12	30	70	1	6	434
13	31	72	0	3	341
14	32	73	0	2	124
15	33	74	1	6	70
16	34	74	1	3	76
17	35	75	0	2	88
18	36	76	0	2	11
19	37	76	1	7	13
20	38	77	1	3	140

THE SUM OF LxMx = .176

r = -.137

LIFE TABLE FOR A COHORT HATCHED IN WEEK 19

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	19	8	195	1000	0
1	20	12	0	0	0
2	21	22	3	14	0
3	22	36	1	6	0
4	23	46	1	6	0
5	24	51	9	45	0
6	25	55	11	57	0
7	26	59	24	123	0
8	27	62	0	1	1143
9	28	65	1	6	681
10	29	67	1	6	1131
11	30	69	4	18	301
12	31	70	2	9	341
13	32	72	0	2	124
14	33	73	2	8	70
15	34	74	1	3	76
16	35	74	0	2	88
17	36	75	0	2	11
18	37	76	1	6	13
19	38	76	1	5	140
20	39	77	1	4	103

THE SUM OF LxMx = .244

r = -.114

LIFE TABLE FOR A COHORT HATCHED IN WEEK 20 NO DATA FOR WEEK 20

LIFE TABLE FOR A COHORT HATCHED IN WEEK 21

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	21	8	85	1000	0
1	22	12	28	331	0
2	23	22	68	805	0
3	24	36	67	787	0
4	25	46	47	558	0
5	26	51	56	656	0
6	27	55	6	71	0
7	28	59	5	62	0
8	29	62	2	20	1131
9	30	65	5	60	301
10	31	67	6	69	236
11	32	69	8	98	86
12	33	70	5	55	70
13	34	72	1	11	76
14	35	73	1	8	88
15	36	74	1	7	11
16	37	74	2	24	13
17	38	75	1	14	140
18	39	76	1	17	103
19	40	76	0	0	0
20	41	77	0	4	310

THE SUM OF LxMx = .761

r = -.025

LIFE TABLE FOR A COHORT HATCHED IN WEEK 22

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	22	8	136	1000	0
1	23	12	70	517	0
2	24	22	93	687	0
3	25	36	181	1332	0
4	26	46	105	775	0
5	27	51	19	137	0
6	28	55	7	53	0
7	29	59	12	91	0
8	30	62	6	43	301
9	31	65	7	50	236
10	32	67	10	76	86
11	33	69	11	84	49
12	34	70	3	22	76
13	35	72	1	5	88
14	36	73	1	6	11
15	37	74	2	15	13
16	38	74	2	12	140
17	39	75	2	13	103
18	40	76	0	0	0
19	41	76	1	4	310
20	42	77	1	5	99

THE SUM OF LxMx = .426

r = -.074

1980/81 BENES DAM

LIFE TABLE FOR A COHORT HATCHED IN WEEK 23

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	23	8	68	1000	0
1	24	12	103	1506	0
2	25	22	139	2040	0
3	26	36	233	3423	0
4	27	46	51	744	0
5	28	51	15	219	0
6	29	55	17	253	0
7	30	59	29	423	0
8	31	62	8	115	236
9	32	65	12	173	86
10	33	67	14	207	49
11	34	69	7	110	52
12	35	70	2	30	88
13	36	72	1	12	11
14	37	73	3	40	13
15	38	74	2	24	140
16	39	74	2	34	103
17	40	75	0	0	0
18	41	76	1	9	310
19	42	76	1	17	99
20	43	77	1	14	83

THE SUM OF LxMx = .735

r = -.027

LIFE TABLE FOR A COHORT HATCHED IN WEEK 24

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	24	8	113	1000	0
1	25	12	81	710	0
2	26	22	103	907	0
3	27	36	163	1437	0
4	28	46	34	296	0
5	29	51	28	250	0
6	30	55	40	349	0
7	31	59	24	210	0
8	32	62	14	121	86
9	33	65	16	142	49
10	34	67	9	81	52
11	35	69	5	45	61
12	36	70	2	21	11
13	37	72	3	26	13
14	38	73	2	19	140
15	39	74	2	20	103
16	40	74	0	0	0
17	41	75	1	6	310
18	42	76	1	10	99
19	43	76	2	14	83
20	44	77	0	4	116

THE SUM OF LxMx = .343

r = -.085

LIFE TABLE FOR A COHORT HATCHED IN WEEK 25

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	25	8	53	1000	0
1	26	12	21	387	0
2	27	22	70	1317	0
3	28	36	76	1427	0
4	29	46	53	1008	0
5	30	51	46	868	0
6	31	55	32	605	0
7	32	59	28	522	0
8	33	62	19	354	49
9	34	65	11	200	52
10	35	67	6	119	61
11	36	69	6	116	7
12	37	70	6	113	13
13	38	72	2	45	140
14	39	73	3	60	103
15	40	74	0	0	0
16	41	74	1	18	310
17	42	75	1	26	99
18	43	76	2	30	83
19	44	76	1	14	116
0	45	0	0	0	0

THE SUM OF LxMx = .622

r = -.038

1980/81 BENES DAM

LIFE TABLE FOR A COHORT HATCHED IN WEEK 26

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	26	8	8	1000	0
1	27	12	15	1984	0
2	28	22	34	4471	0
3	29	36	116	15291	0
4	30	46	52	6911	0
5	31	51	32	4279	0
6	32	55	36	4762	0
7	33	59	23	2999	0
8	34	62	12	1630	52
9	35	65	7	952	61
10	36	67	8	1000	7
11	37	69	13	1687	9
12	38	70	3	430	140
13	39	72	3	460	103
14	40	73	0	0	0
15	41	74	1	127	310
16	42	74	2	243	99
17	43	75	2	254	83
18	44	76	1	99	116
0	45	0	0	0	0
0	46	0	0	0	0

THE SUM OF LxMx = 3.693

r = .107

LIFE TABLE FOR A COHORT HATCHED IN WEEK 27

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	27	8	28	1000	0
1	28	12	8	286	0
2	29	22	28	1003	0
3	30	36	48	1733	0
4	31	46	25	886	0
5	32	51	34	1208	0
6	33	55	28	988	0
7	34	59	17	620	0
8	35	62	8	301	61
9	36	65	9	309	7
10	37	67	16	564	9
11	38	69	5	177	97
12	39	70	4	153	103
13	40	72	0	0	0
14	41	73	1	47	310
15	42	74	2	66	99
16	43	74	3	92	83
17	44	75	1	32	116
0	45	0	0	0	0
0	46	0	0	0	0
0	47	0	0	0	0

THE SUM OF LxMx = .909

r = -.007

LIFE TABLE FOR A COHORT HATCHED IN WEEK 28

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	28	8	44	1000	0
1	29	12	9	194	0
2	30	22	16	355	0
3	31	36	30	690	0
4	32	46	18	414	0
5	33	51	27	609	0
6	34	55	22	492	0
7	35	59	11	251	0
8	36	62	10	230	7
9	37	65	18	410	9
10	38	67	6	139	97
11	39	69	6	128	71
12	40	70	0	0	0
13	41	72	1	33	310
14	42	73	3	58	99
15	43	74	3	58	83
16	44	74	1	27	116
0	45	0	0	0	0
0	46	0	0	0	0
0	47	0	0	0	0
0	48	0	0	0	0

THE SUM OF LxMx = .518

r = -.051

1980/81 BENES DAM

LIFE TABLE FOR A COHORT HATCHED IN WEEK 29

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	29	8	92	1000	0
1	30	12	18	191	0
2	31	22	29	318	0
3	32	36	46	498	0
4	33	46	17	186	0
5	34	51	21	231	0
6	35	55	14	148	0
7	36	59	10	111	0
8	37	62	21	229	9
9	38	65	7	76	97
10	39	67	7	76	71
11	40	69	0	0	0
12	41	70	2	23	310
13	42	72	3	30	99
14	43	73	4	38	83
15	44	74	1	13	116
0	45	0	0	0	0
0	46	0	0	0	0
0	47	0	0	0	0
0	48	0	0	0	0
0	49	0	0	0	0

THE SUM OF LxMx = .296

r = -.099

LIFE TABLE FOR A COHORT HATCHED IN WEEK 30

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	30	8	72	1000	0
1	31	12	62	863	0
2	32	22	66	915	0
3	33	36	26	365	0
4	34	46	14	199	0
5	35	51	13	181	0
6	36	55	12	167	0
7	37	59	17	239	0
8	38	62	8	113	97
9	39	65	8	110	71
10	40	67	0	0	0
11	41	69	4	50	215
12	42	70	3	44	99
13	43	72	4	53	83
14	44	73	2	23	116
0	45	0	0	0	0
0	46	0	0	0	0
0	47	0	0	0	0
0	48	0	0	0	0
0	49	0	0	0	0
0	50	0	0	0	0

THE SUM OF LxMx = .410

r = -.078

1980/81. NGUNI DAM. TRAP RESULTS.

LIFE TABLE FOR A COHORT HATCHED IN WEEK 1

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	1	8	354	1000	0
1	2	11	0	0	0
2	3	20	1	2	0
3	4	34	7	21	0
4	5	46	15	44	0
5	6	53	11	32	0
6	7	59	14	40	0
7	8	65	7	20	2000
8	9	70	14	40	1486
9	10	74	37	105	1175
10	11	78	48	137	754
11	12	82	30	84	735
12	13	86	34	97	583
13	14	88	29	82	620
14	15	91	24	68	1117
15	16	93	11	31	1376
16	17	95	0	0	0
17	18	97	5	15	1278
18	19	99	15	42	1606
19	20	101	6	17	806
20	21	102	6	18	678

THE SUM OF LxMx = 7.256

r = .164

LIFE TABLE FOR A COHORT HATCHED IN WEEK 2

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	2	8	192	1000	0
1	3	11	5	26	0
2	4	20	13	69	0
3	5	34	32	165	0
4	6	46	9	49	0
5	7	53	18	93	0
6	8	59	14	72	0
7	9	65	19	99	1486
8	10	70	63	329	814
9	11	74	48	252	754
10	12	78	61	317	503
11	13	82	46	238	583
12	14	86	44	227	620
13	15	88	27	141	732
14	16	91	27	141	1376
15	17	93	0	0	0
16	18	95	5	28	1278
17	19	97	15	78	1606
18	20	99	26	135	779
19	21	101	6	33	678
20	22	102	10	50	584

THE SUM OF LxMx = 16.579

r = .247

LIFE TABLE FOR A COHORT HATCHED IN WEEK 3

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	3	8	494	1000	0
1	4	11	24	49	0
2	5	20	34	68	0
3	6	34	25	50	0
4	7	46	14	29	0
5	8	53	21	42	0
6	9	59	25	50	0
7	10	65	74	150	814
8	11	70	65	132	522
9	12	74	61	123	503
10	13	78	87	176	399
11	14	82	58	117	620
12	15	86	41	82	732
13	16	88	32	66	902
14	17	91	0	0	0
15	18	93	5	11	1278
16	19	95	15	30	1606
17	20	97	26	52	779
18	21	99	29	58	655
19	22	101	10	19	584
20	23	102	6	12	701

THE SUM OF LxMx = 6.765

r = .168

1980/81 NGUNI DAM

LIFE TABLE FOR A COHORT HATCHED IN WEEK 4

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	4	8	583	1000	0
1	5	11	26	45	0
2	6	20	6	10	0
3	7	34	17	30	0
4	8	46	28	49	0
5	9	53	31	53	0
6	10	59	62	106	0
7	11	65	69	118	522
8	12	70	81	140	348
9	13	74	87	150	399
10	14	78	92	159	424
11	15	82	54	93	732
12	16	86	49	83	902
13	17	88	0	0	0
14	18	91	11	19	1278
15	19	93	15	26	1606
16	20	95	26	44	779
17	21	97	29	50	655
18	22	99	25	43	564
19	23	101	6	11	701
20	24	102	10	18	528

THE SUM OF LxMx = 5.544

r = .143

LIFE TABLE FOR A COHORT HATCHED IN WEEK 5

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	5	8	354	1000	0
1	6	11	0	0	0
2	7	20	5	15	0
3	8	34	54	153	0
4	9	46	34	95	0
5	10	53	56	159	0
6	11	59	61	171	0
7	12	65	85	240	348
8	13	70	99	280	276
9	14	74	92	261	424
10	15	78	84	236	501
11	16	82	65	183	902
12	17	86	0	0	0
13	18	88	12	33	838
14	19	91	30	85	1606
15	20	93	26	73	779
16	21	95	29	82	655
17	22	97	25	71	564
18	23	99	26	72	677
19	24	101	10	29	528
20	25	102	4	11	582

THE SUM OF LxMx = 9.403

r = .188

LIFE TABLE FOR A COHORT HATCHED IN WEEK 6

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	6	8	738	1000	0
1	7	11	10	13	0
2	8	20	13	17	0
3	9	34	85	115	0
4	10	46	53	72	0
5	11	53	56	76	0
6	12	59	75	101	0
7	13	65	93	125	276
8	14	70	104	141	294
9	15	74	84	113	501
10	16	78	95	129	617
11	17	82	0	0	0
12	18	86	18	24	838
13	19	88	30	41	1052
14	20	91	54	74	779
15	21	93	29	39	655
16	22	95	25	34	564
17	23	97	26	35	677
18	24	99	38	51	511
19	25	101	4	5	582
20	26	102	5	7	291

THE SUM OF LxMx = 4.328

r = .120

1980/81 NGUNI DAM

LIFE TABLE FOR A COHORT HATCHED IN WEEK 7

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	7	8	642	1000	0
1	8	11	19	30	0
2	9	20	29	46	0
3	10	34	164	255	0
4	11	46	45	70	0
5	12	53	66	103	0
6	13	59	83	129	0
7	14	65	97	150	294
8	15	70	97	151	347
9	16	74	95	148	617
10	17	78	0	0	0
11	18	82	24	37	838
12	19	86	45	70	1052
13	20	88	57	89	511
14	21	91	56	88	655
15	22	93	25	39	564
16	23	95	26	40	677
17	24	97	38	59	511
18	25	99	22	34	563
19	26	101	5	8	291
20	27	102	3	5	469

THE SUM OF LxMx = 4.985

r = .133

LIFE TABLE FOR A COHORT HATCHED IN WEEK 8

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	8	8	634	1000	0
1	9	11	11	17	0
2	10	20	62	97	0
3	11	34	78	123	0
4	12	46	33	52	0
5	13	53	73	116	0
6	14	59	87	138	0
7	15	65	92	144	347
8	16	70	106	167	427
9	17	74	0	0	0
10	18	78	34	53	573
11	19	82	60	95	1052
12	20	86	86	135	511
13	21	88	55	86	429
14	22	91	46	73	564
15	23	93	26	40	677
16	24	95	38	60	511
17	25	97	22	34	563
18	26	99	20	32	281
19	27	101	3	5	469
20	28	102	4	6	107

THE SUM OF LxMx = 4.874

r = .132

LIFE TABLE FOR A COHORT HATCHED IN WEEK 9

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	9	8	1276	1000	0
1	10	11	35	27	0
2	11	20	37	29	0
3	12	34	71	56	0
4	13	46	35	27	0
5	14	53	79	62	0
6	15	59	85	67	0
7	16	65	98	76	427
8	17	70	0	0	0
9	18	74	34	26	573
10	19	78	71	56	720
11	20	82	114	90	511
12	21	86	82	64	429
13	22	88	42	33	370
14	23	91	39	30	677
15	24	93	38	30	511
16	25	95	22	17	563
17	26	97	20	16	281
18	27	99	18	14	453
19	28	101	4	3	107
20	29	102	2	2	42

THE SUM OF LxMx = 2.298

r = .068

1980/81 NGUNI DAM

LIFE TABLE FOR A COHORT HATCHED IN WEEK 10

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	10	8	2921	1000	0
1	11	11	54	19	0
2	12	20	50	17	0
3	13	34	40	14	0
4	14	46	43	15	0
5	15	53	79	27	0
6	16	59	80	27	0
7	17	65	0	0	0
8	18	70	34	12	397
9	19	74	71	24	720
10	20	78	113	39	349
11	21	82	109	37	429
12	22	86	63	22	370
13	23	88	26	9	444
14	24	91	56	19	511
15	25	93	22	7	563
16	26	95	20	7	281
17	27	97	18	6	453
18	28	99	20	7	103
19	29	101	2	1	42
20	30	102	2	1	22

THE SUM OF LxMx = .832

r = -.015

LIFE TABLE FOR A COHORT HATCHED IN WEEK 11

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	11	8	2959	1000	0
1	12	11	75	25	0
2	13	20	38	13	0
3	14	34	44	15	0
4	15	46	43	14	0
5	16	53	68	23	0
6	17	59	0	0	0
7	18	65	29	10	397
8	19	70	57	19	498
9	20	74	113	38	349
10	21	78	89	30	294
11	22	82	84	28	370
12	23	86	40	13	444
13	24	88	37	13	335
14	25	91	32	11	563
15	26	93	20	7	281
16	27	95	18	6	453
17	28	97	20	7	103
18	29	99	16	5	41
19	30	101	2	1	22
20	31	102	2	1	19

THE SUM OF LxMx = .679

r = -.033

LIFE TABLE FOR A COHORT HATCHED IN WEEK 12

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	12	8	2273	1000	0
1	13	11	78	34	0
2	14	20	42	18	0
3	15	34	49	22	0
4	16	46	42	18	0
5	17	53	0	0	0
6	18	59	18	8	0
7	19	65	36	16	498
8	20	70	83	37	242
9	21	74	89	39	294
10	22	78	58	25	253
11	23	82	53	23	444
12	24	86	56	25	335
13	25	88	21	9	369
14	26	91	36	16	281
15	27	93	18	8	453
16	28	95	20	9	103
17	29	97	16	7	41
18	30	99	31	14	22
19	31	101	2	1	19
20	32	102	2	1	43

THE SUM OF LxMx = .660

r = -.036

1980/81 NGUNI DAM

LIFE TABLE FOR A COHORT HATCHED IN WEEK 13

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	13	8	2573	1000	0
1	14	11	129	50	0
2	15	20	73	28	0
3	16	34	61	24	0
4	17	46	0	0	0
5	18	53	11	4	0
6	19	59	23	9	0
7	20	65	45	17	242
8	21	70	70	27	203
9	22	74	58	22	253
10	23	78	33	13	304
11	24	82	74	29	335
12	25	86	31	12	369
13	26	88	32	12	184
14	27	91	29	11	453
15	28	93	20	8	103
16	29	95	16	6	41
17	30	97	31	12	22
18	31	99	27	10	18
19	32	101	2	1	43
20	33	102	2	1	46

THE SUM OF LxMx = .423

r = -.073

LIFE TABLE FOR A COHORT HATCHED IN WEEK 14

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	14	8	3102	1000	0
1	15	11	157	51	0
2	16	20	140	45	0
3	17	34	0	0	0
4	18	46	8	3	0
5	19	53	15	5	0
6	20	59	37	12	0
7	21	65	42	14	203
8	22	70	67	22	175
9	23	74	33	10	304
10	24	78	78	25	229
11	25	82	42	14	369
12	26	86	48	15	184
13	27	88	22	7	297
14	28	91	37	12	103
15	29	93	16	5	41
16	30	95	31	10	22
17	31	97	27	9	18
18	32	99	32	10	42
19	33	101	2	1	46
20	34	102	0	0	19

THE SUM OF LxMx = .277

r = -.110

LIFE TABLE FOR A COHORT HATCHED IN WEEK 15

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	15	8	3504	1000	0
1	16	11	227	65	0
2	17	20	0	0	0
3	18	34	3	1	0
4	19	46	5	1	0
5	20	53	40	11	0
6	21	59	112	32	0
7	22	65	63	18	175
8	23	70	71	20	210
9	24	74	78	22	229
10	25	78	51	14	252
11	26	82	64	18	184
12	27	86	33	9	297
13	28	88	34	10	68
14	29	91	36	10	41
15	30	93	31	9	22
16	31	95	27	8	18
17	32	97	32	9	42
18	33	99	23	7	44
19	34	101	0	0	19
20	35	102	1	0	27

THE SUM OF LxMx = .243

r = -.126

LIFE TABLE FOR A COHORT HATCHED IN WEEK 16

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	16	8	4818	1000	0
1	17	11	0	0	0
2	18	20	8	2	0
3	19	34	32	7	0
4	20	46	83	17	0
5	21	52	173	36	0
6	22	58	181	37	0
7	23	63	91	19	210
8	24	68	183	38	158
9	25	72	38	8	252
10	26	75	85	18	126
11	27	79	52	11	203
12	28	81	34	7	68
13	29	83	40	8	27
14	30	85	79	16	14
15	31	87	83	17	12
16	32	89	96	20	27
17	33	91	12	2	44
18	34	92	13	3	19
19	35	93	12	2	26
20	36	94	9	2	32

THE SUM OF LxMx = .184

r = -.157

LIFE TABLE FOR A COHORT HATCHED IN WEEK 17

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)

THE SUM OF LxMx = .000 (No DATA)

LIFE TABLE FOR A COHORT HATCHED IN WEEK 18

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	18	8	1674	1000	0
1	19	11	167	100	0
2	20	20	247	148	0
3	21	34	606	362	0
4	22	46	343	205	0
5	23	52	184	110	0
6	24	58	183	109	0
7	25	63	128	77	175
8	26	68	123	73	87
9	27	72	52	31	203
10	28	75	118	71	46
11	29	79	116	70	18
12	30	81	79	47	14
13	31	83	83	50	12
14	32	85	96	57	27
15	33	87	79	47	29
16	34	89	74	44	12
17	35	91	12	7	26
18	36	92	9	5	32
19	37	93	19	11	25
20	38	94	20	12	119

THE SUM OF LxMx = .374

r = -.089

LIFE TABLE FOR A COHORT HATCHED IN WEEK 19

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	19	8	4832	1000	0
1	20	11	437	90	0
2	21	20	310	64	0
3	22	34	719	149	0
4	23	46	224	46	0
5	24	52	214	44	0
6	25	58	187	39	0
7	26	63	123	25	87
8	27	68	111	23	141
9	28	72	89	18	46
10	29	75	155	32	18
11	30	79	188	39	10
12	31	81	83	17	12
13	32	83	96	20	27
14	33	85	79	16	29
15	34	87	74	15	12
16	35	89	78	16	17
17	36	91	9	2	32
18	37	92	19	4	25
19	38	93	20	4	119
20	39	94	25	5	187

THE SUM OF LxMx = .105

r = -.165

1980/81 NGUNI DAM

LIFE TABLE FOR A COHORT HATCHED IN WEEK 20

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	20	8	4162	1000	0
1	21	11	461	111	0
2	22	20	321	77	0
3	23	34	449	108	0
4	24	46	216	52	0
5	25	52	210	51	0
6	26	58	126	30	0
7	27	63	111	27	141
8	28	68	127	31	32
9	29	72	116	28	18
10	30	75	251	60	10
11	31	79	186	45	8
12	32	81	96	23	27
13	33	83	79	19	29
14	34	85	74	18	12
15	35	87	78	19	17
16	36	89	69	17	21
17	37	91	19	4	25
18	38	92	20	5	119
19	39	93	25	6	187
20	40	94	32	8	135

THE SUM OF LxMx = .111

r = -.150

LIFE TABLE FOR A COHORT HATCHED IN WEEK 21

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	21	8	3371	1000	0
1	22	11	219	65	0
2	23	20	236	70	0
3	24	34	355	105	0
4	25	46	164	49	0
5	26	52	143	42	0
6	27	58	114	34	0
7	28	63	127	38	32
8	29	68	144	43	13
9	30	72	188	56	10
10	31	75	248	74	8
11	32	79	221	66	19
12	33	81	79	23	29
13	34	83	74	22	12
14	35	85	78	23	17
15	36	87	69	21	21
16	37	89	60	18	17
17	38	91	20	6	119
18	39	92	25	7	187
19	40	93	32	9	135
20	41	94	21	6	194

THE SUM OF LxMx = .107

r = -.137

LIFE TABLE FOR A COHORT HATCHED IN WEEK 22

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	22	8	2634	1000	0
1	23	11	204	78	0
2	24	20	165	63	0
3	25	34	460	175	0
4	26	46	118	45	0
5	27	52	132	50	0
6	28	58	60	23	0
7	29	63	144	55	13
8	30	68	215	82	7
9	31	72	186	71	8
10	32	75	295	112	19
11	33	79	176	67	20
12	34	81	74	28	12
13	35	83	78	30	17
14	36	85	69	26	21
15	37	87	60	23	17
16	38	89	69	26	78
17	39	91	25	9	187
18	40	92	32	12	135
19	41	93	21	8	194
0	42	0	0	0	0

THE SUM OF LxMx = .140

r = -.125

1980/81 NGUNI DAM

LIFE TABLE FOR A COHORT HATCHED IN WEEK 23

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	23	8	2513	1000	0
1	24	11	188	75	0
2	25	20	203	81	0
3	26	34	215	86	0
4	27	46	126	50	0
5	28	52	68	27	0
6	29	58	94	37	0
7	30	63	215	85	7
8	31	68	196	78	6
9	32	72	221	88	19
10	33	75	234	93	20
11	34	79	161	64	8
12	35	81	78	31	17
13	36	83	69	28	21
14	37	85	60	24	17
15	38	87	69	28	78
16	39	89	84	33	122
17	40	91	32	13	135
18	41	92	21	8	194
0	42	0	0	0	0
0	43	0	0	0	0

THE SUM OF LxMx = .161

r = -.119

LIFE TABLE FOR A COHORT HATCHED IN WEEK 24

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	24	8	3164	1000	0
1	25	11	189	60	0
2	26	20	159	50	0
3	27	34	238	75	0
4	28	46	53	17	0
5	29	52	101	32	0
6	30	58	70	22	0
7	31	63	196	62	6
8	32	68	226	71	13
9	33	72	176	55	20
10	34	75	215	68	8
11	35	79	150	47	12
12	36	81	69	22	21
13	37	83	60	19	17
14	38	85	69	22	78
15	39	87	84	26	122
16	40	89	77	24	89
17	41	91	21	7	194
0	42	0	0	0	0
0	43	0	0	0	0
0	44	0	0	0	0

THE SUM OF LxMx = .126

r = -.138

LIFE TABLE FOR A COHORT HATCHED IN WEEK 25

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	25	8	1984	1000	0
1	26	11	182	92	0
2	27	20	151	76	0
3	28	33	49	25	0
4	29	45	47	24	0
5	30	51	63	32	0
6	31	57	72	36	0
7	32	62	193	97	13
8	33	66	137	69	14
9	34	70	109	55	6
10	35	73	150	75	12
11	36	75	100	50	14
12	37	78	116	58	11
13	38	80	56	28	78
14	39	82	42	21	122
15	40	83	77	39	89
16	41	85	32	16	127
0	42	0	0	0	0
0	43	0	0	0	0
0	44	0	0	0	0
0	45	0	0	0	0

THE SUM OF LxMx = .150

r = -.133

1980/81 NGUNI DAM

LIFE TABLE FOR A COHORT HATCHED IN WEEK 26

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	26	8	1213	1000	0
1	27	11	122	100	0
2	28	20	22	18	0
3	29	33	54	44	0
4	30	45	23	19	0
5	31	51	64	52	0
6	32	57	62	51	0
7	33	62	147	121	14
8	34	66	111	92	6
9	35	70	107	88	8
10	36	73	150	123	14
11	37	75	77	64	11
12	38	78	64	53	53
13	39	80	69	57	122
14	40	82	39	32	89
15	41	83	63	52	127
0	42	0	0	0	0
0	43	0	0	0	0
0	44	0	0	0	0
0	45	0	0	0	0
0	46	0	0	0	0

THE SUM OF LxMx = .245

r = -.101

LIFE TABLE FOR A COHORT HATCHED IN WEEK 27

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	27	8	1524	1000	0
1	28	11	14	9	0
2	29	20	17	11	0
3	30	33	22	15	0
4	31	45	20	13	0
5	32	51	52	34	0
6	33	57	48	31	0
7	34	62	117	77	6
8	35	66	114	75	8
9	36	70	128	84	10
10	37	73	116	76	11
11	38	75	43	28	53
12	39	78	80	53	84
13	40	80	53	35	89
14	41	82	32	21	127
0	42	0	0	0	0
0	43	0	0	0	0
0	44	0	0	0	0
0	45	0	0	0	0
0	46	0	0	0	0
0	47	0	0	0	0

THE SUM OF LxMx = .143

r = -.148

LIFE TABLE FOR A COHORT HATCHED IN WEEK 28

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	28	8	481	1000	0
1	29	11	15	32	0
2	30	20	2	4	0
3	31	33	33	68	0
4	32	45	9	18	0
5	33	51	41	85	0
6	34	57	28	58	0
7	35	62	119	248	8
8	36	66	156	324	10
9	37	70	75	155	8
10	38	73	64	133	53
11	39	75	54	111	84
12	40	78	43	89	61
13	41	80	42	87	127
0	42	0	0	0	0
0	43	0	0	0	0
0	44	0	0	0	0
0	45	0	0	0	0
0	46	0	0	0	0
0	47	0	0	0	0
0	48	0	0	0	0

THE SUM OF LxMx = .392

r = -.077

1980/81 NGUNI DAM

LIFE TABLE FOR A COHORT HATCHED IN WEEK 29

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	29	8	202	1000	0
1	30	11	3	13	0
2	31	20	15	76	0
3	32	33	4	20	0
4	33	45	9	44	0
5	34	51	24	118	0
6	35	57	25	125	0
7	36	62	161	799	10
8	37	66	72	359	8
9	38	70	33	163	37
10	39	73	80	398	84
11	40	75	29	142	61
12	41	78	30	151	87
0	42	0	0	0	0
0	43	0	0	0	0
0	44	0	0	0	0
0	45	0	0	0	0
0	46	0	0	0	0
0	47	0	0	0	0
0	48	0	0	0	0
0	49	0	0	0	0

THE SUM OF LxMx = .716

r = -.030

LIFE TABLE FOR A COHORT HATCHED IN WEEK 30

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	30	8	184	1000	0
1	31	11	5	29	0
2	32	20	8	44	0
3	33	33	9	51	0
4	34	45	5	27	0
5	35	51	21	114	0
6	36	57	27	147	0
7	37	62	75	405	8
8	38	66	23	125	37
9	39	70	36	195	58
10	40	73	43	233	61
11	41	75	20	110	87
0	42	0	0	0	0
0	43	0	0	0	0
0	44	0	0	0	0
0	45	0	0	0	0
0	46	0	0	0	0
0	47	0	0	0	0
0	48	0	0	0	0
0	49	0	0	0	0
0	50	0	0	0	0

THE SUM OF LxMx = .428

r = -.080

1981/82. NGUNI DAM. TRAP RESULTS.

LIFE TABLE FOR A COHORT HATCHED IN WEEK 1

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	1	8	238	1000	0
1	2	11	7	31	0
2	3	20	11	45	0
3	4	34	14	58	0
4	5	47	8	36	0
5	6	56	14	57	0
6	7	62	5	22	682
7	8	67	8	31	1100
8	9	72	5	19	1841
9	10	76	6	24	2470
10	11	80	11	45	1850
11	12	84	7	29	1015
12	13	88	11	48	1312
13	14	91	3	14	1042
14	15	93	0	1	243
15	16	94	0	1	403
16	17	94	0	1	270
17	18	94	0	1	326
18	19	95	0	1	106
19	20	95	0	1	62
20	21	95	0	0	23

THE SUM OF LxMx = 3.353

r = .115

LIFE TABLE FOR A COHORT HATCHED IN WEEK 2

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	2	8	556	1000	0
1	3	11	16	28	0
2	4	20	13	24	0
3	5	34	13	23	0
4	6	45	9	16	0
5	7	53	11	20	0
6	8	59	17	30	0
7	9	65	21	37	1275
8	10	70	11	19	1710
9	11	74	15	28	1266
10	12	79	19	34	694
11	13	83	12	22	1312
12	14	86	16	29	683
13	15	89	3	5	159
14	16	89	2	3	264
15	17	90	2	4	177
16	18	90	0	0	326
17	19	91	0	1	106
18	20	91	0	1	62
19	21	92	0	0	23
20	22	92	0	0	69

THE SUM OF LxMx = 1.895

r = .064

LIFE TABLE FOR A COHORT HATCHED IN WEEK 3

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	3	8	718	1000	0
1	4	11	20	28	0
2	5	20	19	27	0
3	6	31	17	23	0
4	7	40	13	19	0
5	8	49	18	26	0
6	9	56	15	21	0
7	10	62	16	22	1710
8	11	67	28	38	877
9	12	71	23	32	694
10	13	76	24	33	898
11	14	80	34	47	467
12	15	82	4	6	159
13	16	83	3	4	264
14	17	84	4	6	177
15	18	85	2	3	214
16	19	86	3	4	69
17	20	87	4	6	40
18	21	88	2	2	15
19	22	88	2	2	45
20	23	89	2	3	280

THE SUM OF LxMx = 1.505

r = .041

1981/82 NGUNI DAM

LIFE TABLE FOR A COHORT HATCHED IN WEEK 4

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	4	8	574	1000	0
1	5	11	58	102	0
2	6	18	9	15	0
3	7	26	12	20	0
4	8	35	22	38	0
5	9	44	16	28	0
6	10	52	14	24	0
7	11	58	27	47	0
8	12	63	24	42	481
9	13	68	19	34	622
10	14	72	52	91	467
11	15	75	9	16	109
12	16	76	7	13	181
13	17	78	9	15	121
14	18	79	7	13	146
15	19	80	7	12	47
16	20	81	8	13	40
17	21	83	3	6	15
18	22	84	4	6	45
19	23	86	4	6	280
20	24	87	7	12	297

THE SUM OF LxMx = .979

r = -.002

LIFE TABLE FOR A COHORT HATCHED IN WEEK 5

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	5	8	830	1000	0
1	6	10	12	15	0
2	7	14	6	8	0
3	8	21	8	9	0
4	9	30	12	14	0
5	10	39	9	11	0
6	11	46	20	25	0
7	12	52	17	20	0
8	13	57	8	10	0
9	14	62	25	30	323
10	15	65	11	13	75
11	16	67	9	11	125
12	17	69	5	6	84
13	18	71	10	12	146
14	19	72	12	14	47
15	20	74	24	29	28
16	21	77	18	22	10
17	22	79	8	9	31
18	23	81	6	7	280
19	24	84	9	11	297
20	25	86	9	11	336

THE SUM OF LxMx = .251

r = -.089

LIFE TABLE FOR A COHORT HATCHED IN WEEK 6

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	6	8	344	1000	0
1	7	10	6	18	0
2	8	14	7	22	0
3	9	21	6	17	0
4	10	30	9	26	0
5	11	38	19	55	0
6	12	44	10	28	0
7	13	49	7	20	0
8	14	55	16	47	0
9	15	58	7	20	0
10	16	61	9	26	125
11	17	63	6	18	84
12	18	65	11	31	101
13	19	67	16	47	33
14	20	69	29	84	19
15	21	73	24	68	10
16	22	75	11	31	31
17	23	78	15	43	192
18	24	81	12	34	297
19	25	84	10	30	336
20	26	87	3	9	1716

THE SUM OF LxMx = .568

r = -.031

1981/82 NGUNI DAM

LIFE TABLE FOR A COHORT HATCHED IN WEEK 7

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	7	8	167	1000	0
1	8	10	12	74	0
2	9	14	2	9	0
3	10	21	6	38	0
4	11	28	9	53	0
5	12	34	11	66	0
6	13	40	5	29	0
7	14	46	7	43	0
8	15	50	6	38	0
9	16	53	6	36	0
10	17	55	5	32	0
11	18	58	9	52	0
12	19	60	13	78	33
13	20	63	36	216	19
14	21	67	35	212	7
15	22	71	14	82	31
16	23	74	19	111	192
17	24	78	18	105	203
18	25	82	13	75	336
19	26	85	4	22	1716
20	27	87	2	10	3247

THE SUM OF LxMx = 1.472

r = .020

LIFE TABLE FOR A COHORT HATCHED IN WEEK 8

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	8	8	349	1000	0
1	9	10	9	24	0
2	10	14	5	15	0
3	11	20	6	18	0
4	12	26	8	22	0
5	13	33	3	9	0
6	14	39	14	39	0
7	15	43	5	14	0
8	16	46	3	10	0
9	17	49	4	11	0
10	18	52	9	27	0
11	19	54	9	24	0
12	20	58	23	66	0
13	21	63	41	117	7
14	22	67	19	55	21
15	23	71	20	57	192
16	24	75	20	57	203
17	25	80	13	37	230
18	26	83	4	12	1716
19	27	86	2	5	3247
20	28	88	1	3	1382

THE SUM OF LxMx = .737

r = -.017

LIFE TABLE FOR A COHORT HATCHED IN WEEK 9

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	9	8	1008	1000	0
1	10	10	56	55	0
2	11	14	4	4	0
3	12	18	7	7	0
4	13	25	5	5	0
5	14	31	14	13	0
6	15	36	4	4	0
7	16	39	3	3	0
8	17	42	4	4	0
9	18	46	11	10	0
10	19	48	9	9	0
11	20	53	22	22	0
12	21	59	28	27	0
13	22	63	22	21	21
14	23	67	18	18	133
15	24	72	23	23	203
16	25	77	13	12	230
17	26	81	5	5	1716
18	27	85	2	2	3247
19	28	87	1	1	1382
20	29	88	1	1	1664

THE SUM OF LxMx = .276

r = -.072

1981/82 NGUNI DAM

LIFE TABLE FOR A COHORT HATCHED IN WEEK 10

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	10	8	1212	1000	0
1	11	9	81	67	0
2	12	13	5	4	0
3	13	17	5	4	0
4	14	23	9	7	0
5	15	28	4	3	0
6	16	32	3	3	0
7	17	36	4	3	0
8	18	39	13	11	0
9	19	42	10	8	0
10	20	47	22	18	0
11	21	54	25	21	0
12	22	59	23	19	0
13	23	64	21	17	133
14	24	69	27	22	141
15	25	75	14	12	230
16	26	79	5	4	1174
17	27	83	2	2	3247
18	28	86	1	1	1382
19	29	87	1	1	1664
20	30	89	1	0	405

THE SUM OF LxMx = .217

r = -.090

LIFE TABLE FOR A COHORT HATCHED IN WEEK 11

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	11	8	1410	1000	0
1	12	9	35	25	0
2	13	13	4	3	0
3	14	17	7	5	0
4	15	22	5	3	0
5	16	26	3	2	0
6	17	30	6	4	0
7	18	34	14	10	0
8	19	37	8	5	0
9	20	43	23	16	0
10	21	50	26	19	0
11	22	56	25	17	0
12	23	61	21	15	133
13	24	67	31	22	141
14	25	73	15	11	230
15	26	78	5	4	1174
16	27	82	3	2	3247
17	28	85	1	1	1382
18	29	86	1	1	1664
19	30	88	1	0	405
20	31	89	0	0	470

THE SUM OF LxMx = .203

r = -.099

LIFE TABLE FOR A COHORT HATCHED IN WEEK 12

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	12	8	839	1000	0
1	13	9	16	19	0
2	14	13	5	6	0
3	15	17	9	10	0
4	16	22	3	4	0
5	17	26	7	9	0
6	18	30	13	16	0
7	19	34	8	10	0
8	20	40	20	24	0
9	21	47	26	32	0
10	22	53	26	31	0
11	23	59	21	25	0
12	24	65	32	39	141
13	25	72	15	18	230
14	26	77	6	7	1174
15	27	81	3	4	3247
16	28	84	1	2	1382
17	29	86	1	1	1664
18	30	88	1	1	405
19	31	89	0	0	470
20	32	90	0	0	175

THE SUM OF LxMx = .334

r = -.071

1981/82 NGUNI DAM

LIFE TABLE FOR A COHORT HATCHED IN WEEK 13

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	13	8	1331	1000	0
1	14	9	21	16	0
2	15	13	6	5	0
3	16	17	6	4	0
4	17	22	8	6	0
5	18	26	12	9	0
6	19	30	7	5	0
7	20	36	17	13	0
8	21	44	28	21	0
9	22	51	23	17	0
10	23	57	21	15	0
11	24	64	34	25	141
12	25	70	14	11	230
13	26	76	6	4	1174
14	27	80	3	3	3247
15	28	83	2	1	1382
16	29	85	1	1	1664
17	30	87	1	0	405
18	31	89	0	0	470
19	32	90	0	0	115
20	33	91	0	0	503

THE SUM OF LxMx = .227

r = -.103

LIFE TABLE FOR A COHORT HATCHED IN WEEK 14

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	14	8	1101	1000	0
1	15	9	39	36	0
2	16	13	4	4	0
3	17	18	8	8	0
4	18	23	13	12	0
5	19	27	6	5	0
6	20	33	16	15	0
7	21	41	28	25	0
8	22	49	18	17	0
9	23	55	22	20	0
10	24	62	31	28	141
11	25	69	14	12	159
12	26	75	6	6	1174
13	27	79	4	4	2221
14	28	82	2	1	1382
15	29	85	1	1	1664
16	30	86	1	1	405
17	31	88	0	0	470
18	32	89	0	0	115
19	33	90	0	0	503
20	34	91	0	0	225

THE SUM OF LxMx = .244

r = -.105

LIFE TABLE FOR A COHORT HATCHED IN WEEK 15

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	15	8	197	1000	0
1	16	9	14	71	0
2	17	13	6	30	0
3	18	18	32	164	0
4	19	25	15	74	0
5	20	35	17	85	0
6	21	43	28	142	0
7	22	50	20	104	0
8	23	56	21	108	0
9	24	63	33	165	141
10	25	70	14	71	159
11	26	75	6	30	1174
12	27	80	4	19	2221
13	28	83	2	8	1382
14	29	85	1	5	1664
15	30	87	1	3	405
16	31	88	0	1	470
17	32	89	0	1	115
18	33	90	0	0	503
19	34	91	0	1	225
20	35	91	0	0	0

THE SUM OF LxMx = 1.331

r = .023

1981/82 NGUNI DAM

LIFE TABLE FOR A COHORT HATCHED IN WEEK 16

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	16	8	256	1000	0
1	17	9	51	200	0
2	18	13	24	95	0
3	19	18	6	24	0
4	20	25	12	49	0
5	21	35	27	106	0
6	22	43	14	56	0
7	23	50	18	69	0
8	24	58	26	101	0
9	25	66	13	50	159
10	26	72	7	29	1174
11	27	77	5	19	2221
12	28	81	3	10	1382
13	29	83	1	4	1664
14	30	85	1	3	405
15	31	87	0	1	470
16	32	88	0	2	115
17	33	90	0	0	0
18	34	90	0	1	225
19	35	91	0	0	0
20	36	91	0	0	0

THE SUM OF LxMx = 1.080

r = .006

LIFE TABLE FOR A COHORT HATCHED IN WEEK 17

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	17	8	215	1000	0
1	18	9	33	156	0
2	19	13	5	21	0
3	20	18	4	16	0
4	21	26	18	85	0
5	22	35	10	44	0
6	23	43	13	60	0
7	24	52	20	95	0
8	25	61	14	66	159
9	26	69	11	49	813
10	27	74	6	27	2221
11	28	78	6	29	946
12	29	81	1	6	1664
13	30	83	1	4	405
14	31	85	0	2	470
15	32	87	0	2	115
16	33	88	0	0	0
17	34	89	0	1	147
18	35	90	0	1	94
19	36	90	0	0	0
20	37	91	0	0	0

THE SUM OF LxMx = 1.497

r = .037

LIFE TABLE FOR A COHORT HATCHED IN WEEK 18

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	18	8	227	1000	0
1	19	9	9	40	0
2	20	13	2	9	0
3	21	18	5	24	0
4	22	26	5	20	0
5	23	35	17	73	0
6	24	45	14	62	0
7	25	56	16	70	0
8	26	64	13	59	813
9	27	71	8	35	2221
10	28	75	7	32	946
11	29	79	2	10	1139
12	30	81	1	5	405
13	31	83	0	2	470
14	32	85	1	3	115
15	33	87	0	0	0
16	34	88	0	1	147
17	35	88	0	1	94
18	36	89	0	1	223
19	37	90	0	0	338
20	38	90	0	0	0

THE SUM OF LxMx = 1.704

r = .053

1981/82 NGUNI DAM

LIFE TABLE FOR A COHORT HATCHED IN WEEK 19

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	19	8	98	1000	0
1	20	10	4	36	0
2	21	13	3	34	0
3	22	18	0	4	0
4	23	26	11	112	0
5	24	38	8	85	0
6	25	50	12	121	0
7	26	59	12	122	0
8	27	67	12	122	1538
9	28	72	8	83	946
10	29	76	3	26	1139
11	30	79	2	25	277
12	31	81	0	5	470
13	32	84	1	7	115
14	33	85	0	0	0
15	34	86	0	4	147
16	35	87	0	2	94
17	36	88	0	2	223
18	37	89	0	1	338
19	38	89	0	3	143
20	39	90	0	4	36

THE SUM OF LxMx = 3.074

r = .117

LIFE TABLE FOR A COHORT HATCHED IN WEEK 20

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	20	8	65	1000	0
1	21	10	4	60	0
2	22	13	0	0	0
3	23	18	3	39	0
4	24	29	4	67	0
5	25	43	7	108	0
6	26	54	10	154	0
7	27	62	14	217	1538
8	28	68	11	170	655
9	29	72	3	46	1139
10	30	76	3	45	277
11	31	79	2	29	322
12	32	81	1	11	115
13	33	83	0	0	0
14	34	84	0	7	147
15	35	85	0	5	94
16	36	86	0	4	223
17	37	87	0	1	338
18	38	88	0	6	143
19	39	89	0	8	36
0	40	0	0	0	0

THE SUM OF LxMx = 5.242

r = .194

LIFE TABLE FOR A COHORT HATCHED IN WEEK 21

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	21	8	18	1000	0
1	22	10	0	0	0
2	23	13	1	71	0
3	24	21	3	185	0
4	25	34	9	483	0
5	26	47	7	401	0
6	27	57	16	908	0
7	28	64	13	714	655
8	29	69	6	350	788
9	30	72	3	187	277
10	31	76	2	125	322
11	32	79	1	73	79
12	33	81	0	0	0
13	34	82	0	27	147
14	35	83	0	18	94
15	36	84	0	18	223
16	37	85	0	5	338
17	38	86	0	25	143
18	39	87	1	31	36
0	40	0	0	0	0
0	41	0	0	0	0

THE SUM OF LxMx = 8.570

r = .250

1981/82 NGUNI DAM

LIFE TABLE FOR A COHORT HATCHED IN WEEK 22

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	22	8	37	1000	0
1	23	10	0	9	0
2	24	15	3	91	0
3	25	27	13	355	0
4	26	41	4	103	0
5	27	53	17	462	0
6	28	60	11	300	655
7	29	65	8	201	788
8	30	70	4	108	192
9	31	74	3	67	322
10	32	77	2	40	79
11	33	79	1	24	226
12	34	81	1	16	147
13	35	82	0	10	94
14	36	83	0	10	223
15	37	84	0	3	338
16	38	85	1	13	143
17	39	86	1	17	36
0	40	0	0	0	0
0	41	0	0	0	0
0	42	0	0	0	0

THE SUM OF LxMx = 4.145

r = .183

LIFE TABLE FOR A COHORT HATCHED IN WEEK 23

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	23	8	318	1000	0
1	24	11	15	46	0
2	25	20	16	50	0
3	26	33	1	4	0
4	27	46	17	55	0
5	28	54	9	29	0
6	29	60	6	19	788
7	30	65	5	16	192
8	31	70	3	10	223
9	32	73	2	6	79
10	33	76	1	3	226
11	34	78	1	3	101
12	35	79	1	2	65
13	36	81	0	1	223
14	37	82	0	0	338
15	38	83	1	2	143
16	39	84	1	2	36
0	40	0	0	0	0
0	41	0	0	0	0
0	42	0	0	0	0
0	43	0	0	0	0

THE SUM OF LxMx = .225

r = -.179

LIFE TABLE FOR A COHORT HATCHED IN WEEK 24

X	WEEK	SIZE	No. SURV.	Lx	Mx (*100)
0	24	8	312	1000	0
1	25	11	19	59	0
2	26	20	2	5	0
3	27	33	6	19	0
4	28	44	7	22	0
5	29	51	5	15	0
6	30	57	12	37	0
7	31	62	4	13	223
8	32	67	4	14	54
9	33	71	1	4	226
10	34	73	1	4	101
11	35	75	1	3	65
12	36	76	3	10	152
13	37	78	1	2	231
14	38	79	3	10	98
15	39	81	1	3	36
0	40	0	0	0	0
0	41	0	0	0	0
0	42	0	0	0	0
0	43	0	0	0	0
0	44	0	0	0	0

THE SUM OF LxMx = .084

r = -.214
