MONITORING THE CONSERVATION STATUS AND DIVERSITY OF FISH ASSEMBLAGES IN THE MAJOR RIVERS OF THE KRUGER NATIONAL PARK

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DECLARATION

I declare that this thesis is my own, unaided work. It is being submitted for the Degree of Doctor of Philosophy in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other university.

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ABSTRACT

Environmental management for the purpose of conserving biotic diversity entails a universal problem. Diversity from all levels (genes to ecosystems) is a concept that does not translate easily into measurable goals. It is difficult to manage for a goal that cannot be measured, and impossible to monitor what cannot be measured. Without monitoring, the achievement of goals cannot be assessed. This study set out, using Kruger National Park rivers as the field site, to overcome this problem and advance the science of monitoring diverse fish assemblages by identifying methods of data collection, analysis and interpretation that would be appropriate for assessing the achievement of conservation objectives. Two approaches were used:

Firstly, goals pertaining to the distribution of fish in rivers of the Kruger National Park were proposed, with changes resulting from anthropogenic modifications of the aquatic environment considered undesirable. A >35% change in number of localities at which a species was collected signified a significant change in distribution. Testing goal achievement necessitated establishment of causes for distribution changes. This entailed description of the environmental preferences of fish, with three communities (rapids, pools, marginal areas) being described. Changes in the aquatic environment readily explained most long-term changes in the distribution of fish species. These were increased severity of low flows; high solute and suspended solid concentrations; episodic pollution events; artificial barriers to migration; and changes in aquatic plant distribution. Decline in the conservation status of fish communities, indicated by undesirable changes in the distribution of species, was greatest in the Luvuvhu River (12 species), followed by the Olifants (10 species), Letaba (8 species), Crocodile (6 species) and Sabie (2 species) rivers.

The second approach entailed evaluation of six methods of analysis of change in the diversity of fish assemblages (informal description of species abundance; length frequency distribution; alpha-diversity indices; frequency abundance models; condition factors; beta-diversity ordinations) to identify methods appropriate for efficient monitoring. The combination of methods which came closest to filling the criteria of providing interpretable information for assessing the achievement of conservation goals were the informal description of species abundances and the fitting of species abundance models. Application of these methods, together with assessment of species distribution changes, will enable efficient, goal- orientated, monitoring of diverse fish assemblages.

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TABLE OF CONTENTS

Page

ABSTRACT i
ACKNOWLEDGEMENTS ii
TABLE OF CONTENTS iii
LIST OF FIGURES vi
LIST OF TABLES x

1. INTRODUCTION TO THE STUDY 1
  1.1 INTRODUCTION 1
  1.2 REVIEW OF PERTINENT LITERATURE 4
    1.2.1 Describing the conservation status of fish communities 4
    1.2.2 Monitoring to evaluate the achievement of conservation goals 5
      1.2.2.1 Variability in the physical and chemical environment of rivers 6
      1.2.2.2 Spatial and temporal variability in fish assemblages 12
      1.2.2.3 Conservation objectives and operational goals 15
      1.2.2.4 Biotic diversity and its measurement 16
      1.2.2.5 Summary and study approach 24
  1.3 STUDY AREA 27
    1.3.1 Locality 27
    1.3.2 Topography 27
    1.3.3 Climate 29
    1.3.4 Hydrology and development in the Luvuvhu River catchment 30
    1.3.5 Hydrology and development in the Letaba River catchment 35
    1.3.6 Hydrology and development in the Olifants River catchment 38
    1.3.7 Hydrology and development in the Sabie River catchment 42
    1.3.8 Hydrology and development in the Crocodile River catchment 45
2. THE CONSERVATION STATUS OF FISH COMMUNITIES OF KNP RIVERS 49
  2.1 INTRODUCTION 49
  2.2 MATERIALS AND METHODS 58
    2.2.1 Distribution of fish in KNP rivers 58
      2.2.1.1 Sample site selection 58
      2.2.1.2 Fish sampling methods 65
      2.2.1.3 Identification of fish species 69
      2.2.1.4 Describing long-term changes in the distribution of fish 69
    2.2.2 Environmental preferences of fish 71
      2.2.2.1 Description of geomorphological features 71
      2.2.2.2 Flow Velocity 71
      2.2.2.3 Turbidity 72
      2.2.2.4 Nature of the substratum 73
      2.2.2.5 Presence of aquatic plants 73
      2.2.2.6 Mathematical techniques to define the environmental preferences of fish 74

2.2.3 Environmental factors causative of fish distributional change 75
2.2.3.1 The effects of flow reductions on fish habitat availability 75
2.2.3.2 Physical and chemical water quality 83
2.2.3.3 The distribution of aquatic plants 85
2.3 RESULTS AND DISCUSSION 85
2.3.1 Changes in the distribution of fish species 85
2.3.2 Environmental preferences of fish species 90
2.3.2.1 Fish species occurrence in different geomorphological features 92
2.3.2.2 Fish species distribution in relation to water flow velocity 97
2.3.2.3 Fish species occurrence in relation to water turbidity 99
2.3.2.4 Fish species occurrence over different substrata 101
2.3.2.5 Fish species occurrence in relation to aquatic plants 105
2.3.2.6 Associations between fish species: defining fish communities 107
2.3.3 Environmental factors causative of fish distributional change 110
2.3.3.1 Habitat loss resulting from reductions in instream flow 111
2.3.3.2 Severity of low flows : frequency, duration and volume of flow 116
2.3.3.3 Physical and chemical water quality: potential effects on the distribution of fish 122
2.3.3.4 Changes in the distribution of aquatic plants: potential effects on fish distribution 131
2.3.3.5 Causes of changes in the distribution of fish in KNP rivers 133
2.3.4 Conservation status of fish communities in KNP rivers 144

3. ESTABLISHING THE CONCEPTUAL AND QUANTITATIVE BASIS FOR MONITORING THE DIVERSITY OF FISH ASSEMBLAGES 149
3.1 INTRODUCTION 149
3.2 MATERIALS AND METHODS 156
3.2.1 Sampling of fish communities 156
3.2.2 Descriptions of fish assemblage diversity 156
3.2.2.1 Length frequency distribution of fish populations 157
3.2.2.2 Description of fish community alpha-diversity using diversity indices 158
3.2.2.3 Description of fish community alpha-diversity using diversity models 162
3.2.2.4 Physical condition of species 167
3.2.2.5 Beta diversity 174
3.3 INFORMAL DESCRIPTIONS OF CHANGE IN THE ABUNDANCE OF FISH SPECIES (1987 to 1989) 177
3.3.1 Results 177
3.3.2 Discussion 184
3.4 LENGTH FREQUENCY DISTRIBUTION OF FISH POPULATIONS 189
3.4.1 Results and discussion 190
3.4.1.1 Minimum sample size for description of the length frequency distribution of fish populations 190
3.4.1.2 Length frequency distribution of selected fish species 192

3.5 ALPHA-DIVERSITY INDICES AS MEASURES OF CHANGE IN THE DIVERSITY OF FISH COMMUNITIES 208
3.5.1 Results and discussion 210
3.5.1.1 Minimum sampling intensity for describing alpha-diversity of fish communities 210
3.5.1.2 Cost-efficiency of monitoring programme using diversity indices 215
3.5.1.3 Interpretability of diversity index results 215
3.5.1.4 Determination of operational goals for index values 221
3.5.2 Summary and conclusions 221
3.6 SPECIES ABUNDANCE MODELS AS MEASURES OF FISH COMMUNITY CHANGE 223
3.6.1 Results and discussion 223
3.6.1.1 Interpretability of species abundance models 223
3.6.1.2 Determination of operational goals for species abundance models 232
3.6.1.3 General discussion and conclusions 234
3.7 CONDITION FACTORS AS MEASURES OF COMMUNITY CHANGE 237
3.7.1 Results 237
3.7.1.1 Condition of fish species in the Luvuvhu River 238
3.7.1.2 Condition of fish species in the Letaba River 243
3.7.1.3 Condition of fish species in the Olifants River 244
3.7.1.4 Condition of fish species in the Sabie River 245
3.7.1.5 Condition of fish species in the Crocodile River 246
3.7.1.6 Comparisons of the condition of fish in relatively pristine and perturbed rivers 246
3.7.1.7 Summary 247
3.7.2 Discussion 247
3.7.3 Summary and conclusions 249
3.8 BETA-DIVERSITY OF FISH COMMUNITIES 250
3.8.1 Results and discussion 252
3.9 SUMMARY AND CONCLUSIONS 259
4. MONITORING FISH ASSEMBLAGES: SUMMARISING DISCUSSION AND CONCLUSIONS 261
4.1 WHY MONITORING OF FISH ASSEMBLAGES IN KNP RIVERS SHOULD BE UNDERTAKEN 261
4.2 GUIDE-LINES ON A COST-EFFECTIVE MONITORING PROGRAMME 262
4.2.1 Hierarchical characterization of biotic diversity 263
4.2.2 Methods of fish collection 268
4.2.3 Selection of sample localities 269
4.2.4 Frequency of sampling 270
4.2.5 Termination of monitoring 270
4.3 RECENT CONCEPTS IN MONITORING FISH ASSEMBLAGES: BIOTIC INTEGRITY 272
4.4 SUMMARY AND CONCLUSIONS 275

LIST OF FIGURES

Page

Figure 1.1 Relationship between response and recovery period and sensitivity to disturbance for different spatial scales associated with rivers systems (Redrawn from Naiman *et al.* 1992)....14

Figure 1.2 Interdependence of information needs and analytical approaches to determine the conservation status of fish communities....25

Figure 1.3 Catchment areas of major rivers flowing through the Kruger National Park showing places and features mentioned in the text....28

Figure 1.4 Total monthly flow in the Luvuvhu (a), Letaba (b), Olifants (c), Sabie (d) and Crocodile (e) rivers measured a Department of Water Affairs and Forestry gauging stations closest to the western boundary of the Kruger National Park....31

Figure 2.1 Framework for designing a monitoring programme. Arrows indicate direction of steps that would be taken and revision stages where necessary (redrawn from Spellerberg (1991))....50

Figure 2.2 Framework for designing a wetland monitoring programme (redrawn from Finlayson (1996))....51

Figure 2.3 Proposed framework for monitoring the status of fish assemblages. Arrows indicate direction of steps....52

Figure 2.4 Map of Kruger National Park indicating localities used to sample fish communities....59

Figure 2.5 Ordination using correspondence analysis of the frequency of occurrence of fish species in the habitats rapids, deep pools (> 1m), shallow pools (< 1m), channel and pool margins, and secondary channels and backwaters....93

Figure 2.6 Ordination using Detrended Correspondence Analysis of sample sites in the Luvuvhu (a), Letaba (b), Olifants (c), Sabie (d) and Crocodile (e) rivers based on the presence and absence of fish species, to distinguish between different habitat types....94

Figure 2.7 Ordination using correspondence analysis of sample sites in the Luvuvhu (a), Letaba (b), Olifants (c), Sabie (d) and Crocodile (e) rivers based on the presence and absence of fish species, to distinguish between different habitat types....95

Figure 2.8 Ordination using correspondence analysis of the frequency of occurrence of fish species under different flow conditions (strong, medium, low and none)....98

Figure 2.9 Ordination using correspondence analysis of the frequency of occurrence of fish species in waters of different turbidities (very turbid, turbid, clear)....100

Figure 2.10 Ordination using correspondence analysis of the frequency of occurrence of fish species in sample sites with different substrata (bedrock, stone, stone & gravel, gravel, mud) to distinguish the habitat preferences of species 102

Figure 2.11 Ordination using correspondence analysis of the frequency of occurrence of fish in sample sites with different substrata (see Figure 3.5), displaying the feeding strategy of different fish species 104

Figure 2.12 Ordination using correspondence analysis of the frequency of occurrence of fish species in sample sites which differ with respect to the relative proximity of submerged and emergent aquatic plants (present at sample site, not present in sample site though in close proximity - fringing, and completely absent from sample site) 106

Figure 2.13 Species composition of fish communities in the major rivers of the Kruger National Park. Categorisation of species undertaken on the basis of the environmental preferences of species, with descriptions of the environmental preferences of species given in brackets obtained from the literature 109

Figure 2.14 Long-term changes in the severity of low flows in Kruger National Park rivers indicated by changes in the frequency with which low flows have been below minimum flow required to achieve flow parameter (optimum wetted perimeter, average 20cm depth, average 30cm s^{-1} velocity) (4.1a to 4.1e), duration of low flow periods (4.1f to 4.1j), and flow volume expressed as percentage below the minimum flow calculated to achieve minimum flow parameter for each river (41.k to 4.1o) 117

Figure 2.15 Cross-sectional profile of the channel of the Luvuvhu River at sample localities number 4 (Bobomenie) (a), and sample locality number 3 (Hapi) (b) 136

Figure 2.16 Conceptual plans of the major causes of change in the distribution of fish species in the major rivers of the Kruger National Park 143

Figure 3.1 Rank abundance plots illustrating the typical shape of four species abundance models: geometric-series, log-series, log-normal and broken-stick (redrawn from Magurran, 1988) 164

Figure 3.2 Plots of the mean percentage similarity (solid lines), 95% confidence limits (dotted lines) and maximum and minimum values (dashes) of the length frequency distribution with increasing sample size for (a) *Micralestes acutidens* (1mm length classes), (b) *Labeo rosae* (10mm length classes), (c) *Oreochromis mossambicus* (5mm length classes) and (d) *Oreochromis mossambicus* (10mm length classes) 191

Figure 3.3 Length frequency distribution of *Brycinus imberi* in the Letaba River sampled in the winter 1987 (a), winter 1988 (b) and winter 1989 (c) sample periods 193

Figure 3.4 Length frequency distribution of *Labeo rosae* in the Letaba River sampled in the winter 1987 (a), summer 1987/88 (b), winter 1988 (c) and winter 1989 (d) sample periods 196

Figure 3.5 Length frequency distribution of *Oreochromis mossambicus* in the Letaba River sampled in the winter 1987 (a), winter 1988 (b) and winter 1989 (c) sample periods........ 198

Figure 3.6 Length frequency distribution of *Barbus marequensis* in the Olifants River sampled in the winter 1987 (a), winter 1988 (b) and winter 1989 (c) sample periods........ 201

Figure 3.7 Length frequency distribution of *Labeo molybdinus* in the Olifants River sampled in the winter 1987 (a), winter 1988 (b) and winter 1989 (c) sample periods........ 202

Figure 3.8 Length frequency distribution of *Barbus viviparus* in the Sabie River sampled in the winter 1987 (a), winter 1988 (b) and winter 1989 (c) sample periods........ 204

Figure 3.9 Length frequency distribution of *Micralestes acutidens* in the Sabie River sampled in the winter 1987 (a), summer 1987/88 (b), winter 1988 (c) and winter 1989 (d) sample periods........ 205

Figure 3.10 The number of fish species sampled (species richness), and alpha-diversity index values for increasing sampling intensity of fish communities sampled in deep pools in the Letaba River during 1988 (a) and 1989 (b)........ 211

Figure 3.11 The number of fish species sampled (species richness), and alpha-diversity index values for increasing sampling intensity of fish communities sampled in rapids in the Sabie River (a) and Olifants River (b)........ 212

Figure 3.12 The number of fish species sampled (species richness), and alpha-diversity index values for increasing sampling intensity of fish communities sampled in marginal habitats in the Olifants River (a) and Sabie River (b)........ 214

Figure 3.13 Species richness (a, e, i), number of individuals sampled (b, f, j), and index values for the log-series-alpha (c, g, k) and Berger-Parker (d, h, l) indices for fish communities in the Luvuvhu (plus), Letaba (star), Olifants (open square), Sabie (cross) and Crocodile (closed square) rivers. Abundance values expressed as CPUE, with sampling effort being ten seine net pulls in deep pools, and 60 minutes electro-fishing in rapids and marginal habitats........ 216

Figure 3.14 Rank abundance plots for fish communities in deep pools, rapids and marginal habitats in the Luvuvhu (a, b, c), Letaba (d, e, f), Olifants (g, h, i) Sabie (j, k, l) and Crocodile (m, n, o) rivers. Fish communities sampled in 1987 indicated by solid lines, 1988 by dotted lines, and 1989 by dashed lines........ 225

Figure 3.15 Condition factor analysis in successive sample years (1987 to 1989) of twenty eight abundant fish in KNP rivers, showing the mean and 95% confidence limits........ 239

Figure 3.16 Ordination display of changes in the beta-diversity of hypothetical samples indicating changes in the position of a sample within the ordination space with (I) the gain (or loss) of bi-habitat generalists, (II) the gain (or loss) of multi-habitat generalists, (III) the gain (or loss) of bi-habitat generalists simultaneously with the gain (or loss) of multi-habitat generalists, and (IV) the gain (or loss) of habitat specialists simultaneously with the gain (or loss) of bi-habitat and multi-habitat generalists 254

Figure 3.17 Ordination display of changes in the beta-diversity of a hypothetical sample with the addition of different combinations of habitat generalist and habitat specialist species. Equal weighting on all species. Open squares = samples; closed squares = idealized communities 256

Figure 3.18 Ordination display of changes in the beta-diversity of a hypothetical sample with the addition of different combinations of habitat generalist and habitat specialist species. Weighting on species, where habitat specialists = 3, bi-habitat generalists = 2, multi-habitat generalists = 1. Open squares = samples; closed squares = idealized communities 257

LIST OF TABLES

Page

Table 2.1 Summary of procedures undertaken in this study to monitor the conservation status of fish communities in the major rivers of the Kruger National Park.......56

Table 2.2 Location and description of sample sites used during fish surveys in the Luvuvhu River.......60

Table 2.3 Location and description of sample sites used during fish surveys in the Letaba River.......61

Table 2.4 Location and description of sample sites used during fish surveys in the Olifants River.......62

Table 2.5 Location and description of sample sites used during fish surveys in the Sabie River.......63

Table 2.6 Location and description of sample sites used during fish surveys in the Crocodile River.......64

Table 2.7 Occurrence of fish at different sample localities in the Kruger National Park as determined in the 1960s (after Piennar 1968, 1978, *pers comm.*; Gaigher 1969) and 1980s (this study), where x = 1960s surveys only; + = 1980s surveys only; and o = both 1960s and 1980s surveys.......86

Table 2.8 Categorisation of fish species in the major rivers of the Kruger National park according to their change in distribution between surveys undertaken in the 1960s, and 1990s.......88

Table 2.9 Summary of the habitat preferences of freshwater fish which occur in eastern Transvaal rivers as described in 41 published papers. Values indicate the number of references in which particular habitat preferences were described. Data after Copley (1958); Greenwood (1958); Jackson (1961a; 1961b; 1962); Crass (1964); Groenewald (1964); Okedi (1965); Jubb (1965; 1968, 1979); Le Roux & Steyn (1968); Wager (1968); Gaigher (1969, 1970, 1973); Ribbink (1971); Fryer & Iles (1972); Kenmuir (1973); Bruton & Boltt (1975); Bell-Cross (1976); Mitchell (1976); Blaber (1978); Bowen (1978); Bruton (1978, 1979); Kok *et al.* (1978); Pienaar (1978); Caulton (1979); Bruton & Kok (1980); Hecht (1980a, 1980b); Kleynhans (1980, 1982, 1984); Skelton & Cambray (1981); Bruton *et al.* (1982); Bruton & Jackson (1983); Cambray (1984); White *et al.* (1984); Merron *et al.* (1985); Skelton *et al.* (1985); Skelton (1986). As several authors did not distinguish between pools and marginal areas these have been combined under the heading of pools.......91

Table 2.10 Minimum flow (cumecs) required to achieve flow parameters (optimum wetted perimeter, average 20cm depth, average 30cm s^{-1} velocity) in rapids and channels at selected localities in the Luvuvhu, Letaba, Olifants, Sabie and Crocodile rivers.......112

Table 2.11 Estimations of the minimum non-consumptive baseflow requirements of the major rivers of the Kruger National Park undertaken in this and other studies.......114

Table 2.12 Water quality parameters as measured at the Department of Water Affairs and Forestry gauging stations closest to the western boundary of the Kruger National Park indicating median values (and range), in mg/l (unless stated otherwise) 123

Table 2.13 Maximum and minimum values for the water quality parameters (water temperature, dissolved oxygen concentration, conductivity, pH and turbidity) measured in the Luvuvhu, Letaba, Olifants, Sabie and Crocodile rivers during Winter 1987, Summer 1987/1988, Winter 1988 and Winter 1989 sample periods 124

Table 3.1a Regression analysis constants, from regression of fork length versus wet body mass, for fish collected in the Luvuvhu River during Winter 1987, 1988 and 1989 surveys 168

Table 3.1b Regression analysis constants, from regression of fork length versus wet body mass, for fish collected in the Letaba River during Winter 1987, 1988 and 1989 surveys 169

Table 3.1c Regression analysis constants, from regression of fork length versus wet body mass, for fish collected in the Olifants River during Winter 1987, 1988 and 1989 surveys 170

Table 3.1d Regression analysis constants, from regression of fork length versus wet body mass, for fish collected in the Sabie River during Winter 1987, 1988 and 1989 surveys 171

Table 3.1e Regression analysis constants, from regression of fork length versus wet body mass, for fish collected in the Crocodile River during Winter 1987, 1988 and 1989 surveys 172

Table 3.2 Number of specimens (CPUE) captured in deep pools (number per 10 seine net pulls), rapids (number per 60 minutes electro-fishing) and marginal habitats (number per 60 minutes electro-fishing) in the Luvuvhu River during 1987, 1988 and 1989 178

Table 3.3 Number of specimens (CPUE) captured in deep pools (number per 10 seine net pulls), rapids (number per 60 minutes electro-fishing) and marginal habitats (number per 60 minutes electro-fishing) in the Letaba River during 1987, 1988 and 19890 179

Table 3.4 Number of specimens (CPUE) captured in deep pools (number per 10 seine net pulls), rapids (number per 60 minutes electro-fishing) and marginal habitats (number per 60 minutes electro-fishing) in the Olifants River during 1987, 1988 and 1989 180

Table 3.5 Number of specimens (CPUE) captured in deep pools (number per 10 seine net pulls), rapids (number per 60 minutes electro-fishing) and marginal habitats (number per 60 minutes electro-fishing) in the Sabie River during 1987, 1988 and 1989 181

Table 3.6 Number of specimens (CPUE) captured in deep pools (number per 10 seine net pulls), rapids (number per 60 minutes electro-fishing) and marginal habitats (number per 60 minutes electro-fishing) in the Crocodile River during 1987, 1988 and 1989 182

Table 3.7 Growth of *Oreochromis mossambicus* in various water bodies in southern Africa. All lengths are expressed as TL with original values given by Bruton and Allanson (1974), Hecht (1980a) and Krupka (1974) being converted from SL to TL using the formula TL = 18.417 + 1.212(SL) after Kok (1980). Values from Le Roux (1961) were read from growth curves and converted from inches to millimetres (M = male; F = Female)........ 199

Table 3.8 Chi-squared test results for the fit of observed fish species abundances from deep pools in the Luvuvhu, Letaba, Olifants and Sabie rivers to species abundances predicted by the geometric-series, log-series, log-normal and broken-stick abundance models........ 226

Table 3.9 Chi-squared test results for the fit of observed fish species abundances from rapids in the Luvuvhu, Olifants, Sabie and Crocodile rivers to species abundances predicted by the geometric-series, log-series, log-normal and broken-stick abundance models........ 227

Table 3.10 Chi-squared test results for the fit of observed fish species abundances from marginal habitats in the Luvuvhu, Letaba, Olifants, Sabie and Crocodile rivers to species abundances predicted by the geometric-series, log-series, log-normal and broken-stick abundance models........ 228

CHAPTER 1

INTRODUCTION

1.1 INTRODUCTION TO THE STUDY

Changes in the attributes of riverine fish assemblages (distribution and abundance of species, age structure of populations, physical dimensions of individuals) in response to both natural and anthropogenic changes in their environment have been documented in several countries (Welcomme 1979; Leidy and Fiedler 1985; Ross *et al.* 1985; Schlosser 1985; Moyle and Leidy 1992; Pusey *et al.* 1993) including South Africa (Hart and Allanson 1984; Day *et al.* 1986; Heeg *et al.* 1986; Merron *et al.* 1993). A properly designed monitoring programme will provide a means of describing the direction, extent and intensity of such biological changes (Hellawell 1978; Spellerberg 1991), and hence enable assessment of changes in the diversity and conservation status of assemblages (Meybeck *et al.* 1992).

Several authors have proposed frameworks for designing monitoring programmes (Macdonald and Grimsdell 1983; Maher and Norris 1990; Spellerberg 1991; Hellawell 1992) which emphasize the importance of identifying methods of collecting, analysing, interpreting and reporting data. The design of a biological monitoring programme can, however, be difficult to establish, particularly in rivers (Finlayson 1994). Difficulties encountered are frequently due to the absence of guidelines on how to measure and interpret changes in these highly dynamic systems. Although there has, in recent years, been a great deal of research effort directed towards developing appropriate techniques for monitoring ecological change in aquatic systems (Finlayson 1994), comparatively little attention has been given to the study of fish assemblages.

An array of monitoring techniques for measuring and expressing changes in the attributes of fish assemblages have been developed. These range from suborganism bioindicators such as the physical condition of individuals (Le Cren 1951), to indicators of the reproductive success of populations (Ricker 1975; Lagler 1978), and mathematical expressions of the relative abundance of species within communities (Whittaker 1972, 1977; Cody 1975). However, when designing a programme for monitoring ecological change, the choice of techniques is only one aspect of the process. Equally important, but infrequently done, the processes for utilizing and interpreting the data need to be defined (Finlayson 1994). Interpreting the significance of change is normally achieved by comparison against pre-established standards (Hellawell 1978), which, in conservation, reflect the desired state as outlined in conservation objectives (Mentis 1984).

The maintenance of biotic diversity and the natural functioning of ecosystems are implicit in the conservation directives of many prominent international conservation agencies (IUCN 1980a, 1991; WRI 1992), as well as the conservation authorities of countries such as the National Parks Board of South Africa (National Parks Board 1987). Maintaining biotic diversity is thus frequently the focus of actions directed towards the conservation of aquatic systems (O'Keeffe 1986a). Criticism has been levelled at the use of broad terms such as "maintenance of biotic diversity" as an objective for a holistic conservation policy because it provides little directive of the acceptable degree of change and how this should be determined (Mentis 1984). This criticism is particularly pertinent to the conservation of aquatic systems, where it is frequently difficult to distinguish between natural dynamism, and adverse biotic changes which typically result from changes in catchment landuse (Chutter *et al.* 1986). This creates a dilemma for nature conservationists, who value the preservation of natural communities (O'Keeffe *et al.* 1989), and yet are frequently unable to assess the significance of recorded changes and hence effectiveness of conservation actions.

The lack of guide-lines on how to describe and interpret changes in fish assemblages is possibly a consequence of the cyclical scientific interest in the science of monitoring (Hellawell 1992). Initial interest in monitoring, predominantly in the 1970s, led to the development of a range of techniques to measure change in the diversity of biotic assemblages. Subsequent disillusionment following the failure of many monitoring initiatives (Finlayson 1994), and hence progressive decline in monitoring activities (Hellawell 1992), resulted in a poor understanding of the cause and effect relationships between fish species and their environment. Consequently we know how to measure biotic diversity, but are frequently unable to interpret and report the data in a manner that enables management decisions to be taken and implemented in a timely manner. Thus although it is frequently emphasized that within a monitoring programme it is essential to have objectives which clearly define the level of acceptable change (Hellawell 1978, 1992; Macdonald and Grimsdell 1983; Mentis 1984; Smith 1985) in the monitoring of aquatic systems this is seldom achieved, except where physico-chemical aspects of water quality are the focus of the study (Finlayson 1994).

The revived interest in monitoring, promoted by greater awareness of environmental issues, has placed the onus on environmentalists to devise cost-effective strategies for describing and interpreting the significance of changes in the diversity and status of fish assemblages, thereby providing data that can be used to address management questions. The dearth of information on monitoring approaches would necessitate the establishment and testing of hypotheses on the direction, extent, intensity and causes of biotic changes before embarking on a full scale programme. A multidisciplinary research programme on the major rivers of the Kruger National Park (KNP) in South Africa provided an opportunity to promote understanding on how to monitor diverse fish communities through study of the effects of environmental change on the conservation status of fish communities, and evaluation of methods of assessing change in the diversity of fish assemblages.

Five major rivers flow through the KNP - Luvuvhu, Olifants and Letaba rivers of the Limpopo system, and the Sabie and Crocodile rivers of the Inkomati system. The portions of the major rivers which flow through the KNP are, as occurs with most large rivers in conservation areas, only small components of much larger aquatic systems (Sheldon 1988; Davies *et al.* 1993). Factors outside the boundaries of the conservation area influence the dynamics of the systems which results in conservation authorities having limited control over the detrimental elements of variability. Concerns have been expressed by conservation authorities about the effect that catchment development has had on the quantity and quality of water in KNP rivers and the conservation status of aquatic biota (Joubert 1985, 1986a, 1986b). These concerns were the initial driving force behind the initiation of the Kruger National Park Rivers Research Programme, which had the goal of developing means to predict the effect of changing flow régimes and water quality on KNP river systems, and using this as the basis for managing the allocation of water for ecological purposes (Breen *et al.* 1994). The objective of this study was to advance the science of monitoring diverse riverine fish assemblages by (i) describing long-term changes in the conservation status of fish communities in KNP rivers and (ii) evaluating sampling approaches and methods of data analysis used to determine the achievement of conservation objectives in terms of fish assemblages.

1.2 REVIEW OF PERTINENT LITERATURE

Issues reviewed below relate to the objectives of this study which are to describe the conservation status of fish communities in KNP rivers and establish a monitoring program to evaluate the achievement of conservation goals in terms of fish assemblages.

1.2.1 Describing the conservation status of fish communities.

Conservation status has become an omnibus term which, although widely used in conservation biology, has come to mean different things depending on the context in which it is used. Assessments of the conservation status of biomes, biogeographic areas or ecosystems typically entail descriptions of the environmental threats to classification units, and the land area which has been granted long-term conservation status (Hilton-Taylor and Le Roux 1989; Geldenhuys and MacDevette 1989; Cooper and Berruti 1989, Breen and Begg 1989). Procedures for describing the conservation status of rivers have been proposed by Macmillan (1983) and O'Keeffe *et al.* (1986), with conservation status being defined as "a measure of the importance of a river for conservation, and the extent to which it has been disturbed from its natural state" (O'Keeffe *et al.* 1987). Related procedures have been described by Rabie and Savage (1979), Collier and McColl (1992) and Collier (1993) who favour use of the terms "natural value" (Collier and McColl 1992; Collier 1993) and "aquatic natural area" (Rabie and Savage 1979) as opposed to conservation status. The objectives of these procedures are, however, similar to those of Macmillan (1983) and O'Keeffe *et al.* (1986), namely to classify rivers on the basis of the degree, or sensitivity to anthropogenic disturbances, and deviation from a natural state.

Implicit in all methods for describing the conservation status of rivers is the need to define change from a natural state. Data defining a natural state frequently does not exist, or is very limited (Danilewitz *et al.* 1988). Even where such data are available, a distinction needs to be made between natural disturbance régimes (Naiman *et al.* 1992) and anthropogenic disturbances. Limited understanding of these processes suggest that the subjectivity of such assessments is invariably high (Kleynhans 1994).

Several studies have attempted to describe the conservation status of freshwater fish, both in South Africa (Gaigher *et al.* 1980; Kleynhans 1986; Kleynhans and Engelbrecht 1988; Mayekiso and Hecht 1988; Skelton *et al.* 1995) and elsewhere in the world (Horwitz 1994; Mrakovcic *et al.* 1995; Rakaj and Fllogo 1995; Elvira 1995; Changeux and Pont 1995). A wide range of methodologies have been employed. These include assessments of change in distribution based on field surveys (Gaigher *et al.* 1980; Kleynhans 1986; Kleynhans and Engelbrecht 1988) and museum collections (Skelton *et al.* 1995). Comprehensive assessments of changes in the size and geographical distribution of populations, severity of habitat or other environmental disturbances, and level of protection due to conservation measures taken, have also been attempted (Skelton 1987; Mayekiso and Hecht 1988). Most studies, however, appear to broadly follow the International Union for Conservation of Nature and Natural Resources (IUCN) guide-lines for the description of threatened species (IUCN 1980b, 1986) with subjective categorisation of species as endangered, vulnerable or rare.

The lack of standardized methods for assessing the conservation status of a species, population or community, results in it being left up to the researcher to establish the most appropriate means of assessment and expression. A common theme to all measures of the conservation status of aquatic biota, however, as described for rivers above, is that they contain some measure or description of the level of change from a pristine condition. A common failing of most assessments is their subjectivity. They are basically expressions of one or more persons impressions (albeit frequently based on quantitative data) of the degree of environmental threat to a species, and necessity for conservation actions to ensure perpetuation. Confidence in such assessments would be dependant on the ability to convincingly describe changes in the distribution and/or abundance of species (using either historical data, or well motivated hypotheses of pristine conditions) and relate described changes to anthropogenic environmental disturbances. The primary motivation for this study was the concern amongst conservation authorities about change in the status of fish communities in KNP rivers. Consequently, in order to address this concern there was a need to describe (i) the development in river catchments and how this has affected river conditions, (ii) fish communities and how they have changed over recorded history, and (iii) environmental conditions which might indicate causal relationships.

1.2.2 Monitoring to evaluate the achievement of conservation goals

Monitoring is defined by Mentis (1984) as the maintenance of regular surveillance to test the null hypothesis of no change in predefined properties of a system which is vulnerable to impacts. There are two major issues contained within this definition that are briefly discussed below to provide background and motivation for approaches used in this study. These issues, along with a description of subjects reviewed are:

(i) Variability in the environment can have a significant effect on the distribution and abundance of fish species, with the purpose of a monitoring programme being to highlight such changes. Consequently, the types of environmental changes that can potentially affect fish communities are introduced below, as are the temporal and spatial scales of such changes.

(ii) Monitoring necessitates that goals detailing limits of change be predefined, and that the monitoring methods employed enable testing of the achievement of these goals. In this vein, the conservation objectives and goals pertaining to fish communities in KNP rivers are reviewed, along with analytical methods which could be used to test goal attainment.

1.2.2.1 Variability in the physical and chemical environment of rivers

Fluvial systems are dynamic, characterised by both short- and long-term changes in their physical and chemical qualities (Day *et al.* 1986). This dynamism influences the temporal and spatial abundance of aquatic biota, with important variables including instream flow, suspended particle loads, temperature, dissolved oxygen and solute concentrations (Calow and Petts 1992; Allan 1995).

Long-term variations in instream flow

"Instream flow" is defined as the amount of water in a channel as measured at a given time and place (Estes and Orsborn 1986). Long-term variations in instream flow of a river are caused primarily by climatic variation and by human modifications of the drainage basin. Tyson and Dyer (1978) have illustrated an 18-20 year wet and dry cycle in the summer rainfall region of South Africa, with corresponding variations in streamflow. Human effects on streamflow can be classified into two groups (Ward and Robinson 1990): (i) direct effects such as the construction of impoundments, abstractions for domestic supply and irrigation, and streamflow diversions, and (ii) indirect effects which change the conditions governing runoff formation in the river basin such as agricultural practices, deforestation, urbanization and drainage of wetlands.

There exist a vast literature on the physico-chemical and biological effects of anthropogenic modification of flow through either water abstraction, diversion or impoundment. The major consequences of flow modifications, and in particular impoundment, have been summarised by Ward and Stanford (1979), Ward *et al.* (1984), Petts (1984), Craig and Kemper (1987), Gore and Petts (1989) and Petts *et al.* (1989), with Davies and Day (1986) and Davies *et al.* (1993) providing a review of the consequences of flow regulation in southern African rivers. In brief, alterations in flow patterns can result in changes in the natural range of several physico-chemical factors (for example temperature, turbidity, turbulence, water level, light penetration, chemical and oxygen concentrations, pH), with resultant changes in the plant and animal life of the river. Impoundment and abstraction can significantly alter a river's natural periodicity of flow thereby decreasing the variability of hydrological and disturbance régimes. Environmental instability has long been recognised as an important determinant of the structure of communities (Thiery 1982), and increase in the predictability and hence stability of flow régimes has implication for both the physical and ecological functioning of rivers.

Numerous analytical techniques have been developed and applied in the United States of America to determine the instream flow requirement of fish (Wesche and Rechard 1980). These include the Tennant (Tennant 1976), Wetted Perimeter (Milhous 1978; Bovee and Milhous 1978), Habitat Retention (Nehring 1979) and Instream Flow Incremental Methodologies (IFIM) (Bovee and Milhous 1978; Bovee 1982). IFIM in particular is widely used in USA, to determine minimum acceptable flow for both aquatic invertebrates and fish (Allan 1995). This method has also been employed in a preliminary evaluation of the instream flow requirements of the Sabie River in KNP (Gore *et al.* 1992). IFIM, however, has been heavily criticised, particularly for poor testing of hydraulic simulations which are often difficult to calibrate (Mathur *et al.* 1985; Osborne *et al.* 1988). Further criticism is that there is little evidence for the assumption that generated values of weighted usable area and fish biomass are correlated (Morehardt 1986; Scott and Shirvell 1987). King and Tharme (1993) concluded that IFIM would largely be unsuitable for instream flow predictions in South African rivers, with a major limitation being the extensive time and expertise requirement to effectively operate the program modules.

Several locally derived methods of assessing the instream flow requirements of rivers have either been suggested, or are currently being developed (King and O'Keeffe 1989; Bruwer 1991a; O'Keeffe and Davies 1991; Arthington *et al.* 1992). Early instream flow assessments for KNP rivers tended to concentrate on the Sabie system (O'Keeffe and Davies 1991; Gore *et al.* 1992). The "Skukuza Method" (King and O'Keeffe 1989; Bruwer 1991a), however, has been applied to all five major rivers, and more recently the "Building Block Method" (King and Tharme 1993) has been applied to both the Luvuvhu (Louw 1996) and Letaba (Weston 1996) rivers in KNP. The Olifants and Crocodile rivers have received the least attention with respect to instream flow assessments for fish of other biota. Proposed modified flow régimes for all KNP rivers have yet to be realised by active management of water resources by river managers.

Despite decades of ichthyological work in southern Africa, the flow requirements of fish are poorly understood (Ferrar 1989). Instream flow assessments undertaken in South Africa are heavily reliant on the general knowledge, and best guess-work, of aquatic scientists (Bruwer 1991a; King and Tharme 1993; Louw 1996; Weston 1996). Research initiatives such as the KNP Rivers Research Programme, however, should ultimately produce more in-depth answers and guidance (King and Tharme 1993).

Suspended particles

Suspended particles are defined as fine grained materials, greater than 0.45μm in diameter, which are transported in suspension, with their weight supported by the upward component of fluid turbulence (Kirk 1985). Suspended particles can be either organic (pollen, micro-organisms, seeds) or inorganic (products of weathering) (Gippel 1989) though in African and Australian waters generally consist primarily of sediments (mostly silts and clays) eroded in the upstream basin (Kirk 1985). High sediment particle loads in South African rivers are, in most cases, associated with periods of high discharge (Chutter 1969), though other factors such as time elapsed since a previous storm event and source of material may also be important.

Erosion of land surfaces and subsequent transport of eroded materials in rivers is a natural process (Webb and Walling 1992). Several anthropogenc processes, however, can accelerate erosion and result in increased loads of suspended solids in rivers. These include poor land-use practices such as overgrazing, non-contour ploughing and removal of riparian vegetation (McColl and Hughes 1981), mining (Herbert and Richards 1991) and construction work (Barton 1977; Taylor and Roff 1986; Ogbeibu and Victor 1989). Elevated suspensoid levels can also result from the release of industrial and urban effluents (Davis *et al.* 1988; CSIR 1991) and the management of impoundments (Gray and Ward 1982).

Most rivers in South Africa carry high sediment loads (Rooseboom undated, 1978). The friable nature of many of the soils and rocks of the subcontinent, combined with severe anthropogenic disturbances have exacerbated sediment yield to many rivers (Davies *et al.* 1993).

The presence of suspended particles in river water has both direct and indirect effects on aquatic life. The effects of suspensoids on fish are known to be either detrimental or beneficial (Blaber and Blaber 1980; Blaber 1981), depending primarily on their concentration, as well as the timing and duration of exposure (Bruton 1985). Suspensoids impair the visual clarity of water (Kirk 1985) which can indirectly affect fish by reducing light penetration and hence photosynthesis of micro- and macrophytes, resulting in reduced food and cover availability, and reduction in the visibility of pelagic food (Bruton 1985; Scholtz *et al.* 1988). Direct detrimental consequences of high suspensoid concentrations on fish include reduced availability of benthic food due to smothering, and clogging of gillrakers and gill filaments (Bruton 1985).

Low concentrations of suspended particles, resulting in moderate turbidities (<15 NTU) are, however, thought to be beneficial for most fish species (Bruton 1985), providing juvenile fish with protection from piscivorous birds and fish, and increasing habitat diversity.

Water temperature

Temperature is an important physical characteristic of river water, influencing the distribution and ecology of aquatic organisms (Rose 1967). Most rivers exhibit seasonal, daily and diel changes in water temperature affected by meteorological conditions (Ward 1985). Water temperatures also respond to changing flow conditions, with low flows increasing both water temperature maxima and the range of diel fluctuation (Ward 1985).

Several anthropogenic causes of change in water temperature in southern African rivers have been described by Dallas and Day (1993). Causes potentially effective in rivers in Mpumalanga and the Northern Province include stream regulation (Pitchard and Visser 1975; Ward and Stanford 1982) and reduced shading through loss of riparian vegetation (Graynorth 1979). Changes in water temperature which are unrelated to natural variation can have a significant detrimental effects on fish, including alterations in growth, reproduction, fry survival, and egg hatchability (Brungs 1971), and in extreme cases, mortality resulting from metabolic malfunctions (Cherry and Cairns 1982).

Relatively little is known about the thermobiology of southern African fish species, with only the commercially exploited cichlids *Oreochromis mossambicus* (Peters, 1852) and *Tilapia rendalli* (Boulenger, 1896) being well researched (Caulton 1978, 1979). Preliminary guide-lines on temperature ranges for the protection of aquatic biota in the Luvuvhu River (17 to 30°C) and Sabie River (8 to 25°C) have been proposed by Moore *et al.* (1991).

Dissolved oxygen concentration

The concentration of dissolved oxygen in water is one of the most important abiotic factors relating to the survival of aquatic organisms (Allan 1993). The dissolved oxygen concentration of river water is subject to physical, chemical and biological controls, including elevation, volume of flow and turbulence, water temperature, and rates of respiration and photosynthesis (Wetzel and Likens 1979).

Many rivers exhibit an annual régime of dissolved oxygen which is inversely related to an annual cycle in water temperature (Ball and Bahr 1975), with lower concentrations in the warmer summer months. Dissolved oxygen concentrations in water also fluctuate diurnally in response to diel temperature changes, photosynthesis by plants, and respiratory activity of aquatic organisms (Lloyd and Swift 1976; Gower 1980) with minimum saturation levels occurring at night. Nocturnal reductions in oxygen saturation of up to 50% have been reported in European rivers with extensive benthic algal growth (Butcher *et al.* 1937 cited in Calow and Petts 1992).

Changes in dissolved oxygen concentrations unrelated to natural variations can result from increases in aquatic plants (and hence photosynthesis and respiratory activity) due to nutrient enrichment (Lloyd and Swift 1976; Simonsen and Harremoës 1978; Gower 1980), as well as the addition of organic (BOD) and inorganic (COD) oxygen-demanding effluents (Dratnal and Kasprzak 1980; Okoronkwo and Odeyemi 1985; Hellawell 1986).

The dissolved oxygen requirements of southern African fish have been poorly researched with the exception of the commercially exploited cichlids (Caulton 1979). Concentrations below 4 mg l^{-1} are, however, thought to be detrimental to most freshwater fish species (Davis 1975; Kempster *et al.* 1980).

Solute concentrations

A variety of different parameters can be used to describe the solute load of a river, and include major cation and anion concentrations, trace metals, organic constituents and pesticide levels (Dallas and Day 1993; Allan 1995).

Rivers derive their solute loads from a variety of sources, including the atmosphere (Walling 1980; Cryer 1986; Meybeck *et al.* 1989), chemical reactions between water, rock and soil minerals (Walling 1980), biological processes (Fiebig *et al.* 1990) and anthropogenic inputs (Wetzel and Likens 1979; Allan 1995). The solute content and composition of rivers varies greatly in space and time depending on the particular sources, processes and pathways that are dominant in a given drainage basin (Webb and Walling 1992; Allan 1995). Recent studies of the major ion chemistry of South African rivers (King *et al.* 1992) show strong geographical patterns which can be linked to underlying geology. In lowveld rivers in Mpumalanga and the Northen Province there is a dominance by several ions (Ca^{2+}, Mg^{2+}, HCO_3^-, Na^+, Cl^-) (Day and King 1995) with both geology and rainfall governing water quality.

Solute concentrations in rivers are strongly influenced by temporal changes in discharge levels. Most rivers exhibit decreasing total dissolved solute concentrations with increasing flow, as runoff is translated more rapidly to the river channel and has less opportunity for solute pickup (Walling and Webb 1983; Bishop *et al.* 1990). At low flows, solute concentrations are high because of evapotranspirational losses, and runoff is supplied from groundwater where water has a long residence time and solute release is promoted (Walling and Webb 1983). Both seasonal and longer term flow reductions can result in increases in solute concentrations (Sutcliffe and Carrick 1973; Houston and Brooker 1981). Long-term changes in water chemistry may reflect either natural, or more likely, man-induced changes in the processes occurring in the soil and vegetation of the river basin (Allan 1995).

The effects of changing water chemistry on southern African fish species is poorly understood. Nevertheless, guide-lines have been proposed on the expected tolerance limits of fish to several ions and trace metals (Kempster *et al.* 1980; Moore *et al.* 1991).

Summary

The major issue forthcoming from the above brief review is that the physical and chemical environment in rivers is in a continual state of flux, as a result of both natural processes and man's development of catchment basins. Changes in the physical environment vary spatially, temporally and quantitatively, and can affect fish assemblages in these same scales and dimensions. The effect of changes in the physical and chemical environment of southern African rivers on fish communities is however still poorly understood.

1.2.2.2 Spatial and temporal variability in fish assemblages

Spatial and temporal variability in the diversity of fish assemblages is governed by both abiotic (hydrology, water chemistry) and biotic (predation, competition, disease, parasitism) processes within the aquatic environment (Grossman *et al.* 1982; Herbold 1984; Rahel *et al.* 1984; Yant *et al.* 1984; Grossman *et al.* 1985). Disruption of these processes within a river, as a consequence of either natural environmental fluctuations or human activities within the river basin, can have profound cumulative effects on fish (Harris 1988; Moyle and Williams 1990).

The effect of environmental disturbances on fish assemblages depends on the timing (especially in relation to recruitment dynamics), frequency and magnitude of the events, and the ability of different species to persist in unfavourable conditions (Freeman *et al.* 1988). Unfortunately, there has been very little research to quantify the effects of environmental disturbances (both natural and man-induced) on the spatial and temporal variability of fish assemblages in South African rivers (O'Keeffe 1986b). Most studies have been devoted to fish distribution *vide*: Crass (1960, 1964); Jubb (1967); Gaigher (1973); Cambray (1977, 1982); Pienaar (1978); Gaigher *et al.* 1980; Kleynhans (1980); Skelton and Cambray (1981); Skelton (1986a, 1986b), though some have attempted to describe the spatial and temporal effects of anthropogenic disturbances *vide*: Cambray (1984), Skelton (1987). Understanding of these processes is derived mainly from studies of North American and European river systems, with resultant theories on how environmental units (microhabitats, habitats, reach, river, drainage basin) in rivers, and in turn fish assemblages, are spatially and temporally influenced by development of river catchments (Frissell *et al.* 1986).

Frissell *et al.* (1986) utilised ideas from hierarchy theory (Allen and Starr 1982) to illustrate a continuum of habitat sensitivity to disturbance and recovery time (Figure 1.1) in which microhabitats in rivers are the most susceptible to disturbance, and drainage basins the least. It is also implied that environmental disturbances which affect smaller-scale habitat characteristics may not affect larger-scale system characteristics, whereas large disturbances can directly influence smaller-scale features of rivers (Naiman *et al.* 1992). On a temporal scale, disturbance in the smaller-scale environmental units in rivers (microhabitats, habitats) may disrupt the biotic community over the short term, though the system may recover quickly to pre-disturbance levels if the disturbance is limited in scope and intensity, (Niemi *et al.* 1990). The response time of large-scale environmental units (drainage basin, river) to disturbance is greater, as is the recovery period once environmental conditions are normalised.

Taking cognisance of the spatial and temporal scales of environmental units in rivers, and the manner in which they are correlated with and influenced by development of the river catchment can influence decisions taken and conclusions reached during the design and interpretive phases of fluvial ecosystem structure and process studies. For example, on the basis of the Frissell *et al.* (1986) habitat sensitivity model, it could be concluded that monitoring of biological change in smaller-scale environmental units would provide greater resolution of the effects of low-key or proximate disturbances. Such small-scale relationships, however, may not necessarily maintain their predictive quality when extrapolated to larger scales (Noss 1990). Using a combination of small and large scales (for example, fish community diversity changes in different habitats throughout a river segment) may thus be appropriate in a monitoring program (Noss 1990), thereby obtaining the best mix of sensitivity and representativeness. A similar conclusion could be reached when one investigates the scale of effects of environmental processes on fish assemblages. The effect of biotic processes within the aquatic environment in structuring fish assemblages are frequently (though not exclusively) apparent at smaller spatial scales such as river reach, whereas the effects of abiotic processes are frequently apparent in larger spatial scales (Townsend 1989). Thus, using a combination of small and large spatial scales would appear appropriate to monitor change in the qualities of riverine fish assemblages (Noss 1990). Finally, it

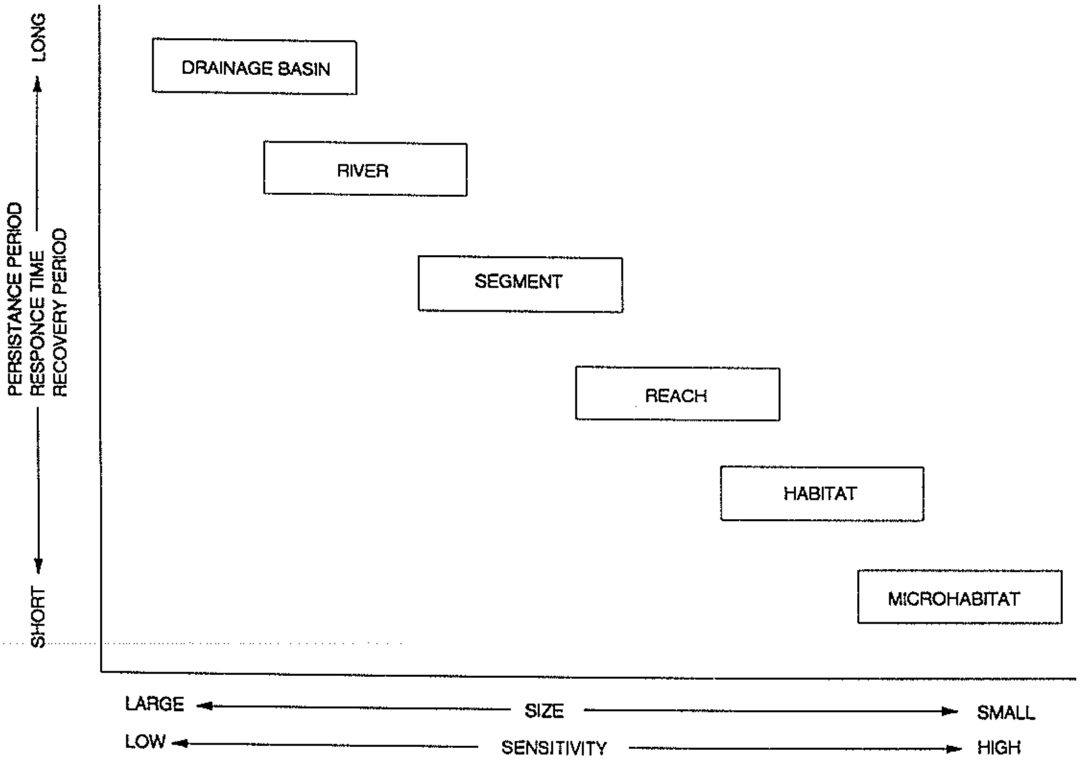

Figure 1.1 Relationship between response and recovery period and sensitivity to disturbance for different spatial scales associated with rivers systems (Redrawn from Naiman *et al.* 1992).

could be argued that the scale of study of biological change should be targeted at the level appropriate for management (Noss 1990). In the case of KNP rivers, this is "river segments", and the extrapolation of monitoring results to larger-scale units (river, drainage basin) would be inappropriate.

Regular measurement of change in the qualities of fish assemblages is important for determining the effects of environmental change caused by both natural events and human effects. Long-term data series are a partial solution to assessing the responses of fish to unpredictable disturbances or long-term environmental changes (Calow and Petts 1992). Alternatively, concurrent studies in systems with comparable habitats and communities can be used to better understand the effects of environmental disturbances (for example when different disturbances affect fish in subsets of the systems being monitored) (Calow and Petts 1992). The degree that the qualities of fish assemblages depart from a norm can serve as an indicator of environmental stress on the fish assemblage. Such norms are ideally phrased or quantified as operational goals (Mentis 1984), which in turn are based on the stated objectives for conservation and management of the river in question.

1.2.2.3 Conservation objectives and operational goals

The need for clearly stated objectives for conservation has been emphasized by Mentis (1984). The conservation objectives of the National Parks Board (National Parks Board 1987) have a universal frame of reference in that they are an endorsement of the objectives formulated by IUCN (1980a).

The objectives for conserving living resources are defined by IUCN (1980a) as:

(i) to maintain essential ecological processes and life support systems...;
(ii) to preserve genetic diversity...;
(iii) to ensure sustainable utilization of species and ecosystems.

The objectives of the IUCN are aimed at fostering sustainable development through the conservation of natural resources (IUCN 1980), and propose a framework which can be tailored by different countries or organisations to develop conservation principles and strategies appropriate to their specific circumstances.

Conservation principles for the KNP entail (Joubert 1986b):

(i) Preservation of the intactness of the individual components of the ecosystem.
(ii) Preservation of the dynamic nature of the interactions between the constituent components of the ecosystem.
(iii) Maintenance of natural cycles, which are an essential attribute of life.

For the purpose of evaluating the effect of environmental disturbances on fish assemblages, the above statements of intent of both the IUCN and the KNP suffer the drawback of being so generally stated that they are not amenable to quantification. Mentis (1984) argues at length on the necessity for the translation of objectives into precise goals, or alternatively rewriting in operational terms. The translation of IUCN objectives suggested by Mentis (1984) is "to maintain biotic diversity", which is compatible with the conservation strategy of the KNP which embodies "preservation of the qualities, interdependencies, and the structural and species diversity of aquatic ecosystems..." (Joubert 1986b).

It has been argued that the conservation objective "to maintain biotic diversity" embodies the IUCN objective of "maintenance of essential ecological process" (and possibly "preservation of the qualities of aquatic ecosystems" with respect to the KNP management strategy) (Mentis 1984). There has long been considered to exist a duality between biotic diversity and environmental conditions (Whittaker 1978), with biotic diversity being used to index environmental quality.

1.2.2.4 Biotic diversity and its measurement

A number of characterizations of the term biotic diversity, as a description of the variability of biological elements of the natural world, have been proposed. Early authors emphasized the variety of interrelated components (Whittaker 1972, 1977; Peet 1974; Cody 1975), which comprise:

(i) Structural diversity: both populations and communities have structural components such as size distribution and densities.
(ii) Intraspecific genetic diversity: genetic information contained in individuals and populations.
(iii) Species diversity: the variety and abundance of living organisms.

(iv) Ecosystem diversity: the variety of habitats, communities and ecological processes.

Noss (1990, 1994) provides a comparable, though broader description of the biotic components of biodiversity. Noss (1990, 1994) and later Karr (1993), however, have tended to differentiate more clearly than earlier authors between the range of organizational scales (genes, populations, communities and landscapes) which each have compositional, structural and functional attributes.

Biotic diversity is thus defined as the variety of the earths naturally occurring biological elements, which extend over a broad range of organizational scales from genes to populations, communities, ecosystems and landscapes (Karr 1993).

The multifaceted nature of biotic diversity results in it not being practical to regularly measure changes at all scales and levels in a cost-efficient monitoring programme. Indicators as measurable surrogates for environmental endpoints thus need to be selected (Noss 1990). Indicators must fit the purpose for monitoring (Noss 1990), which in this study is to assess change in the diversity of fish assemblages. Consequently, in this study, the aspects of landscape and ecosystem diversity are not dealt with directly, beyond identification of landscape processes and disturbances which potentially influence the diversity of fish assemblages. Ecosystem diversity and community diversity are generally considered to be correlated (Pielou 1975; Whittaker 1977; Statzner and Higler 1985) in that diverse communities are generally indicative of a diverse ecosystem. Thus, measures of community diversity could provide an index of ecosystem diversity.

Direct measurement of genetic diversity was also considered beyond the scope of this study, because of the complexity and expense of determinative methodologies (Mentis 1984; Noss 1990). The interrelation between different components of biotic diversity has been emphasized by several authors (Whittaker 1972; Peet 1974; Noss 1990). Thus monitoring the abundance (or indices of abundance) of individuals in populations is thought to provide an indirect means of measuring genetic diversity (Mentis 1984).

This study, thus, concentrated primarily on measurement of change in the population and community levels of biotic diversity. Indicators which have frequently been used to evaluate changes in the diversity of fish populations and communities are briefly reviewed below.

Population diversity

Monitoring the composition aspect of populations is generally undertaken by determining change in the absolute or relative abundance of individuals (Noss 1990, 1994). There are numerous studies undertaken in South Africa (Bok 1979; Hamman 1980; Gaigher *et al.* 1981; Cambray 1984; White *et al.* 1984; Merron *et al.* 1985) and elsewhere in the world (Kenmuir 1973, 1984; Hortle and Lake 1983; Udoidiong 1988; Kinsolving and Bain 1993) in which describe the abundance and distribution of fish as measures of the diversity of populations.

The structural and functional attributes of fish populations have been studied using length frequency distributions as a measure of age distribution, and condition factors. The study of length frequency distribution entails subjective assessment of length frequency histograms to describe the occurrence and abundance of different size classes (Ricker 1975). Knowledge of the growth rate of the species under investigation is used to assign ages to the different size classes, with the occurrence and relative size of age classes providing an indication of the reproductive competency and/or success of the population (Cushing 1981; Everhart and Youngs 1981; Gulland 1985). A proportionally large number of 0+ year old individuals would indicate successful reproduction in the year of assessment (Ricker 1975; Cushing 1981). One of the greatest limitations to the use of length frequency distributions in studies of South African freshwater fish is the poor understanding of the growth rate of most species (Skelton 1993).

Condition factors are either quantitative or qualitative descriptions of the fatness or "well-being" of either individuals or groups of fish (Le Cren 1951). The condition of fish is one of three components of the Index of Biotic Integrity (IBI) (Karr 1981; Fausch *et al.* 1990) that has been successfully applied to evaluate river health in both the United States of America (Plafkin *et al.* 1989; Fausch *et al.* 1990) and France (Oberdorff and Hughes 1992). Condition factors based on the mathematical relationship between the mass and length of individuals or groups of fish have previously been used to assess environmental stress on fish populations in southern Africa (Schoonbee *et al.* 1972; Kenmuir 1973; Marshall and Van der Heiden 1977;

Baird and Fourie 1978), with the inference of the lower the environmental stress, the higher the condition factor and hence better physical condition of the population.

Several methods have been described and used in the literature to enumerate or display, and hence compare, the condition of fish based on the length and mass of individuals (Le Cren 1951; Schoonbee *et al.* 1972; Kenmuir 1973; White *et al.* 1984). Of these methods, two basic groupings can be identified. The first entails variations of the allometric growth equation (M/cL^n where M = mass, L = length, c and n = regression constants). Either the product of the equation (Fulton 1911, cited in Ricker 1975; Le Cren 1951; Schoonbee *et al.* 1972; Baird and Fourie 1978), equation constants (Le Cren 1951), or direct plotting of the length-mass regression (White *et al.* 1984) have been used as a means of defining the physical condition of fish populations. The second type of condition factor, used by Kenmuir (1973) in a study of *Hydrocynus vittatus* Castelnau, 1861 populations in Lake Kariba, entailed calculation of the mean mass of fish falling within selected length groups.

All condition factors suffer from the criticism that the significance of change is frequently difficult to assess as results can be affected by both intrinsic (age, sex, maturity, racial variation in morphometrics) and extrinsic (time and method of sampling) factors that are not related to environmental stress (Le Cren 1951).

Despite the limitations of both length frequency distributions and condition factors, they continue to be used in studies of the diversity of fish populations, and hence their inclusion in this assessment of methods of monitoring change in the diversity of fish in KNP rivers.

Community diversity

Whittaker (1972, 1977) and Cody (1975) described two types of community diversity, each with a number of scales of measurement.

(i) Inventory diversity:

- point diversity - diversity within a sample
- alpha diversity - diversity within a habitat
- gamma diversity - diversity within a geographic area
- epsilon diversity - diversity within a region

(ii) Differentiation diversity:

- pattern diversity - diversity between samples
- beta diversity - diversity between habitats
- delta diversity - diversity between geographic areas

The terms alpha diversity and beta diversity are today almost synonymous with the terms inventory diversity and differentiation diversity, respectively (Mentis 1984; Bond 1989; Cowling *et al.* 1989). This reflects of the most frequently used scale of measurement of biotic diversity in environmental studies, namely the diversity of communities within and between habitats. A community can be defined at any size, scale or level within a hierarchy of habitats (Begon *et al.* 1986), consequently the scale of measurement of community diversity would be largely dictated by the study objectives. One of the objectives of this study was to identify changes in environmental (habitat) conditions which might indicate reasons for changes in the distribution and abundance of fish species. In order to achieve this it was necessary to identify fish communities in KNP rivers which consisted of species with similar habitat preferences and would thus respond in similar ways to changes in their environment. Consequently the scale of diversity measurement used in this study equate with Whittaker's (1977) alpha and beta diversity, therefore these terms are used forthwith.

Alpha diversity consists of three components (Peet 1974), namely (i) species richness or the number of species in the sampling unit, (ii) evenness or equitability or how equally abundant species are, and (iii) heterogeneity which is a combination of richness and equitability. Beta diversity in turn is a measure of the similarity of habitats, principally in terms of species richness, and sometimes abundance (Southwood 1980; Magurran 1988). The complexities involved in trying to incorporate these different component's biotic diversity into a single measure has contributed to the development of a wide array of analytical approaches, as discussed below.

Alpha-diversity indices as measures of community change

Diversity indices are commonly employed to characterise community diversity using a single number, with the intention of simplifying some of the complex properties of the structure and dynamics of communities (Dearden 1978). A variety of diversity indices have been proposed by various authors, from which two main groupings can be identified. These differ primarily in the relative weighting that they give to evenness and species richness (Magurran 1988).

There are two schools of thought on the validity and usefulness of diversity indices for evaluating change in communities. Several workers (Whittaker 1972; May 1975; Grieg-Smith 1983; Gotmark *et al.* 1986; Noss 1990) have questioned the ecological value of diversity indices. Southwood (1980) regards diversity indices as merely a "distraction rather than an asset in ecological analysis ... with the ecological insights gained not being proportional to the mathematical sophistication and complexity of the methods". These statements are based on Southwood's (1980) conclusion that neither theoretical studies, nor empirical studies on field data, have given much support to the value of the indices as a means of measuring diversity.

On the other hand, there are several studies where diversity indices have been successfully used to monitor and evaluate change in the diversity of fish communities *vide*: Bechtel and Copeland (1970); Gorman and Karr (1978); Udoidiong (1988); Penczak *et al.* (1995). Magurran (1988) reviewed the use of diversity indices in community studies, and concluded that they can be informative, and thus have a role in environmental assessment. The log-series-α and Berger-Parker indices, in particular, were considered to be valuable measures in assessment work (Magurran 1988). The interpretational pitfalls of many indices are now well known (Ludwig and Reynolds 1988), and their wide use in ecological studies is evidence of their importance in the understanding of community ecology.

Alpha-diversity models as measures of community change

The probability of all species within a community being equally abundant is unlikely, and it was during some of the early studies of the species-abundance relationship of communities (Fisher *et al.* 1943) that similar patterns of species abundances in different communities were observed. Further study of species-abundance relationships, niche competition and resource partitioning (Whittaker 1970, 1972; May 1975) has culminated in the development of numerous species abundance models, of which four are widely recognised. These are the geometric-series, logarithmic (or log) series, log-normal and MacArthur's broken-stick models (Magurran 1988).

One of the primary advantages of diversity models as a means of describing community diversity is that they incorporate all of the information on species abundance (Magurran 1988). Thus, diversity models are considered to provide the most complete mathematical description of species abundance data. This is a distinct advantage over indices of diversity which frequently involve a loss of information (James and Rathbun 1981). Consequently, the use of such models as a basis for examining community diversity has been strongly advocated by several workers (May 1975, 1981; Southwood 1980). The diversity of a community may thus be described by referring to the model which provides the closest fit to the observed pattern of species abundances (Southwood 1980; Magurran 1988).

Theoretical studies have indicated that communities with different species abundances can be characterized by differences in species richness and dominance, the number and severity of governing environmental conditions, degree of niche preemption and successional stage (Whittaker 1965, 1970, 1972; May 1974, 1975; Sugihara 1980).

The geometric-series pattern of species abundance is found primarily in species-poor communities, occurring under a harsh environmental régime or in the very early stages of a succession (Whittaker 1965, 1970, 1972). In such communities, niche preemption or unevenness is maximal, resulting in a few species being numerically dominant, with the remainder fairly uncommon (May 1975). In these communities, one invariably finds that only one or a few environmental factors dominate the ecology of the community (Whittaker 1972).

As succession proceeds, or as environmental conditions become less severe, species abundance patterns grade into those of a log-series, where species of intermediate abundance become more common. Several workers (Southwood 1980; Magurran 1988) make the distinction between the log-series and the geometric-series distribution models. However, as May (1975) notes, the geometric-series and log-series models are closely related. Thus, many of the characteristics of communities which approach a geometric-series distribution, described above, also apply to communities approaching a log-series distribution. The primary difference, however, is increased species equitability in communities conforming to the log-series abundance model (Magurran 1988).

In large species-rich communities, the distribution of species abundances is usually log-normal (May 1975; Sugihara 1980). In communities with a log-normal distribution there are usually a number of environmental factors which dominate the ecology of the community (May 1975).

At the end of the spectrum is the MacArthur broken-stick distribution in which "species are as equally abundant as is ever observed in the real world" (Magurran 1988). The apportionment of resources between species is more even (May 1974, 1975) with a good fit of the broken-stick model being found primarily in narrowly defined communities of taxonomically related organisms (May 1975).

In several instances, these theories have been verified by field observations of real communities. For example, it has frequently been illustrated that stressed communities are characterized by a change in species abundance, and display a reduction in diversity (Schafer 1973; Rosenberg 1976; Wu 1982) and shift backwards through succession from a log-normal distribution to the less equitable log-series or geometric-series distribution (May 1981).

Beta-diversity

A common approach to investigations of beta-diversity is the description of changes in species abundances along environmental gradients (Whittaker 1972; Cody 1975; Wilson and Mohler 1983). A second approach to beta-diversity is to compare the species compositions of different communities (Whittaker 1972). The fewer species that the different communities or gradient positions share, the higher the beta-diversity will be Magurran 1988).

Two approaches to quantifying beta-diversity have been developed. Firstly, numerous indices have been proposed to measure beta-diversity along transects or environmental gradients using both quantitative and qualitative data (Wilson and Shmida 1984). More commonly used indices have been reviewed by Wilson and Mohler (1983) and Wilson and Shmida (1984). Evaluation of indices in terms of ability to measure community turnover, additivity, and independence from species richness and sample size (Wilson and Shmida 1984) revealed that the index proposed by Whittaker (1960) fulfilled most criteria with fewest restrictions. Beta-diversity of pairs of sites may also be measured by use of similarity coefficients (Clifford and

Stephenson 1975), of which the Jaccard, Sorenson and Morisita-Horn indices have been widely used (Janson and Vegelius 1981).

An alternative approach to measuring beta-diversity is to investigate the degree of association or similarity of samples using the multivariate techniques of ordination or classification (Southwood 1980; Grieg-Smith 1983; Gauch 1984). These methods do not give any direct measure of beta-diversity *per se* but may be used to identify major groupings and infer the number of communities present (Magurran 1988).

Fish community diversity as measures of river health

Biological communities integrate the effects of ecological conditions over different temporal and spatial scales and hence are considered to be sensitive indicators of river health (Kleynhans 1994). The Index of Biotic Integrity (IBI) (Karr 1981), which incorporates components of both the compositional and functional diversity of fish communities (Karr 1981; Fausch *et al.* 1990), is currently receiving substantial attention as a measure of the environmental health of river (Miller *et al.* 1988; Steedman 1988; Plafkin *et al.* 1989; Fausch *et al.* 1990). IBI was not applied in this study as its intended use is to address policies related to river health (Karr 1981), rather than this study's objective of evaluating the achievement of management goals pertaining to the diversity of fish assemblages. Study of the applicability of using diversity measures described above to decribe the diversity of fish assemblages, however, should facilitate identification of IBI metrics applicable to KNP river.

1.2.2.5 Summary and study approach

The preceding review indicates some of the complexities pertaining to the functioning of river ecosystems, and in particular biotic diversity and its measurement. One of the more striking points emanating from the above review is how little is known about the functioning of river ecosystems in general, and southern African rivers in particular. Knowledge of the effects of changes in the physical, chemical and biological environment on fish assemblages is limited (section 1.2.2.1) as is the ability to distinguish between natural biotic fluctuation and those resulting from catchment development (section 1.2.2.2). Consequently, description of what level of change in biotic diversity would occur under pristine environmental conditions is problematic, with resultant difficulty in determining the acceptability (in terms of the objectives for conservation), of measured fluctuations. Stated conservation objectives provide little clarity in that they are so broadly phrased so as to provide little indication as to what level of fluctuation in biotic diversity is desirable or how it should be measured (section 1.2.2.3). Finally, we are faced with an array of analytical techniques to measure biotic diversity (section 1.2.3.4) but very little indication as to which would be appropriate (both in terms of cost efficiency and ability to understand biotic changes) to test for the achievement of conservation goals that are as yet undefined.

For the purpose of monitoring change in the biotic diversity of fish communities, the above described lack of information results in a circular argument (Figure 1.2). To determine the desirability of biotic changes, one needs to have identified the level of biotic change that is considered acceptable (operational goals) as well as an appropriate method of measurement. In order to define operational goals for conservation it is necessary to be able to distinguish between biotic changes resulting from natural environmental fluctuations, and those which are the consequence of man's development of river catchments. Operational goals need to be phrased such

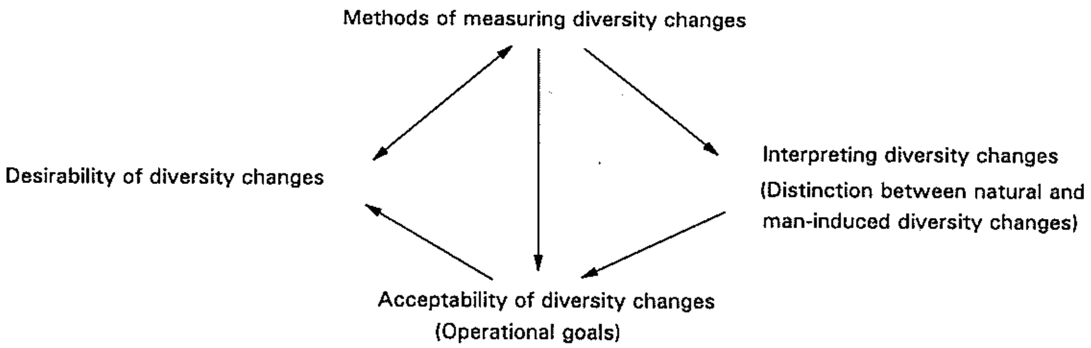

Figure 1.2 Interdependence of information needs and analytical approaches to determine the conservation status of fish communities.

that the method of diversity measurement is readily apparent. Finally, to be able to differentiate between natural and man-induced biotic changes, it is necessary to have identified analytical methods which provide interpretable information on changes in the aspects of biotic diversity which have been identified (by means of operational goals) as being important to conserve.

Clearly the key to breaking this cycle (Figure 1.2) is to identify analytical methods which provide clear, interpretable measures of change in those aspects of the diversity of fish assemblages for which it is possible to define preliminary operational goals. Where such analytical techniques are applied in a monitoring programme, subsequent assessments of changes in the diversity of fish assemblages could, in conjunction with understanding of the causes for such changes (necessitating knowledge of changes in abiotic and biotic process in rivers and the environmental preferences of fish species), enable continued refinement of operational goals. Consequently, the focus of a portion of this study (Chapters 3 and 4) has been on the assessment of analytical methods which could be used in a cost-efficient monitoring programme to determine the direction, degree and significance of changes in the diversity of fish assemblages in KNP rivers.

A second approach to breaking the cycle (Figure 1.2) is to make the assumption that, for the purpose of conservation, changes in the diversity of fish communities resulting from man's development of river catchments are undesirable. Where such biotic changes could be demonstrated and probable causes identified, statements could be made about the conservation status of fish communities. Such an assessment of the conservation status of fish communities in KNP rivers was made possible by the availability of historical data on the type and levels of development of the catchments of the rivers flowing through KNP (Section 1.3) and resultant changes in the aquatic environment (Chapter 2), as well as the distribution of fish species in KNP rivers (Gaigher 1969; Pienaar 1978). These data were used to describe changes in the physical, chemical and biological environment of rivers and the distribution of fish species (Chapter 2). Description of changes in the aquatic environment, in conjunction with descriptions of the environmental preferences of fish species, were used to identify probable causes for recorded changes in the distribution of fish species, thereby enabling an assessment of the conservation status of fish communities in KNP rivers.

1.3 STUDY AREA

Description of physical features and development in the drainage areas of the Luvuvhu, Letaba, Olifants, Sabie and Crocodile rivers provides an overview of factors influencing the physical, chemical and biological processes within these rivers. To avoid repetition, natural features which are similar for the different river basins (for example locality, topography and climate) are discussed collectively for all KNP rivers. Features characteristic to each river (for example hydrology, catchment land use, present and predicted catchment development, and the effects of catchment development on consumptive water use and water quality) are discussed separately for each river.

1.3.1 Locality

All five major rivers flowing through the KNP originate in the high altitude (> 1000m amsl) north-eastern region of South Africa, and flow eastward into the Indian ocean (Figure 1.3). The Luvuvhu and Letaba river catchments are located entirely within the Northern Province, whereas the Crocodile River catchment is located entirely within Mpumalanga. The Sabie and Olifants river catchments cut across provincial boundaries, with the Sabie River catchment located within both Mpumalanga and Northern Province, and the Olifants River catchment in Gauteng, Mpumalanga and Northern Province.

1.3.2 Topography

The topography of the catchments of the five major rivers of the KNP can be divided into three broad zones:

(i) A mountainous zone in the western portions of the catchments formed by the Soutpansberg mountain range in the north and the Drakensberg mountain range in the south. These mountains run in a north-south direction, with the upper plateau generally being higher than 2 100 m above mean sea level (amsl). The upper plateau is commonly referred to as the Highveld.

(ii) A low mountain and foothill zone with a broken undulating topography. Altitude varies between 1 200 and 600 m amsl. This mountainous area is commonly referred to as the escarpment.

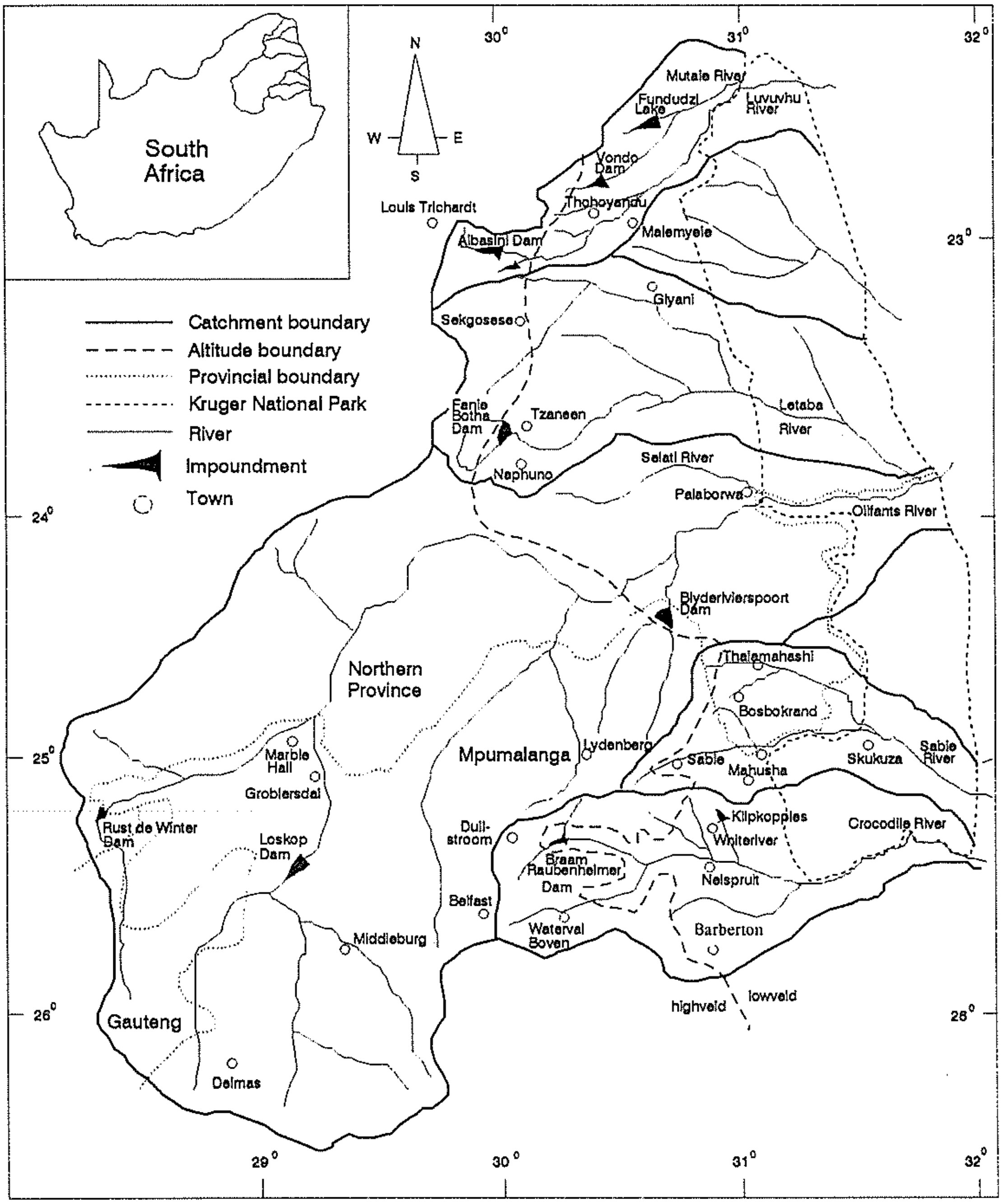

Figure 1.3 Catchment areas of major rivers flowing through the Kruger National Park showing places and features mentioned in the text.

(iii) A plains area in the eastern portion of the catchments with a gently undulating topography, characterized by shallow river divides, isolated koppies and areas of enclosed drainage (Walmsley *et al.* 1987). Altitude varies between 600 and 100 m amsl. This plains area is commonly referred to as the Lowveld.

The Kruger National Park is situated exclusively on the lowveld plains (Figure 1.3).

1.3.3 Climate

The average annual rainfall decreases from west to east across the river catchments. At the headwaters of the Letaba and Sabie rivers, the annual rainfall can be as high as 2 000 mm y^{-1}. (Walmsley *et al.* 1987; Chunnett, Fourie and Partners 1987). In the Olifants River catchment, rainfall varies from c 600 mm y^{-1}. in the upper reaches of the highveld to c 1 000 mm y^{-1}. in the Drakensburg (Theron, Prinsloo and van Tonder 1987). In the Crocodile River catchment, an average rainfall of 1 200 mm y^{-1}. has been recorded in the mountainous highveld (Department of Water Affairs 1987). Approximately 700 mm y^{-1}. falls along the foot hills of the escarpment, and in the lowveld, annual rainfall varies between c 730 mm in the Sabie River catchment, to less than 500 mm y^{-1}. in the Luvuvhu catchment (Gertenbach 1980). Much of the lowveld receives between 500 and 600 mm y^{-1}. (Gertenbach 1980). Mean annual precipitation in the river catchments are 731 mm y^{-1}. (Luvuvhu River), 671 mm y^{-1}. (Letaba River), 693 mm y^{-1}. (Olifants River), 833 mm y^{-1}. (Sabie River), and 879 mm y^{-1}. (Crocodile River) (Departement van Waterwese 1986).

Rainfall is strongly seasonal with about 80% of mean annual precipitation occurring in the summer months, from November to April (Theron, Prinsloo and van Tonder 1987), with the highest rainfall occurring from December to February. An 18 to 20 year wet-dry cycle occurs, with the even numbered decades ('20s, '40s, '60s, '80s) tending to have below average rainfall, and the odd numbered decades ('30s, '50s, '70s) experiencing above average rainfall (Walmsley *et al.* 1987).

Air temperature increases from west to east across the catchments (Chunnett, Fourie and Partners 1987; Walmsley *et al.* 1987). On the escarpment, winters are cold and summers cool, with average monthly temperatures about 10°C less than in the lowveld (Department of Water Affairs 1987). The annual temperature range on the escarpment is c 14°C to 20°C, whereas in the lowveld the annual range is about 11°C, from an average of 17°C in winter to 28°C in mid-summer (Walmsley *et al.* 1987).

Mild winters are characteristic of the lowveld, while summers are generally hot with temperatures as high as 46.5°C having been recorded (Department of Water Affairs 1987).

Evaporation also increases from west to east across the catchments (Walmsley, *et al.* 1987; Department of Water Affairs 1987; Chunnett, Fourie and Partners 1987; Theron, Prinsloo and van Tonder 1987). Mean annual evaporation is much higher than annual rainfall, and varies from a low of c̲ 1 400 mm y^{-1}. over the escarpment (Department of Water Affairs 1987; Chunnett, Fourie and Partners 1987) to as high as 1 900 mm y^{-1}. in the eastern reaches of the lowveld (Theron, Prinsloo and van Tonder 1987).

1.3.4 Hydrology and development in the Luvuvhu River catchment

Hydrology

The major tributaries of the Luvuvhu River are the Mutale and Mutshindudi rivers, with the total river catchment being 5 956 km^2 in extent (Departement van Waterwese 1986) of which 2 487 km^2 falls in the Mutale catchment. The Luvuvhu River is approximately 250 km long from its source in the Soutpansberg mountains near Louis Trichardt to its confluence with the Limpopo River on the eastern boundary of the KNP. Total length within the KNP is 64 km (Venter 1991). Virgin mean annual runoff (MAR) of the Luvuvhu and Mutshindudi rivers combined is 328×10^6 m^3 y^{-1}., and the Mutale River 201×10^6 m^3 y^{-1}. (Departement van Waterwese 1986).

There are no records of runoff in the lower portions of the Luvuvhu River basin. However, flow records from gauging station A9M01A located at Schuynshoogte (30°06'45"E; 30°23'30"S), approximately two thirds down the length of the river, illustrate marked seasonality of flow (Figure 1.4a). Flow in the Luvuvhu River before 1949 is thought to have been perennial (U de V Pienaar, *pers. comm.*)[1]. Zero flow conditions were first recorded in the lower portions of the river in 1949 (Venter and Deacon 1991), and since this time, the frequency and duration of zero flow periods has increased. Between 1982 and 1987, zero flow conditions were experienced in the low rainfall months in the lower reaches of the Luvuvhu for up to six months at a time (F. Venter, *pers. comm.*)[2]. Perenniality of flow was restored in 1988 and 1989 (Figure

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[1] U. de V. Pienaar, Retired Park Warden, Skukuza, Kruger National Park, South Africa.

[2] F. Venter, Senior Research Officer, Skukuza, Kruger National Park, South Africa.

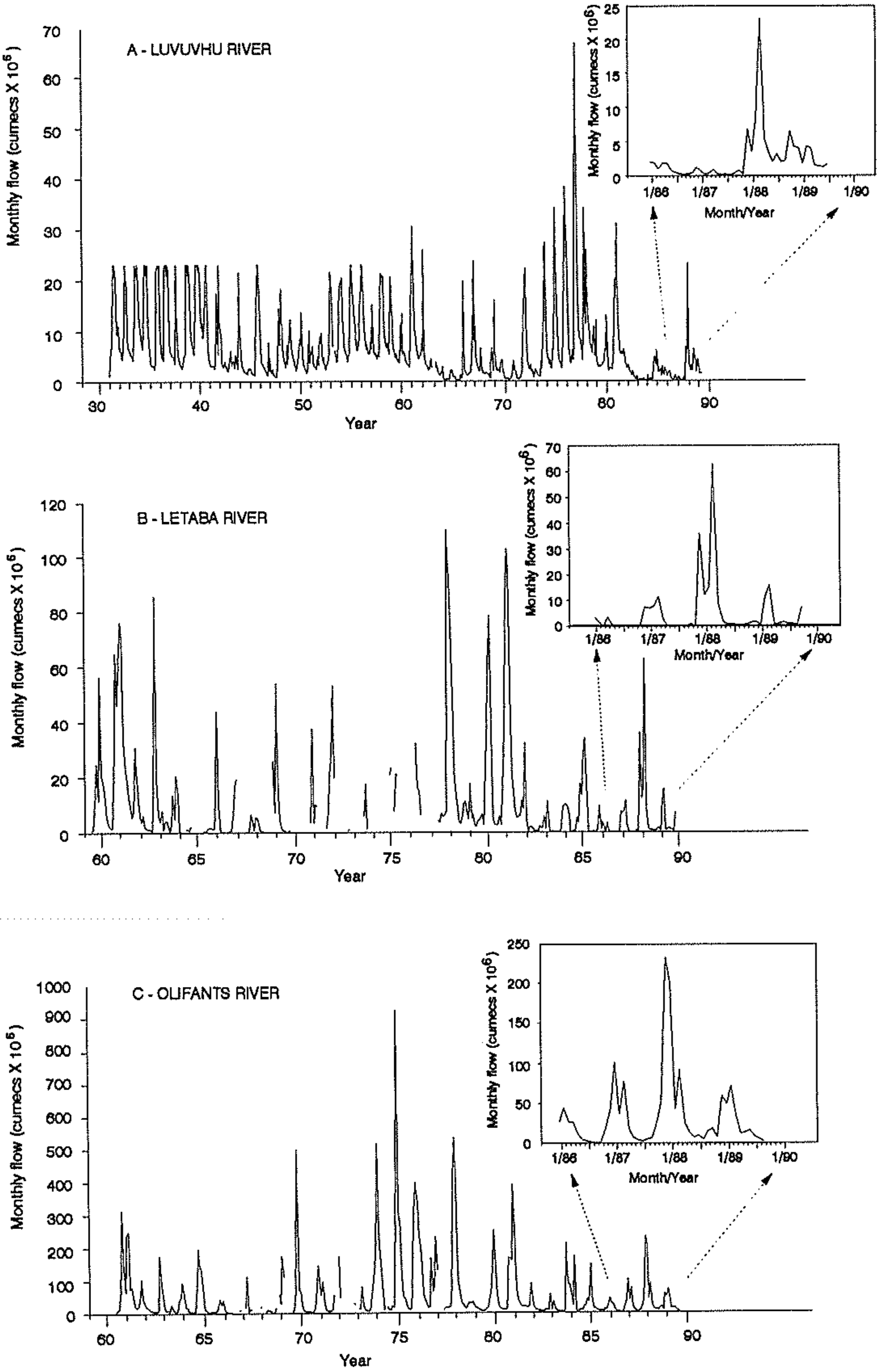

Figure 1.4 Total monthly flow in the Luvuvhu (a), Letaba (b), Olifants (c), Sabie (d) and Crocodile (e) rivers measured a Department of Water Affairs and Forestry gauging stations closest to the western boundary of the Kruger National Park.

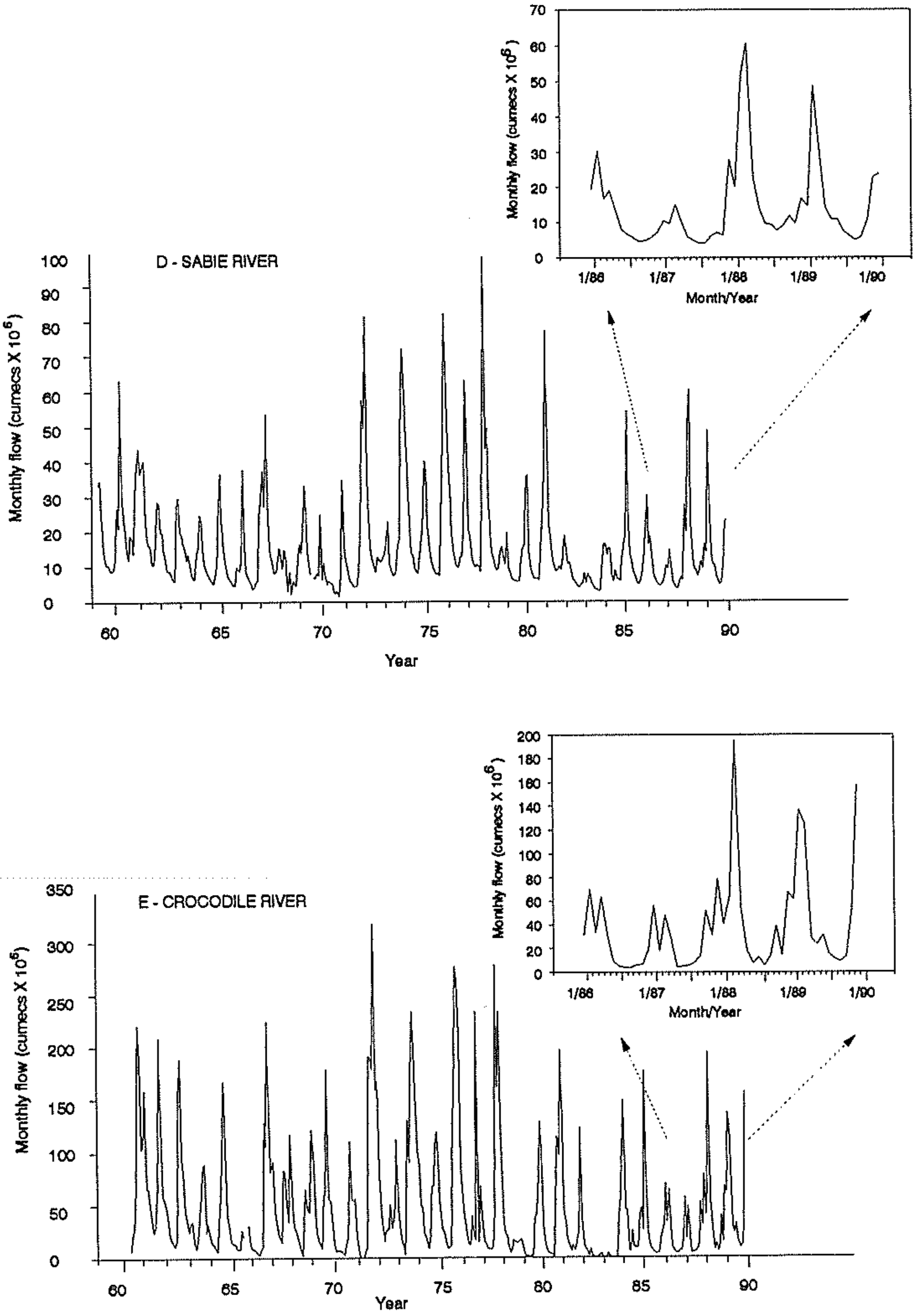

Figure 1.4 cont.

1.4a). Flow during the duration of this study (1987 to 1989) was variable, with no summer floods in 1987, high summer floods in 1988, and small floods in 1989 (Figure 1.4a).

Existing water resources development

Four large impoundments exist in the Luvuvhu River, all located in the upper reaches of the catchment area. These include the Albasini Dam (capacity 25.6 x 10^6 m^3), Vondo Dam (capacity 5.3 x 10^6 m^3), Phiphidi Dam (capacity 0.3 x 10^6 m^3) and Mambedi Dam (capacity 7.0 x 10^6 m^3) (Hill Kaplan Scott Inc. 1987). The Fundudzi lake occurs in the upper catchment of the Mutale River, capacity unknown. The Vondo and Phiphidi dams provide domestic and industrial water to Thohoyandu, whereas water from the Albasini and Mambedi dams are used primarily for irrigation (Hill Kaplan Scott Inc. 1987).

Current infrastructure and land use

There are no major towns in the river catchment, though several small settlement nodes exist.

Approximately 5 500 ha of the Luvuvhu catchment (excluding the Mutale catchment area) is currently under irrigation, requiring approximately 59.3 x 10^6 m^3 y^{-1}. (18.1% MAR) (Hill Kaplan Scott Inc. 1987). This value is only an estimate (I. Nielson, *pers. comm.*)[3] as records of use of water for irrigation purposes exist only for the Albasini Dam, coupled with 'unknown' quantities of water being extracted directly from the river.

Exotic forests cover 4.2% of the catchment (14 600 ha). In view of such forests having largely replaced pre-existing natural montane forest, their effect on the reduction of natural runoff is considered to be minor (Hill Kaplan Scott Inc. 1987).

The watering of livestock in the catchment is estimated to annually consume 0.5 x 10^6 m^3 (0.2% MAR), whereas domestic consumption and industrial water for light industries in Louis Trichardt, Malemulele and Vondo Scheme is calculated to total 9.2 x 10^6 m^3 y^{-1}. (2.8% MAR) (Hill Kaplan Scott Inc. 1987). A total of 2.5 x 10^6 m^3 y^-

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[3] I. Nielson, Hill Kaplan Scott INC. Consulting Engineers, South Africa.

^{1}. of treated sewage effluent from the Thohoyandu sewage treatment scheme is discharged into the Luvuvhu River via the Mvudi and Dzini rivers (Hill Kaplan Scott Inc. 1987).

The total amount of water removed from the Luvuvhu River annually, excluding evapotranspirational losses, is 69.0 x 10^6 m^3 or 21% MAR. This value is probably an underestimate of the real amount of water extracted from the Luvuvhu River as it does not take into consideration private abstraction directly from the river.

Water chemistry

The concentrations of ionic salts in the Luvuvhu River between 1983 and 1989 was low (Van Veelen 1990, 1991; Moore *et al.* 1991) with concentrations increasing inside the KNP.

The concentration of aluminium in water samples from the Luvuvhu River collected in March 1983 exceed 100 $\mu g\ l^{-1}$ (Chutter and de Moor 1983) which is considered to be hazardous to aquatic life (Environmental Protection Agency 1973). The concentration of other metals in the water, sediment and organisms in the Luvuvhu River is unknown.

Tests for pesticides in water samples collected in 1974 and 1975 revealed the periodic occurrence of high concentrations of both alpha-endosulfan (1.9 and 6.4 $\mu g\ l^{-1}$) and beta-endosulfan (5.5 $\mu g\ l^{-1}$) (Van Dyk 1978).

Predicted future development

An expansion in industrial development is to be expected (I. Nielson, *pers. comm.*) though the extent will to a large degree depend on the availability of external financing. It has been proposed that a further 1 700 ha of land be included in the irrigation scheme in the middle reaches of the Luvuvhu River (Hill Kaplan Scott Inc. 1987). There is also a proposal to supply areas in the Shingwedzi catchment with water from the Luvuvhu River (Walmsley *et al.* 1987).

Summary

The catchment of the Luvuvhu River is not extensively developed, with the capacity of impoundments only 11.6% of MAR, and no major human settlements. Known abstraction is low (21% MAR), yet flow has decreased substantially, with zero flow conditions frequently experienced in the 1980s during low rainfall months, indicating extensive unreported abstraction directly from the river. The concentrations of ionic salts is low, though periodic high concentrations of pesticides are cause for concern. Predicted future development is not extensive though increased abstraction appears inevitable.

1.3.5 Hydrology and development in the Letaba River catchment

Hydrology

The Letaba River catchment is 13 850 km² in extent (Departement van Waterwese 1986) and is drained by three major river - the Klein, Middle and Groot Letaba rivers. The Groot Letaba River is 490 km long from its source to the confluence with the Olifants River seven kilometres west of the South Africa/Mocambique border (Walmsley *et al.* 1987). Total length within the KNP is 98 km (Venter 1991). Virgin MAR from the Letaba catchment at the Olifants confluence is estimated to be 819 x 10^6 m^3 y^{-1}. (Departement van Waterwese 1986). The sources of all three tributaries of the Letaba River lie in high rainfall areas, and most of the runoff is generated in the upper reaches of the catchment - 472 x 10^6 m^3 y^{-1}. from 11% of the catchment area (Walmsley *et al.* 1987). Flow is intermittent, depending on the rainfall season.

The Letaba River used to be have perennial flow, though in recent years, flow, particularly in the lower reaches, has become increasingly intermittent. Zero flow conditions were first recorded in 1936 (Venter and Deacon 1991). Since this date, seasonality of flow has increased to the current state where extended periods of zero flow occur annually (Figure 1.4b). The current observed MAR is approximately 25% of the long-term virgin MAR (Chutter *et al.* 1991) illustrating the degree that natural river flow has been reduced. Flow during the duration of this study (1987 to 1989) was variable, with small summer floods in 1987 and 1989, high summer floods in 1988, and a reduction in the duration of zero flow conditions in 1988 and 1989 (Figure 1.4b).

Existing water resources development

Forty three impoundments which could have an influence on regulating river flow have been constructed on rivers in the Letaba River catchment (Walmsley *et al.* 1987). Five of these impoundments are classified as major storage facilities, and include the Ebenezer, Fanie Botha, Middle Letaba, Hudson Ntsanwisi and Thabina dams (Walmsley *et al.* 1987). Four small impoundments have been constructed within the boundaries of the KNP. Name and year of construction of these impoundments are Engelhart (1970/71), Shimweni (1972/73), Minkerhout (1973/74) and Black Heron (1974/75) (Joubert 1986b). The number of 'farm dams' in the catchment is estimated at 300 (Walmsley *et al.* 1987). An inter-basin transfer of between 15 and 19 x 10^6 m^3 y^{-1}. from the headwaters of the Groot Letaba River provides Pietersburg with water (Walmsley *et al.* 1987).

Current infrastructure and land use

In 1985, approximately one million people (85 per km^2) were estimated to be living in the Letaba River catchment (Walmsley *et al.* 1987). Most settlements are located in the foothill areas below the escarpment, and concentrating along the main river valleys and lines of communication (Walmsley *et al.* 1987). There are seven main settlement areas, Tzaneen, Letaba River Valley, Giyani, Ritavi, Naphuno, Sekgosese and Molototsi.

A relatively small portion of the Letaba River catchment (c 50 000 ha) is currently under exotic afforestation, with forestry activity generally confined to the higher elevations (Walmsley *et al.* 1987). The Letaba catchment was declared a Category 1 catchment in 1972, hence no new areas can be afforested (Walmsley *et al.* 1987). Thus, the area under forestry should remain fairly constant.

In 1987, approximately 34 000 ha were under irrigation with a further 22 000 ha under dry-land agriculture (Walmsley *et al.* 1987). Water required for irrigation purposes is conservatively estimated to be 350 x 10^6 m^3 y^{-1}. (43 % MAR) (T. van Schalkwyk, *pers. comm.*)[4]. This value is probably an underestimate of the true volume of water extracted from the Letaba River for irrigation, as it does not take into consideration private abstraction directly from the river. Apart from the alluvial soils along the rivers, the remainder of the catchment is characterized by shallow sandy

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[4] T. van Schalkwyk, Chunnet, Fourie and Partners, Consulting Engineers, Pretoria, South Africa.

loam soils which tend to be infertile (Walmsley *et al.* 1987). These areas are used primarily for livestock farming. In many areas, removal of the vegetative cover by overgrazing has led to accelerated soil erosion and gully development, resulting in increased sediment loads in the rivers (Walmsley *et al.* 1987).

Industrial activity is small, being essentially confined to the canning industry with a water requirement of approximately 0.5×10^6 m^3 y^{-1}. (0.06% MAR) (Walmsley *et al.* 1987). Major domestic consumers of water include the towns of Tzaneen (c 3.5 x 10^6 m^3 y^{-1}. - 0.4 % MAR) and Pietersburg (c 15 x 10^6 m^3 y^{-1}. - 1.8% MAR) (Walmsley *et al.* 1987).

In the Letaba River catchment water demand currently exceeds supply (T. van Schalkwyk, *pers. comm.*).

Water chemistry

The concentrations of ionic salts in the Letaba River between 1983 and 1989 has been described as "moderate" (Van Veelen 1990, 1991; Moore *et al.* 1991), with occasional high ammonia (NH_4) concentrations.

The concentration of aluminium in water samples from the Letaba River collected in March 1983 exceeded 100 $\mu g\ l^{-1}$ (Chutter and de Moor 1983) which is considered to be hazardous to aquatic life (Environmental Protection Agency 1973). The concentration of other metals in the water, sediment and organisms in the Letaba River is unknown.

Despite extensive farming in the catchment of the Letaba River, previous investigations have found the levels of organics and pesticides in the surface waters of this river to be low (Walmsley *et al.* 1987). Out of an approximate 104 water samples collected for chemical analysis in 1974 and 1975, five were found to contain insecticide residues (Van Dyk 1978). These included alpha-endosulfan (0.1 $\mu g\ l^{-1}$), beta-endosulfan (0.5 $\mu g\ l^{-1}$), Dieldrin (1.6 $\mu g\ l^{-1}$) and DDT (0.5 and 1.0 $\mu g\ l^{-1}$).

Episodic pollution events have also occurred in the Letaba River. In 1983 the Letaba River was polluted with Thiodane immediately to the west of the KNP boundary (Pienaar 1983a; Venter and Deacon 1991). Fish kills were recorded after this pollution event (Pienaar 1983a).

Predicted future development

Human population in the Letaba River catchment is expected to increase at a rate of up to 10% y^{-1}. (Walmsley *et al.* 1987). Industry in the catchment is almost entirely related to agriculture and agricultural services, with expected increased growth in these sectors. Tzaneen, Nkowankowa and Giyani have been identified as three industrial development sites (Walmsley *et al.* 1987).

Most agricultural development in the future is expected to be related to irrigation. It is predicted that the amount of land under irrigation will increase from 34 000 ha (2.4% of the catchment) to 48 000 ha (3.5% of the catchment) (Walmsley *et al.* 1987). However, in view of limited water availability, increases in irrigation-agriculture would be at the expense of forestry, dryland agriculture and nature conservation.

Summary

The catchment of the Letaba River is extensively developed. This has resulted in water demand exceeding supply, and declines in water chemistry (particularly increases in the concentrations of aluminium and ionic salts, and increased incidence of episodic pollution events). The Letaba River has been altered from a perennial to a seasonal river. There are no new water development options available in this catchment, only water management options. Nevertheless, extensive irrigation-agricultural development is predicted, which will take place at the expense of nature conservation.

1.3.6 Hydrology and development in the Olifants River catchment

Hydrology

Major tributaries of the Olifants River include the Blyde, Steelpoort and Selati rivers with the total river catchment within South Africa being 54 434 km^2 (Departement van Waterwese 1986). Virgin MAR at the eastern boundary of the KNP is estimated to be 2 284 x 10^6 m^3 (Theron, Prinsloo, and van Tonder 1987). Length within the KNP is c 100km (Venter 1991).

Despite extensive abstraction of water from the Olifants River, perenniality of flow has been maintained. Zero flow conditions have been recorded only once - in 1968, for three days (KNP, unpublished data). For a period during 1983, an exceptionally dry year, perenniality of flow was maintained only by the release of 0.57 cumecs from the Blyderivierspoort Dam (F. Venter, *pers. comm.*). There is a large seasonal variation in flow (Figure 1.4c) with summer floods occurring most years. Base-flow within KNP rarely falls below two cumecs. Flow during the duration of this study (1987 to 1989) was variable, with moderate summer floods in 1987 and 1989, and high summer floods in 1988 (Figure 1.4c).

Existing water resources development

Several large impoundments have been constructed in the upper and middle reaches of the Olifants River, primarily to supply water for crop irrigation (Theron, Prinsloo and van Tonder 1987). These include the Loskop Dam (capacity 348 x 10^6 m^3), Renosterkop Dam (capacity 206 x 10^6 m^3), Blyderivierspoort Dam (capacity 56 x 10^6 m^3), Rust de Winter Dam (capacity 30 x 10^6 m^3) and Arabie Dam (capacity 104 x 10^6 m^3) (Theron, Prinsloo and van Tonder 1987). A total volume of 780 x 10^6 m^3 (c 50% MAR) can be impounded. Inter-basin imports from the Komati, Usutu and Vaal rivers are undertaken to augment bulk supplies (Theron, Prinsloo and van Tonder 1987).

Current infrastructure and land use

A large number of towns occur in the Olifants River catchment, the larger of which are Witbank, Middelburg, Groblersdal, Marble Hall, Belfast, Lydenburg, Lebowakgomo, Tafelkop and Phalaborwa.

Approximately 103 000 ha are currently under irrigation in the Olifants catchment, requiring about 700 x 10^6 m^3 y^{-1}. (30% MAR) (Theron, Prinsloo and van Tonder 1987). Heavy industrial development, including mining and power generation, concentrated in the Bronkhorstspruit-Witbank-Middelburg axis has created a demand for water far in excess of that which can be supplied by local sources (Theron, Prinsloo and van Tonder 1987). Hence inter-basin imports of water are undertaken from the Komati, Usutu and Vaal rivers. However, most of the imported water is delivered directly to the users without entering the river system, and a large portion is used consumptively and thus does not appear as effluent (Theron, Prinsloo and van

Tonder 1987). Catchment development is such that after regulation and abstraction, spillage from major dams are significant only in very wet periods (Theron, Prinsloo and van Tonder 1987).

Water chemistry

The concentrations of ionic salts in the Olifants River between 1983 and 1989 was high (Van Veelen 1990, 1991; Moore *et al.* 1991). During this period, occasionally high sulphate levels (>600 mg l^{-1}) and consistently high fluoride concentrations (>0.7 mg l^{-1}) rendered water in the Olifants River unfit for household use (Van Veelen 1990, 1991). Furthermore, high fluoride levels in the Olifants River are thought to pose a threat to tooth and skeletal development in vertebrates (Raubenheimer *et al.* 1990).

The concentration of aluminium in water samples from the Olifants Rivers collected in March 1983 exceed 100 $\mu g\ l^{-1}$ (Chutter and de Moor 1983) which is considered to be hazardous to aquatic life (Environmental Protection Agency 1973). In this same study, it was found that concentrations of cadmium, chromium, nickel and copper in the Olifants River were low, and could not be considered as toxic or hazardous. However, concentrations of lead (70 $\mu g\ l^{-1}$) and zinc (770 $\mu g\ l^{-1}$) exceeded suggested tolerable levels of 3 $\mu g\ l^{-1}$ and 180 $\mu g\ l^{-1}$ respectively (Kempster *et al.* 1980). The concentration of other metals in the water, sediment and organisms in the Olifants River is unknown.

High concentrations of the organochlorine insecticide Dieldrin (2.8 $\mu g\ l^{-1}$) have been reported in a water sample collected in April 1974 (Van Dyk 1978), whereas during extensive sampling in 1974 and 1975, no traces of either DDT or endosulfan were recorded. More recent investigations have indicated that the levels of polychlorinated biphenyls (PCB's) and the chlorinated hydrocarbons DDT, DDD and DDE in the surface water, sediments, and body tissues of fish species are acceptably low (Grobler 1991). Residues of DDT and its metabolites DDD and DDE were found to be present in fish throughout the system, with the highest concentrations being recorded in specimens of *Schilbe intermedius* (Rüppell 1832) captured in the Phalaborwa barrage on the western boundary of the KNP (t-DDT = 205 $\mu g\ kg^{-1}$ wet wt) and Loskop Dam (t-DDT = 202 $\mu g\ kg^{-1}$ wet wt). These recorded whole body residue values are below the standards established for the protection of aquatic life as determined for various countries (for example North America 1 000 $\mu g\ kg^{-1}$ (wet wt) (National Academy of

Science and National Academy of Engineering 1972)), and hence the current level of contamination is unlikely to detrimentally affect fish species in the Olifants River. However, of some concern is the relatively high ratio of DDT to its metabolites DDD and DDE, particularly in fish captured in the Phalaborwa Barrage, indicating recent or continuous contamination of the Phalaborwa Barrage catchment area.

Several episodic pollution events have occurred in the Olifants River which could have detrimentally affected fish communities in the KNP. On four occasions, high silt levels have occurred in the Olifants River resulting from the flushing of the Phalaborwa Barrage. The first occurred in January 1983 when silt levels as high as 25% by mass (Rooseboom 1991) or 77 000 mg l^{-1} (Venter and Deacon 1991) were recorded. This event resulted in the mortality of fish over a distance of 30 km in the KNP (U de V Pienaar, *in litt.*). The number of individuals killed was estimated to be "several million" and the opinion was expressed that "sensitive species such as the rare minnow *Opsaridium zambezense* and the catlets *Chiloglanis* spp. could be almost totally exterminated" (U de V Pienaar, *in litt.*). Subsequent elevated high suspensoid levels were recorded in 1984 (26 851 mg l^{-1}), and twice in 1987 (24 665 mg l^{-1} and 44 665 mg l^{-1}) (Venter and Deacon 1991). All of these elevated suspensoid concentrations are substantially higher than the 12 860 mg l^{-1} level which results in total deoxygenation of water (Bruton 1985), and hence, not unexpectedly, resulted in fish kills in the Olifants River (Venter and Deacon 1991).

In February 1982, large volumes of phosphoric acid were released into the Selati River, a tributary of the Olifants River (Joubert 1986a). Subsequent surveys revealed excessively high concentrations of fluorides, chlorides and sulphates in the Olifants River below its confluence with the Selati River (Joubert 1986a). Fish kills were recorded after this pollution event (U de V Pienaar, *pers. comm.*).

Predicted future development

Urbanization can be expected to increase substantially in the Olifants River basin (Theron, Prinsloo and van Tonder 1987). Industrial development will probably be related to the mineral industries with an associated increase in demand for industrial water (Theron, Prinsloo and van Tonder 1987). Pressure exists for increased irrigation development along the Olifants River, particularly in the lowveld (Theron, Prinsloo and van Tonder 1987). Additional water storage facilities will be required in some cases. Furthermore, it is foreseen that, in the future, water will have to be exported from the Olifants River basin to meet the growing demand at Pietersburg (Theron, Prinsloo and van Tonder 1987).

Summary

The catchment of the Olifants River is extensively developed, with several industrial, residential and agricultural nodes of development throughout the catchment. Impoundment is extensive with concurrent reductions in flow volumes and increased flow regulation. Water quality is poor, with frequent episodic pollution events (phosphoric acid and high silt concentrations) having substantial detrimental effects on fish. Future development of the catchment is likely to be extensive.

1.3.7 Hydrology and development in the Sabie River catchment

Hydrology

The major tributaries of the Sabie River are the Sand and Marite Rivers. Area of the Sabie River catchment within South Africa is between 6 252 km^2 (Chunnett, Fourie and Partners 1987) and 6 437 km^2 (Chunnett, Fourie and Partners 1992), of which 1 965 km^2 is in the Sand River catchment. The total river length is 180km (Chunnett, Fourie and Partners 1992), with 111 km falling within the KNP (Venter 1991).

There is considerable variability in assessments of virgin MAR of the Sabie River drainage basin, with estimates ranging from 849 x 10^6 m^3 (Departement van Waterwese 1986), to 764 x 10^6 m^3 (Sellick and Bonthuys 1990), with approximately 603 x 10^6 m^3 estimated to originate in the Sabie River, and 158 x 10^6 m^3 in the Sand River sub-catchment (Chunnett, Fourie and Partners 1987). Afforestation is thought to have further reduced runoff in the Sabie River to 436 x 10^6 m^3 (O'Keeffe and Davies 1991).

Zero flow conditions have never been recorded in this river, and winter base flow rarely falls below two cumecs (Figure 1.4d). The lowest flow condition recorded prior to 1990 occurred in 1983, with 0.82 cumecs being measured at Skukuza, and 0.77 cumecs at Lower Sabie (Pienaar 1983b). Flow during the duration of this study (1987 to 1989) was variable, with marked seasonality in flow, and small summer floods in 1987, and high summer floods in both 1988 and 1989 (Figure 1.4d).

Existing water resources development

Existing storage dams in South Africa are generally small, with an estimated gross storage capacity of 29 x 10^6 m^3, of which the bulk of 14 x 10^6 m^3 is provided by the Da Gama Dam (Chunnett, Fourie and Partners 1992). The Zoeknog Dam would have added a further 9 x 10^6 m^3 storage capacity, though the dam failed in 1993 shortly after completion. The Corumana Dam in Mocambique close to the eastern border of the KNP is large, with a storage capacity of 1 200 x 10^6 m^3 (Chunnett, Fourie and Partners 1992). The construction of several large impoundments in the Sabie, Sand and Marite rivers are currently being investigated (F. van Zyl, *pers. comm.*)[5]. Two of these impoundments, the Inyaka Dam (101 x 10^6 m^3) and the Madras Dam (230 x 10^6 m^3), could regulate up to 80% of the runoff of the Sabie River under conditions of present development (C. Sellick, *pers. comm.*)[6].

Current infrastructure and land use

Large towns within the Sabie River catchment include Sabie, Graskop, Skukuza, Thulamahashi, Bosbokrand, Mkhuhlu and Mahusha.

Principle land uses in the Sabie River catchment upstream of Mocambique include conservation, livestock and crop farming and forestry (Chunnett Fourie and Partners 1987). Approximately half of the Sabie River catchment falls into conservation areas (C. Sellick, *pers. comm.*). In 1987 game and livestock within the catchment amounted to approximately 110 000 large stock units (Chunnett, Fourie and Partners 1987). Irrigation farming land totals approximately 11 320 ha (6,8% of the total irrogable soils outside the conservation areas in the catchment) (Sellick and Bonthuys 1990). Exotic afforestation is confined to the western portion of the catchment and amounts to approximately 72 000 ha (Chunnett, Fourie and Partners 1987). Natural annual runoff of the Sabie River system is estimated to have been reduced from 764 x 10^6 m^3 to 633 x 10^6 m^3 (17.15%) due to afforestation (Sellick and Bonthuys 1990). In contrast O'Keeffe and Davies (1991) maintain that afforestation has reduced MAR from a naturally occurring 603 x 10^6 m^3 to 436 x 10^6 m^3 (27.7%).

Mining activity is limited to five small gold mines near the towns of Sabie and Graskop, and industrial activity is small, being essentially confined to the processing

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[5] F. van Zyl, Department of Water Affairs and Forestry, Pretoria, South Africa.
[6] C. Sellick, Chunnet, Fourie and Partners, Consulting Engineers, Pretoria, South Africa.

of wood and small service industries (Chunnett, Fourie and Partners 1987; Sellick and Bonthuys 1990).

Total water requirements from the Sabie River upstream of Mocambique, not including evapotranspiration, were, in 1987, estimated to be 240 x 10^6 m^3 y^{-1}. or 31.5% of virgin MAR (Chunnett, Fourie and Partners 1987). Of this total, 192 x 10^6 m^3 came from the Sabie River and 49 x 10^6 m^3 from the Sand River (C. Sellick, *pers. comm.*).

Water chemistry

The concentrations of ionic salts in the Sabie River between 1983 and 1989 was low (Van Veelen 1990, 1991; Moore *et al.* 1991). In this period pH was low (6.0 to 6.5) although it was generally higher than 7.0 below the confluence of the Sand River (Van Veelen 1990, 1991).

The pesticides DDT, Dieldrin, alpha-endosulfan and beta-endosulfan were not present in water samples collected in 1974 and 1975 (Van Dyk 1978).

Episodic pollution events have occurred in the Sabie River. In October 1983, the derailing of a train carrying diesel fuel at the Rolle Bridge near Acornhoek resulted in approximately 455 000 litres of diesel being spilled in the Sand River, the major tributary of the Sabie River (Pienaar 1983b). Fish kills were recorded after this pollution event (U de V Pienaar, *pers. comm.*).

Predicted future development

In 1987, the human population in the catchment was estimated to be between 338 000 and 340 000, with a further 80 000 persons outside the catchment being dependent on water supplies from the Sabie River (Chunnett, Fourie and Partners 1987; Sellick and Bonthuys 1990). The average growth rate for the total population has been 5% y^{-1}. from 1980 to 1985 (Sellick and Bonthuys 1990). The total population in the Sabie River catchment is expected to double by the year 2010 (Chunnett, Fourie and Partners 1987), with a total population of 860 000 being dependant on water from the Sabie River catchment (Sellick and Bonthuys 1990). Rate of industrial growth is not expected to be significantly different from the rate of population growth, with development expected primarily in light service industries (Sellick and Bonthuys

1990). Irrigation development is expected to develop from the 11 320 ha in 1985 to approximately 23 100 ha by the year 2010 (Sellick and Bonthuys 1990). The potential for expansion of mining activities is limited, and thus is unlikely to significantly affect the water resource (Sellick and Bonthuys 1990). It is predicted that by the year 2000 the primary water use could increase by a further 55 x 10^6 m^3 y^{-1}. to a total of 295 x 10^6 m^3 y^{-1}. or 38.7% of virgin MAR (Chunnett, Fourie and Partners 1987), with the largest increase being in water for domestic use.

Summary

Industrial and urban development in the Sabie River catchment is not extensive, which is reflected in minor changes in water quality. Afforestation has, however, resulted in moderate (17-27%) declines in flow. The Sabie River is the least perturbed of the five major rivers in the KNP. Predicted future catchment development and impoundment can result in substantial modifications, principally reductions in flow volumes and increased flow regulation.

1.3.8 Hydrology and development in the Crocodile River catchment

Hydrology

The major tributaries of the Crocodile River are the Elands, Kaap, Sand and Mbyamiti rivers. The total drainage area of Crocodile River catchment is 10 526 km^2 (Department of Water Affairs 1987) and has a total length of approximately 320 km from its source in the northern regions of the Mpumalanga highveld to its confluence with the Komati River at Komatipoort. The last 116 km of the Crocodile River forms the southern boundary of the KNP. Virgin MAR for the Crocodile River catchment at Komatipoort is estimated to be between 1 238 x 10^6 m^3 (Departement van Waterwese 1986) and 1 360 x 10^6 m^3 (Department of Water Affairs 1987).

Although essentially a perennial river, impoundment and extraction of water has resulted in low flow conditions frequently having been recorded in the lower reaches since 1956 (Figure 1.4e). Impoundment has also resulted in the regulation of flows, with high winter base flows being maintained, and summer flood peaks being dampened. Flow during the duration of this study (1987 to 1989) was variable, with marked seasonality in flow, and small summer floods in 1987, and high summer floods in both 1988 and 1989 (Figure 1.4e).

Existing water resources development

Eleven large impoundments have been constructed in the Crocodile River basin, the largest of which are the Braam Raubenheimer Dam (capacity 160.6 x 10^6 m^3) on the Crocodile River, Klipkoppies Dam (capacity 12.1 x 10^6 m^3) on the White River, and the Witklip Dam (capacity 12.9 x 10^6 m^3) on the Sand River (Department of Water Affairs 1987). Most of these impoundments have been constructed primarily to provide water for irrigation and have a total capacity of more than 196 x 10^6 m^3 (Department of Water Affairs 1987), or approximately 15% of MAR.

Current infrastructure and land use

The five largest towns in the Crocodile River catchment are Barberton, Dullstroom, Nelspruit, Pilgrims Rest and Waterval Boven, with a total urban and rural population (in 1985) of 213 670 (Department of Water Affairs 1987).

The principle water use in the Crocodile catchment is for irrigation, with large volumes also being lost due to afforestation (Department of Water Affairs 1987). Calculations of the amount of water used for irrigation appear to be confused, as Department of Water Affairs (1987) calculated this value for 1985 as being between 270 x 10^6 m^3 and 400.8 x 10^6 m^3 y^{-1}. (20-30% MAR), based on the estimation of between 36 400 and 58 590 ha. being under irrigation. In the same document, however, it is maintained that in reality 87 398 ha was under irrigation in 1985, though this area was not included in the calculation of the amount of water used from the Crocodile River catchment for irrigation purposes. Using the conversion ratio for area under irrigation vs volume per area, as used by Department of Water Affairs (1987), it is calculated that the total amount of water used for irrigation in the Crocodile River catchment would be approximately 648.3 x 10^6 m^3 y^{-1}. or 51% virgin MAR.

In 1985 approximately 170 000 ha was under afforestation (Anonymous 1987) with preliminary investigations by Department of Water Affairs (1987) estimating the water requirements for forestry to be 210 x 10^6 m^3 y^{-1}. (15.5% MAR).

Other water consumers include domestic, municipal, industrial and mining uses, which utilize approximately 20 x 10^6 m^3 y^{-1}. (1.5% MAR) and exports to the Komati catchment - 11.4 x 10^6 m^3 y^{-1}. (0.8% MAR) (Department of Water Affairs 1987).

Including losses due to evapotranspiration (estimated to total 128.8 x 10^6 m^3 y^{-1}. or 9.5% MAR), the Department of Water Affairs (1987) estimated the total annual input of water into the Crocodile River catchment minus the total annual output to be 598.6 x 10^6 m^3 y^{-1}. or 52.7% MAR. In light of the above discussed inconsistencies in calculations of water used for irrigation, total annual flow could be as low as 220.3 x 10^6 m^3 or 22% virgin MAR.

Water chemistry

The concentrations of ionic salts in the Crocodile River between 1983 and 1989 has been described as "moderate" (Van Veelen 1990; 1991; Moore *et al.* 1991), with concentrations increasing inside the KNP. Between 1983 and 1989 there was a significant upward trend in the concentrations of NH_4 and phosphate (PO_4), a positive increase in pH (van Veelen 1990 1991; Moore *et al.* 1991), and an upward trend in fluoride concentrations (Raubenheimer *et al.* 1990).

The concentration of aluminium in water samples from the Crocodile River collected in March 1983 exceeded 100 µg l^{-1} (Chutter and de Moor 1983) which is considered to be hazardous to aquatic life (Environmental Protection Agency 1973). The concentration of other metals in the water, sediment and organisms in the Crocodile River is unknown.

Tests for pesticides in water samples collected in 1974 and 1975 revealed the periodic occurrence of alpha-endosulfan (0.09 and 1.2 µg l^{-1}) (Van Dyk 1978).

Predicted future development

Future development of the Crocodile River catchment, and hence water demands, are inevitable. Department of Water Affairs (1987) projects a water demand of 510.6 m^3 x 10^6 y^{-1}. by the year 2000, though the accuracy of this prediction is questionable since it is substantially less than the conservative calculation of total water usage in 1985 (640.2 m^3 x 10^6) given in the same document, and the more probable water usage in 1985 of 1 019 m^3 x 10^6 (see discussion on land use above). It is foreseen that the area under irrigation could increase by a further 36 000 ha (Department of Water Affairs 1987), causing agricultural demand to rise by a further 270 x 10^6 m^3 y^{-1}. Further demands on water from the Crocodile River are expected to be exerted by expansion of plantations around the Ngodwana pulp mill (up to 48 000 ha), industrial and urban development in the White River, Nelspruit, Barbeton and Waterval-Boven areas, and diversion of cooling water for power stations (Department of Water Affairs 1987).

Summary

The catchment of the Crocodile River is extensively developed, in particular the agricultural sector. Impoundment and abstraction of water for irrigation has resulted in substantial reductions in flow volumes and increased flow regulation. Water quality is moderate, with significant increases in plant nutrients and fluoride over the past 10 years. Periodic high concentrations of metals and pesticides is problematic. Significant future catchment development can be expected with concurrent reductions in flow and declines in water quality.

CHAPTER 2

THE CONSERVATION STATUS OF FISH COMMUNITIES OF KRUGER NATIONAL PARK RIVERS

2.1 INTRODUCTION

Development of the catchments of KNP rivers, and consequent changes in stream flow and water quality (Chapter 1) have lead to concerns being expressed by conservation authorities (Joubert 1985, 1986a, 1986b) and other interested parties (Bruwer 1991a) about potential changes in the conservation status of their fish communities.

The frequent haphazard approach to defining the conservation status of freshwater fish (section 1.2.1) is reflective of the lack of a framework for undertaking such studies. Several investigations have been undertaken in South Africa (Gaigher *et al.* 1980; Kleynhans 1986; Kleynhans and Engelbrecht 1988; Mayekiso and Hecht 1988; Skelton *et al.* 1995) and elsewhere in the world (Horwitz 1994; Mrakovcic *et al.* 1995; Rakaj and Flloko 1995; Elvira 1995; Changeux and Pont 1995) which claim to assess the conservation status of aquatic biota. Few authors, however, define what they mean by the term "conservation status", define their objectives, or describe how they interpret the significance of recorded biotic changes. Consequently, a failing of most assessments is their subjectivity. The overcoming of such subjectivity through thorough planning and design of investigative programmes, which includes definition of objectives and goals, has been emphasized by several authors (Macdonald and Grimsdell 1983; Maher and Norris 1990; Spellerberg 1991; Hellawell 1992; Finlayson 1994; Centre for Water in the Environment 1996).

The conceptual plans for monitoring suggested by Spellerberg (1991) (Figure 2.1) and Finlayson (1994) (Figure 2.2) could serve as a basis for undertaking assessments of the conservation status of fish communities. The emphasis in assessments of conservation status on describing historical changes in the distribution or abundance of species (ideally from a pristine state (Kleynhans and Engelbrecht (1988)) resulting from anthropogenic changes to the environment, however, indicates the necessity for two additional processes (Figure 2.3).

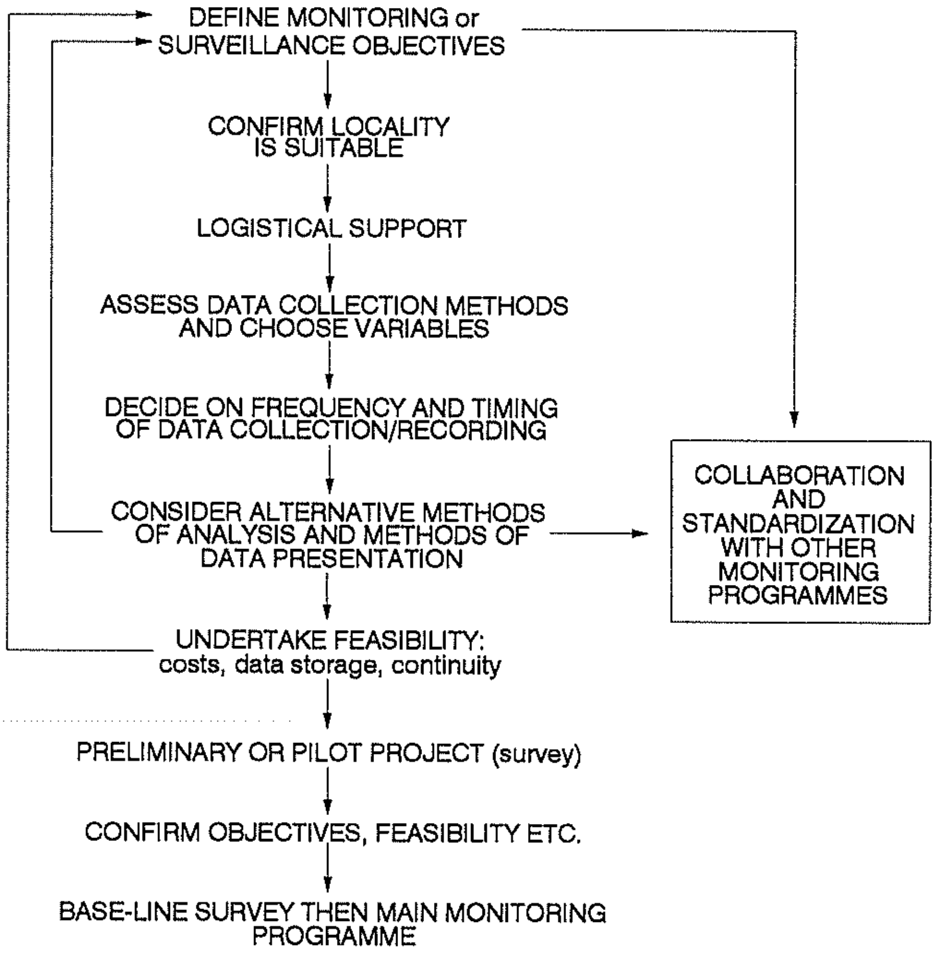


Figure 2.1 Framework for designing a monitoring programme. Arrows indicate direction of steps that would be taken and revision stages where necessary (redrawn from Spellerberg 1991).

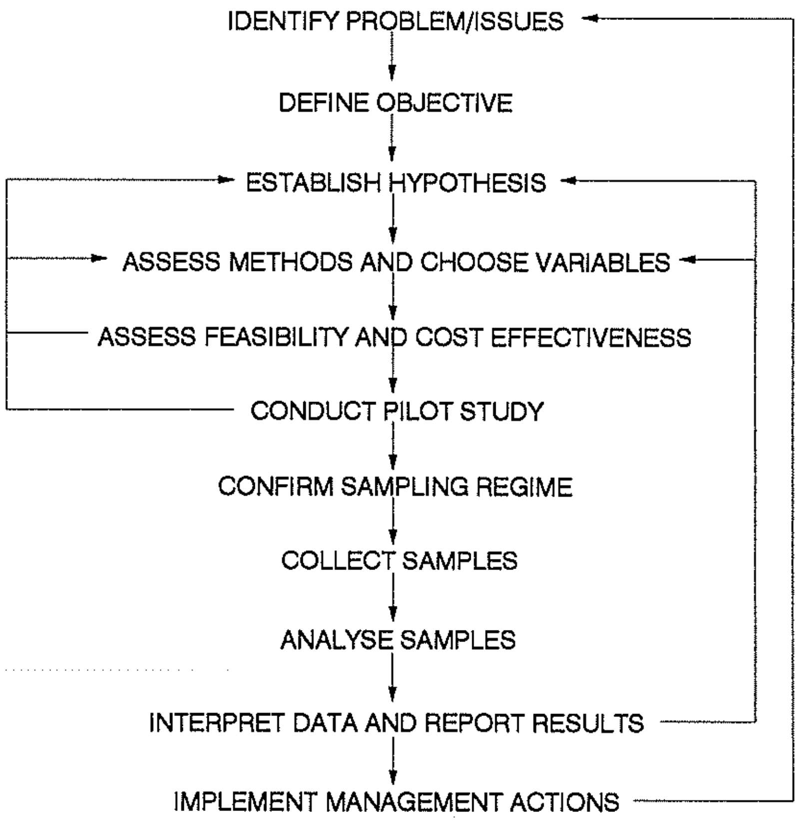


Figure 2.2 Framework for designing a wetland monitoring programme (redrawn from Finlayson (1996))

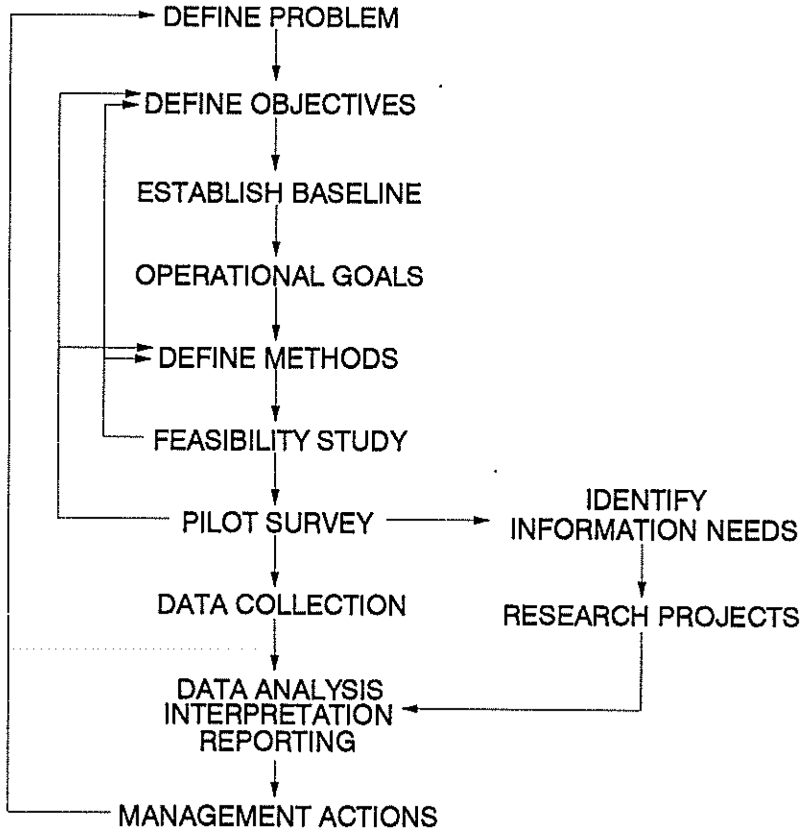


Figure 2.3 Proposed framework for monitoring the status of fish assemblages. Arrows indicate direction of steps.

Firstly it is necessary to describe what the historical state was, before quantifiable goals can be formulated on the type and degree of acceptable change. This can be problematic as frequently the distribution or abundance of fish under pristine conditions is unknown (Danilewitz *et al.* 1988). This problem pertains to KNP rivers, where historical data on the distribution of fish in the KNP were collected between 1959 and 1963 (Pienaar 1968, 1978; Gaigher 1969), whereas man's modification of the river catchments commenced prior to these surveys (sections 1.3.4 to 1.3.8). Consequently, the distribution of fish in KNP rivers under pristine conditions is unknown. Therefore, assessments of change in the conservation status of fish in KNP rivers using comparisons of the distribution of fish species during past (1959-1963) and present (1987-1989) surveys would be based on distribution changes over a 30 year period (1959-1989) rather than from a pristine state.

The second suggested addition to the conceptual plan entails the identification of additional studies or reviews necessary to distinguish between the effect of natural and anthropogenic disturbances on fish distribution. Numerous studies both in southern Africa (Jackson 1961a; Crass 1964; Kok *et al.* 1978; Gaigher *et al.* 1980; Kleynhans 1986; Skelton 1987) and elsewhere (Petr 1967; Lelek 1973; Grossman *et al.* 1982; Herbold 1984; Rahel *et al.* 1984; Yant *et al.* 1984; Grossman *et al.* 1985) have shown that changes in the abiotic environment of rivers can influence the spatial and temporal variability in the abundance of fish. The conservation objectives of the National Parks Board of South Africa (National Parks Board 1987) embody the concept of conserving natural fluctuations in the distribution and abundance of biota (section 1.2.2.3). Thus, changes resulting from natural variations in the aquatic environment, such as long-term variability in stream flow resulting from cyclical variations in rainfall (Tyson 1978), would not signify a decline in conservation status. Alternatively, changes in the distribution of fish resulting from anthropogenic changes to the aquatic environment would signify a change in conservation status (Kleynhans and Engelbrecht 1988). The distinction between these two processes, however, is frequently difficult (Naiman *et al.* 1992) due to inadequate understanding of the natural variability of abiotic processes in rivers, and the environmental factors which govern the distribution and abundance of biota.

Catchment development in KNP rivers has been substantial (sections 1.3.4 to 1.3.8) thus both natural and anthropogenic environmental changes could be expected to simultaneously influence the distribution of fish species. The formulation of plausible hypotheses of the causes of observed changes in KNP fish communities, and hence justifiable statements on the conservation status, would necessitate understanding the environmental preferences of fish species, as well as the types and probable effects of physical, chemical and biological changes in the aquatic environment.

Arguably one of the most problematic components of any investigative programme dealing with complex, and frequently poorly understood ecosystem processes, is the definition of operational goals which define limits of change in relation to conservation objectives. The necessity for definition of operational goals prior to sampling and analysis has been emphasized in several recent publications on monitoring methodology (Spellerberg 1991; Hellawell 1992; Finlayson 1994), and forms the basis of evaluating conservation success (Mentis 1984). No references could be located which define operational goals pertaining to the distribution of freshwater fish. Without such guidance, it was therefore necessary to independently define such goals.

In attempting to define operational goals for KNP fish communities, cognisance was taken of the primary conservation objective of maintaining biotic diversity (section 1.2.2.3) which encompasses conservation of the diversity of fish assemblages, as well as the dynamic functioning of the aquatic ecosystems. Thus operational goals for these communities had to be broad enough to encompass species distributional changes resulting from natural environmental changes, yet exclude distributional changes resulting from man-induced, deleterious environmental changes. Historical descriptions of KNP fish communities (Pienaar 1968, 1978; Gaigher 1969) detail only the distribution of species. Therefore evaluation of change in the conservation status of fish communities could only be undertaken at this level of community description. Consequently, it is suggested that the following changes in the distribution of fish species would indicate a decline in the conservation status of fish communities and hence departure from conservation objectives:

(i) A decrease (>35% decline in number of localities collected in different surveys) in the distribution of an indigenous fish species that is permanently resident in a river and where the reason for the decline is the consequence of man-induced changes in the aquatic environment.

(ii) An increase (>35% increase in number of localities collected in different surveys) in the distribution of a permanently resident, indigenous fish species, where the reason for the increase is the consequence of man-induced changes in the aquatic environment and where the increased distribution of said species threatens the conservation status of any other species.

(iii) The establishment or increase in the distribution of an alien fish species.

Alternatively, the following changes in the distribution of fish species would not indicate a decline in the conservation status of fish communities, and hence would not represent a departure from the National Parks Board's conservation objectives:

(iv) Either an increase or decrease in the distribution of an indigenous fish species resulting from natural changes in the aquatic environment; or where, after comprehensive study of the environmental preferences of the species and man-induced changes in the physical, chemical and biological environment, no obvious cause for the observed change in distribution can be identified.

(v) A decline in the distribution of a widespread fish species whose widespread distribution is the consequence of man-induced changes in the aquatic environment.

(vi) An increase in the distribution of an indigenous fish species, resulting from man-induced changes in the aquatic environment, where the increased distribution does not threaten the conservation status of any other species.

(vii) A decline in the distribution of an introduced or alien fish species.

(viii) A decline in the distribution of occasional migrant fish species.

Definition of the terms "increase in distribution" and "decrease in distribution", and the frequency and scope of surveys required to determine such changes are open to debate. More detailed discussion of these topics are, for the purpose of this assessment of change in the conservation status of fish communities, given in section 2.2.

The procedure used in this study to assess the conservation status of KNP fish communities is summarised in Table 2.1. The general problem relating to anthropogenic modification of KNP rivers has been discussed in Chapter 1 and briefly outlined above. The above discussion has also outlined operational goals for a study which has the objective of assessing the conservation status of fish in KNP rivers by

Table 2.1 Summary of procedures undertaken in this study to monitor the conservation status of fish communities in the major rivers of the Kruger National Park.

General problem:	■ Catchment development ■ Water abstraction and impoundment ■ Water quality deterioration
Specific problem:	■ Anthropogenic modifications of aquatic ecosystem could result in changes in the distribution and abundance of freshwater fish species
Objective:	■ Assess the conservation status of fish communities by establishing the occurrence of long-term changes in the distribution of species resulting from anthropogenic modifications of the aquatic environment.
Baseline:	■ Historical data on fish distribution (Pienaar 1978; Gaigher 1969)
Goals:	The conservation status of fish community would have declined if one or more of the following conditions apply: ■ A decrease in the distribution of an indigenous fish species that is permanently resident in a river and where the reason for the decline is the consequence of man induced changes in the aquatic environment. ■ An increase in the distribution of a permanently resident, indigenous fish species, where the reason for the increase is the consequence of man induced changes in the aquatic environment and where the increased distribution of said species threatens the conservation status of any other species. ■ The establishment or increase in the distribution of an introduced or alien fish species.
Methods:	■ Sampling methods employed (seine net & electro-fishing) ■ Assess limitations of techniques ■ Sample site selection
Feasibility:	■ Equipment availability ■ Logistical support ■ Time
Pilot:	■ Preliminary surveys to establish suitability of sample methods ■ Test equipment under field conditions and check reliability of recordings ■ Train staff in species identification
Information & Research:	■ Environmental preferences of fish ■ Minimum flow requirements to maintain fish habitat ■ Review of water quality requirements
Sampling:	■ Survey species distribution
Analysis & Interpretation:	■ Comparison of species distribution to baseline data ■ Identify probable causes of change ■ Evaluate achievement of operational goals
Evaluate:	■ Review effectiveness of procedures ■ Identify research needs to improve accuracy of assessments

assessing long-term changes in the distribution of species. The issues of data collection and analysis used, and the limitations of such methods, are discussed in section 2.2. The major emphasis of this chapter is on the last four components of conservation status assessment (information and research; sample collection; analysis and interpretation; evaluation) which entailed:

(i) Determination of long-term changes in the distribution of fish species by comparing data from past (1960s) and present (1980s) surveys.

(ii) Description of the environmental preferences of fish species by correlating the distribution of fish species with environmental conditions at sample sites. Description of fish communities consisting of species with similar environmental preferences, to facilitate identification and description of changes in the distribution of ichthyofauna.

(iii) Description of changes in the physical, chemical and biological environment of rivers that could potentially affect fish species distribution.

(iv) Formulation of hypotheses on probable reasons for changes in the distribution of fish species (based on data from points i to iii above), thereby facilitating the formulation of justifiable statements on the conservation status of fish communities.

(v) Evaluation of the conservation status by determining the achievement of conservation goals relating to the extent and causes of changes in the distribution of fish species.

Evaluation of the approach used to assess the conservation status of fish is undertaken throughout the chapter, with the highlighting of limitations of the data, and deficiencies with regard to understanding of environmental process which hamper data interpretation. Emphasis is placed on identifying potential future areas of research which could facilitate assessments of the cause for, and significance of changes in fish communities.

2.2 MATERIALS AND METHODS

2.2.1 Distribution of fish in KNP rivers

The distribution of fish in KNP rivers was described to enable evaluation of long-term changes by comparison with historical data.

2.2.1.1 Sample site selection

Sampling of fish communities was undertaken at 35 sample localities (Figure 2.4), comprising 86 sample sites (Tables 2.2 to 2.6) situated on the Luvuvhu, Letaba, Olifants, Sabie and Crocodile rivers. All sample localities were within the boundaries of the KNP, and were the same as those used by Pienaar (1968 and 1978) and/or Gaigher (1969) to facilitate comparison of the distribution of fish species (see section 2.2.1.4).

Time constraints precluded the use of all sample localities originally selected by Pienaar (1968, 1978). Sample localities used were selected judgmentally according to the following criteria:

(i) It was necessary to have the sample localities distributed along the entire length of the river sections falling within the boundaries of the KNP, to enable description of the distribution of species throughout the KNP.

(ii) Sample localities were selected for their accessibility from an established road, and effective operation of fish sampling apparatus.

(iii) An attempt was made to sample as wide a variety of different geomorphological features as possible.

Wherever possible, fish surveys were undertaken in the same localities in successive sample years. In some instances, this was not possible due to the presence of hippopotamuses, and therefore an alternative locality was selected. These alternative localities were geographically as close as possible to the original abandoned sample locality, and included geomorphological features similar to the abandoned locality.

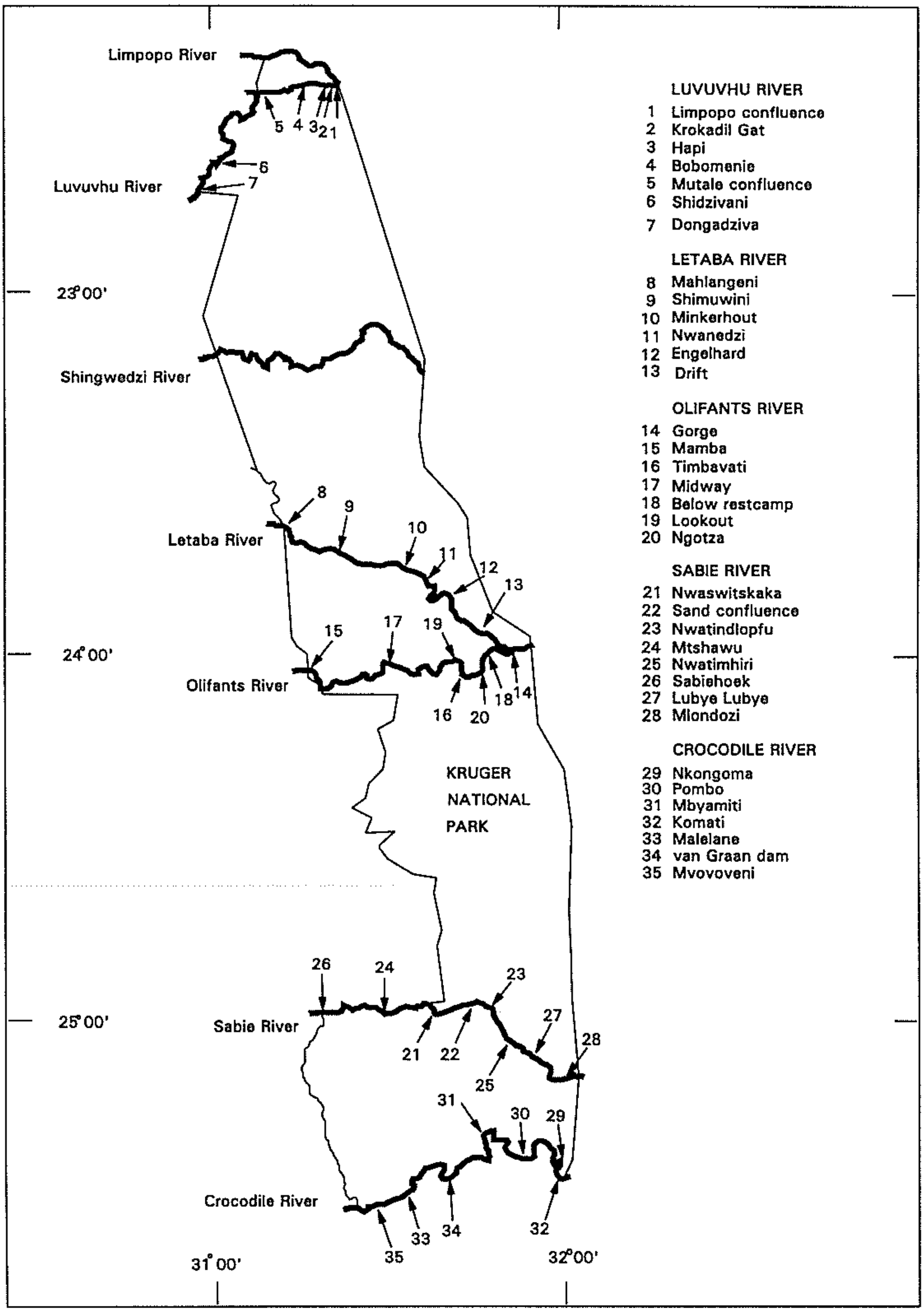


Figure 2.4 Map of Kruger National Park indicating localities used to sample fish communities.

Table 2.2 Location and description of sample sites used during fish surveys in the Luvuvhu River.

Sample site No.	 Name	Habitat description	Lat (S)	Long (E)	Map No.
1a	Limpopo confluence	Deep pool in main channel	22°25'31"	31°18'25"	2231AD
1b	Limpopo confluence	Pool edge in main channel	22°25'31"	31°18'25"	2231AD
2	Krokadil gat	Deep pool in main channel	22°25'55"	31°17'44"	2231AD
3	Hapi	Deep pool in main channel	22°25'41"	31°15'07"	2231AD
4a	Bobomeni	Deep pool in main channel	22°25'41"	31°12'35"	2231AC
4b	Bobomeni	Rapid	22°25'41"	31°12'35"	2231AC
4c	Bobomeni	Shallow pool and pool edges	22°25'41"	31°12'35"	2231AC
5a	Mutale	Deep pool in main channel	22°26'50"	31°04'53"	2231AC
5b	Mutale	Rapid (fast) in Luvuvhu	22°26'50"	31°04'53"	2231AC
5c	Mutale	Pool edge (*Lightfootia*)	22°26'50"	31°04'53"	2231AC
5d	Mutale	Rapid (slow) in Mutale	22°26'50"	31°04'53"	2231AC
6a	Shipale	Deep pool in main channel	22°30'31"	31°00'56"	2231CA
6b	Shipale	Rapid	22°30'31"	31°00'56"	2231CA
6c	Shipale	Shallow pools (*Phragmites*)	22°30'31"	31°00'56"	2231CA
6d	Shipale	Pool edge & 2° channel	22°30'31"	31°00'56"	2231CA
7a	Shidzivane	Main channel	22°38'08"	30°57'25"	2230DB
7b	Shidzivane	Shallow pool	22°38'08"	30°57'25"	2230DB
7c	Shidzivane	Rapid	22°38'08"	30°57'25"	2230DB
7d	Shidzivane	Pool edge (*Phragmites*)	22°38'08"	30°57'25"	2230DB

Table 2.3 Location and description of sample sites used during fish surveys in the Letaba River.

Sample site No	Name	Habitat description	Lat (S)	Long (E)	Map No.
8a	Mahlangeni	Deep pool in main channel	23°38'41"	31°09'07"	2311CA
8b	Mahlangeni	Rapid	23°38'41"	31°09'07"	2311CA
9a	Shimoweni	Deep pool in main channel	23°42'48"	31°17'50"	2331CB
9b	Shimoweni	Shallow pool	23°42'48"	31°17'50"	2331CB
10a	Minkerhout	Deep pool below dam wall	23°45'31"	31°30'00"	2331CD
10b	Minkerhout	Shallow pool in main channel	23°45'31"	31°30'00"	2331CD
11	Nwanedzi	Deep pool in main channel	23°48'08"	31°34'07"	2331DC
12	Engelhart	Shallow pool (*Lightfootia*)	23°50'11"	31°38'15"	2331DC
13a	Drift	Deep pool in main channel	23°56'37"	31°44'12"	2331DC
13b	Drift	Pool edges (*Phragmites*)	23°56'37"	31°44'12"	2331DC

Table 2.4 Location and description of sample sites used during fish surveys in the Olifants River.

Sample site		Habitat description	Lat (S)	Long (E)	Map No.
No	Name				
14a	Gorge	Deep pool in main channel	23°59'19"	31°49'36"	2331DD
14b	Gorge	Rapid	23°59'19"	31°49'36"	2331DD
15	Mamba	Rapid	24°02'33"	31°12'53"	2431AA
16a	Timbavati	Deep pool in main channel	24°03'21"	31°40'35"	2431BA
16b	Timbavati	Rapid	24°03'21"	31°40'35"	2431BA
16c	Timbavati	2° channels (*Phragmites*)	24°03'21"	31°40'35"	2431BA
17	Midway	Main channel (shallow)	24°02'12"	31°33'03"	2431BA
18a	Below restcamp	Deep pool in main channel	23°59'02"	31°46'19"	2331DD
18b	Below restcamp	Rapid	23°59'02"	31°46'19"	2331DD
18c	Below restcamp	Pool edges (*Phragmites*)	23°59'02"	31°46'19"	2331DD
19a	Lookout	Pool edges (*Phragmites*)	24°01'45"	31°40'18"	2431BA
19b	Lookout	Rapid (slow)	24°01'45"	31°40'18"	2431BA
20a	Ngotza	Deep pool in main channel	24°03'10"	31°43'40"	2431BA
20b	Ngotza	Rapid	24°03'10"	31°43'40"	2431BA
20c	Ngotza (Balule)	Deep pool off main channel	24°03'10"	31°43'40"	2431BA
20d	Ngotza (Balule)	Pool edge (*Phragmites*)	24°03'10"	31°43'40"	2431BA
20e	Ngotza (Balule)	Rapid	24°03'10"	31°43'40"	2431BA

Table 2.5 Location and description of sample sites used during fish surveys in the Sabie River.

Sample site					
No	Name	Habitat description	Lat (S)	Long (E)	Map No.
21a	Skukuza	Deep pool in main channel	24°59'06"	31°35'14"	2431DC
21b	Skukuza	Pool edge in main channel	24°59'06"	31°35'14"	2431DC
21c	Skukuza	Rapid	24°59'06"	31°35'14"	2431DC
22a	Sand confluence	Deep pool in main channel	24°57'37"	31°42'23"	2431DC
22b	Sand confluence	Pool edges (*Phragmites*)	24°57'37"	31°42'23"	2431DC
22c	Sand confluence	Rapid	24°57'37"	31°42'23"	2431DC
22d	Sand confluence	Pool edges (*Pistia*)	24°57'37"	31°42'23"	2431DC
22e	Sand confluence	Shallow pool	24°57'37"	31°42'23"	2431DC
23a	Ntwatindlopfu	Main channel	24°58'36"	31°46'11"	2431DD & 2432CC
23b	Ntwatindlopfu	Pool edges & 2° channel	24°58'36"	31°46'11"	2431DD & 2432CC
23c	Ntwatindlopfu	Deep pool in 2° channel	24°58'36"	31°46'11"	2431DD & 2432CC
24a	Mtshawu	Deep pool in main channel	24°58'29"	31°21'30"	2431CD
24b	Mtshawu	Shallow pool & pool edges	24°58'29"	31°21'30"	2431CD
24c	Mtshawu	Rapid	24°58'29"	31°21'30"	2431CD
25	Ntwatinhiri	Pool edges in main channel	25°03'02"	31°48'37"	2531BB & 2532AA
26a	Sabiehoek	Pool edges in main channel	25°01'04"	31°15'00"	2531AA
26b	Sabiehoek	Main channel (shallow)	25°01'04"	31°15'00"	2531AA
26c	Sabiehoek	2° channel (*Phragmites*)	25°01'04"	31°15'00"	2531AA
27a	Lubye Lubye	Deep pool in main channel	25°05'47"	31°53'05"	2531BB & 2532AA
27b	Lubye Lubye	Pool edges in main channel	25°05'47"	31°53'05"	2531BB & 2532AA
27c	Lubye Lubye	Rapid	25°05'47"	31°53'05"	2531BB & 2532AA
27d	Lubye Lubye	Shallow pool & 2° channel	25°05'47"	31°53'05"	2531BB & 2532AA
28a	Mlondozi confl.	Deep pool in 2° channel	25°09'46"	31°59'57"	2531BB & 2532AA
28b	Mlondozi confl.	Shallow pools in 2° channel	25°09'46"	31°59'57"	2531BB & 2532AA
28c	Mlondozi confl.	Pool edges (*Pistia*)	25°09'46"	31°59'57"	2531BB & 2532AA
28d	Mlondozi confl.	Rapid	25°09'46"	31°59'57"	2531BB & 2532AA
28e	Mlondozi confl.	Main channel (shallow)	25°09'46"	31°59'57"	2531BB & 2532AA

Table 2.6 Location and description of sample sites used during fish surveys in the Crocodile River.

Sample site No	Name	Habitat description	Lat (S)	Long (E)	Map No.
29	Nkangoma	Channel edges (*Phragmites*)	25°23'28"	31°58'30"	2531BD & 2532AC
30	Pombo	Shallow pool & channel edges	25°22'16"	31°51'58"	2531BD & 2532AC
31a	Mbyamiti	Channel edges (Phragmites)	25°18'55"	31°44'56"	2531BA
31b	Mbyamiti	Rapid	25°18'55"	31°44'56"	2531BA
32a	Komati confluence	Channel edges	25°26'18"	31°58'24"	2531BD & 2532AC
32b	Komati confluence	Rapid	25°26'18"	31°58'24"	2531BD & 2532AC
33a	Malelane	Main channel (deep)	25°27'27"	31°32'08"	2531BA
33b	Malelane	Rapid	25°27'27"	31°32'08"	2531BA
33c	Malelane	Channel edges	25°27'27"	31°32'08"	2531BA
34a	van Graan	Shallow pool	25°26'12"	31°38'09"	2531BA
34b	van Graan	Channel edges	25°26'12"	31°38'09"	2531BA
35a	Mvovoveni	Main channel (deep)	25°30'12"	31°27'15"	2531CB
35b	Mvovoveni	2° channel	25°30'12"	31°27'15"	2531CB

Samples were collected during four surveys, comprising three winter surveys (May to September) in 1987, 1988 and 1989 in all five rivers, and one summer survey (November 1987 to February 1988) at four localities in the Luvuvhu River, six localities in the Letaba River, and eight localities in the Sabie River. The single summer survey was undertaken to compare catch compositions in different seasons. A more comprehensive summer sampling program was precluded by time constraints, coupled with difficulties experienced with operating sampling gear in strongly flowing rivers during summer months.

2.2.1.2 Fish sampling methods

Two methods of sampling fish communities were used in all surveys, namely seine netting and electro-fishing. These methods were selected as they had previously been employed in fish surveys of the major rivers in Mpumalanga and the Northern Province in South Africa (Gaigher 1969; U de V Pienaar *pers. comm.*).

Seine nets were used in pools that were relatively free of obstructions such as sunken logs, large stones and dense stands of macrophytes. Two beach seine nets were used with dimensions 25m x 2m x 35mm, and 40m x 1m x 12mm. The 35mm net had a 2m trailing purse, with a stretched mesh size of one millimetre. A 30m warp was attached at each end of both nets. The maximum sampling area of the nets was $750m^2$ and $1200m^2$ respectively.

The 35mm net was used in deep pools and in strongly flowing water, as its greater depth proved more effective in deeper waters, and its larger mesh size offered less resistance, and hence more efficient recovery, in strongly flowing water. The 12mm net was used exclusively in slow flowing, shallow waters.

Nets were set from a rowing boat by first playing out one of the warps at right angles to the bank/direction of flow. The net was set parallel to the bank opposite the landing area. Where flow was strong, the upstream end of the net was loosely tied to the fringing *Phragmites* reeds or other marginal vegetation to stabilize the position of the net within the channel. Where no marginal vegetation occurred the net was placed on the bank at the waters edge. The remaining warp was played out back to the landing area. The net was hauled in manually by pulling on the warps (effectively breaking the connection where the net had been tied to the opposite bank vegetation).

Between two and eight effective seine net pulls were undertaken at each suitable sample site during each survey. Sampling at a locality was generally terminated before the number of specimens collected exceeded that which could be identified, weighed and measured, during the same day that sampling was undertaken.

An electrical shocking apparatus was used to collect fish in fast flowing water, shallow pools with a stony substratum, and amongst inundated or floating vegetation. The apparatus consisted of a portable generator (220 volts, 1200 watts, AC) with hand held electrodes on a 30m electrical cable.

In shallow rapids, pools and amongst vegetation, the equipment operator walked at right angles to the bank, while simultaneously moving the electrodes in an arc in the water. Once having walked to the far bank of the river, or alternatively, until the electrical cable was extended to its maximum length, the operator would walk upstream (parallel to the river bank) for three to four meters, and then work back towards the original bank, once again with the electrodes in the water. Sampling was undertaken in an upstream direction to minimize the obscuring of vision from mud disturbed by the operators feet. The operator carried a hand net, and was assisted by two persons also equipped with hand nets, with which stunned fish were scooped up. The assistants walked on either side and slightly behind the operator. The generator was moved along the river bank when necessary. In most instances, the generator was operated whilst standing on the river bank, however it was occasionally placed in a boat and pulled along behind the operator. This was done in order to achieve greater freedom of movement within the sample area.

In fast flowing rapids, the most effective method of fish collection was to position as many assistants as possible towards the bottom of the rapid, each with a handnet that was held permanently in the water with the open mouth of the net facing the direction of flow. The operator then walked from the top of the rapid downwards, where possible moving in the same zigzag manner as described above. The electro-narcotisized fish would be swept down the rapid, and most would be retained in the handnets.

The period of use varied according to the size of the area being sampled, though in most instances this was greater than 30 minutes per sample site per survey. As with seine netting, electro-fishing was generally terminated before the number of specimens collected exceeded that which could be identified, weighed and measured, during the same day that sampling was undertaken. Where both seine netting and electro-fishing were undertaken at the same locality on the same day, cognisance was taken of sample returns from both sample methods when deciding on sampling intensity.

Limitations of fish sampling methods

As only two methods of fish sample collection were employed, it is pertinent to detail some of the selectivity characteristics of these methods, and how they could have influenced catch composition.

Effective sampling of pools in which the maximum depth exceeded two meters was limited by the maximum seine net depth. Sampling was only undertaken during daylight hours for reasons of personal safety. The majority of sampling was undertaken in winter, since high flow during summer frequently rendered seine netting impossible. Therefore, seine netting resulted largely in the capture of fish that frequented the shallower sandy bottomed type habitats during the day.

Species that were probably undersampled included large, highly mobile species that predominantly frequent deep pools (*Labeo congoro* Peters, 1852; *Labeo rosae* Steindachner, 1894; *H. vittatus*; and large cichlids); species that occur predominantly in fast flowing rapids (*Chiloglanis pretoriae* Van der Horst, 1931; *Chiloglanis anoterus* Crass 1960); as well as species that are predominantly nocturnally active (*Petrocephalus catostoma* (Günther, 1866), and *Marcusenius macrolepidotus* (Peters, 1852), (Kok 1980)). The number of adult *L. rosae* and *T. rendalli* were probably also undersampled due to the habit of netted individuals frequently jumping the headrope of the seine net. Adult *Clarias gariepinus* (Burchell, 1822) are also known to frequently avoid capture by escaping underneath the footrope of seine nets (Kok 1980).

Sampling with the electro-fishing apparatus was undertaken primarily in the winter months, and only during daylight hours. Due to the dangers posed by crocodiles, electro-fishing was not undertaken in highly turbid waters or in areas where water depth exceeded one meter.

The effectiveness of the electro-fishing apparatus was dependant on a number of factors, including the species of fish, the physical size of the specimens, and the conductance of the water.

Different fish species were found to differ in their degree of resistance to electro-induced paralysis. The Mormyridae were highly resistant, requiring physical contact with one of the electrodes to be completely immobilized. Most of the cyprinids and cichlids were highly susceptible, and were completely immobilized even when a couple of meters from the electrodes.

Fish species also differed in their ability to avoid the electrical field created by the approaching sampler. Most of the highly mobile, open water species such as *H. vittatus* and *L. rosae* were able to avoid capture, whereas others species such as *C. gariepinus* and most of the species that frequent rapids, were more easily captured. Most fish species floated to the water surface immediately after being electro-narcotisized. However, *Chiloglanis* species and *C. gariepinus* tended to remain on the bottom, making them difficult to see and therefore collect, particularly in turbid water.

Size of the specimen also influenced sampling effectiveness. Large individuals were more successful in avoiding the electrical field, despite the documented greater capture probability of larger specimens when electro-fishing (Cross and Scott 1975; Bohlin and Sundstrom 1977).

Lastly, the greater the electrical conductance of the water, the more effective was the sampling apparatus. Effectiveness of the sampling apparatus was found to be highest in the Olifants River due to the high conductance of the water (Table 2.13), whereas sampling effectiveness in the Sabie River was substantially lower due largely to lower conductance levels.

In summary, sampling methods employed emphasized the capture of fish species that frequented rapids, shallow pools and marginal areas during daylight hours in winter. Predominantly slower swimming species and physically small specimens were captured, whereas highly mobile species and large specimens were potentially undersampled. Electro-fishing was most effective in the Olifants River, and least effective in the Sabie River. Seine netting was most effective in the slow flowing, shallow waters of the Luvuvhu and Letaba rivers, and least effective in the faster flowing Crocodile and Sabie rivers. Although fish collection methods used may have biased sampling to some extent towards specific habitats or species, it is believed that the combination of methods used provided the best possible sampling strategy in these rivers.

2.2.1.3 Identification of fish species

Captured fish were identified using generic and specific keys (Pienaar 1978), and descriptions of species (Jubb 1967). Where specimens could not be identified using these references, they were preserved in 10% formalin and transported to the J.L.B. Smith Institute of Ichthyology (Grahamstown) where identification was undertaken by freshwater fish taxonomists.

During the first two years of field work (1987 and 1988), all *Glossogobius* species identified in the field by the author were classified as *Glossogobius giuris* (Hamilton-Buchanan, 1822). However, in the third year of the study (1989) some of the *Glossogobius* specimens from the Sabie River sent to J.L.B. Smith Institute as voucher specimens were identified as *Glossogobius callidus* (Smith, 1937) (P. Skelton, *in litt.*), a species not previously recorded in KNP rivers. This raised the suspicion that some of the *Glossogobius* specimens collected in 1987 and 1988 may have been misidentified. Consequently during all analyses, no distinction is made between *G. giuris* and *G. callidus* and the two species are treated as a single group referred to as *Glossogobius* spp.

Voucher specimens of all fish species were preserved in 10% formalin and housed in the J.L.B. Institute of Ichthyology museum in Grahamstown, and the National Parks Board research department museum at Skukuza.

2.2.1.4 Describing long-term changes in the distribution of fish

Change in the distribution of fish species within the KNP was assessed by subjective comparison of descriptions of species distribution determined in past (1960s) (Pienaar 1968, 1978; Gaigher 1969) and present (1980s) surveys. Fish were categorised into the following groups (definitions given in parentheses):

(i) Species not found; with two subgroups described as:

  (a) Previously widespread
  (Described by Pienaar (*in litt.*) as being abundant in the 1960s, and collected at 50% or more, of the suitable localities sampled, per river, in the 1960s, and not collected during this study).

  (b) Previously scarce
  (Described by Pienaar (*in litt.*) as being scarce in the 1960s, and collected at less than 50% of the suitable localities sampled, per river, in the 1960s, and not collected during this study).

(ii) Species with decreased distribution
(Collected at fewer localities, per river, in this survey compared to surveys in the 1960s, where the difference in the number of localities collected is greater than 35% of all suitable localities surveyed).

(iii) Species with increased distribution
(Collected at more localities, per river, in this survey compared to surveys in the 1960s, where the difference in the number of localities collected is greater than 35% of all suitable localities surveyed).

(iv) New species record
(Not collected in a river in the 1960s, but collected during this study).

(v) Species with unchanged distribution
(Collected in a river in the 1960s and during this study, where the difference in the number of localities collected is not greater than 35% of all localities sampled)

For the purpose of assessing the achievement of operational goals (see section 2.1) the inability to sample a species (previously either widespread or scarce) after three consecutive surveys was interpreted as indicating a decline in distribution. New species records were interpreted as indicating an increase in distribution.

2.2.2 Environmental preferences of fish

The environmental preferences of fish species were described by comparison of environmental conditions at sample sites (geomorphological feature, flow velocity, nature of the substratum, water turbidity and the presence of aquatic plants) and the distribution of fish species. Environmental data was intended for use in a species frequency by environmental variable matrix to be analysed using multivariate statistics. Both discrete (geomorphological features, substratum, aquatic plants) and continuous (flow velocity, turbidity) data were collected. To be accommodated in the matrix format, continuous data was classified into three or four categories, which encompassed ranges measured during sampling.

2.2.2.1 Description of geomorphological features.

All sample sites were categorized according to the following key:

(i) Rapids - generally characterized by a steep gradient, stony substratum and high flow velocity.
(ii) Deep pools - >1m maximum depth.
(iii) Shallow pools - <1m maximum depth.
(iv) Marginal areas - areas around the margins of pools and typically with inundated or floating aquatic plants.
(v) Secondary channels - narrow (<5m wide), usually shallow (<1m deep) channels adjacent to the primary river channels, generally characterized by low flow velocity.

2.2.2.2 Flow Velocity.

Flow velocity varies according to both horizontal and vertical position in the river channel as well as with river discharge. Velocity of flow is considered as one of the environmental variables that determines the suitability of an area for different fish species (Prewitt and Carlson 1980; Annear and Conder 1984).

Flow velocity was measured at five or more regularly spaced points across the river channel at each sample site. Flow velocity was measured with an OSK 3203 Hirois electric current meter at two thirds depth, that has in previous studies (Smith and

Stopp 1987) been found to correspond closely with average velocity within the vertical profile.

Mean flow velocities within sample sites were categorized into four groups:

(i) None (0 m s^{-1})
(ii) Little (0.1 m s^{-1} to 1.5 m s^{-1})
(iii) Medium (1.6 m s^{-1} to 3.0 m s^{-1})
(iv) Strong (>3.0 m s^{-1}).

2.2.2.3 Turbidity.

Turbidity is a visual property of water implying muddiness or lack of clarity, and is due to the presence of solid or colloidal particles, generally larger than 0.22 µm, that are held in suspension in the water (Kirk 1985).

The influence of suspensoids on fish is complex (Bruton 1985), and includes reduction in light penetration and thus photosynthesis, resulting in reduced food availability and plant biomass; reduced visibility of pelagic food; reduced availability of benthic food due to smothering; clogging of gillrakers and gill filaments and reduced aerial predation risk. Turbidity was measured at each survey locality and during each annual sample session in order to define the environmental preferences of fish.

In 1987 and 1988 turbidity at sample sites was assessed by visual inspection, and water samples classified into three categories: Clear, Turbid, and Very turbid.

In 1989, a Hach Model 16800 turbidity meter was used to determine turbidity of all water samples with results expressed in Nephelometric Turbidity Units (NTU). Using both visual categorisation and direct measurement of turbidity during 1989 demonstrated that the approximate NTU ranges of turbidity categories where:

(i) Clear (<5 NTU)
(ii) Turbid (5.1 to 15 NTU)
(iii) Very turbid (>15 NTU)

All samples measured in 1989 where categorised as either clear, turbid or very turbid to provide a discrete data set compatible to that collected in 1987 and 1988.

2.2.2.4 Nature of the substratum.

The nature of the substratum was described at one meter intervals along three or more profiles spanning all the sites of the sample locality, and orientated across the river channel. The nature of the substratum was described by either visual inspection in clear, shallow waters, or by feel using a sounding rod in deep pools and turbid waters. The general nature of the substratum at each sample site was classified into one of seven categories:

(i) Detritus
(ii) Mud (<0.05mm)
(iii) Gravel (5mm to 0.05mm)
(iv) Stone (>5mm)
(v) Stone and gravel
(vi) Stone and algae
(vii) Bedrock

2.2.2.5 Presence of aquatic plants.

Aquatic plants are an important component of the habitat of several fish species, being a food source, a substratum from which food can be obtained and onto which adhesive eggs can be attached (Bell-Cross 1976; Bruton *et al.* 1982), and provide protective cover from predators (Skelton 1986b).

Emergent and submerged aquatic plants at all sample sites were subjectively described in the field in terms of presence (present, absent), proximity (within 10m of sample site, further than 10m from sample site), and abundance (sparse, abundant, very abundant). For the purpose of multivariate analyses, aquatic plants at each sample site was classified into one of three categories:

(i) Present (abundant in sample area)
(ii) Fringing (absent or sparse within sample site, though abundant in close proximity to sample area)
(iii) Absent (not present within or in close proximity to sample site).

2.2.2.6 Mathematical techniques to define the environmental preferences of fish.

The relationship between fish species distribution and physical (geomorphological features, flow speed, nature of the substratum, turbidity) and biological (proximity to aquatic plants) environmental variables was explored using correspondence analysis (Greenacre 1989) and DECORANA (Hill 1979) to define the environmental preferences of fish species and to describe fish communities. These methods were used since the data consisted of counts (frequency of species recorded with correlated environmental variables) for which methods based on reciprocal averaging (such as correspondence analysis and DECORANA) are an appropriate means of analysis (James and McCulloch 1990). The related procedure of principle components analysis, although widely used in studies of the relationships between community variation and environmental gradients (James and McCulloch 1990), was not selected as it is unable to capture nonlinear relationships (Miles and Ricklefs 1984). Consequently, for most community data sets, particularly those consisting of counts, or percentages, ordination methods based on reciprocal averaging provide a superior means of analysis (Gauch 1984).

The use of different fish sampling techniques and variable sampling intensity in different sample sites necessitated that all fish abundance data be expressed as a percentage of the number of times species were sampled at sites with a specific environmental variable. This was undertaken to re-weight the species profiles, hence placing the different environmental variables on a par with one another for purposes of comparison (Greenacre 1989).

Initially seven categories were used to describe the predominant substratum at sample sites (section 2.2.2.4). Sampling of sites with substratum consisting predominantly of 'Detritus' or 'Stones and algae' were too infrequent for meaningful analysis. Consequently, these were grouped with the substratum categories 'Mud' and 'Stone' respectively.

Ordination axes (correspondence analysis) were selected on the basis of their having sufficient variance to represent inherent data structure and hence exhibit maximal community variation (Hill 1979). The relationships between species and environmental variables were assessed by visual inspection of the geometric dispersion of sample points within the ordination space. Outlyers were removed from the data bases to facilitate data interpretation.

In correspondence analysis, the dispersion of row (species) and column (environment) profiles in the ordination space are approximately the same (Greenacre and Hastie 1987), thus frequent occurrence of fish species under an environmental condition was indicated by their being located close together within an ordination space. The environmental preferences of fish species were in turn inferred from observations of their frequency of occurrence under different environmental conditions, with species frequently co-occurring under similar environmental conditions grouped into communities.

Possible instability of the first two axes of the ordination of geomorphological features was indicated by the similarity of their contributions to the total inertia. Axis stability was tested using jackknifing by sequential removal of species from the data base (Greenacre 1989) and re-plotting the resulting scatter diagrams.

The data set for frequency of occurrence of fish species in different geomorphological features was reanalysed using DECORANA (Hill 1979) to assess the influence of the arch effect and axis compression (Gauch *et al.* 1977) on the interpretation of scatter diagrams produced using correspondence analysis. Community beta diversity in terms of standard deviation units was determined from the DECORANA output.

2.2.3 Environmental factors causative of fish distributional change.

Long-term changes in the physical (flow reductions), chemical (water chemistry) and biological (distribution of aquatic plants) environment of KNP rivers were described to enable formulation of hypotheses on the effect of changing environmental conditions on the distribution of fish species.

2.2.3.1 The effects of flow reductions on fish habitat availability.

Assessment of the effects of flow reductions on fish habitat availability was undertaken using hydraulic models to define minimum base flows for maintaining fish habitats. Base flow estimates where, in turn, compared to historical flow data to determine frequency and duration of loss of fish habitat resulting from low flows.

Modeling of flow to define minimum flows for maintaining fish habitats.

Growing world-wide concern about the detrimental environmental effects of modified flow régimes has resulted in the development of several methods for calculating the instream flow requirements of aquatic biota. Although it was not the objective of this study to assess the instream flow requirements of KNP rivers, various instream flow methodologies were investigated as potentially providing a basis for defining minimum flows for maintaining fish habitats.

Computational difficulties associated with the hydrological components of IFIM (see section 1.2.2.1) precluded its use in this study. Although the conceptual basis of most other, mathematically simpler, instream flow methodologies may differ from one another, all incorporate a similar hydrological and ecological approach. Analyses are either wholly (Wetted Perimeter; Habitat Retention) or partially (Skukuza; Building Block) based on flow simulations in river cross-sections (usually using Manning's equation), to determine flow conditions at which predefined environmental parameters are retained (Milhous 1978; Bovee and Milhous 1978; Nehring 1979 cited in Annear and Conder 1984; Bruwer 1991a; King and Tharme 1993). Environmental parameters used include water depth (Milhous 1978; Bovee and Milhous 1978; Nehring 1979; Bruwer 1991a), flow velocity (Nehring 1979; Bruwer 1991a; King and Tharme 1993), and wetted perimeter (Milhous 1978; Bovee and Milhous 1978; Nehring 1979). Furthermore, all are based on the largely untested assumption that flow conditions lower than the determined minima will negatively influence aquatic biota (Nehring 1979; Prewitt and Carlson 1980; King and Tharme 1993).

The concept of modeling flow to establish discharge required to meet certain environmental parameters, as used in most "biological response" type instream flow analyses (Mosley 1985), was used in this study. This entailed application of Manning's equation to simulate flow in river cross-sections to establish the minimum flow at which predefined environmental parameters (mean depth, velocity and wetted perimeter) are retained. This study was also based on the assumption that flow lower than a determined minima, in a specific river, will negatively influence fish species.

The methodology used in this study most closely approaches the Habitat Retention method (Nehring 1979). This method is believed to be more suitable for identifying minimum flows necessary to maintain fish habitats than previous attempts (O'Keeffe 1991; Chutter *et al.* 1991; Rooseboom 1991; Davies 1991; Bruwer 1991d; Gore *et al.*

1992; Louw 1996; Weston 1996) at defining instream flow requirements in KNP rivers, for the reasons discussed below.

The first reason relates to the objective for undertaking instream flow assessments. In the case of rivers flowing through the KNP, objectives include the concept of managing flows to "ensure the long-term conservation of aquatic communities" (Department of Water Affairs and Forestry 1993). How this conservation status will be assessed has unfortunately not been defined, though it is reasonable to assume that the acceptable (in terms of the conservation objectives) ecological state could differ from a pristine state. It is re-emphasized that this study was not undertaken to define the instream flow requirements of rivers, but rather to identify baseflow levels below which there would be a reduction in the availability of suitable habitat for fish. Thus no judgements needed to be made whether flow reductions where acceptable or not in terms of conservation objectives. It was assumed that any loss of suitable habitat would have a detrimental effect on the distribution and abundance of fish. This in turn could result in higher minimum flow assessments when compared to instream flow methodologies where habitat loss may, at times, be acceptable. Thus, for the purpose of this study, the method of flow assessment used was considered superior to previously used instream flow methodologies as it enabled focusing on the issue of the effects of flow reductions on fish, and sidestepping (at this point of the study) of the contentious debate of limits of acceptable change.

Secondly, it is a comparatively simple technique which avoids the mathematical complexities of IFIM. Orth and Leonard (1990) have demonstrated reasonable correspondence between predictions from IFIM and simpler discharge based methods, suggesting use of simpler methodologies does not automatically imply decreased accuracy of flow assessments. The need for simplicity in the methodology used for assessing minimum acceptable flows has been emphasized by Allan (1995) until such time as complex modeling procedures (such as IFIM) can be rigourously tested against the biological variables they are intended to predict.

Thirdly, unlike early applications of the Skukuza method which used hypothetical cross-sections through rapids (Davies 1991), this study used actual cross-section and slope measurements, through both rapids and sandy bottomed river channels. The use of real rather than hypothetical data, measured in a variety of geomorphological features, is likely to increase the accuracy of flow assessments.

Before modeling of flow could be undertaken it was first necessary to quantify minimum limits for the environmental parameters - mean depth, velocity and wetted perimeter. This was undertaken to enable identification of the flow volume below which accelerated loss of fish habitat would occur. Quantification of environmental parameters was essentially a subjective decision. However, in view of the substantial influence that the defined limits have on the interpretation of flow modeling results, it was considered necessary to justify these decisions. Consequently, the following section includes a discussion of the literature used to aid quantification environmental parameters for KNP rivers.

Quantification of environmental parameters necessary for maintenance of fish habitats

For large North American rivers (wetted perimeter greater than 30m) a flow providing at least 60 percent of an optimum wetted perimeter has been suggested (Prewitt and Carlson 1980). This parameter was considered inappropriate for KNP rivers since flows less than that which provide optimum wetted perimeter (typified by the point at which the water surface recedes from the river banks, or in certain instances secondary channel) (Annear and Conder 1984), could result in substantial loss of marginal habitats characterised by the presence of inundated plants (usually *Phragmites mauritianus* Kunth.). The vulnerability of fish species that occur predominantly in marginal areas to reductions in flow has been highlighted by Russell and Rogers (1989). Consequently, optimum wetted perimeter, identified as the first inflection point on a flow versus wetted perimeter graph, was considered an appropriate flow characteristic for evaluation of minimum base flows for the maintenance of adult fish habitats in KNP rivers.

Mean flow velocity, suitable for the maintenance of fish habitats in Colorado USA have been specified as 0.30 to 0.45 m s^{-1} (Prewitt and Carlson 1980), with Annear and Conder (1984) distinguishing different velocities for rapids (0.30 m s^{-1}), runs (0.15 m s^{-1}) and pools (0.03 m s^{-1}). These recommendations concurred with preliminary assessments of the environmental preferences of three fish in the Sabie River (Gore *et al.* 1992), namely the marginal habitat dwelling *Serranochromis meridianus* Jubb, 1967 (0 to 0.05 m s^{-1}) and *Barbus viviparus* Weber, 1897 (0 to 0.20 m s^{-1}), as well as *Chiloglanis swierstrai* Van der Horst, 1931 (0.30 m s^{-1}) which occurs predominantly on sandy runs. With the assumption that provision of flow velocity for the fish species with the highest flow requirement will also cater for the habitat requirements of other fish species, a mean flow velocity of 0.30 m s^{-1} was considered to be adequate for the maintenance of fish habitats in open river channels (runs) in the KNP rivers.

No data exist on the flow velocity preferences of rapid dwelling fish species which occur in the KNP rivers. However, Gore *et al.* (1991) recorded preferred flow velocities of 0.15 m s^{-1} and 0.30 m s^{-1} for the rapid-dwelling *Austroglanis barnardi* (Skelton 1981) and *Austroglanis gilli* (Barnard 1943), respectively, in the Olifants river (western Cape). It was assumed that the flow velocity preferences of rapid-dwelling *Chiloglanis* species in KNP rivers would not differ substantially from that of the closely related *Austroglanis* species in the western Cape. Thus a mean flow velocity of 0.30 m s^{-1} was also considered to be adequate for the maintenance of fish habitats in rapids in KNP rivers.

Mean depth evaluation is usually based on the maximum body depth of the largest fish present (Prewitt and Carlson 1980; Annear and Conder 1984), which for large rivers in North America is generally in the order of 0.18 to 0.30m. Cambray *et al.* (1989) suggested an average depth of 0.50m in riffles of perennial streams in South Africa as a minimum for the breeding and survival of 'sensitive' species, but there are no data to support this suggestion. In preliminary evaluations of the flow requirements of KNP rivers, an average depth of 0.20m has been considered essential for the medium- and short-term maintenance of fish communities in the Luvuvhu river (O'Keeffe 1991), whereas only 0.10m was considered essential in the Sabie river (Davies 1991). The 0.10m average depth suggested for the Sabie river is inadequate, as this value is substantially less than the maximum body depth recorded for several large fish specimens collected in surveys during the current study (maximum body depth for the two largest specimens, *T. rendalli* - 181mm; *C. gariepinus* - 192mm). Based on recorded maximum body depth of such fish species, a minimum mean water depth of 0.20m would seem more appropriate for the maintenance of fish communities in open river channels. This corresponded with the depth resulting in maximum habitat suitability for *C. swierstrai* in the Sabie river (Gore *et al.* 1992). Several large bodied fish species (maximum body depth larger than 100mm) such as *Barbus marequensis* A. Smith, 1841; *Labeo molybdinus* Du Plessis, 1963; and *Labeo cylindricus* Peters, 1852 frequently occur in rapids (see section 2.3.2.1), thus necessitating a mean depth greater than 0.10m in these areas. Furthermore, passage flows across rapids are considered to be as important as maintenance flows in pool and run areas (Prewitt and Carlson 1980), which indicates that a minimum mean water depth of 0.20m would also be appropriate in rapids in KNP rivers.

In summary, flow parameters used in hydraulic modeling were mean depth $\geq$ 0.20m, mean flow velocity $\geq$0.30 m s^{-1}, and optimum wetted perimeter.

River cross-sections

Between three and six river cross-sections were measured at each sample locality to enable measurement, and modeling of flow. River cross-sections consisted of three components, namely a water depth profile and two river bank profiles.

Water depth profile

Water depth profiles consisted of a series of regularly spaced (1 meter intervals) water depth measurements across a river channel, orientated perpendicular to the direction of flow.

Depth measurements in deep pools (>1m) were taken from a boat, with a nylon rope firmly anchored on both river banks to aid manoeuvrability in a straight line across the river channel. Depth measurements were taken to the nearest centimetre, using a one meter wooden ruler (0.5cm graduations) in shallow waters, and a three meter stainless steel pole (1.0cm graduations) in deeper waters.

Water depth profiles were spaced such that they spanned the area in which fish sampling was undertaken. The average distance between profiles at any sample locality was 30m.

River bank profiles

River bank profiles consisted of a series of regularly spaced, relative height measurements, along both banks of a river, starting at the end points of the water depth profile at the waters edge and orientated perpendicular to the direction of flow.

Relative changes in height were determined at either one or two meter intervals (closer spacing for more variable topography) along a glass-fibre tape measure stretched over the ground, using a Wild Leitz dumpy level and a 5m metric staff.

Where possible, river bank profiles were extended to the outer edges of the riparian vegetation zone.

Hydraulic model

Modeling of flow through cross-sections of different geomorphological features involved manipulation of the Manning's formula (see below), with calculations undertaken using a spreadsheet (QPRO) on a personal computer.

$$V = S^{1/2}.R^{2/3}/n$$

where V = Velocity
S = Slope
R = Hydraulic radius
n = roughness coefficient

Slope was calculated by surveying the endpoints of the water depth profile using a Wild Leitz dumpy level and a 5m metric staff. Roughness coefficients were obtained from tables compiled by Rooseboom and Van Zyl (1978) based on the nature of the substratum (section 2.2.2.4) and aquatic plants (section 2.2.2.5) within the survey locality.

Calibration of the flow simulation model was undertaken using measurements of river discharge ($m^3\ s^{-1}$ or cumec), which was calculated using water depth profile and flow velocity (section 2.2.2.2) data. Calculation of river discharge involved dividing the water depth profile into panels with a single flow velocity measurement point midway in each panel (Smith and Stopp 1987). This measurement of flow velocity was taken to represent the average flow velocity of the section of the river channel within the corresponding panel. Discharge (cumecs) per panel was determined by multiplying the total area of the panel (m^2) with flow velocity ($m\ s^{-1}$). The sum of the discharge in all panels of the water depth profile yielded river discharge. Discharge calculations were undertaken using a spreadsheet (QPRO) operated on a personal computer.

Calibration of the flow simulation model involved comparing simulated and calculated discharges with hydraulic radius as a constant. Where necessary, the model constants for roughness coefficient and slope were adjusted until calculated and measured discharge values were within 0.5 cumec of one another. If large adjustments to the model constants (n >0.05; slope >10% of measured value) were required for calibration of flow simulations through a river cross-section, then these data were excluded.

The minimum flow required for the maintenance of fish habitats within a river was described as the average of the lowest flows calculated for the retention of all three environmental parameters in different geomorphological features.

The effect of flow reductions on fish habitat conditions

The effect of flow modifications on the availability of fish habitats was confined to the study of flow reductions (rather than increases in flow), as water abstractions for offstream use constitute the major anthropogenic modification to flow régimes rather than flow increases through interbasin transfers or dam releases during low flow periods (sections 1.3.4 to 1.3.8). The effects of low flows on fish habitats was investigated by calculating, as measures of the severity of low flow (Arthington 1991), the frequency and duration of low flow periods, as well as the extent to which flows fell below minima required for the maintenance of fish habitats. The frequency of low flows was expressed as the percentage of monthly flow records in a calendar year where mean runoff (m^3 s^{-1}) was below calculated minima to maintain fish habitats. The duration of low flow was expressed as the number of consecutive months where mean runoff was below calculated minima to maintain fish habitats. The extent to which mean monthly flows fell below calculated minima to maintain fish habitats was expressed as the percentage of flow between the calculated minimum and zero flow, where average monthly flow equal to the calculated minimum for a river was zero percent, and zero flow was 100 percent.

Monthly flow records for KNP rivers used in the above described assessments of flow reductions on fish habitat conditions were obtained from South African Department of Water Affairs and Forestry (DWAF) managed gauging stations closest to the western boundary on the KNP. Monthly flow record available for the Luvuvhu River, however, underestimate discharge reaching the western boundary of the KNP because:

(i) Flow records do not include runoff from the ungauged Mutale River, a major tributary of the Luvuvhu River (section 1.3.4).

(ii) The gauging station for the Luvuvhu River is situated approximately midway in the catchment. Thus flow emanating from approximately 30% of the catchment outside the western boundary of the KNP is not gauged.

These inaccuracies in the flow record of the Luvuvhu River were compensated for by:

(i) Increasing runoff by 38% which is the proportionate runoff from the Mutale River (section 1.3.4).

(ii) Increasing runoff by a further 30% to compensate for runoff originating in the lower portions of the catchments. This percentage increase is equivalent to the area of ungauged catchment, as Mean Annual Precipitation in Luvuvhu catchment is less than average rainfall for the lowveld region (section 1.3.3) thus there are unlikely to be major differences in runoff from the upper and lower reaches.

Regression analysis was used to determine whether significant temporal (1960 to 1990) changes occurred in the frequency and duration of low flows, and reduction in flow volumes.

2.2.3.2 Physical and chemical water quality

The physical and chemical water quality of KNP rivers was described, and compared to existing guide-lines (Kempster *et al.* 1980; Environmental Affairs Department 1980; Environment Canada 1987; Gardiner and Zabel 1989; Moore *et al.* 1991) on the water quality requirements of aquatic biota, to determine the effect of past water quality on the distribution of fish species. Two sources of water quality data were used:

(i) DWAF unpublished water quality data consisting of measurements of electrical conductivity, total dissolved solids, pH, and concentrations of Na, Mg, Ca, F, Cl, NO_3+NO_2, SO_4, PO_4, $CaCO_3$, Si, K and NH_4 (data used were from sample sites closest to the western boundary of the KNP).

(ii) Water quality parameters measured at sample localities during fish surveys were conductivity, dissolved oxygen concentration, temperature, pH and turbidity. Method of measurement of turbidity is described above (section 2.2.2.3) and other water quality parameters below.

Conductivity

Conductivity provides a measure of the concentration and dissociation of dissolved salts (Yellow Springs Instrument Co. 1981), and was measured in the field at each sample locality, and during each annual sample period with a YSI 33 S-C-T meter.

Dissolved oxygen concentration and temperature

Oxygen production during photosynthesis, and consumption during respiration, results in temporal and spatial variability in the dissolved oxygen concentration of waterbodies. Temperature influences the solubility of oxygen in water and hence its availability to aquatic organisms (Wetzel and Likens 1979). Both oxygen concentration and water temperature are factors that affect the distribution of fish species (Rose 1967; Davis 1975).

Measurements were undertaken in the field with a YSI model 51B oxygen/temperature meter and a YSI 5739 oxygen/temperature probe. In view of diel changes in both dissolved oxygen concentration and temperature in most waterbodies, all measurements of dissolved oxygen and temperature were taken as close to 12h00 as possible.

pH

The pH of a waterbody is determined primarily by the equilibrium of CO_2, HCO_3^- and $CO_3^=$. In most waterbodies, changes in pH are regulated by the buffering effects that additional carbonates have on this equilibrium (Wetzel 1983). The equilibrium can be shifted by photosynthetic activity of aquatic plants when the uptake of CO_2 results in an increase in the proportion of HCO_3^- and $CO_3^=$ and hence reduction in the concentration of hydrogen ions (Wetzel 1983). Thus, pH increases during periods of high photosynthetic activity, and decreases during periods of low productivity.

The measurement of pH in the field was undertaken with a Schott and Gerhard electronic pH meter. In view of diel changes in pH in waterbodies, all pH measurements were taken as close to 12h00 as possible.

2.2.3.3 The distribution of aquatic plants

The distribution of emergent (*Phragmites mauritianus* Kunth.), floating (*Pistia stratiotes* L.; *Eichhornia crassipes* (Mort.) Solms.) and submerged (*Cladophera* spp.) aquatic plants along the course of the perennial rivers in the KNP was noted during low-level (<100m altitude) aerial surveys during 1987, and from ground observations during field surveys. These observations, along with descriptions of the past distribution of aquatic plants obtained from the literature, were used to describe gross changes in the distribution of aquatic plants, and predict the probable effect of such changes on the distribution of fish species.

2.3 RESULTS AND DISCUSSION

2.3.1 Changes in the distribution of fish species

Since both past (1960s) and present (1980s) fish surveys were comprehensive, a comparative reduction (section 2.2.1.4) in the number of sample localities at which a species was collected (Table 2.7) was interpreted as a reduction in distribution. Conversely an increase in collection localities was interpreted as an increase in distribution.

The largest number of changes involving reduction in the distribution of fish species was recorded in the Luvuvhu River (Table 2.8). Four previously widespread species (*B. annectens, B. toppini, B. trimaculatus, B. unitaeniatus*), and six species with previous limited distributions (*Amphilius uranoscopus* (Pfeffer, 1889), *Aplocheilichthys johnstoni* Günther, 1893, *A. aeneofuscus, Carcharhinus leucas* (Valencienness, 1839), *C. swierstrai, P. philander*) were not found in this study. A further three species (*B. marequensis, B. radiatus, B. viviparus*) were found to have decreased distributions in the Luvuvhu River within the KNP.

In the Letaba River both declines and increases in species distribution were recorded (Table 2.8). Six species (*B. annectens, C. swierstrai, Anguilla marmorata* Quoy & Gaimard, 1824, *A. aeneofuscus, C. pretoriae, L. congoro*) were not recorded during this study, and the distribution of *H. vittatus* was found to have declined within the KNP. The decreased distribution of *A. aeneofuscus, A. marmorata, C. swierstrai* and *H. vittatus* in the Letaba River in KNP has been confirmed by Chutter and Heath

Table 2.7 Occurrence of fish at different sample localities in the Kruger National Park as determined in the 1960s (after Piennar 1968, 1978, *pers comm.*; Gaigher 1969) and 1980s (this study), where x = 1960s surveys; + = 1980s surveys; and o = both 1960s and 1980s surveys.

River and site number	Luvuvhu River							Letaba River						Olifants River						
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Acanthopagrus berda	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Amphilius uranoscopus	.	.	.	.	x	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Anguilla bengalensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Anguilla marmorata	.	.	.	.	.	.	.	x	.	.	.	.	.	x	.	.	.	.	.	.
Anguilla mossambica	.	.	.	x	.	+	.	.	+	.	.	.	.	.	.	.	.	x	.	.
Aplocheilichthys johnstoni	.	.	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Awaous aeneofuscus	x	.	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.	.	.	.
Barbus afrohamiltoni	o	+	o	o	x	x	.	o	+	+	o	o	o	.	.	.	.	.	x	.
Barbus annectens	.	.	.	.	x	x	.	.	.	.	x	x	x	.	x	.	.	.	.	.
Barbus argenteus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Barbus eutaenia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Barbus marequensis	x	x	.	o	x	x	o	o	+	o	o	o	o	+	o	o	+	o	o	o
Barbus mattozi	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	.
Barbus paludinosus	+	.	.	.	x	.	.	.	.	+	.	+	+	.	.	+	.	+	.	.
Barbus radiatus	x	.	.	x	x	o	.	o	.	+	o	+	+	.	.	+	+	+	.	x
Barbus toppini	.	.	x	x	x	x	.	+	+	+	o	+	o	.	x	o	+	o	o	x
Barbus trimaculatus	x	x	x	x	x	x	.	o	+	o	o	o	o	+	o	o	+	+	o	o
Barbus unitaeniatus	.	.	.	x	x	x	.	o	+	+	+	+	o	.	x	.	.	.	x	.
Barbus viviparus	.	.	.	x	x	o	x	o	+	o	o	o	o	.	o	o	+	o	o	o
Brycinus imberi	o	o	o	+	o	+	o	o	o	o	o	+	o	o	x	x	.	.	.	.
Carcharinus leucas	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Chetia brevis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Chiloglanis anoterus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Chiloglanis paratus	x	+	.	o	o	+	+	o	+	o	x	+	x	+	+	o	+	o	o	+
Chiloglanis pretoriae	.	.	.	.	x	.	o	.	.	.	.	.	x	+	+	.	.	o	x	+
Chiloglanis swierstrai	x	.	.	.	.	.	.	.	.	x	x	x	x	.	.	o	.	x	+	+
Clarias gariepinus	o	o	o	o	o	o	o	o	o	o	o	o	o	+	o	o	+	o	o	o
Glossogobius spp.	o	o	o	+	o	o	+	o	+	+	o	o	o	+	x	.	+	+	.	.
Hydrocynus vittatus	o	o	o	o	o	o	x	x	.	o	x	x	o	o	.	.	.	x	x	.
Labeo congoro	.	+	.	o	x	.	+	.	.	.	.	x	x	+	x	.	x	+	x	+
Labeo cylindricus	x	.	x	o	o	o	o	o	+	o	o	+	o	+	o	x	+	o	x	o
Labeo molybdinus	.	.	.	o	o	+	+	+	+	+	o	o	o	o	+	o	+	o	o	o
Labeo rosae	o	o	o	o	x	+	.	o	+	+	o	o	o	+	x	o	.	o	x	o
Labeo ruddi	o	o	o	x	.	.	+	+	+	+	o	o	o	.	x	o	.	o	x	o
Marcusenius macrolepidotus	.	.	.	x	x	+	o	x	o	+	o	o	x	.	x	.	.	x	o	x
Mesobola brevianalis	.	+	.	.	x	x	o	o	+	+	o	o	.	.	x	x	.	.	o	.
Micralestes acutidens	o	o	.	o	o	o	o	o	.	+	o	x	o	.	x	x	.	x	x	x
Opsaridium zambezense	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	x	.	x	x	.
Oreochromis mossambicus	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	+	o	o	o
Petrocephalus catostoma	+	.	.	.	.	o	o	.	.	.	.	o	x	.	.	.	.	.	o	x
Pseudocrenilabrus philaber	.	.	.	.	x	.	.	.	.	.	.	o	.	.	.	.	+	.	+	.
Schilbe intermedius	o	o	o	o	x	+	+	o	o	+	+	o	+	.	.	o	.	.	o	.
Serranochromis meridianus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Synodontis zambezensis	o	o	o	o	.	.	.	+	+	o	x	x	o	+	x	.	+	x	o	o
Tilapia rendalli	o	+	o	o	o	o	+	+	o	+	o	o	o	+	x	o	.	x	x	x
Tilapia sparrmanii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table 2.7 Continued

River and site number	Sabie River								Crocodile River						
Species	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Acanthopagrus berda	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.
Amphilius uranoscopus	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.
Anguilla bengalensis	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.
Anguilla marmorata	+	x	.	.	x	.	x	x	.	.	x	o	x	.	.
Anguilla mossambica	.	x	.	+	+	x	o	.	+	.	.	+	.	.	x
Aplocheilichthys johnstoni	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Awaous aeneofuscus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Barbus afrohamiltoni	.	.	.	.	+	.	x	+	+	.	.	.	.	x	.
Barbus annectens	x	+	+	x	+	o	+	+	.	.	.	.	.	.	.
Barbus argenteus	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.
Barbus eutaenia	.	+	.	+	+	o	+	.	.	+	+	.	x	.	x
Barbus marequensis	o	o	o	o	o	o	o	o	+	o	+	+	o	o	o
Barbus mattozi	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Barbus paludinosus	.	.	+	.	.	+	.	.	.	.	.	.	+	+	.
Barbus radiatus	x	o	+	.	+	o	o	+	+	+	+	.	x	+	+
Barbus toppini	x	+	+	.	.	x	+	.	.	.	.	.	x	+	.
Barbus trimaculatus	o	+	o	+	+	o	o	o	o	o	+	.	o	o	o
Barbus unitaeniatus	x	x	+	+	+	o	o	.	.	.	.	.	o	+	o
Barbus viviparus	o	o	o	o	+	o	o	+	+	+	+	+	o	o	o
Brycinus imberi	x	x	x	x	.	.	x	o	+	x	.	x	.	o	o
Carcharinus leucas	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Chetia brevis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Chiloglanis anoterus	+	.	.	+	.	x	x	.	.	x	.	.	x	.	.
Chiloglanis paratus	o	+	.	o	.	o	o	.	+	o	o	+	o	.	x
Chiloglanis pretoriae	.	+	.	.	.	x	.	.	.	x	x	x	x	x	x
Chiloglanis swierstrai	x	o	.	o	.	o	+	.	.	x	+	+	x	.	.
Clarias gariepinus	x	o	o	x	o	o	o	o	o	o	o	o	o	o	o
Glossogobius spp.	o	x	o	.	o	.	x	+	+	x	.	+	x	.	.
Hydrocynus vittatus	x	x	x	x	.	.	x	o	.	x	.	o	.	.	.
Labeo congoro	x	o	.	+	.	x	x	x	+	o	+	o	x	+	.
Labeo cylindricus	o	o	.	o	+	o	o	o	o	o	+	o	o	o	o
Labeo molybdinus	o	o	.	o	+	o	o	+	.	o	+	+	o	+	x
Labeo rosae	o	o	o	+	.	x	x	o	+	x	.	x	x	x	+
Labeo ruddi	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x
Marcusenius macrolepidotus	o	o	o	+	+	o	+	+	o	+	+	o	+	+	x
Mesobola brevianalis	o	o	o	+	.	x	o	+	.	x	+	.	o	+	o
Micralestes acutidens	o	o	o	o	+	o	o	o	+	o	+	o	o	o	o
Opsaridium zambezense	o	o	o	o	.	x	o	.	.	x	+	.	x	.	o
Oreochromis mossambicus	o	o	o	o	x	o	o	o	o	o	o	o	o	o	o
Petrocephalus catostoma	x	+	.	+	+	.	+	o	.	x	+	.	x	.	x
Pseudocrenilabrus philaber	o	o	+	+	+	o	o	+	+	.	+	.	o	o	+
Schilbe intermedius	x	x	x	+	+	x	o	+	+	+	+	+	o	o	.
Serranochromis meridianus	o	o	o	o	o	o	o	o	.	.	.	.	.	.	.
Synodontis zambezensis	+	x	.	.	.	.	.	x	.	.	.	x	x	.	.
Tilapia rendalli	o	o	o	o	o	o	o	o	+	o	+	o	o	o	o
Tilapia sparrmanii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+

Table 2.8 Categorisation of fish species in the major rivers of the Kruger National park according to their change in distribution between surveys undertaken in the 1960s, and 1980s.

Luvuvhu	Letaba	Olifants	Sabie	Crocodile
Group 1 - species not found				
Previously widespread				
B. annectens	*B. annectens*	*M. acutidens*	-	*C. pretoriae*
B. toppini	*C. swierstrai*	*O. zambezense*	-	-
B. trimaculatus	-	-	-	-
B. unitaeniatus	-	-	-	-
Previously scarce				
A. uranoscopus	*A. marmorata*	*A. marmorata*	*A. uranoscopus*	*A. bengalensis*
A. johnstoni	*A. aeneofuscus*	*A. mossambica*	*B. argenteus*	*A. berda*
A. aeneofuscus	*C. pretoriae*	*B. afrohamiltoni*	-	*C. anoterus*
C. leucas	*L. congoro*	*B. annectens*	-	*L. ruddi*
C. swierstrai	-	*B. mattozi*	-	*S. zambezensis*
P. philander		*B. unitaeniatus*		-
Group 2 - Decreased distribution				
B. marequensis	*H. vittatus*	*M. macrolepidotus*	*A. marmorata*	*L. rosae*
B. radiatus	-	*T. rendalli*	*B. imberi*	-
B. viviparus	-	-	*H. vittatus*	-
			L. congoro	
Group 3 - Increased distribution				
-	*B. radiatus*	*B. trimaculatus*	*B. annectens*	*B. radiatus*
-	*B. toppini*	*C. paratus*	*B. eutaenia*	*S. intermedius*
-	*B. unitaeniatus*	-	*B. trimaculatus*	*B. viviparus*
-	*L. molybdinus*	-	*M. macrolepidotus*	-
-	*L. ruddi*	-	*P. catostoma*	-
-	*S. intermedius*	-	*P. philander*	-
Group 4 - New species				
-	*A. mossambica*	*B. paludinosus*	*B. paludinosus*	*B. paludinosus*
-	*B. paludinosus*	*P. philander*		*C. brevis*
-	-	-		*T. sparrmanii*
Group 5 - Unchanged distribution				
A. mossambica	*B. afrohamiltoni*	*B. marequensis*	*A. mossambica*	*A. marmorata*
B. afrohamiltoni	*B. marequensis*	*B. radiatus*	*B. afrohamiltoni*	*A. mossambica*
B. paludinosus	*B. trimaculatus*	*B. toppini*	*B. marequensis*	*B. afrohamiltoni*
B. imberi	*B. viviparus*	*B. viviparus*	*B. radiatus*	*B. eutaenia*
C. paratus	*B. imberi*	*B. imberi*	*B. toppini*	*B. marequensis*
C. pretoriae	*C. paratus*	*C. pretoriae*	*B. unitaeniatus*	*B. toppini*
C. gariepinus	*C. gariepinus*	*C. swierstrai*	*B. viviparus*	*B. trimaculatus*
Glossogobius spp.	*Glossogobius spp.*	*C. gariepinus*	*C. anoterus*	*B. unitaeniatus*
H. vittatus	*L. cylindricus*	*Glossogobius spp.*	*C. paratus*	*B. imberi*
L. congoro	*L. rosae*	*H. vittatus*	*C. pretoriae*	*C. paratus*
L. cylindricus	*M. macrolepidotus*	*L. congoro*	*C. swierstrai*	*C. swierstrai*
L. molybdinus	*M. brevianalis*	*L. cylindricus*	*C. gariepinus*	*C. gariepinus*
L. rosae	*M. acutidens*	*L. molybdinus*	*Glossogobius spp.*	*Glossogobius spp.*
L. ruddi	*O. mossambicus*	*L. rosae*	*L. cylindricus*	*H. vittatus*
M. macrolepidotus	*P. catostoma*	*L. ruddi*	*L. molybdinus*	*L. congoro*
M. brevianalis	*P. philander*	*M. brevianalis*	*L. rosae*	*L. cylindricus*
M. acutidens	*S. zambezensis*	*O. mossambicus*	*M. brevianalis*	*L. molybdinus*
O. mossambicus	*T. rendalli*	*P. catostoma*	*M. acutidens*	*M. macrolepidotus*
P. catostoma	-	*S. intermedius*	*O. zambezense*	*M. brevianalis*
S. intermedius	-	*S. zambezensis*	*O. mossambicus*	*M. acutidens*
S. zambezensis	-	-	*S. intermedius*	*O. zambezense*
T. rendalli	-	-	*S. meridianus*	*O. mossambicus*
-	-	-	*S. zambezensis*	*P. catostoma*
-	-	-	*T. rendalli*	*P. philander*
-	-	-	-	*T. rendalli*

(1993). The distribution of six species (*B. radiatus, B. toppini, B. unitaeniatus, L. molybdinus, L. ruddi, S. intermedius*) was found to have increased, and *B. paludinosus* and *Anguilla mossambica* Peters, 1852 where recorded for the first time in the Letaba River in the KNP.

The second largest number of changes involving reduction in the distribution of species was recorded in the Olifants River (Table 2.8). Two previously widespread species (*M. acutidens, O. zambezense*), and six species with previously limited distribution (*A. marmorata, A. mossambica, B. afrohamiltoni, B. annectens, Barbus mattozi* Guimaraes, 1884, *B. unitaeniatus*) were not found within the KNP during this study. A further two species (*M. macrolepidotus* and *T. rendalli*) were found to have decreased distributions. The distribution of two species (*B. trimaculatus, C. paratus*) was found to have increased, and two species (*B. paludinosus, P. philander*) were recorded for the first time in the Olifants River in the KNP.

The least number of changes involving a reduction in the distribution of fish species was recorded in the Sabie River (Table 2.8). Two species with previously limited distribution (*A. uranoscopus, Barbus argenteus* Günther 1868) were not recorded in this study, and four species (*A. marmorata, B. imberi, H. vittatus, L. congoro*) were found to have decreased distribution. The distribution of six species (*B. annectens, B. eutaenia* Boulenger, 1904, *B. trimaculatus, M. macrolepidotus, P. catostoma, P. philander*) was found to have increased, and one species (*B. paludinosus*) was recorded for the first time in the Sabie River in the KNP.

In the Crocodile River, both declines and increases in species distribution were recorded (Table 2.8). One previously widespread species (*C. pretoriae*), and five species with previously limited distribution (*Anguilla bengalensis* Peters, 1852, *Acanthopagrus berda* (Forsskål, 1775), *C. anoterus, L. ruddi, S. zambezensis*) were not recorded in this study. The distribution of one species (*L. rosae*) decreased, whereas the distribution of three species (*B. radiatus, B. viviparus, S. intermedius*) was found to have increased. Three species (*B. paludinosus, Chetia brevis* Jubb, 1968, *T. sparrmanii*) were recorded for the first time in the Crocodile River within the KNP.

In summary, the fish surveys revealed complex changes in species distribution both between and within rivers (Table 2.8). While some species recorded in the 1960s were not recovered during this study, the distribution of others was found to have increased. On the whole fish communities in the rivers of the Limpopo system

(Luvuvhu, Letaba, Olifants) have undergone greater changes than have those of the Inkomati system (Sabie, Crocodile). Changes have been specific to each river, but the general pattern has been a net reduction in the distribution of species.

There is a vast literature describing changes in the distribution of freshwater fish, both in South Africa (Skelton 1987; Merron *et al.* 1993) and elsewhere in the world (Moyle and Leidy 1992; Allan and Flecker 1993). A variety of factors have been identified as causative of such changes, including alteration of flows due to abstraction and impoundment (Moyle and Nichols 1974; Stanford and Ward 1986; Scudder 1989; Moyle *et al.* 1992; Merron *et al.* 1993; Moyle 1995), changes in physical and chemical water quality (Almaça 1995; Balik 1995) and habitat loss (Hortle and Lake 1983; Penczak *et al.* 1995), and more commonly, a combination of these factors (Crass 1969; Coad 1981; Senanayake and Moyle 1982; Cadwallader 1986; Udoidiong 1988; Moyle and Williams 1990; Mrakovcic *et al.* 1995; Elvira 1995; Economidis 1995). Identifying probable causes for fish distributional changes in KNP rivers is necessary to assess changes in the conservation status of species (section 1.2.2.5). To hypothesize probable causes requires knowledge of the environmental preferences of fish species and changes in the physical, chemical and biological environment of KNP rivers. These issues are addressed below.

2.3.2 Environmental preferences of fish species

Present understanding of environmental preferences of fish in the lowveld regions of rivers in Mpumalanga and the Northern Province was considered inadequate for this study as they are based largely on opinions formed during sampling in various southern and east African rivers rather than on quantitative data (Copley 1958; Greenwood 1958; Jackson 1961a, 1961b; Crass 1964; Jubb 1968; Bell-Cross 1976; Pienaar 1978; Cambray 1984). Furthermore, for several species, only few, or contrary data are available (Table 2.9). Consequently, it was considered necessary to adopt a more formalized and rigourous approach to describe the environmental preferences of fish in KNP rivers. This was achieved by using ordination techniques to explore relationships between the distribution of fish species in relation to each other and to various environmental variables such as geomorphological features, water flow velocity, water turbidity, type of substratum and the presence of aquatic plants. Differences between observed environmental preferences and those reported in the literature (Table 2.9) are discussed below.

Table 2.9 Summary of the habitat preferences of freshwater fish which occur in eastern Transvaal rivers as described in 41 published papers. Values indicate the number of references in which particular habitat preferences were described. Data after Copley (1958); Greenwood (1958); Jackson (1961a; 1961b; 1962); Crass (1964); Groenewald (1964); Okedi (1965); Jubb (1965; 1968, 1979); Le Roux & Steyn (1968); Wager (1968); Gaigher (1969, 1970, 1973); Ribbink (1971); Fryer & Iles (1972); Kenmuir (1973); Bruton & Boltt (1975); Bell-Cross (1976); Mitchell (1976); Blaber (1978); Bowen (1978); Bruton (1978, 1979); Kok *et al.* (1978); Pienaar (1978); Caulton (1979); Bruton & Kok (1980); Hecht (1980a, 1980b); Kleynhans (1980, 1982, 1984); Skelton & Cambray (1981); Bruton *et al.* (1982); Bruton & Jackson (1983); Cambray (1984); White *et al.* (1984); Merron *et al.* (1985); Skelton *et al.* (1985); Skelton (1986). As several authors did not distinguish between pools and marginal areas these have been combined under the heading of pools.

	Fs			Hab			Sub				Cov		Cla		
Species	F	S	I	P	R	I	S	R	M	I	V	I	C	T	I
Acanthopagrus berda	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Amphilius uranoscopus	4	.	.	.	3	.	.	4	.	.	.	.	1	.	.
Anguilla bengalensis	.	.	.	1	.	.	.	2	.	.	.	.	.	.	1
Anguilla marmorata	.	1	.	2	.	.	.	2	.	.	.	.	.	.	1
Anguilla mossambica	.	$\boxed{.}$	2	.	$\boxed{.}$	1	.	2	.	$\boxed{.}$	$\boxed{.}$	.	$\boxed{.}$	.	1
Aplocheilichthys johnstoni	.	5	.	2	.	.	.	.	.	.	7	.	3	.	.
Awaous aeneofuscus	.	.	1	3	.	.	2	.	.	.	.	.	.	.	.
Barbus afrohamiltoni	.	$\boxed{4}$	.	$\boxed{5}$	.	.	.	.	$\boxed{.}$	.	1	$\boxed{.}$	.	$\boxed{.}$	.
Barbus annectens	.	$\boxed{2}$	.	$\boxed{3}$	.	.	.	.	.	$\boxed{.}$	$\boxed{1}$	1	$\boxed{.}$	.	.
Barbus argenteus	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
Barbus eutaenia	6	.	.	.	1	.	.	1	.	.	1		4	.	.
Barbus marequensis	$\boxed{4}$	.	1	.	3	$\boxed{2}$	1	$\boxed{3}$	.	.	.	$\boxed{.}$	.	.	$\boxed{.}$
Barbus mattozi	.	1	1	4	.	.	.	.	.	1	.	.	.	.	.
Barbus paludinosus	.	$\boxed{7}$	.	$\boxed{7}$	.	2	.	.	.	$\boxed{1}$	$\boxed{5}$	.	.	.	$\boxed{1}$
Barbus radiatus	.	$\boxed{3}$	.	$\boxed{4}$	.	.	.	.	.	$\boxed{.}$	$\boxed{2}$	.	.	.	$\boxed{1}$
Barbus toppini	.	$\boxed{2}$	.	$\boxed{3}$	.	.	.	.	.	$\boxed{.}$	1	$\boxed{.}$	.	.	$\boxed{.}$
Barbus trimaculatus	.	$\boxed{4}$	.	$\boxed{5}$	.	.	1	.	.	$\boxed{.}$	8	$\boxed{.}$	1	.	$\boxed{1}$
Barbus unitaeniatus	.	$\boxed{.}$	1	$\boxed{1}$	.	1	.	.	.	$\boxed{.}$	1	$\boxed{.}$	.	.	$\boxed{1}$
Barbus viviparus	.	$\boxed{5}$	.	$\boxed{3}$	.	1	.	.	.	$\boxed{.}$	$\boxed{3}$	.	1	.	$\boxed{.}$
Brycinus imberi	.	$\boxed{2}$	.	$\boxed{4}$	.	.	.	.	.	$\boxed{1}$	.	$\boxed{1}$	.	$\boxed{.}$	.
Chetia brevis	.	1	.	2	.	.	1	.	.	.	1	.	.	.	.
Chiloglanis anoterus	2	.	.	.	4	.	.	3	.	.	.	.	1	.	.
Chiloglanis paratus	$\boxed{4}$	.	.	.	$\boxed{4}$	2	.	$\boxed{4}$	.	.	.	$\boxed{.}$	.	.	$\boxed{.}$
Chiloglanis pretoriae	$\boxed{2}$	.	.	.	$\boxed{4}$	.	.	$\boxed{2}$	.	.	.	$\boxed{.}$	.	.	$\boxed{.}$
Chiloglanis swierstrai	$\boxed{5}$	3	.	4	$\boxed{.}$	.	$\boxed{9}$	.	.	.	.	$\boxed{.}$	$\boxed{.}$	.	.
Clarias gariepinus	.	$\boxed{4}$	1	$\boxed{5}$	.	2	.	.	.	$\boxed{2}$	$\boxed{3}$	.	.	.	$\boxed{1}$
Cyprinus carpio	.	2	.	2	.	.	1	.	1	.	.	.	.	.	.
Glossogobius spp.	.	4	$\boxed{.}$	4	.	$\boxed{.}$	$\boxed{1}$	2	.	.	2	$\boxed{.}$	.	.	$\boxed{.}$
Hydrocynus vittatus	.	$\boxed{1}$	.	$\boxed{2}$	.	.	1	.	$\boxed{.}$	1	4	$\boxed{.}$	1	$\boxed{.}$	.
Labeo congoro	2	$\boxed{1}$	.	3	.	$\boxed{.}$	.	$\boxed{5}$	.	.	.	$\boxed{.}$	.	.	$\boxed{.}$
Labeo cylindricus	$\boxed{2}$	.	.	.	1	$\boxed{5}$	.	$\boxed{4}$	.	.	.	$\boxed{.}$	.	.	$\boxed{.}$
Labeo molybdinus	$\boxed{.}$	.	1	.	.	$\boxed{4}$	.	$\boxed{3}$	.	.	.	$\boxed{.}$	.	.	$\boxed{.}$
Labeo rosae	.	$\boxed{2}$	.	$\boxed{3}$	.	.	1	.	.	$\boxed{2}$	.	$\boxed{.}$	.	$\boxed{1}$	.
Labeo ruddi	.	$\boxed{4}$	.	$\boxed{6}$	.	.	1	.	$\boxed{2}$	.	.	$\boxed{.}$	.	$\boxed{.}$	.
Marcusenius macrolepidotus	.	$\boxed{2}$	.	$\boxed{4}$	.	.	.	2	.	1	$\boxed{4}$	.	.	.	$\boxed{.}$
Mesobola brevianalis	.	$\boxed{4}$	2	$\boxed{5}$	.	1	.	.	.	$\boxed{.}$	4	$\boxed{.}$	1	.	$\boxed{.}$
Micralestes acutidens	.	.	$\boxed{3}$	$\boxed{.}$	.	2	1	1		$\boxed{1}$	$\boxed{.}$	.	2	.	$\boxed{.}$
Opsaridium zambeziense	$\boxed{4}$	.	1	$\boxed{3}$	.	1	3	2	.	$\boxed{.}$	.	$\boxed{1}$	$\boxed{4}$	.	.
Oreochromis mossambicus	.	$\boxed{2}$	.	$\boxed{4}$	.	.	.	.	.	$\boxed{.}$	$\boxed{1}$	.	.	.	$\boxed{.}$
Petrocephalus catostoma	.	$\boxed{3}$	.	4	.	$\boxed{.}$	.	$\boxed{1}$	.	.	$\boxed{3}$	.	.	.	$\boxed{.}$
Pseudocrenilabrus philander	.	$\boxed{1}$	3	$\boxed{2}$	.	2	2	1	.	$\boxed{.}$	$\boxed{6}$	.	1	.	$\boxed{.}$
Schilbe intermedius	.	$\boxed{2}$	1	$\boxed{4}$	.	.	.	.	.	$\boxed{.}$	.	$\boxed{.}$	.	$\boxed{.}$	.
Serranochromis meridianus	.	$\boxed{1}$	.	$\boxed{1}$	.	.	1	.	.	$\boxed{.}$	$\boxed{1}$	.	$\boxed{.}$	.	.
Synodontis zambezensis	.	$\boxed{2}$	.	$\boxed{3}$	.	.	.	1	$\boxed{.}$	2	.	$\boxed{.}$	.	$\boxed{.}$	.
Tilapia rendalli	.	$\boxed{2}$	1	$\boxed{4}$	.	.	.	.	.	$\boxed{.}$	$\boxed{.}$	.	.	.	$\boxed{.}$
Tilapia sparrmanii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Legend

Fs = flow speed
where F = preferred fast flow
S = preferred slow flow
I = either fast or slow flow

Hab = preferred habitat
where P = pools
R = rapids
I = either pools or rapids

Sub = preferred substratum
where S = sand or gravel
R = rocky
M = mud
I = substratum irrelevant

Cov = vegetation as cover
where V = vegetation for cover
I = vegetation irrelevant

Cla = clarity of water
where C = preferred clear water
T = preferred turbid water
I = water clarity irrelevant

☐ = environmental preference as determined in this study

2.3.2.1 Fish species occurrence in different geomorphological features

The principle inertias of the ordination profiles of fish occurring in pools, rapids, secondary channels and marginal areas were y_1 = 0.2247 (45.75%), y_2 = 0.1781 (36.25%), y_3 = 0.0644 (13.11%) and y_4 = 0.0240 (4.89%) respectively (Figure 2.5). Therefore, a two-dimensional correspondence analysis (Axis 1 vs Axis 2), containing 82% of the total inertia, was a good display of the profiles (Figure 2.5). Possible instability of the first two ordination axes was indicated by the similarity in their principal inertias. However, jackknifing, by means of deletion from the database of each row (species) profile in turn, indicated internal stability of the planar displays.

The influence of "arch distortion" (Gauch 1984) on the Simplified Correspondence Analysis (SIMCA) (Greenacre 1989) ordinational display was evaluated by ordinating an identical database using Detrended Correspondence Analysis (DCA) (Hill and Gauch 1980), and visually comparing the outputs. Although a slight "horseshoe effect" was apparent when using correspondence analysis (Figure 2.5), this had little influence on the ability to interpret the relative positioning of geomorphological features and species within the ordination space. The DCA output did, however, tend to better emphasize the association of *P. catostoma, M. macrolepidotus* and *Barbus paludinosus* Peters, 1852 with shallow pools (Figure 2.6). Gradient lengths of the first two axes were 3.09 sd and 2.28 sd respectively, indicating only moderate beta-diversity.

Differentiation of geomorphological features along Axis 1 was primarily between rapids and other geomorphological features, whereas, differentiation along Axis 2 was primarily between deep pools and other geomorphological features (Figure 2.5). The distinction between shallow pools, channel margins and secondary channels was not clearly defined in the ordination space. Therefore fish abundance data for these three geomorphological features were combined, and conglomeratively called "marginal areas".

Consistent differentiation of three geomorphological features (rapids, deep pools, marginal areas) in all five rivers was confirmed using ordinations of sample sites based on the presence or absence of fish species (Figures 2.7a to 2.7e), with relatively little species overlap between geomorphological features. Furthermore, in all rivers, there was little distinction between shallow pools, channel margins and secondary

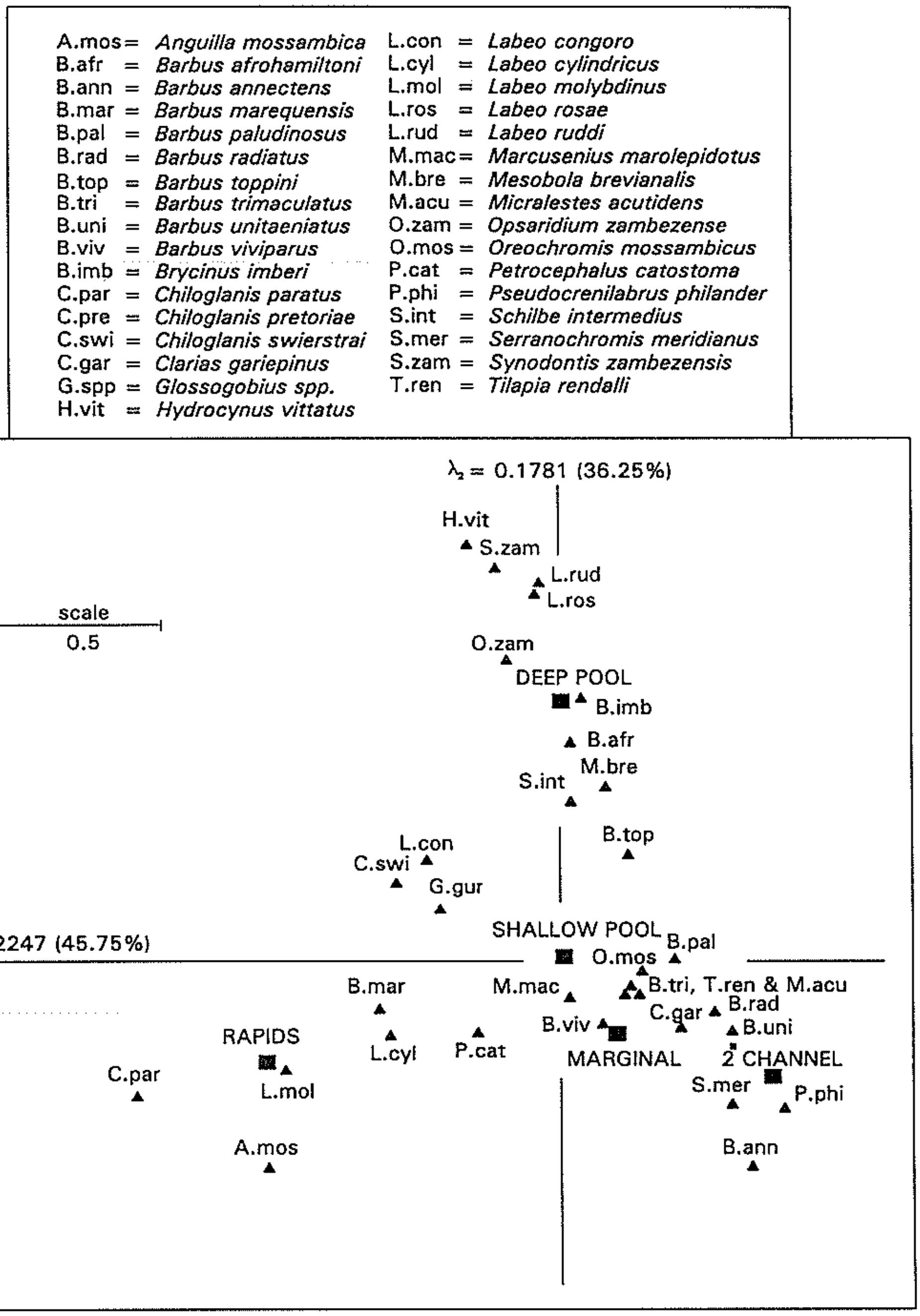


Figure 2.5 Ordination using correspondence analysis of the frequency of occurrence of fish species in the habitats rapids, deep pools (> 1m), shallow pools (< 1m), channel and pool margins, and secondary channels and backwaters.

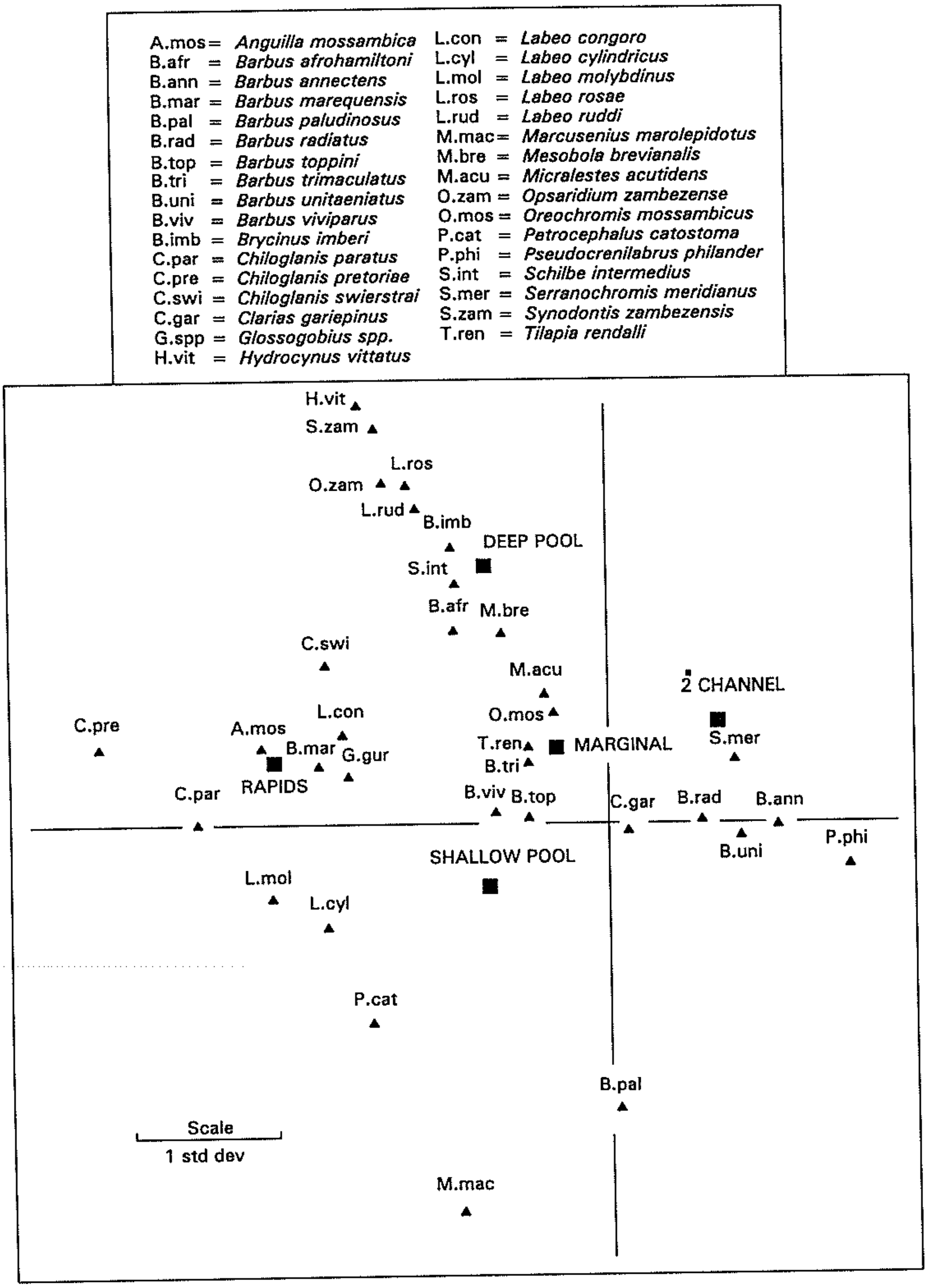


Figure 2.6 Ordination using Detrended Correspondence Analysis of the frequency of occurrence of fish species in the habitats rapids, deep pools (> 1m), shallow pools (< 1m), channel and pool margins, and secondary channels and backwaters.

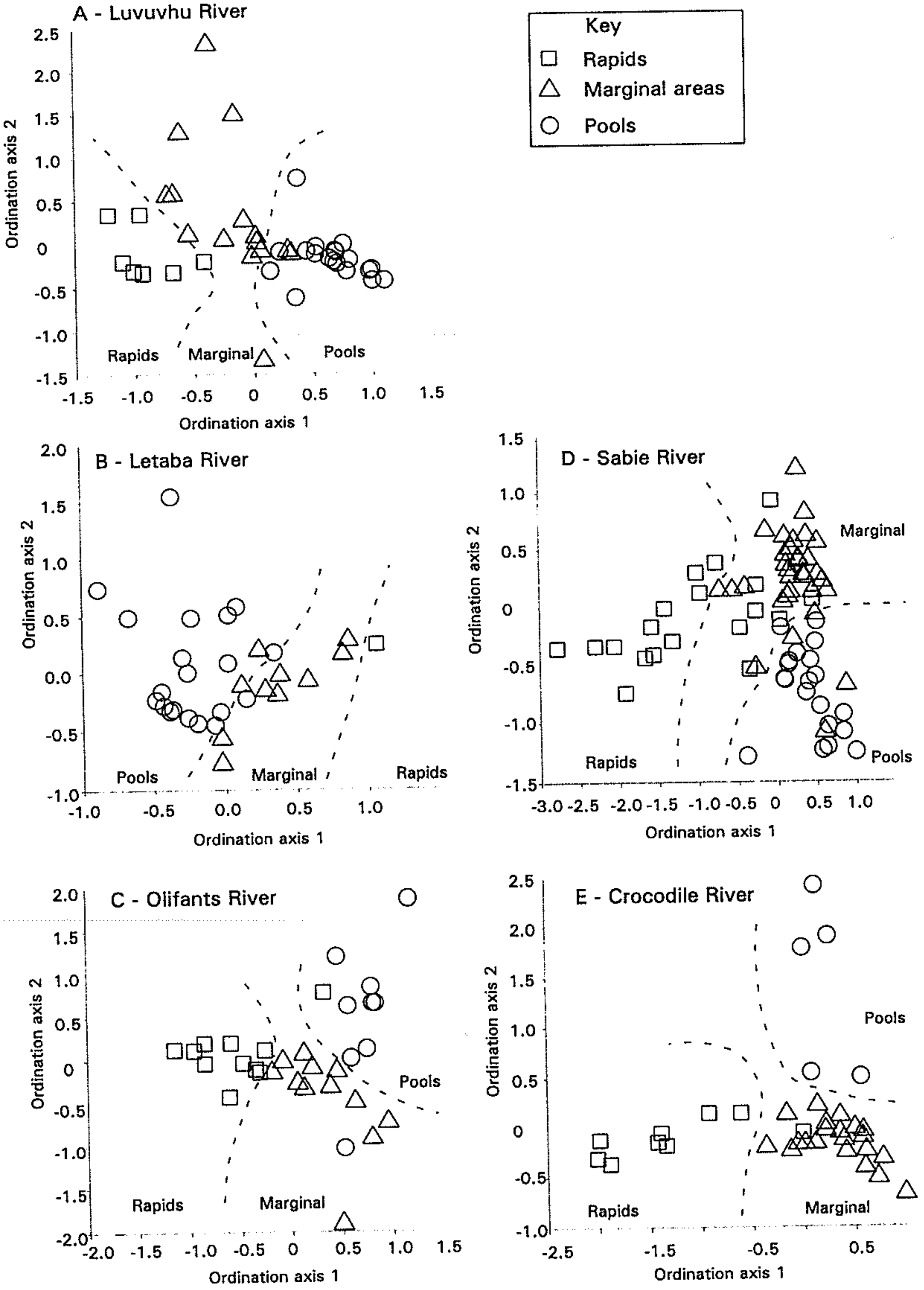


Figure 2.7 Ordination using correspondence analysis of sample sites in the Luvuvhu (a), Letaba (b), Olifants (c), Sabie (d) and Crocodile (e) rivers based on the presence and absence of fish species, to distinguish between different habitat types.

channels in terms of species occurrence, confirming the validity of combining them into a single unit for the purpose of describing the environmental preferences of fish.

Fish species frequently associated with rapids were *Chiloglanis paratus* Crass, 1960, *C. pretoriae*, *A. mossambica* and *L. molybdinus*. The latter two species, despite frequent occurrence in rapids (56% and 48% of distribution observations, respectively) were also frequently recorded in marginal areas (44% and 45% respectively). The environmental preferences of *A. mossambica* and *L. molybdinus* can thus not be described as being predominantly rapids. Similarly, *B. marequensis, L. cylindricus* and *P. catostoma* fell approximately midway between the rapid and marginal area groupings, also because of frequent recordings in both geomorphological features. The frequent occurrence of *P. catostoma* in rapids indicates broader environmental preferences than suggested in previous studies (Crass 1964; Gaigher 1969, 1973; Bell-Cross 1976; Pienaar 1978; Bruton *et al.* 1982) where it has been reported to occur primarily in slow flowing water.

Species most frequently associated with marginal areas were *M. macrolepidotus, C. gariepinus* and *Micralestes acutidens* (Peters, 1852), the cyprinids *B. paludinosus, Barbus annectens* Gilchrist and Thompson, 1917, *Barbus trimaculatus* Peters, 1952, *Barbus viviparus, Barbus unitaeniatus* Günther, 1866, and *Barbus radiatus* Peters, 1853, as well as the cichlids *O. mossambicus, T. rendalli, S. meridianus* and *Pseudocrenilabrus philander* (Weber, 1897). The observed high frequency of occurrence of *P. philander* in marginal areas (CPUE = 93%) is similar to the findings of Crass (1964) and Pienaar (1978), and indicates more specialised environmental preferences than occurs in the Orange River (South Africa) where it has been recorded in a variety of geomorphological features including rocky rapids, rocky shores, sandy open waters, vegetated belts, backwaters and flowing channels (Skelton and Cambray 1981).

Fish species generally associated with deep pools were *H. vittatus, Synodontis zambezensis* Peters, 1852, *Labeo ruddi* Boulenger, 1907, *L. rosae, Opsaridium zambezense* (Peters, 1852), *Brycinus imberi* (Peters, 1852), *Barbus afrohamiltoni* Crass, 1960, *Schilbe intermedius* Rüppell, 1832, and *Mesobola brevianalis* (Boulenger, 1908). The observed high frequency of occurrence of *M. brevianalis* in deep pools is similar to the findings of Crass (1964), Gaigher (1973) and Pienaar (1978), and indicates more specialised environmental preferences than occurs in the Orange River (South Africa) where it has been recorded in several different geomorphological features, including fast flowing channels and rapids, open water portions of the mainstream and backwater channels (Skelton and Cambray 1981; Cambray 1984).

Barbus toppini Boulenger, 1916 fell approximately midway between the deep pool and marginal area groupings as a result of frequent recordings in both geomorphological features. *Labeo congoro*, *C. swierstrai*, and *Glossogobius* spp. occupied a central position in the ordination space (Figure 2.5) and consequently can be assigned to all three of the species groupings. The frequent occurrence of *Glossogobius* spp. in rapids (28% of all specimens collected), particularly in the Luvuvhu River (100% of the rapids sampled; 1988 = 33%, 1989 = 13% of the specimens collected), indicated broader environmental preferences than suggested in previous studies (Crass 1964; Gaigher 1969, 1973; Bell-Cross 1976; Pienaar 1978; Hecht 1980b; Bruton *et al.* 1982) where it has been reported to primarily occur in slow flowing water.

2.3.2.2 Fish species distribution in relation to water flow velocity

The principle inertias of the ordinational profiles of occurrence of fish species in different water flow velocities (Figure 2.8) and their percentage contribution to total inertia were $y_1 = 0.1967$ (79.16%), $y_2 = 0.0366$ (14.73%) and $y_3 = 0.0152$ (6.11%) respectively. Therefore, a two-dimensional correspondence analysis (Axis 1 vs Axis 2), containing 93.89% of the total inertia was a good display of the profiles, with the majority of the variation indicated on the primary axis.

The percentage contributions of different flow velocity categories to the principle inertia (strong = 58.5%, medium = 5.4%, low = 14.0% and none = 22.1%) highlights differences in the fish species composition between sites with strong flow and those with medium to zero flow. The distinction between sites where flow velocities were described as medium and low appears to be unsubstantiated, as they were located close to one another within the ordination space.

Similarities can be drawn between the species composition of sites with different flow velocities and species composition of different geomorphological features (section 2.3.2.1). These similarities were most evident in rapids and strongly flowing waters. Fish species most frequently associated with strong flowing waters were the rapid dwelling *C. pretoriae*, *C. paratus* and *L. molybdinus*. Although, as described above

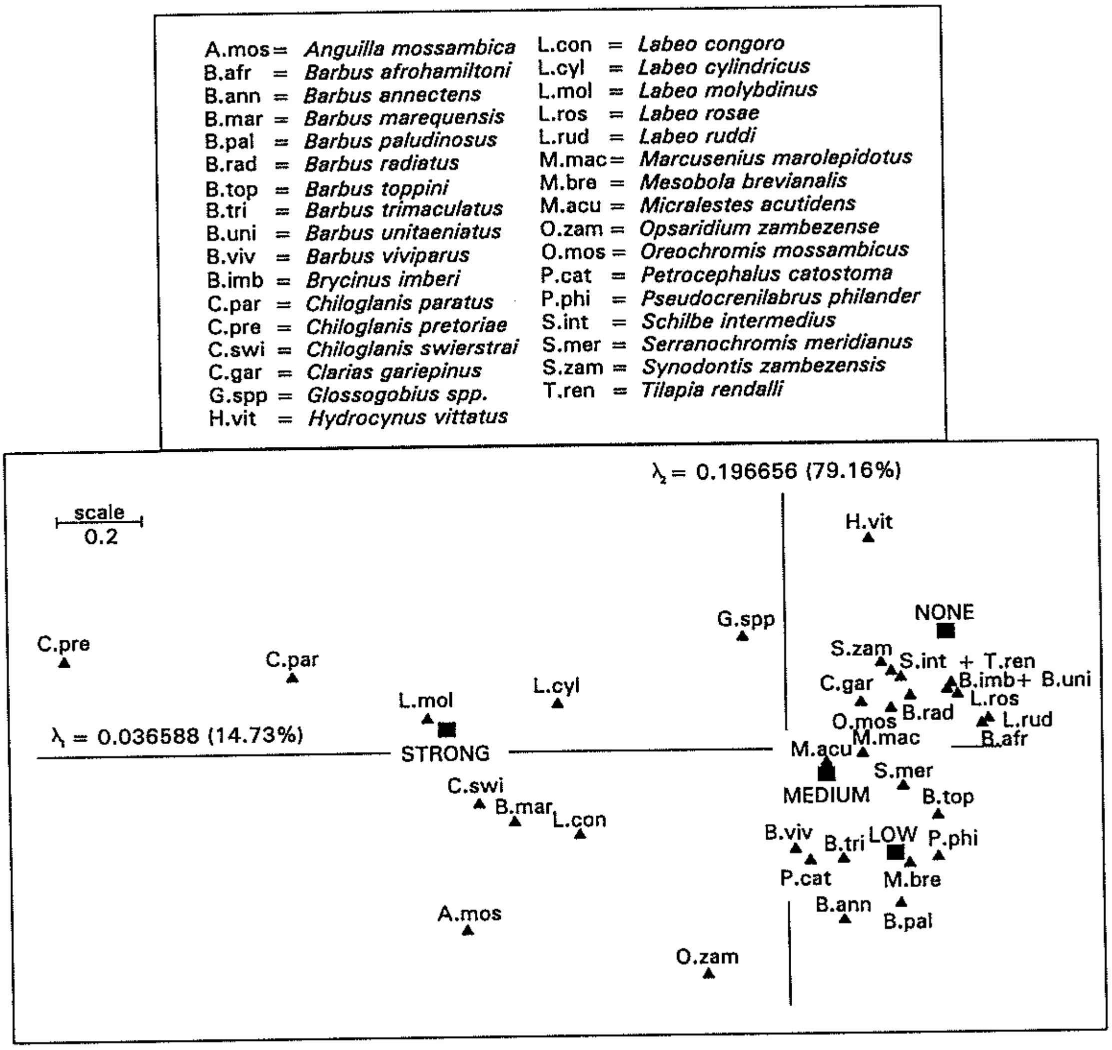


Figure 2.8 Ordination using correspondence analysis of the frequency of occurrence of fish species under different flow conditions (strong, medium, low and none).

(section 2.3.2.1), *C. swierstrai*, *L. cylindricus* and *B. marequensis* were not always associated with rapids, they were frequently associated with strongly flowing waters (Figure 2.8). Similarly, *O. zambezense*, despite occurring primarily in pools, was more frequently associated with strongly flowing water than other pool dwelling species. *Chiloglanis paratus* has been reported by several authors to occur exclusively in strongly flowing waters (Crass 1964; Gaigher 1973; Bruton and Kok 1980; White *et al.* 1984). Although *C. paratus* was frequently recorded in rapids in KNP rivers, it was also, on occasion, recorded in deep pools in the Luvuvhu river, which have a muddy substratum and in which zero flow conditions prevail for several months of the year. This concurs with the findings of Kleynhans (1980) who found that *C. paratus* was able to endure relatively stagnant conditions.

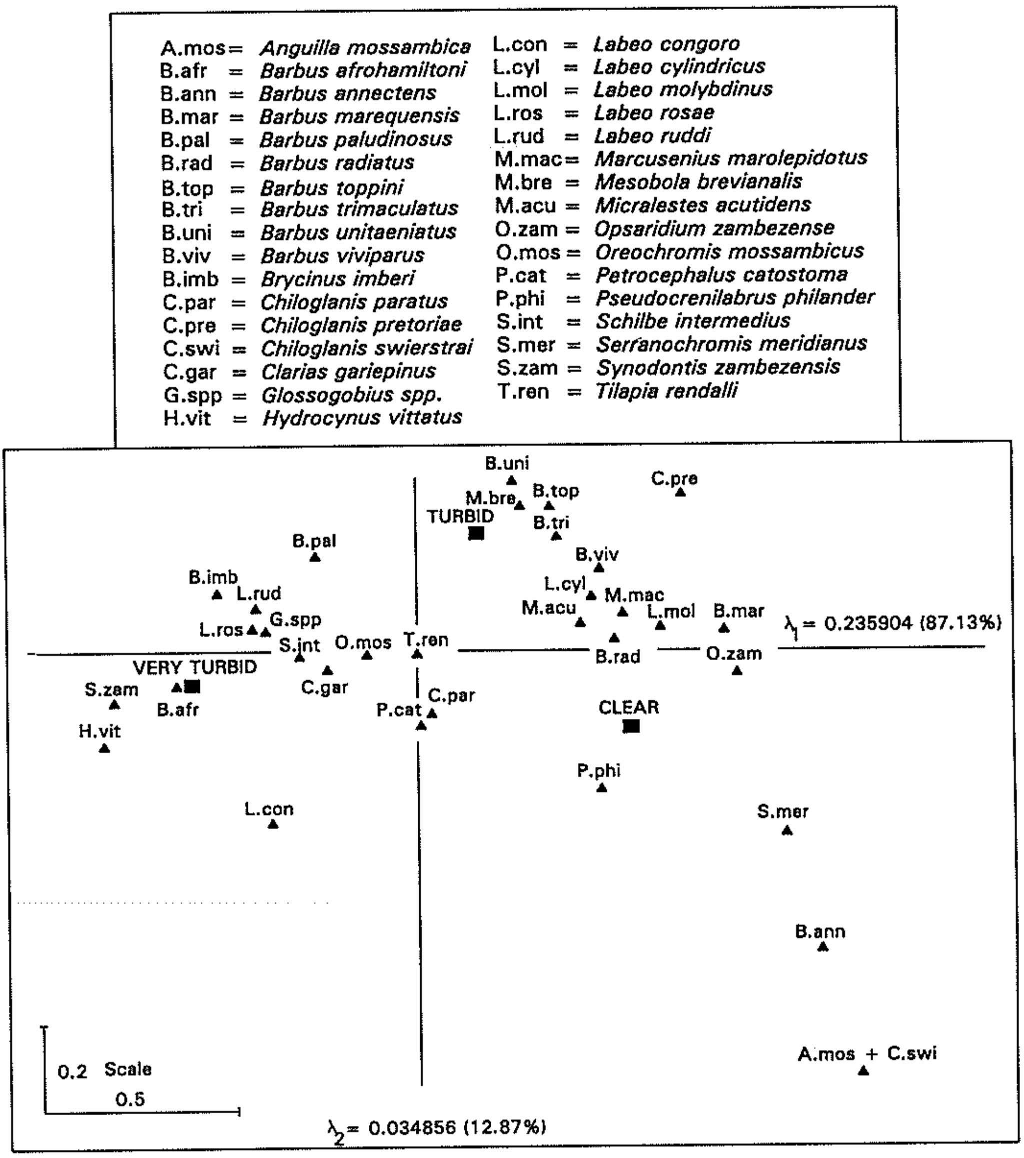
Species most frequently associated with zero flow conditions included most species that occurred primarily in deep pools, namely *H. vittatus*, *S. zambezensis*, *S. intermedius*, *B. imberi*, *L. ruddi*, *L. rosae*, and *B. afrohamiltoni*, as well as several species frequently associated with marginal areas, namely *O. mossambicus*, *T. rendalli*, *B. unitaeniatus* and *B. radiatus*.

With the exception of *Glossogobius* spp., all other species recorded occurred primarily in either medium or low flow conditions. *Glossogobius* spp., by virtue of their having being recorded in strong flowing rapids, pools with zero flow, as well as marginal areas with varying flow velocities cannot be described as occurring predominantly under any distinct flow-velocity category.

2.3.2.3 Fish species occurrence in relation to water turbidity

The principle inertias of the ordination profiles of fish species in waters of different turbidities (Figure 2.9) and percentage of total inertia were $y_1 = 0.2359$ (87.13%), and $y_2 = 0.0348$ (12.87%), respectively. Therefore, the majority of the variation in the profiles is displayed on the primary axis. Consequently, the ability to interpret this output is not severely limited, despite the ordination showing a marked horseshoe effect (Figure 2.9).

The separation of turbidity classes (very turbid, turbid, clear) along the primary axis was from very turbid to clear waters. The major contributors to the total inertia of the primary axis were the classes Very Turbid (55.7%) and Clear (40.7%), with species contributors being *B. marequensis* (12.0%) and *H. vittatus* (10.0%). There was a



A.mos = *Anguilla mossambica*
B.afr = *Barbus afrohamiltoni*
B.ann = *Barbus annectens*
B.mar = *Barbus marequensis*
B.pal = *Barbus paludinosus*
B.rad = *Barbus radiatus*
B.top = *Barbus toppini*
B.tri = *Barbus trimaculatus*
B.uni = *Barbus unitaeniatus*
B.viv = *Barbus viviparus*
B.imb = *Brycinus imberi*
C.par = *Chiloglanis paratus*
C.pre = *Chiloglanis pretoriae*
C.swi = *Chiloglanis swierstrai*
C.gar = *Clarias gariepinus*
G.spp = *Glossogobius spp.*
H.vit = *Hydrocynus vittatus*
L.con = *Labeo congoro*
L.cyl = *Labeo cylindricus*
L.mol = *Labeo molybdinus*
L.ros = *Labeo rosae*
L.rud = *Labeo ruddi*
M.mac = *Marcusenius marolepidotus*
M.bre = *Mesobola brevianalis*
M.acu = *Micralestes acutidens*
O.zam = *Opsaridium zambezense*
O.mos = *Oreochromis mossambicus*
P.cat = *Petrocephalus catostoma*
P.phi = *Pseudocrenilabrus philander*
S.int = *Schilbe intermedius*
S.mer = *Serranochromis meridianus*
S.zam = *Synodontis zambezensis*
T.ren = *Tilapia rendalli*

Figure 2.9 Ordination using correspondence analysis of the frequency of occurrence of fish species in waters of different turbidities (very turbid, turbid, clear).

progression from left to right across the ordination space of species frequently recorded in very turbid waters, to those recorded almost exclusively in clear waters.

Species frequently recorded in turbid waters were predominantly those found to occur in deep pools, namely *H. vittatus, S. zambezensis, B. afrohamiltoni, B. imberi, L. rosae, L. ruddi* and *S. intermedius*. These results do not necessarily indicate that these species actively select more turbid waters, but rather that they were able to survive turbid conditions. *Hydrocynus vittatus* is a visual pursuit predator, and is therefore reputed to require clear water for prey location (Crass 1964; Skelton *et al.* 1985). In this study, however, *H. vittatus* was frequently recorded (CPUE = 78%) in turbid (15-80 NTU) pools, particularly in the Luvuvhu River. The supposed dependence of *H. vittatus* on clear waters thus appears unjustified.

Species recorded predominantly in clear water were recorded in a variety of different geomorphological features, namely *C. swierstrai, A. mossambica, B. annectens, S. meridianus* and *O. zambezense*.

2.3.2.4 Fish species occurrence over different substrata

The principle inertias of the ordination profiles of fish species sampled over different substrata (Figure 2.10), and their percentage contribution to total inertia were y_1 = 0.1326 (64.40%), y_2 = 0.0373 (18.12%), y_3 = 0.0203 (9.88%) and y_4 = 0.0157 (7.60%) respectively. Thus, a two-dimensional correspondence analysis (Axis 1 vs Axis 2), containing 82.52% of the total inertia, was a good display of the profiles.

Major contributors to the inertia of the primary axis were Mud (26.2%) and Stone (44.8%). Thus, the primary axis separates substratum types based on size fraction, with the conglomerate class, Stone and Gravel, occupying a central position within the ordination space. Major contributors to the inertia of the secondary axis were Bedrock (44.7%) and Stone (21.7%). The environmental gradient represented along this axis was unclear.

Species frequently occurring in sites with a predominantly stony substratum were the rapid dwelling species, *C. pretoriae, C. paratus* and *L. molybdinus*, as well as species frequently recorded in rapids, namely *B. marequensis, L. cylindricus, L. congoro* and *P. catostoma*.

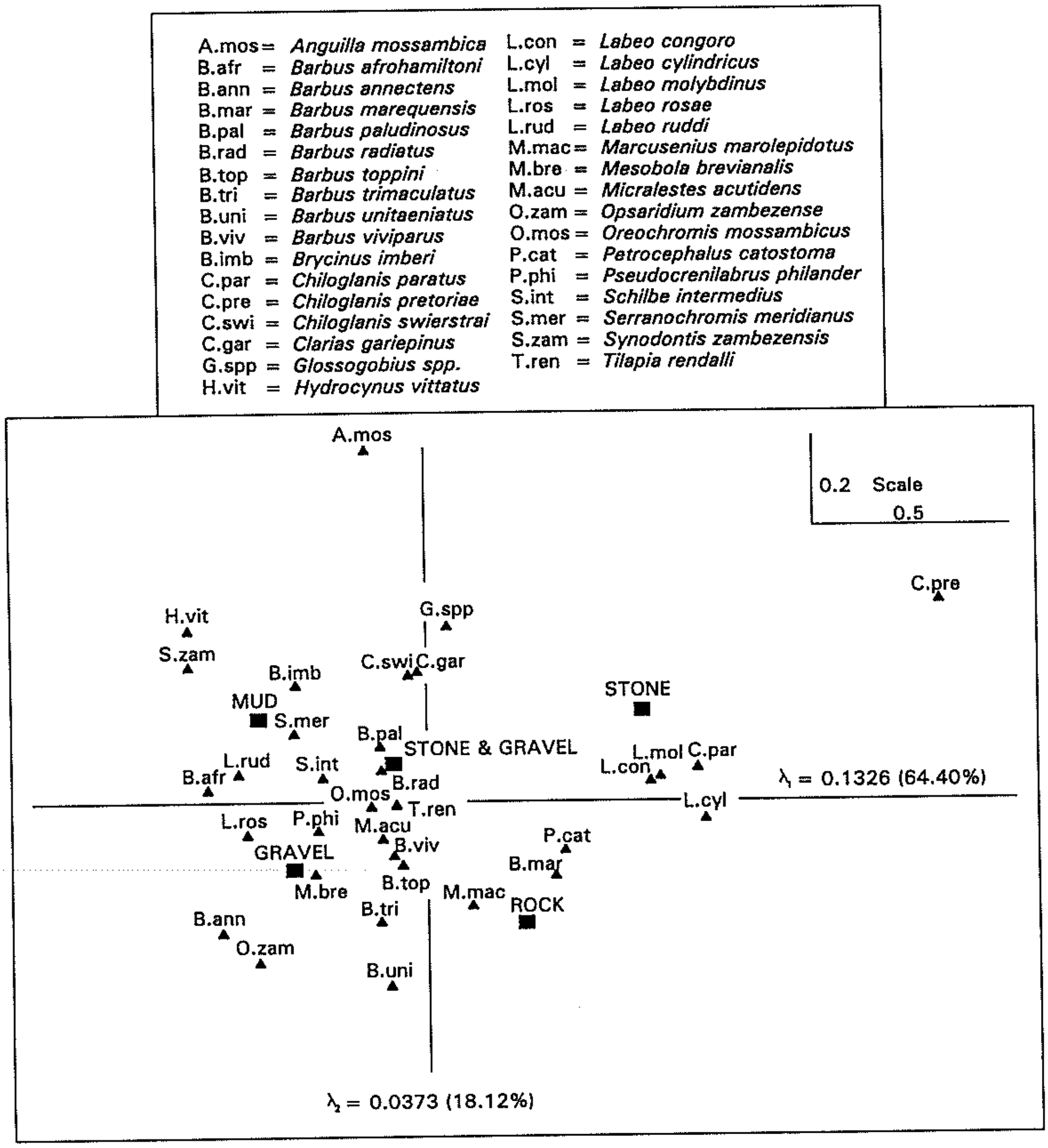


Figure 2.10 Ordination using correspondence analysis of the frequency of occurrence of fish species in sample sites with different substrata (bedrock, stone, stone & gravel, gravel, mud) to distinguish the habitat preferences of species.

Species frequently recorded in localities with a predominantly muddy substratum were *H. vittatus*, *S. zambezensis*, *B. afrohamiltoni* and *L. ruddi*, all of which were sampled predominantly in deep pools (section 2.3.2.1) with little or no flow (section 2.3.2.2). *Chiloglanis swierstrai* occurred predominantly over gravel or a combination of stone and gravel (63% of observations).

The importance of substrate to the diversity and biota of running waters, and in particular benthic invertebrates, has been demonstrated in several studies (Hynes 1970; Allan 1995). Many fish require particular substrate conditions for cover, spawning and feeding (Hynes 1970). Epibenthic fish species, such as the darters of North America, frequently occur on or near particular substrata (Lee *et al*. 1980). Similarly, burrowing taxa in KNP rivers, such as *C. swierstrai*, are likely to be specific in the particle size of substrate they inhabit. Most North American fish select hard substrata for reproduction, and it is thought that the availability of substrate for spawning affects the distribution and abundance of many fishes (Hynes 1970). The substrate preferences of bottom spawning fish in rivers in the lowveld regions of Mpumalanga and the Northern Province are unknown.

The effect that the nature of the substratum has on the distribution of fish species with different feeding strategies is illustrated by the superimposing of this species characteristic onto the ordination space (Figure 2.11). Bottom-feeding periphytivores and bottom-feeding insectivores were associated primarily with stony and bedrock substrata. Both detritivores and piscivores, which would be expected to be independent of the presence of stones for feeding, were associated primarily with substrata consisting either of mud or gravel. Multiple-level insectivores commonly occurred over a gravel or stone and gravel substrata, and occurred only infrequently over substrata consisting predominantly of either mud, stone or bedrock. Omnivorous species occurred over a wide variety of substrata, though were recorded infrequently over substrata consisting primarily of stone or bedrock.

The diversity of benthic invertebrates has been found to be related to the size, stability and heterogeneity of substrata (Minshall 1984). In general, invertebrate diversity and the number of individuals is higher in stable, heterogeneous substrata, and increasing with median particle size, and declining with stones at or above the size of cobbles (>64mm diameter) (Minshall and Minshall 1977; Wise and Molles 1979; Minshall 1984). The correlation between insectivorous fish, and stony and gravel substrata, in

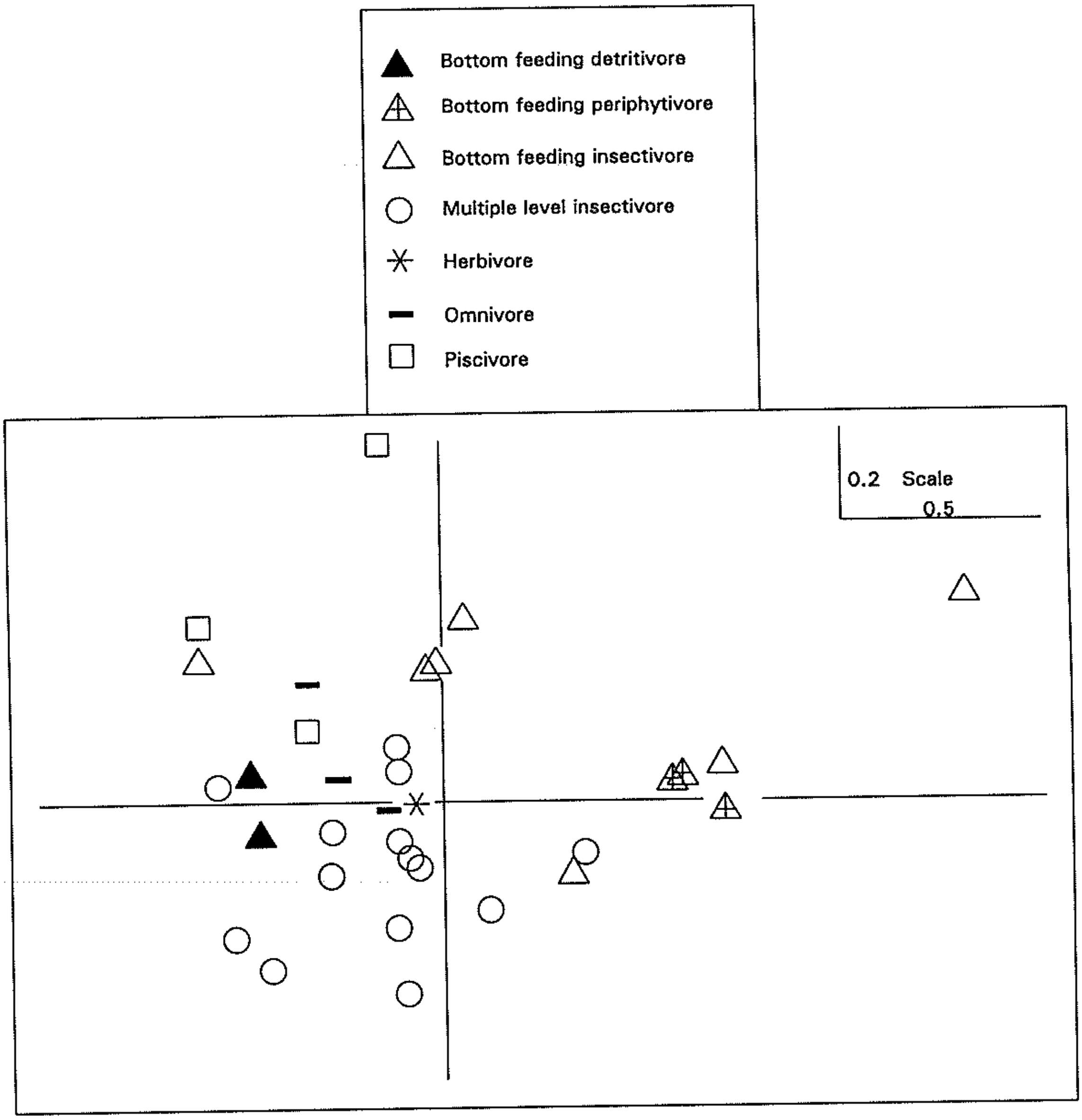


Figure 2.11 Ordination using correspondence analysis of the frequency of occurrence of fish in sample sites with different substrata (see Figure 2.10), displaying the feeding strategy of different fish species.

KNP rivers is possibly related to the preferred substratum of aquatic invertebrates and hence food availability.

Although previous qualitative studies of fish communities in the lowveld regions of rivers in Mpumalanga and the Northern Province in South Africas have been unable to illustrate correlations between the occurrence of species and the nature of the substratum (Gaigher 1969; 1973) the findings of this study indicate that substrate does play a role in the distribution of ichthyofauna.

2.3.2.5 Fish species occurrence in relation to aquatic plants

The principle inertias of the ordination profiles of fish species relative to the occurrence of aquatic plants (Figure 2.12), and their percentage contribution to total inertia were $y_1 = 0.1086$ (69.53%), and $y_2 = 0.0476$ (30.47%) respectively. Thus, the majority of the information in the profiles was displayed on the first principle axis. There was a marked distinction between sites where aquatic plants were present and those where they were entirely absent or occurred only in close proximity to the sample area, suggesting the importance of this environmental variable to several fish species.

Major contributors to the inertia of the primary axis were *P. philander* (14.9%), a species found to occur almost exclusively either amongst or in close proximity to aquatic plants, and *L. ruddi* (6.2%) and *L. rosae* (5.7%), both pool dwelling detritivores (section 2.3.2.4) which were found to occur only infrequently amongst inundated aquatic plants.

There was a progression from left to right across the ordination space of species found to occur frequently amongst aquatic plants to those which were independent of the presence of aquatic plants. Thus, species that frequently occurred amongst aquatic plants were *P. philander, B. annectens, P. catostoma, S. meridianus, B. radiatus, B. paludinosus, M. macrolepidotus, M. acutidens* and *B. viviparus*. The high frequency of occurrence of *P. philander* amongst aquatic plants (CPUE = 69%) is similar to the findings of Crass (1964) and Pienaar (1978), and indicates more specialised environmental preferences than occurs in the Orange River (South Africa) where it was frequently recorded in areas devoid of aquatic plants (Skelton and Cambray 1981). Species frequently recorded amongst aquatic plants, but which were also found

A.mos = *Anguilla mossambica*
B.afr = *Barbus afrohamiltoni*
B.ann = *Barbus annectens*
B.mar = *Barbus marequensis*
B.pal = *Barbus paludinosus*
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B.uni = *Barbus unitaeniatus*
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T.ren = *Tilapia rendalli*

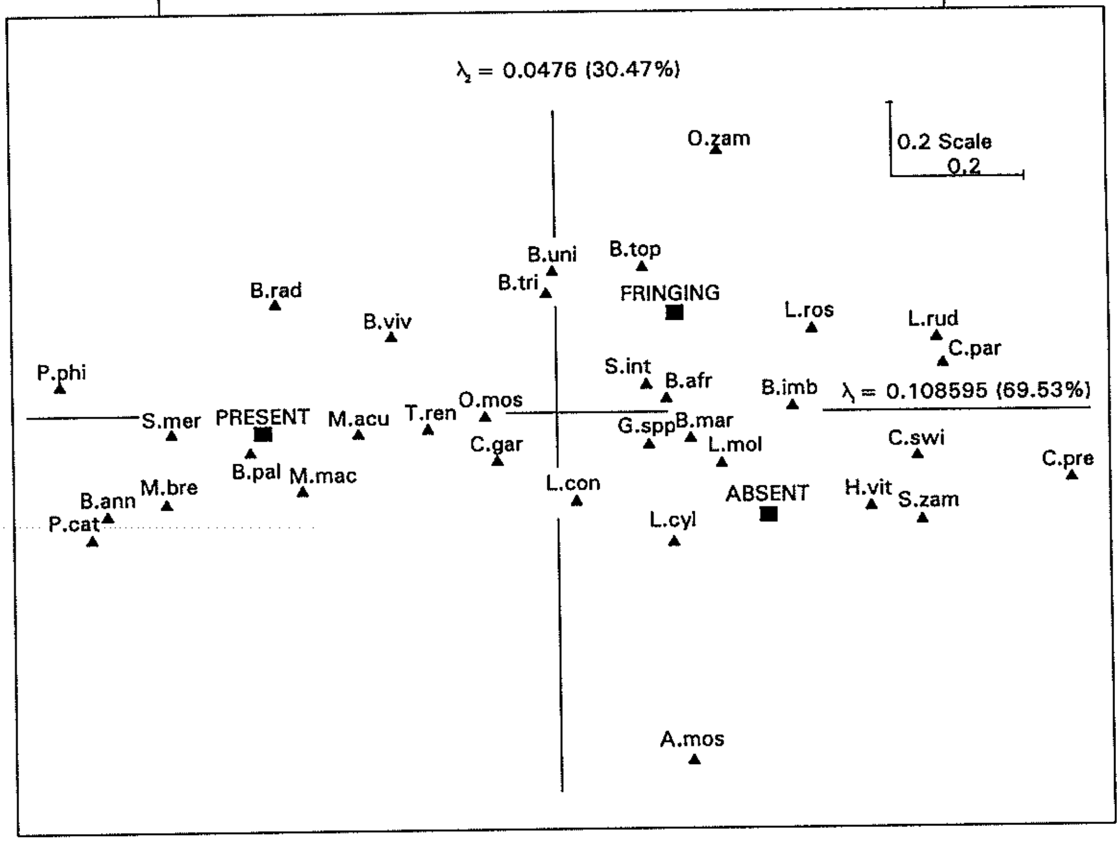

Figure 2.12 Ordination using correspondence analysis of the frequency of occurrence of fish species in sample sites which differ with respect to the relative proximity of submerged and emergent aquatic plants (present at sample site, not present in sample site though in close proximity - fringing, and completely absent from sample site).

to be widespread in localities devoid of vegetative cover were *T. rendalli, O. mossambicus, C. gariepinus* and *A. mossambica*.

Only *C. pretoriae* was never recorded amongst aquatic vegetation, though several other species, including *C. paratus, C. swierstrai, S. zambezensis, H. vittatus, L. ruddi, L. rosae* and *B. imberi* were apparently also independent of the presence of aquatic plants.

Finally, there was a large group of species that were recorded either predominantly in sites with fringing vegetation, though were not collected amongst the aquatic vegetation; or alternatively were recorded with similar frequency in sites both with and without aquatic plants. These were *O. zambezense, S. intermedius, Glossogobius* spp., *L. molybdinus, L. cylindricus, L. congoro, B. marequensis, Barbus toppini* Boulenger, *B. unitaeniatus, B. trimaculatus* and *B. afrohamiltoni*. The dependence of these species on aquatic plants is unknown, though is most likely low. The environmental preferences of *B. trimaculatus* have been described as shallow, slow flowing, well vegetated margins of pools and river channels (Jackson 1961a; Crass 1964; Bell-Cross 1976; Pienaar 1978; Skelton and Cambray 1981; Cambray 1984; Skelton 1986a). Similarly, Bell-Cross (1976) maintained that *B. afrohamiltoni* is frequently found in association with aquatic plants. The frequent recording in this study of both *B. trimaculatus* and *B. afrohamiltoni* in areas without aquatic vegetation (CPUE = 77% and 73% respectively), however, indicates broader environmental preferences for these species than suggested in previous studies.

Both *P. catostoma* and *M. brevianalis* have previously been reported to occur predominantly amongst aquatic plants (Crass 1964; Okedi 1965; Bell-Cross 1976; Pienaar 1978). In this study, however, both species were frequently recorded in areas devoid of plants (CPUE = 20% and 71% respectively) including fast flowing channels and rapids, which is similar to the findings of Skelton and Cambray (1981) and Cambray (1984) in the Orange River. Consequently, the implied strong association of *P. catostoma* and *M. brevianalis* with aquatic plants appears unfounded in KNP rivers.

2.3.2.6 Associations between fish species: defining fish communities

There are many similarities between the groups of species described relative to environmental factors in sections 2.3.2.1 to 2.3.2.5 above. These similarities are not unexpected given the interaction between environmental factors in rivers (Allan 1995), where, for example, high flow velocities, large substrate particulate size and an absence of aquatic plants are often correlated. The description of species from a prescribed area or physical habitat, and which hence frequently co-occur in space and time is the basis for describing a community (Odum 1971; McNaughton and Wolf 1979). Three such groupings are apparent in KNP rivers (Figure 2.13), namely:

(i) Rapid communities - consisting predominantly of bottom-feeding periphytivores and insectivores that occur in rapids with fast flowing water, over a predominantly stony or bedrock substratum, and largely independent of the presence or close proximity of rooted aquatic plants.

(ii) Pool communities - consisting predominantly of detritivores, piscivores and omnivores that occur in deep pools with little or no flow, over either a gravel or muddy substratum, and largely independent of the presence or close proximity of rooted aquatic plants.

(iii) Marginal area communities - consisting predominantly of multiple level insectivores that occur in shallow pools and marginal areas which have little or no flow, generally with a substratum of either gravel or a combination of gravel and stones, and frequently closely associated with rooted aquatic plants.

The differentiation between communities occurring predominantly in pools and rapids is recognised in many studies of riverine fish (Welcomme and Merona 1988; Pusey *et al.* 1995). This common distinction is possibly due to the readily apparent rapid-pool sequence in most alluvial rivers (Dunne and Leopold 1978). Recognition of the association between distinctive groups of species and the shallow margins of pools (frequently in association with aquatic plants), however, is less common, though it has been described by some authors (Mitchell 1976, 1978; Cambray *et al.* 1978; Hortle and Lake 1983; Weeks *et al.* 1996). The importance of cover provided by aquatic plants and other submerged objects in shallow marginal areas is well documented (Walker 1986; Rozas and Odum 1988; Savino and Stein 1989; Pusey *et al.* 1993), and the creation of artificial cover forms the focus of many river restoration works (Brookes 1987).

Several studies have demonstrated substantial variability in the habitat specificity of different fish within communities (Hynes 1970; Harris 1988). This variability in

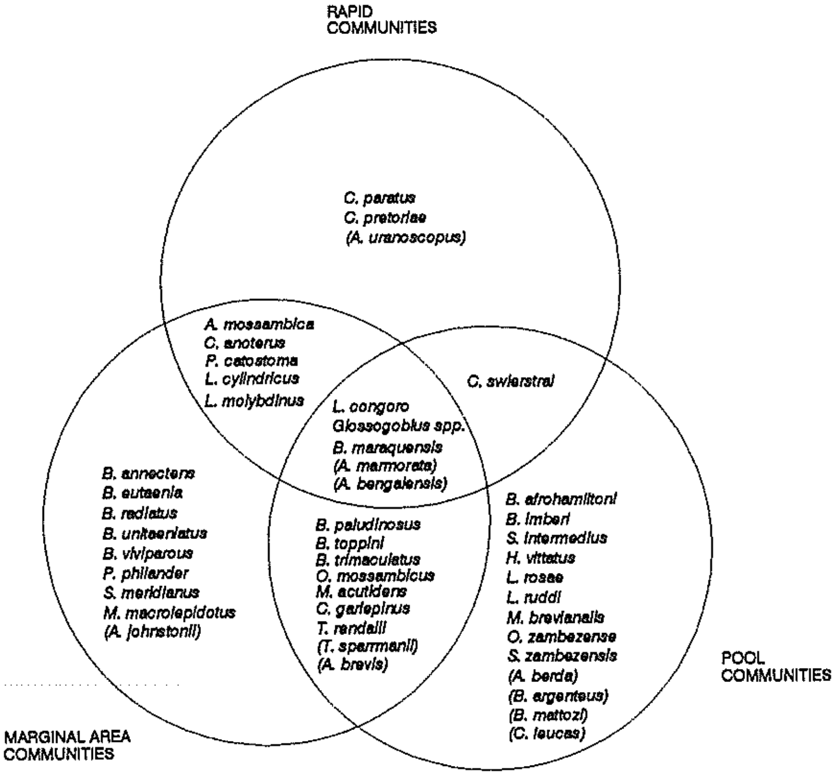

Figure 2.13 Species composition of fish communities in the major rivers of the Kruger National Park. Categorisation of species undertaken on the basis of the environmental preferences of species, with descriptions of the environmental preferences of species given in brackets obtained from the literature.

habitat specificity also occurs amongst fish in KNP rivers, where some species can be considered as habitat specialists in that they require specific environmental conditions (for example *C. pretoriae* recorded only in strongly flowing water in rapids) and hence are exclusive to a particular community (Figure 2.13). Other species are habitat generalists, recorded under a variety of environmental conditions (for example *Glossogobius* spp.), and hence occur in two or three communities (Figure 2.13). Habitat specialists would be expected to be more susceptible to detrimental changes in specific habitat conditions than would habitat generalists (Harris 1988; Moyle and Williams 1990). Reductions in flow could, for example, through the dewatering of rapids and marginal areas, be expected to be more detrimental to rapid and marginal area communities, and particularly to habitat specialists in these communities, than to pool communities. Alternatively, changes in non-habitat specific environmental factors, such as water quality, could be expected to have detrimental effects on a wide variety of biota. Thus evaluation of change in community diversity (species richness and abundance) can, with knowledge of the environmental preferences of species, provide a basis for evaluating the effect of a changing environment on aquatic biota. Description of fish communities consisting of combinations of species that occurred together under similar environmental conditions thus forms the basis for measuring and evaluating biotic change at the community level in this and subsequent chapters.

2.3.3 Environmental factors causative of fish distributional change

Many factors can contribute to the decline of fish species, and it is often difficult to identify a single cause due to inadequate data or, often, because multiple factors play a role (Allan and Flecker 1993). In a review of the influence of man on the loss of diversity of riverine fish fauna in several countries throughout the world, Moyle and Leidy (1992) highlighted several proximal causes of fish species decline. Principal amongst these were the partial or total desiccation of aquatic systems, pollution, and habitat changes such as the elimination of instream cover and riparian vegetation. Similarly, Soulé (1991) and Allan and Flecker (1993) identified six primary causes for species extinctions, namely habitat loss and degradation (resulting primarily from impoundment, land transformations and agriculture), the spread of alien species, overexploitation, secondary extinctions, chemical and organic pollution, and climate change.

Overexploitation can be discounted as a potential cause for changes in KNP fish communities as species are neither commercially nor recreationally exploited.

Similarly, the spread of alien fish is unlikely to be a significant factor as only two alien species occur in KNP rivers (*Cyprinus carpio*, *Chetia brevis*) (Pienaar 1978), neither of which are widespread or abundant (Table 2.7). The causal links between potential global climatic changes and freshwater fishes are speculative (Allan and Flecker 1993) and were considered beyond the scope of this study. The remaining potential causes for changes in fish distribution are assessed below, and include habitat loss resulting from reduction in instream flow, changes in water quality, and changes in the distribution of aquatic plants, including the introduction of alien plant species. The potential effect of interactions between fish species is also briefly discussed below.

2.3.3.1 Habitat loss resulting from reductions in instream flow

Instream flow is defined as the amount of water in a channel measured at a given time and place (Estes and Orsborn 1986). Development in the catchments of KNP rivers (sections 1.3.4 to 1.3.8) has resulted in altered instream flow patterns (Bruwer 1991c), with resultant concerns for the effect on aquatic biota (Bruwer 1991b). The objective of this section is to assess the probable effect of habitat loss, resulting from past low flows, on the distribution of fish in KNP rivers. This was undertaken by:

(i) Modeling flow in geomorphological features (rapids and channels) of rivers to calculate the minimum base flows required to maintain habitats for adult fish.

(ii) Using DWAF flow records (1960 to 1989) to describe the frequency, duration and magnitude of low flows (below that required to maintain fish habitats) to enable formulation of hypotheses on the influence of past river flows on fish habitats and hence fish communities.

Minimum flow required to meet the defined environmental parameters (0.20m mean depth, 0.30 m s^{-1} mean velocity, and optimum wetted perimeter - see section 2.2.3.1), and hence maintain habitats for adult fish, was highest for the Luvuvhu River at 137.4 x 10^6 m^3 y^{-1}. (4.4 cumec), and lowest for the Letaba River at 58.3 x 10^6 m^3 y^{-1}. (1.9 cumec) (Table 2.10). Minimum base flow in other rivers in the KNP fell between these two extremes, with 82.0 x 10^6 m^3 y^{-1}. (2.6 cumec) for the Sabie River, 84.0 x 10^6 m^3 y^{-1}. (2.7 cumec) for the Olifants River, and 87.8 x 10^6 m^3 y^{-1}. (2.8 cumec) for the Crocodile River (Table 2.10). The above discharges reflect minimum flow required at any locality within the boundaries of the KNP, and consequently, for the

Table 2.10 Minimum flow (cumecs) required to achieve flow parameters (optimum wetted perimeter, average 20cm depth, average 30cm s^{-1} velocity) in rapids and channels at selected localities in the Luvuvhu, Letaba, Olifants, Sabie and Crocodile rivers.

River	Site name	Description	Wetted Perimete (optimum)	Depth (20cm)	Velocity (30 cm/s)	Max	Annual runoff (cubic meters)	MAR (%)
Luvuvhu	Bobomenie	Rapid	2.0	5.0	0.1	5.0		
	Hapie	Channel	3.8	2.0	2.0	3.8		
	Limpopo 1	Channel	1.0	1.5	1.5	1.5		
	Limpopo 2	Channel	4.0	1.5	1.5	4.0		
	Limpopo 3	Channel	3.0	1.4	1.5	3.0		
	Limpopo 4	Channel	5.0	1.1	1.0	5.0		
	Limpopo 5	Channel	5.0	1.2	1.3	5.0		
				Avg rapid		5.0		
				Avg channel		3.7		
				Avg all		4.4	137.4E+06	25.98
Letaba	Minkerhout	Channel	2.0	0.6	0.25	2.0		
	Nwanedzi	Channel	0.5	1.7	0.8	1.7		
				Avg all		1.9	58.3E+06	7.12
Olifants	Gorge 1	Rapid	2.0	0.3	0.04	2.0		
	Gorge 3	Rapid	1.8	1.1	0.2	1.8		
	Gorge 5	Rapid	0.5	1.4	0.3	1.4		
	Gorge 6	Rapid	2.0	2.2	0.1	2.2		
	Gorge 7	Rapid	1.5	2.0	0.2	2.0		
	Lookout 3	Channel	1.5	3.2	3.5	3.5		
	Lookout 4	Channel	1.5	7.0	3.5	7.0		
	Lookout 5	Channel	1.5	2.8	1.7	2.8		
	Midway 1	Channel	2.0	1.0	1.5	2.0		
	Midway 3	Channel	0.5	2.0	3.0	3.0		
	Midway 4	Channel	1.2	2.0	3.0	3.0		
	Midway 5	Channel	1.2	2.0	2.9	2.9		
				Avg rapid		1.9		
				Avg channel		3.5		
				Avg all		2.7	84.2E+06	3.68
Sabie	Sabiehoek	Channel	3.0	1.3	1.8	3.0		
	Ntwatindlopfu 1	Channel	1.0	1.2	0.5	1.2		
	Ntwatindlopfu 3	Channel	2.2	1.0	0.4	2.2		
	Ntwatindlopfu 4	Channel	4.0	0.7	0.5	4.0		
				Avg all		2.6	82.0E+06	10.73
Crocodile	Mbyamite 3	Rapid	2.5	1.3	0.5	2.5		
	Komati 1	Rapid	4.5	4.7	0.3	4.7		
	Komati 2	Rapid	0.7	2.0	1.0	2.0		
	Mbyamite 2	Channel	2.0	2.5	1.2	2.5		
	Nkangoma 2	Channel	2.5	0.5	0.5	2.5		
	Nkangoma 3	Channel	2.5	1.4	1.5	2.5		
				Avg rapid		3.1		
				Avg channel		2.5		
				Avg all		2.8	87.8E+06	7.09

purpose of flow management, should represent minimum instream flow at the eastern boundary of the park.

Direct comparison of the above minimum base flow estimates with previous evaluations of the flow requirements of KNP rivers are difficult because, as pointed out in section 2.2.3.1, the objectives and hence conceptual basis of the different approaches differ. Instream flow estimates are frequently made with the understanding that adherence will result in periodic habitat loss (Davies 1991; O'Keeffe 1991). This is countered by catering for periodic flow increases, primarily to stimulate and enable reproductive processes and facilitate particle transport (Weston 1996; Louw 1996) thereby ensuring the perpetuation of species and their habitat. In contrast, this study focuses solely on the effects of flow reductions on the availability of habitat for fish, without being judgmental on the acceptability (in terms of management objectives) of habitat loss. Thus, baseflow estimates from this study are likely to be higher than those of other instream flow estimates.

Despite these differences there is a high degree of similarity between baseflow estimates for the Sabie River derived from this and other studies (Table 2.11). The slightly higher flow estimates of Davies (1991) and O'Keeffe and Davies (1991) incorporated seasonal variation in flow, though excluded spring and mid-summer "freshets" and larger floods. None of these variables were included in lower base flows estimates of Gore *et al.* (1992) or this study. Similarity between baseflow estimates for the Sabie River provides some basis for confidence that they are appropriate for the maintenance of fish habitats.

In contrast, preliminary estimations of minimum base flow (not including seasonal variations in flow) for the Luvuvhu (O'Keeffe 1991; Louw 1996), Letaba (Chutter *et al.* 1991; Weston 1996), Olifants (Rooseboom 1991) and Crocodile (Bruwer 1991d) rivers were all substantially lower than flows calculated in this study (Table 2.11). Several possible reasons exist for these differences, other than the conceptual differences between methodologies discussed above. The most likely of these reasons is that flow estimates from studies using the Skukuza method were largely based on the necessity for an average depth of 0.10m for aquatic invertebrates in rapids (O'Keeffe 1991; Chutter *et al.* 1991; Rooseboom 1991; Davies 1991; Bruwer 1991d), as opposed to the 0.20m for adult fish used in this study. The approximate doubling of minimum base flow estimates in the Crocodile, Olifants and Letaba rivers from

Table 2.11 Estimations of the minimum non-consumptive baseflow requirements of the major rivers of the Kruger National Park undertaken in this and other studies.

River	Annual discharge	Objective	Method	Source
Luvuvhu	31.0×10^6	Maintain environmental condition	Skukuza	O'Keeffe (1991)
	11.5×10^6	Maintain environmental condition	Building Block	Louw (1996)
	137.4×10^6	Maintain fish habitats	Habitat retention	This study
Letaba	16.0×10^6	Maintain environmental condition	Skukuza	Chutter *et al.* (1991)
	22.5×10^6	Maintain environmental condition	Building Block	Weston (1996)
	59.9×10^6	Maintain fish habitats	Habitat retention	This study
Olifants	45.7×10^6	Maintain environmental condition	Skukuza	Rooseboom (1991)
	81.9×10^6	Maintain fish habitats	Habitat retention	This study
Sabie	99.0×10^6	Maintain environmental condition	Skukuza	Davies (1991)
	63.0×10^6	Maintain minimum fish diversity	IFIM	Gore *et al.* (1992)
	94.0×10^6	Worst drought	Hydraulic simulation	O'Keefe & Davies (1991)
	81.9×10^6	Maintain fish habitats	Habitat retention	This study
Crocodile	37.8×10^6	Maintain environmental condition	Skukuza	Bruwer (1991d)
	87.9×10^6	Maintain fish habitats	Habitat retention	This study

studies based on the Skukuza method compared to flow estimates from this study could, in part, have resulted from a doubling of the average depth requirement.

A further reason for different baseflow estimates between this study and previous assessments based on the Skukuza method is the inclusion, in this study, of habitat parameters other than water depth. Achievement of 0.30 m s^{-1} flow velocity and optimum wetted perimeter frequently required a higher discharge than achievement of 0.20m depth alone (Table 2.10). Thus the inclusion of additional habitat parameters in this study would have resulted in comparatively higher baseflow estimates.

Other factors which could have contributed to the differences in baseflow estimates for the Luvuvhu, Letaba, Olifants and Crocodile rivers include the use of hypothetical cross-sectional profiles by the above authors, which could have resulted in underestimations of flow. Furthermore, overestimation of baseflow required to maintain fish habitats in this study could have resulted from subjective assessment of inflection points on flow versus wetted perimeter graphs. Finally, inaccurate estimations of Manning's n values, and the assumption, within the flow simulation model used in this study, that water will flow uninhibited along a channel, without deflection or cross-channel movement resulting from changes in channel geometry and restrictions to flow above or below the point of profile measurement, could have resulted in overestimation of flow.

The same difficulties regarding comparison between baseflow estimates from this study and instream flow estimates for KNP rivers, as discussed above, pertains to comparison with instream flow assessments from elsewhere in the world. Reasonable comparisons could only be made with published accounts where techniques which emphasise baseflow requirements, such as the "Aquatic Base Flow" method (US Fish and Wildlife Service 1981) and Montana method (Tennant 1976) were used.

Estimated minimum base flows for the Letaba, Crocodile and Sabie rivers, expressed as percentage MAR (Table 2.10), demonstrate reasonable correspondence with recommended minimum flows to maintain fish habitats in four streams in Virginia (USA) determined using the comparatively simple aquatic base flow method (US Fish and Wildlife Service 1981). The ABF method uses the median daily flow for the low flow months of the year, with estimates generally ranging between 10 and 20% MAR. Flow estimates for the Luvuvhu and Olifants rivers, however, differ substantially from this predicted range. Minimum base flow estimates for the Letaba, Olifants and

Crocodile rivers also differ from minimum flow recommendations based on the Montana method (Tennant 1976) where 10% MAR is considered to provide minimal habitat, and 30% MAR to provide good habitat for fishes.

Dissimilarity between baseflow estimates form this and previous studies suggests the need for further study of the hydrology of KNP rivers, and in particular the Luvuvhu, Letaba, Olifants and Crocodile rivers, to evaluate the accuracy of flow estimates.

Arthington (1991) has suggested that in highly unpredictable environments such as rivers, stochastic factors such as low flows, and in particular the "severity" of low flows (frequency, duration and flow volume) could be major determinants of fish community structure. There are numerous accounts from throughout the world of the detrimental effects on fish of disruptions of natural flow régimes in rivers, and in particular flow reductions and changes in flow patterns resulting from impoundment and water diversions (Ward and Stanford 1979; Cross and Moss 1987; Moyle and Leidy 1992; Allan 1995). Recent studies of fish communities in the Sabie River system during drought conditions have also demonstrated that substantial changes in fish community composition can result from reductions in flow (Pollard *et al.* 1993). Both the extent and duration of low flows in the Sabie river system were found to influence the extent of fish species loss during drought conditions, with low flow sequences as short as two months likely to cause changes to the community from which species could take years to recover (O'Keeffe *et al.* 1996). The frequency and duration of low flow periods, as well as the extent to which flows fall below those calculated as the minimum requirement for fish in KNP rivers are discussed below to assess the probable influence of past low flows on fish communities.

2.3.3.2 Severity of low flows : frequency, duration and volume of flow

Frequency of low flows

In all five rivers there were several months between 1960 and 1989 (the period between comparative fish surveys) in which average monthly flow was less than recommended minima described for maintaining the habitat of adult fish (Figures 2.14a to 2.14e). The frequency of low flows was highest in the Luvuvhu River (79.9% of months for which flow records exist) followed by the Letaba (46.8%), Olifants (24.8%), Sabie (21.5%) and Crocodile (17.4%) rivers.

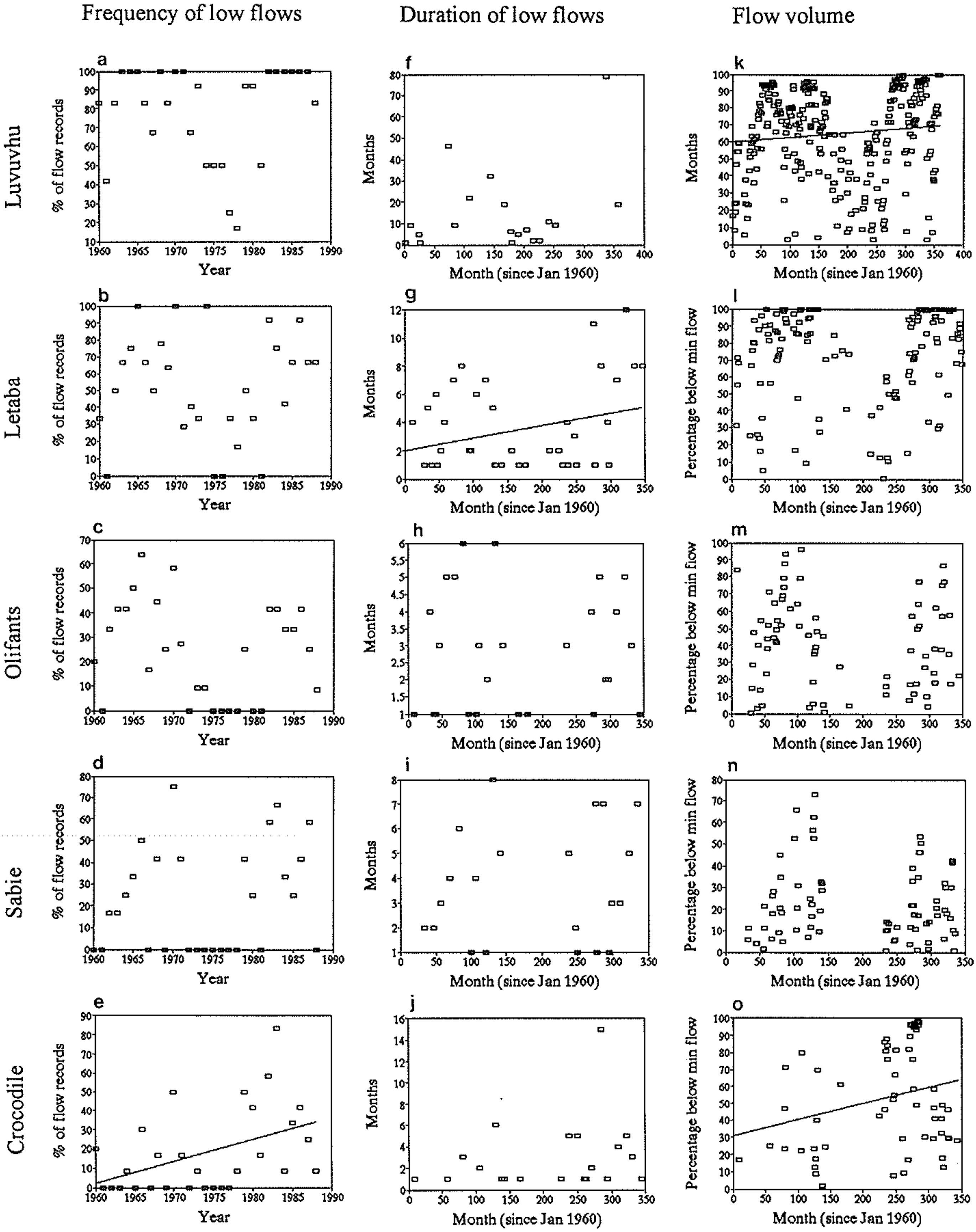

Figure 2.14 Long-term changes in the severity of low flows in Kruger National Park rivers indicated by changes in the frequency with which low flows have been below minimum flow required to achieve flow parameter (optimum wetted perimeter, average 20cm depth, average 30cm s^{-1} velocity) (2.14a to 2.14e), duration of low flow periods (2.14f to 2.14j), and flow volume expressed as percentage below the minimum flow calculated to achieve minimum flow parameter for each river (2.14k to 2.14o). Solid lines show significant trend.

Potential inaccuracies in the calculated percentages include:

(i) Runoff from larger tributaries below gauging stations in the Letaba, Olifants and Sabie rivers (Klein Letaba for the Letaba; Selati and Timbavati rivers for the Olifants; Sand River for the Sabie) have not been taken into consideration as no flow records exist for these rivers. Flow in these tributaries is seasonal, and it was difficult to accurately assess the effect of their flow on the above monthly flow calculations.

(ii) Flow records are from gauging stations located near the western boundary of KNP, whereas calculated minimum flows required to maintain fish habitat reflected that required at the eastern boundary of the park. Thus, reductions in surface flow within the KNP due to losses to ground, evaporation and consumptive use have not been incorporated into the calculations. Volumes associated with such losses are unknown.

Consequently, estimates of the frequency which average monthly flows have been below the minimum to maintain fish habitats should be considered as conservative (based on the best available information) which could be improved by further research of the hydrology of KNP rivers.

A significant increase in the frequency of low flow periods was apparent only in the Crocodile River ($F=6.417$, $p<0.05$) (Figure 2.14e) resulting from increased abstraction and impoundment (section 1.3.8). These long-term changes would suggest increased environmental stress on flow dependant fish species (section 2.3.2.6). In none of the rivers was a significant decrease in the frequency of low flows recorded over the thirty year study period (Figures 2.14a to 2.14e).

Duration of low flows

The duration of low flow periods was longest in the Luvuvhu River, with three periods between 1960 and 1989 where, for each period, average monthly flow was below the minimum necessary to maintain fish habitats for 30 consecutive months (Figure 2.14f). The most recent of these extended low flow periods occurred in the 1980s, where an average monthly flow below that required to maintain fish habitats persisted for 79 consecutive months, suggesting recent environmental stresses on fish species. Extended (>6 months) low-flow periods have also frequently occurred in the

Letaba River (nine occasions between 1960 and 1989) (Figure 2.14g) and once in both the Sabie (Figure 2.14i) and Crocodile (Figure 2.14j) rivers. The construction of the Braam Raubenheimer Dam in the Crocodile River (section 1.3.8) resulted in instream flow falling substantially below that required to maintain fish habitats for 15 consecutive months. Low flows in the Olifants river have never persisted for longer than six months (Figure 2.14h).

A weak trend of increasing low flow duration could be demonstrated only in the Letaba River ($F=3.10$, $p<0.1$). Thus despite the recent incidence of extended low flow periods in most rivers, it cannot be demonstrated that low flow prior to, or during these fish surveys were of significantly longer duration than during comparable surveys undertaken in the 1960s (Gaigher 1969; Pienaar 1978). Consequently, increased duration of low flows cannot be demonstrated as causative of long-term changes in fish distribution in KNP rivers.

Flow volume during low flow periods

Flow volumes (relative to minimum flow necessary to maintain fish habitats) during low flow periods have been lowest in the Letaba (Figure 2.14l) and Luvuvhu (Figure 2.14k) rivers. In these rivers, less than half the minimum flow required for the maintenance of fish habitats was recorded in 80% (Letaba) and 73% (Luvuvhu) of the low flow months, and less than one tenth of the minimum flow was recorded in 42% (Letaba) and 23% (Luvuvhu) of the low flow months. Furthermore, zero flow has been recorded in the Letaba River in 13% of the low flow months. Low flow volumes have also frequently occurred in the Crocodile river (Figures 2.14o), with less than half the minimum flow required to maintain fish habitats occurring in 48% of the low flow months, and less that one tenth of the minimum flow in 18% of the low flow months. Flow volumes, relative to minimum flow, were highest in the Olifants and Sabie rivers (Figures 2.14m and 2.14n) with less than half of the minimum flows occurring in 38% (Olifants) and 10% (Sabie) of the low flow months. In the Olifants River, less than one tenth of the minimum flow required to maintain fish habitats occurred in three percent of the low flow months. Flow records indicated that zero average monthly flow has never been recorded in the Luvuvhu, Olifants, Sabie and Crocodile rivers. These data were possibly incorrect for the Luvuvhu River in the KNP, as extended periods of zero surface flow were observed during field surveys undertaken between 1987 and 1989 (*pers. obs.*).

Significant long-term decreases in flow volumes have occurred in both the Luvuvhu (F=5.67, $p<0.05$) and Crocodile (F=4.36, $p<0.05$) rivers. These long-term trends would suggest increased environmental stress on flow dependant fish species in these rivers (section 2.3.2.6).

Hypothesized influence of low flows on fish distribution.

Long-term increases in the severity of low flows below that required to maintain fish habitats in the Luvuvhu and Crocodile rivers, coupled with extensive impoundment (sections 1.3.4 and 1.3.8) and frequent incidence of low or zero-flow conditions in the Letaba River, could be expected to have resulted in decreases in the distribution of flow dependant species (*C. paratus*, *C. pretoriae*, *C. swierstrai* and *Amphilius uranoscopus* (Pfeffer, 1889) - see section 2.3.2.2) in these rivers. Species which occur predominantly in marginal areas (Figure 2.13), the first area to be dewatered during low flow periods (section 2.3.3.5), would be expected to have decreased distributions. Furthermore, species favouring seasonal rivers or zero-flow conditions and/or non flood-dependant breeders (*L. ruddi*, *B. toppini*, *B. paludinosus*, *Tilapia sparrmanii* A. Smith, 1840) would be expected to have increased distributions. The absence of long-term changes in the severity of low flows in the Sabie and Olifants rivers suggests that habitat loss resulting from low flow is unlikely to be the cause of changes in the distribution of fish in these rivers.

It is pertinent to detail here some of the limitations in our understanding of the effects of changes in the periodicity and magnitude of flow on fish communities. This in turn limits our ability to assess the influence of past flow régimes on fish distribution in KNP rivers.

A major factor which complicates assessments of the detrimental effects of flow reductions on fish communities is the difficulty of distinguishing between changes in fish distribution resulting from natural and man-induced flow variations. This distinction is necessary in order to assess the conservation status of communities (section 2.1). High variability in short-term flow patterns is typical in most southern hemisphere rivers (Alexander 1985; Braune 1985) and is evident in most South African rivers (Davies *et al*. 1993). Consequently, periodic low flows could be expected, even under virgin flow conditions, particularly during the dry phases of the 18 to 20 year wet and dry cycle in the summer rainfall areas (Abbott and Dyer 1976; Tyson and Dyer 1978).

The effect of long-term rain cycles on river discharge is evidenced in all KNP rivers, though most clearly illustrated in the Luvuvhu River (Figure 1.4a) with low flows having been recorded since the 1930s (when reductions in flow from water impoundment and abstraction would be expected to have been minimal). The effects of naturally occurring low flows on KNP fish communities are unknown. The strong influence of environmental variability on the structure of lotic communities (LeRoy Poff and Ward 1989; Jowett and Duncan 1990; LeRoy Poff and Allan 1995; Death and Winterbourn 1995), however, suggests that changes in fish communities resulting from natural flow variations could be substantial. This study was undertaken during a dry cycle, whereas comparable surveys (Pienaar 1968, 1978; Gaigher 1969) were undertaken towards the end of a wet cycle (Preston-Whyte and Tyson 1988). Consequently, natural and man-induced changes in fish distribution are likely to have occurred simultaneously and hence would be difficult to distinguish one from the another.

Limited understanding of effects of flow reduction on fish, and in particular natural flow variations, emphasized the need for studies on natural community fluxes to improve the interpretive and predictive capabilities of studies emphasizing the flow requirements of fish. Most studies of lotic ecosystems tend to concentrate on perturbed river systems (Davies *et al.* 1993). Study of community fluxes in relatively pristine river systems (such as the Sabie River in KNP), however, are essential to gain a better understanding of the causes and range of natural changes in the diversity of fish assemblages.

A limitation of this study is that emphasis was placed on only a single aspect of the influence of flow variation on fish communities, namely the influence of low flows on the availability of fish habitats. Other environmental factors, however, such as the necessity for seasonal variations in flow and the environmental requirements of early life history stages of fish, have also been recognised as being important in determining the suitability of the fluvial environment for fish (Ward and Stanford 1979; Welcomme 1979; Ward *et al.* 1984; Cambray *et al.* 1989). Little is known about these aspects of the flow requirements of fish, though recent attempts have been made to define the seasonal flow requirements of fish in the Luvuvhu (Louw 1996) and Letaba (Weston 1996) rivers. The authenticity of such assessments, however, remains to be assessed. The paucity of knowledge of the environmental requirements of aquatic biota, and in particular fish (Ferrar 1989) emphasises the continuing need for development, and testing, of techniques for determining the environmental requirements of fish with respect to periodicity and magnitude of flow.

2.3.3.3 Physical and chemical water quality: potential effects on the distribution of fish.

The occurrence of long-term changes in water quality in KNP rivers was difficult to assess since only those water samples collected and analysed by the DWAF after 1985 were regularly preserved (with $HgCl_2$) and filtered. This brings into doubt the accuracy of measurements of several chemical parameters from samples collected prior to 1985. However, as these are the only data available on the water quality in KNP rivers spanning the period between fish surveys (1960-1989) (Table 2.12) pragmatism necessitated their use to assess the suitability of environmental conditions for fish species.

Water quality variables in KNP rivers (Tables 2.12 and 2.13) were, for the most part, found to be within expected ranges for a southern African fluvial freshwater system (Dallas and Day 1993). However, some anomalies were observed in water quality data collected in KNP (Table 2.13), as well as DWAF water quality data collected at gauging stations outside the western boundary of KNP (Table 2.12), as discussed below.

Temperature

Periodic high water temperatures were recorded in both the Luvuvhu (maximum 34.9°C) and Letaba (maximum 32.1°C) rivers (Table 2.13). Temperatures lower than 14.0°C were not recorded during this study (Table 2.13). Although rapid declines in water temperature following hailstorms have previously been recorded in lowveld rivers (Appelton 1976) these were not recorded during this study.

The maximum and minimum temperature, and temperature ranges of rivers are dependant on hydrology (source and rate of flow), climatological (air temperature, cloud cover, wind speed, vapour pressure, precipitation events) and structural features of the catchment area (vegetation cover, channel form, water volume, depth and turbidity) (Ward 1985). Extended low flow periods in the Luvuvhu and Letaba rivers (section 2.3.3.1), and consequent reductions in water volume and depth, have possibly contributed to periodic high water temperatures.

Table 2.12 Water quality parameters as measured at the Department of Water Affairs and Forestry gauging stations closest to the western boundary of the Kruger National Park indicating median values (and range), in mg/l (unless stated otherwise)

Variable	River (sample size)				
	Luvuvhu (44-48)	Letaba (112-115)	Olifants (100-110)	Sabie (137-142)	Crocodile (126-129)
EC (mS/m)	11.5 (8.9-15.5)	35.8 (11.9-147.0)	56.3 (21.9-88.5)	10.1 (4.9-15.9)	35.9 (8.4-82.3)
TDS	83 (51-106)	242 (75-1011)	402 (131-586)	69 (28-124)	269 (88-599)
pH	6.9 (5.9-7.9)	7.4 (5.0-8.6)	7.9 (6.4-8.9)	7.0 (5.3-8.7)	7.7 (5.8-8.7)
Na	7.5 (2.0-11.5)	37.3 (8.5-217.0)	46.2 (8.2-99.3)	3.7 (1.4-9.0)	30.0 (8.0-83.6)
Mg	4.8 (2.4-7.0)	11.2 (2.0-45.9)	25.9 (3.2-42.5)	4.8 (1.5-7.4)	17.6 (3.3-37.0)
Ca	6.8 (3.8-10.1)	16.4 (5.8-45.3)	28.1 (14.8-42.7)	7.5 (2.6-18.9)	18.5 (3.4-41.5)
F	0.2 (0.03-0.6)	0.2 (0-0.77)	0.3 (0-0.59)	0.1 (0-1.36)	0.3 (0-3.04)
Cl	8.3 (2.6-15.0)	42.5 (9.0-263.0)	51.5 (16.2-116.3)	3.7 (0.7-3.2)	19.3 (5.8-66.1)
NO3	0.1 (0-0.61)	0.2 (0-1.93)	0.3 (0-1.84)	0.2 (0-0.57)	0.5 (0-2.01)
SO4	2.7 (0-7.0)	12.0 (0-84.9)	21.4 (1.5-81.1)	3.9 (0-15.7)	17.6 (0-63.2)
PO4	0.01 (0-0.81)	0.01 (0-0.41)	0.01 (0-0.2)	0.01 (0-0.04)	0.01 (0-0.15)
CaCO3	42.6 (16.2-61.0)	94.1 (7.6-293)	175.6 (13.9-249.6)	35.8 (4.3-73.6)	138.8 (27.1-288.7)
Si	11.1 (8.32-13.74)	8.2 (1.69-11.8)	8.7 (5.66-11.35)	5.9 (3.81-10.2)	11.4 (4.74-23.6)
K	1.0 (0.67-3.04)	2.3 (0.59-7.02)	2.3 (1.36-4.16)	0.6 (0.02-2.08)	1.0 (0.08-3.78)
NH4	0.04 (0-0.21)	0.06 (0.1-0.42)	0.04 (0-5.9)	0.03 (0-0.26)	0.04 (0-0.45)

Table 2.13 Maximum and minimum values for the water quality parameters (water temperature, dissolved oxygen concentration, conductivity, pH and turbidity) measured in the Luvuvhu, Letaba, Olifants, Sabie and Crocodile rivers during Winter 1987, Summer 1987/1988, Winter 1988 and Winter 1989 sample periods.

Variable	River	Sample time			
		Winter 1987	Summer 1987/88	Winter 1988	Winter 1989
Temperature (C)	Luvuvhu	19.2 - 27.5	28.9 - 31.1	17.4 - 34.9	17.0 - 22.3
	Letaba	14.0 - 20.8	26.8 - 32.1	17.0 - 27.3	17.5 - 25.3
	Olifants	17.3 - 24.0	-	15.9 - 21.8	17.5 - 21.5
	Sabie	17.1 - 19.8	25.1 - 28.1	16.9 - 22.8	13.9 - 27.9
	Crocodile	21.0 - 24.9	-	20.4 - 23.9	18.2 - 22.5
Dissolved Oxygen (mg.l)	Luvuvhu	4.7 - 8.6	6.1 - 7.2	-	7.4 - 8.6
	Letaba	5.7 - 10.6	-	4.4 - 9.8	6.9 - 7.4
	Olifants	9.2 - 12.4	-	6.8 - 8.4	7.5 - 8.9
	Sabie	6.6 - 8.8	5.6 - 8.1	6.7 - 7.5	-
	Crocodile	6.0 - 9.2	-	6.2 - 9.0	-
Conductivity (uS.cm)	Luvuvhu	99 - 253	101 - 190	91 - 98	89 - 100
	Letaba	249 - 376	160 - 252	133 - 500	263 - 336
	Olifants	826 - 1188	-	610 - 760	520 - 660
	Sabie	94 - 122	99 - 130	88 - 116	80 - 119
	Crocodile	301 - 436	-	232 - 530	220 - 366
pH	Luvuvhu	6.6 - 7.6	7.6 - 7.9	6.3 - 7.3	7.3 - 7.9
	Letaba	7.7 - 8.4	7.5 - 7.9	-	7.6 - 8.0
	Olifants	7.3 - 9.4	-	-	8.3 - 8.5
	Sabie	6.5 - 8.0	6.8 - 7.4	7.5 - 8.1	7.3 - 8.0
	Crocodile	7.6 - 8.4	-	7.4 - 8.7	7.8 - 8.5
Turbidity (NTU)	Luvuvhu	-	-	-	13.5 - 23.0
	Letaba	-	-	-	9.3 - 36.5
	Olifants	-	-	-	12.4 - 20.0
	Sabie	-	-	-	2.0 - 5.6
	Crocodile	-	-	-	2.0 - 14.5

The effects of temperature changes on fish include alterations in growth, reproduction, fry survival, and egg hatchability (Brungs 1971), and in extreme cases, mortality resulting from metabolic malfunctions (Cherry and Cairns 1982). The temperature tolerances or preferred range of most southern African fish are unknown. The LC_{50} of coldwater North American Salmonidae such as *Salvelinus fontinalus* are as low as 26.1°C, whereas LC_{50} for warm water species such as *C. carpio* are as high as 35.7°C (McKee and Wolf 1963). The possibility exists for both lethal and sub-lethal effects from high water temperatures in both the Luvuvhu and Letaba rivers.

Long-term temperature ranges greater than 17°C to 30°C for the Luvuvhu River, and 8°C to 25°C for the Sabie River are considered to be detrimental for fish species (Moore *et al.* 1991). These ranges, however, where based on "best guesses" by workshop delegates rather that investigative studies (Moore *et al.* 1991). The upper limit of the range for the Sabie River is possibly unrealistically low, as temperatures of up to 28.1°C were recorded in this study, and there is no reason to suspect that these temperatures were a consequence of man-induced changes to the physical environment. Maximum temperatures recorded in the Luvuvhu and Letaba River were in excess of the suggested range for the Luvuvhu (Moore *et al.* 1991), and would be expected to exceed the upper temperature tolerance of species such as *A. uranoscopus*, which predominate in cold mountain streams (Pienaar 1978). The potential effects of high water temperatures on other species is unknown.

pH

Median pH values in KNP rivers indicated that the Luvuvhu and Sabie rivers tend towards neutral, whereas the Letaba, Olifants and Crocodile river are frequently slightly alkaline (Table 2.12). Low pH values have been periodically recorded in both the Letaba (pH = 5.0 - January 1992) and Sabie (pH = 5.3 - July 1981) rivers (Table 2.12). Furthermore, pH values below 6.0 were recorded in several sample months in both the Sabie and Crocodile rivers during 1980 and 1984 (DWAF unpublished data). In contrast, high pH values (pH = 9.4) were periodically recorded in the Olifants River during the course of this study (Table 2.13).

Freshwater can vary widely in pH due to natural causes such as photosynthetic activity (Wetzel 1983) and the leaching of organic acids from the vegetation (Gardiner 1988; Britton 1991; Gale 1992), as well as anthropogenic inputs such as industrial and mining effluents and acid precipitation (Dallas and Day 1993; Allan

1995). Most fresh waters, including most in South Africa, are relatively well buffered, with pH ranges around 6 to 8 (Dallas and Day 1993). Extensive development of KNP river catchments (Chapter 1), and resultant industrial and mining effluents, as well as acid precipitation in the highveld regions of Mpumalanga (Tyson *et al.* 1988) may be causative of pH in KNP rivers periodically exceeding this expected natural range.

Most studies of the toxic effects of pH on fish deal with acidification (Driscoll *et al.* 1980; Baker and Schofield 1982; Ingersoil *et al.* 1985; Hall 1987). Detrimental influences of acidification are related primarily to altered solubility of ions, and include the mobilization of toxic metals (particularly aluminium) (Campbell and Tessier 1987), and decrease in the solubility of certain essential elements such as Selenium (Mushak 1985). Failure of fish eggs to develop following lowered pH have been reported by Carrick (1979) and Burton *et al.* (1985). Alkalinization is also reported to have detrimental effects on fish such as the conversion of non-toxic NH_4^+ to toxic NH_3^+ (Gammeter and Frutiger 1990) the effects of which can include reduction in hatching success, reduction in growth rate, and pathological changes in gill, liver and kidney tissues (USEPA 1986 cited in Hart *et al.* 1992).

The pH tolerances of freshwater fish in KNP rivers are unknown. The pH tolerance of aquatic organisms in general in South Africa is thought to vary between 6.0 and 9.0 (Kempster *et al.* 1980). Critical pH ranges for aquatic life in KNP rivers are estimated to be substantially wider (Moore *et al.* 1991), with a maximum range of 4.0 to 10.5 estimated for the Luvuvhu River. Quality ranges given for northern hemisphere countries include 5.0 to 10.0 for the United States of America (Environmental Affairs Department 1980), and 6.9 to 9.0 for both Canada (Environment Canada 1987) and the United Kingdom (Gardiner and Zabel 1989). Where different criteria are given by various authors, the difficulty arises in deciding which to use for evaluating the suitability of environmental conditions for fish species. A pH of between 6.0 and 9.0 is the most widely accepted range for protection of aquatic life, and hence was used in this evaluation. pH in all KNP rivers has exceeded the 6 to 9 range, with periodic acidification indicated in the Letaba, Sabie and Crocodile rivers, and alkalinization in the Olifants River (Tables 2.12 and 2.13). Although it is impossible to discount the effect of past variability in pH on fish communities, the effects, like the pH changes, are likely to be transient. Exceedance of the 6 to 9 range has occurred recently only in the Olifants River, hence only fish species of this system are likely to have shown recent harmful effects.

Turbidity

Turbidity in the Luvuvhu, Letaba and Olifants rivers frequently exceeded 15 NTU (Table 2.13) during winter months, and thus can be considered as high (Bruton 1985). Significantly higher values were recorded in both the Luvuvhu (110 NTU) and Olifants (70 NTU) rivers during summer floods. In contrast, turbidity ranges recorded in the Crocodile River were moderate, and low in the Sabie River (Table 2.13).

The effects of suspensoids on fish are known to be either detrimental or beneficial (Blaber and Blaber 1980; Blaber 1981; Cyrus 1983), depending primarily on the concentration of suspended particles, as well as the timing and duration of exposure (Bruton 1985). In most instances, moderate turbidities (<15 NTU) are thought to be beneficial for most species (Bruton 1985), providing juvenile fish with protection from piscivorous birds and fish, and increasing habitat diversity. Detrimental effects of high turbidity include reduction in light penetration leading to a decrease in photosynthesis and hence primary production (Ryan 1991), smothering of benthic biota leading to reduced foraging efficiency and growth, reduction in the food-searching behaviour of visually-hunting predators, and impairment of gill function (Bruton 1985).

Turbidities recorded in the Sabie and Crocodile rivers during winter months were for the most part substantially lower than the 20 NTU critical level given by Moore *et al.* (1991). Thus even turbidity intolerant species such as *C. swierstrai*, *B. annectens*, *S. meridianus* and *O. zambezense* (section 2.3.2.3) are unlikely to have been detrimentally affected. In the Luvuvhu, Letaba and Olifants rivers, however, turbidity levels were frequently in excess of the proposed 20 NTU critical level, with highly turbid conditions recorded during summer floods. Moderate turbidities are a natural feature of arid zone rivers (Harrison and Elsworth 1958; Shafron *et al.* 1990), and many fish species are adapted to withstand short-term increases in turbidity due to natural floods (Bruton 1985). However, sustained high turbidities in the Letaba River, and particularly the Luvuvhu River, have undoubtedly led to the observed "blanketing" of the substratum with fine silts and clays in many reaches (*pers. obs.*). Such "blanketing" would be expected to limit food availability and retard successful breeding of bottom breeding species. It has been well established that sustained periods of high turbidity have a long-term detrimental effect on fish communities (Bruton 1985), and this effect would not be unexpected in the rivers of the Limpopo system.

Conductivity and major inorganic ions

Concentrations of inorganic ions reported in this study, measured at gauging stations closest to the western boundary of KNP from the 1960s to 1989 (Table 2.12) were similar to those given by van Veelen (1990, 1991) and Moore *et al.* (1991) recorded within the KNP between 1983 and 1989. These data, along with description of concentrations of various trace metals and biocides have been discussed in section 1.3.

Low conductivities measured in the Luvuvhu River during the course of this study (89 to 253 μS cm^{-2}; Table 2.13) were indicative of a low concentration of inorganic ions. This was reflected in the low concentrations of total dissolved salts (TDS) (generally below 100 mg l^{-1}; maximum = 106 mg l^{-1}) recorded between 1966 and 1989 (Table 2.12).

Conductivities in the Letaba river varied between 133 and 500 μS cm^{-2} (Table 2.13), and TDS concentrations were generally below 400 mg l^{-1} (although a maximum of 1011 mg l^{-1} was recorded in July 1985) (Table 2.12) indicating moderate concentrations of inorganic ions. Periodic high concentrations of some inorganic ions have been recorded, with calcium exceeding 45 mg l^{-1} in July 1985, chloride reaching concentrations of 263 mg l^{-1} in September 1982, and the concentration of sodium reaching 217 mg l^{-1} in July 1985 (Table 2.12). The concentration of calcium, chloride, fluoride, sodium and sulphate were, in general, higher during winter and early summer (May to September), whereas the concentration of silicon shows the reverse seasonal trend, being lower during winter months (DWAF unpublished data).

Conductivities in the Olifants River varied between 520 and 1188 μS cm^{-2} (Table 2.13), and TDS concentrations ranged between 131 and 585 mg l^{-1} with a median value of 402 mg l^{-1} indicating high concentrations of inorganic ions (Table 2.12). Calcium concentrations invariably exceeded 30 mg l^{-1} during winter months, with occasional high concentrations of both sodium (>99 mg l^{-1}) and chloride (>116 mg l^{-1}) recorded between 1980 and 1984 (Table 2.12). The concentrations of most inorganic ions varied seasonally, with higher concentrations occurring in winter and early summer. Only silicon showed the reverse seasonal trend, with concentrations being lower during winter months (DWAF unpublished data).

Conductivities in the Sabie River varied between 80 and 122 µS cm^{-2} (Table 2.13), and TDS concentrations were typically less than 100 mg l^{-1} (only twice exceeding 120 mg l^{-1}, once in 1976, and again in 1977) indicating low concentrations of inorganic ions (Table 2.12). Fluoride concentrations were usually low (<0.2 mg l^{-1}), though did reach a maximum of 1.36 mg l^{-1} in December 1986 (Table 2.12).

Conductivities in the Crocodile River varied between 220 and 530 µS cm^{-2} (Table 2.13), and TDS concentrations were typically above 200 mg l^{-1} (frequently exceeding 500 mg l^{-1} between 1979 and 1983) indicating moderate concentrations of inorganic ions (Table 2.12). Concentrations of calcium and sodium frequently exceeded 30 mg l^{-1} and 60 mg l^{-1} respectively, with occasional high concentrations of chloride (>50 mg l^{-1}; August to October 1983) and fluoride (>3.0 mg l^{-1}; October 1986) also having been recorded (Table 2.12). The concentrations of several inorganic ions varied seasonally, with higher concentrations of calcium, chloride, fluoride, magnesium, sodium and sulphate occurring in winter months (July to September) (DWAF unpublished data).

Very little is known about the effects of changes in the concentrations of most ions on aquatic biota, and in particular fish. Studies of the effects of salinization on riverine fish in Australia (Williams and Williams 1991) and America (Pimentel and Bulkley 1983) have demonstrated that most species are relatively unaffected by considerable increases in salinity (c. 800 - 1200 µS cm^{-2}) provided concentrations increase slowly over a number of days. High fluoride concentrations are thought to detrimentally affect tooth and skeletal development in vertebrates (Raubenheimer *et al.* 1990). Many ions, such as sulphate, bicarbonate and carbonate, are themselves not toxic (Hellawell 1986) though can influence other abiotic factors such as pH (Allan 1995). Ions such as chloride are not known to have any toxic effects on living organisms (Dallas and Day 1993). Kok (1980) has suggested that the mormyrids *M. macrolepidotus* and *P. catostoma* are unable to tolerate high conductivities as this effects their ability to electrolocate. The tolerance ranges of these species, however, is unknown, though persistently high conductivity in the Olifants River could be detrimental.

In terms of the water quality criteria of Kempster *et al.* (1980) the concentration of chloride in the Letaba, Olifants and Crocodile rivers, and fluoride in the Crocodile River were, on occasion, unsuitable for the maintenance of biological processes. Calcium concentrations in these three rivers were also frequently higher than the 30 mg l^{-1} critical level suggested for the Sabie River by Moore *et al.* (1991), though the biological authenticity of this standard is unknown. High fluoride concentrations in the Olifants River, although not demonstrated in this analysis of DWAF water quality data, have previously been reported by van Veelen (1990, 1991).

Limited understanding of the effect of periodically high concentrations of inorganic ions on fish make it difficult to assess the likely consequences of long-term changes on species distributions. The influence of changes in water chemistry is likely to be most evident in the Olifants, and to a lesser extent, Crocodile rivers, where consistently high concentrations of several inorganic ions have been recorded, particularly during low-flow winter months. The low toxicity of most inorganic ions which have been regularly monitored (section 2.2.3.2), however, suggests that the biological effects of periodic elevations are unlikely to have been substantial.

Dissolved oxygen

Dissolved oxygen concentrations measured at 12h00 ranged in all rivers between 4.4 and 10.6 mg l^{-1}, though were typically above 7.0 mg l^{-1} (Table 2.13). A low of 4.4 mg l^{-1} was recorded during winter 1988 in the Letaba River, with minimum values of 4.7 mg l^{-1} recorded in the Luvuvhu River and 5.6 mg l^{-1} in the Sabie River (Table 2.13).

A dissolved oxygen concentration of below 4.0 mg l^{-1} in freshwater systems is considered to be detrimental for fish (Moore *et al.* 1991) and other aquatic life (Kempster *et al.* 1980). Although low oxygen concentrations (<5.0 mg l^{-1}) were periodically recorded in KNP rivers, values below the 4.0 mg l^{-1} critical level were never recorded. Furthermore, the incidences of low dissolved oxygen concentration were always found to be localised. Thus, it was unlikely that oxygen concentrations recorded in this study would have substantially influenced the abundance or distribution of fish species. However, numerous factors influence the dissolved oxygen concentration of water, including reairation from the atmosphere (dependant on turbulence and oxygen deficit), atmospheric pressure, salinity, water temperature, photosynthesis by aquatic plants, respiration of aquatic organisms, aerobic decomposition and chemical breakdown of pollutants (Allan 1995). Pollard *et al.* (1993) have recorded a negative relationship between overhead cover and dissolved oxygen in pools in the Sabie River system, with photosynthetic activity by algae in unshaded pools thought to increase daytime oxygen concentrations. Dissolved oxygen concentrations in water fluctuate diurnally in response to temperature changes, photosynthesis by plants, and respiratory activity of aquatic organisms (Lloyd and Swift 1976). It is therefore possible that oxygen concentration below minima recorded in this study may periodically occur, particularly after daylight hours. Coldwater fish generally require higher concentrations of dissolved oxygen than do warmwater species (Boyd 1982), thus species such as *A. uranoscopus*, which predominate in cold mountain streams (Pienaar 1978) may be detrimentally affected by periodic low oxygen concentrations, particularly in the slow flowing Letaba and Luvuvhu rivers.

In summary, with the exception of increases in suspended particles and hence turbidity, most water quality changes (high or low pH, high ionic particle concentrations, low dissolved oxygen concentrations) appear to have been short-lived, and their direct influence on the distribution and abundance of fish species remains to be assessed. High water temperatures would be expected to have reduced the distribution of the cold water species *A. uranoscopus*. High suspensoid levels, particularly in rivers of the Limpopo system, recorded both during fish surveys, and as episodic events (Chapter 1) are likely to have resulted in a decline in the abundance and distribution of turbidity intolerant fish species.

2.3.3.4 Changes in the distribution of aquatic plants: potential effects on fish distribution.

Aquatic plants in the Luvuvhu river were sparse and sporadically distributed. Dense stands of *P. mauritianus* (reeds) occurred only at Dongadzivha (sample locality No. 7) (Figure 2.4), and sparse rafts of *P. stratiotes* (water lettuce) were observed in isolated pools.

Aquatic plants were previously more widespread and abundant in the Luvuvhu River, with aerial photograph analysis revealing a marked decline in the distribution of *P. mauritianus* over the past 30 years (A. Carter, *pers. comm.*)[7]. Similarly, *P. stratiotes* after first having been recorded in the Luvuvhu river in 1981 (Joubert 1986b), rapidly increased in distribution and abundance, being particularly abundant in slow flowing pools in the lower reaches of the river. The introduction of the parasitic weevil *Neohydronomus pulchellus* in December 1985 (Cilliers 1987), however, combined with periodic high flows, have been instrumental in reducing the abundance of *P. stratiotes* in the Luvuvhu river.

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Emergent aquatic plants are widespread in the Letaba River, with dense stands of *P. mauritianus* occurring in an approximately 26 km long stretch below the Engelhard Dam (sample locality No. 12) (Figure 2.4). In the remainder of the Letaba River in the KNP, *P. mauritianus* occurs in sparse stands along the margins of the secondary channels, usually in association with bedrock outcrops. Long-term declines in reed cover have been recorded (Carter and Rogers 1989), with a 14.4% increase observed between 1942 and 1965, followed by a 32.6% decline in reed cover between 1965 and 1988.

Dense stands of *P. mauritianus* occur only in a relatively short (c 18km long) portion of the Olifants River upstream of the Olifants restcamp (sample locality No. 18) (Figure 2.4). Along the remainder of the Olifants River in the KNP, *P. mauritianus* is either absent or occurs in sparse, isolated patches, usually in association with bedrock outcrops. Long-term changes in the distribution of *P. mauritianus* in the Olifants River have been noted (Carter 1990), with a net decrease occurring between 1965 to the mid-1970s, followed by increases up to the mid-1980s. Submerged or floating aquatic plants are neither widespread nor abundant.

Dense stands of *P. mauritianus* occur on sandbanks along much of the lengths of the Sabie River in the KNP. Long-term changes in the distribution of *P. mauritianus* have been recorded (Carter and Rogers 1989), with increases in reed cover having occurred between 1940 and 1965, and subsequent declines between 1965 and 1984.

The floating macrophyte *P. stratiotes* was first recorded in the Sabie river in 1981 (DWAF unpublished data; Joubert 1986b), since which time it has become widespread and abundant, forming dense rafts in slow flowing reaches. The parasitic weevil *N. pulchellus* was introduced into the Sabie River in 1988, (L. Braack, *pers. comm.*)[8], though its effect to date on reducing the abundance of *P. stratiotes* appears to be minimal.

Aquatic plants are widespread and abundant in the Crocodile River. Dense stands of *P. mauritianus* occur on sandbanks and islands along much of the lengths of the river in the KNP. An increase in the distribution of *P. mauritianus* in the Crocodile River since the early 1940s has been recorded by Carter and Rogers (1989).

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[8] L. Braack, Manager: Scientific Services, Skukuza, Kruger National Park, South Africa.

Eichhornia crassipes (water hyacinth) was first recorded in the Crocodile river in 1972 (DWAF unpublished data), and within the boundaries of the KNP in 1976 (Joubert 1986b), and is now widespread and abundant, particularly in dams and weirs. *Pistia stratiotes* was first recorded in the Crocodile river in 1985 (DWAF unpublished data) and is now widespread though not abundant. In the lower reaches of the Crocodile river filamentous algae (possibly *Cladophora* spp.) are abundant, in places forming dense mats of organic matter on the substratum (*pers. obs.*).

Is summary, changes recorded in aquatic plant communities include substantial increases in the abundance and distribution of floating hydrophytes in the Sabie and Crocodile rivers (Joubert 1986b; DWAF unpublished data), and nett decreases in the distribution of *P. mauritianus* in all five major rivers in KNP (Carter and Rogers 1989; Carter 1990; A. Carter, *pers. comm.*).

Aquatic plants form an important component of the habitat of several freshwater fish species in providing a food source, and shelter for breeding and nursery areas (Jackson 1961b; Crass 1964; Bell-Cross 1976; Pienaar 1978; Skelton and Cambray 1981; Bruton *et al.* 1982; Bruton and Jackson 1983; Cambray 1984; Skelton 1986a). Furthermore, the adults of several small as well as skotophilic fish species frequently occur in vegetated marginal areas and under floating macrophyte mats which provide defensive cover from predators (Mitchell 1976; section 2.3.2.5). Consequently, changes in the distribution and abundance of aquatic plants would be expected to have a significant effect on the diversity of fish communities.

In the Olifants and Luvuvhu rivers, where there are extensive areas with few or no *Phragmites* reeds, the abundance of phytophilous fishes (for example *M. macrolepidotus*, *A. johnstoni*, *P. philander*, small *Barbus* species) would be limited. In contrast, in the Sabie and Crocodile rivers, recent increases in the abundance and distribution of floating aquatic plants could be predicted to have resulted in an increase in the abundance and distribution of phytophilous fishes.

2.3.3.5 Causes of changes in the distribution of fish in KNP rivers

Hypotheses of causes for changes in fish distribution have been formulated with the understanding that the distribution of species can be dependant on a variety of environmental factors, only a few of which have been regularly monitored. Correlation between environmental and species changes does not necessarily demonstrate causation (Allan 1995). Detailed impact and experimental studies would be required to test any suggestions made regarding the interaction between species and their environment. Identification of probable causes (of either natural or anthropogenic origin) for species distributional changes is necessary for the assessment of the conservation status of fish communities (section 1.2.2.5).

Luvuvhu River

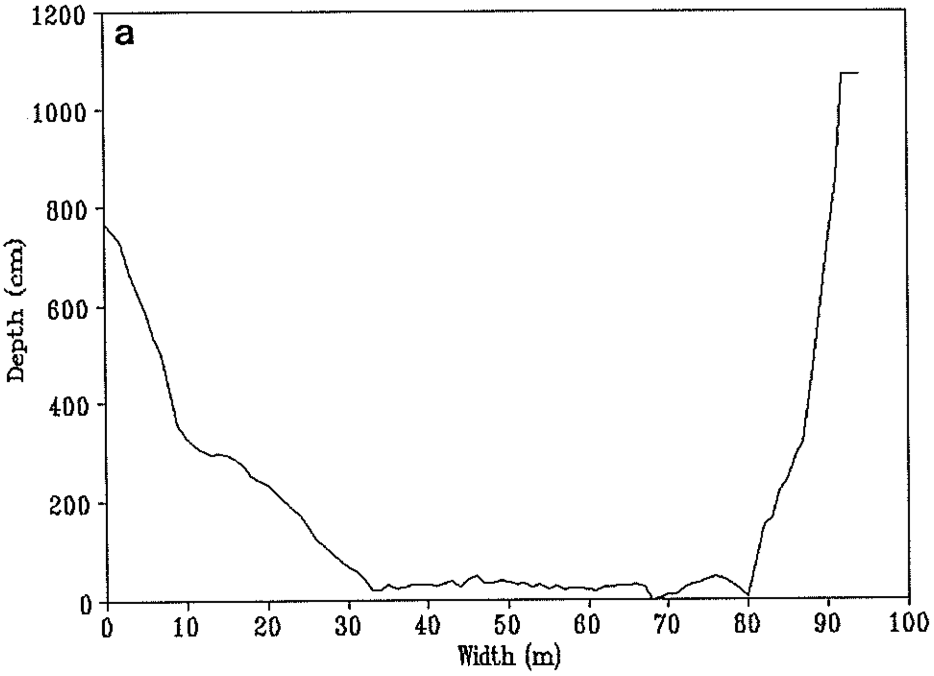
A number of probable causes for observed species declines in the Luvuvhu River can be identified. Increased severity of low flows (section 2.3.3.2) and the occurrence of zero flow conditions between 1982 and 1989 (section 1.3.4) are among the main physical changes that have occurred in this once perennial river. It is therefore not surprising that *C. swierstrai* and *A. uranoscopus*, which are dependant on perenniality of flow (Crass 1964; Gaigher 1969, 1973; Bell-Cross 1976; Gaigher 1978; Bruton *et al.* 1982) were amongst those species not recorded in the Luvuvhu River during this study. Reductions in flow could also have contributed to the decline of *B. marequensis* which frequently occurs in strongly flowing waters (section 2.3.2.2).

Water diversions and consequent reductions in instream flow have been identified as a major cause of declines in freshwater fish on most continents, including North America (Moyle and Nichols 1974; Stanford and Ward 1986; Moyle and Williams 1990; Moyle *et al.* 1992; Moyle 1995), Australia (Cadwallader 1986), Asia (Coad 1981; Senanayake and Moyle 1982), Europe (Mrakovcic *et al.* 1995; Elvira 1995; Economidis 1995) and Africa (Crass 1969; Scudder 1989; Merron *et al.* 1993). Flow reductions can be the direct cause of decline of flow dependant species (as appears to be the case with *C. swierstrai* and *A. uranoscopus*), though indirect effects, such as habitat alteration and loss of refugia, may also effect non-flow dependant species (Moyle and Leidy 1992). The decline of *B. toppini, B. trimaculatus, B. unitaeniatus, B. radiatus, B. viviparus* and *B. annectens* in the Luvuvhu River does not appear to have been as a direct result of reduced flow. The independence of these species from perennial flow is evidenced by their being widespread in seasonal rivers (Pienaar 1978), and most have persisted in the Letaba River which now dries up every year (section 1.3.5). Indirect effects of reduced flow, however, cannot be discounted as causative factors.

Four of the species not recorded in the Luvuvhu River during this study (*B. annectens, B. unitaeniatus, P. philander, A. johnstoni*), and two species with decreased distribution (*B. radiatus, B. viviparus*) occur primarily along the margins of pools and channels (section 2.3.2.1) and utilise instream or inundated marginal vegetation for defensive cover or as feeding sites. A further two previously widespread species not recorded in this study (*B. toppini, B. trimaculatus*) also frequently occur amongst inundated aquatic vegetation (section 2.3.2.5). As stated previously, there has been a marked decline in marginal vegetation in the Luvuvhu River (in particular *P. mauritianus*) over the past 30 years, with the western reaches of this river now being largely devoid of such plants (section 2.3.3.4). Whether the frequent occurrence of low flows have been causative of such habitat changes in the Luvuvhu has yet to be conclusively shown, though erratic flow is thought to be responsible for destabilization of marginal vegetation in other perennial rivers in the KNP (Carter and Rogers 1989). Increased severity in low flows (section 2.3.3.2), however, and reduction in the frequency and magnitude of flood events in the Luvuvhu River during the 1980s (Figure 1.4a), have undoubtedly limited both the duration and frequency of inundation of what marginal vegetation remains.

Channel morphology and the distribution of submerged and emergent aquatic plants within the channel of the Luvuvhu River have contributed to the vulnerability of marginal area dwelling species to low flows. Much of the Luvuvhu River channel in the KNP is "U" shaped, with high (>5m) steeply sloping banks. Descriptions of channel morphology of the Luvuvhu River are given by Venter (1991), and typical cross-sections illustrated in Figures 2.15a and 2.15b. There are few secondary channels and water generally flows in the centre of the primary channel. Aquatic macrophytes and trailing marginal plants are not abundant and are restricted primarily to the edges of channels (section 2.3.3.4). As discharge and consequently water depth within the river channel decreases, the first areas to be de-watered are the shallow vegetated areas along the margins of the channel. De-watering of marginal areas will force marginal area dwelling species into the mainstream where they are more vulnerable to predation. Increased predation and reduced availability of their favoured habitat will result in declines in the distribution and abundance of marginal-dwelling species.

Declines in freshwater fish resulting from loss in vegetative cover have been recorded in several countries (Senanayake and Moyle 1982; Hortle and Lake 1983; Moyle and Williams 1990; Penczak *et al.* 1995). Reasons cited for the loss of vegetation include canalisation (Hortle and Lake 1983), increased turbidity (Penczak *et al.* 1995) and direct removal during mining operations (Senanayake and Moyle 1982). These differ



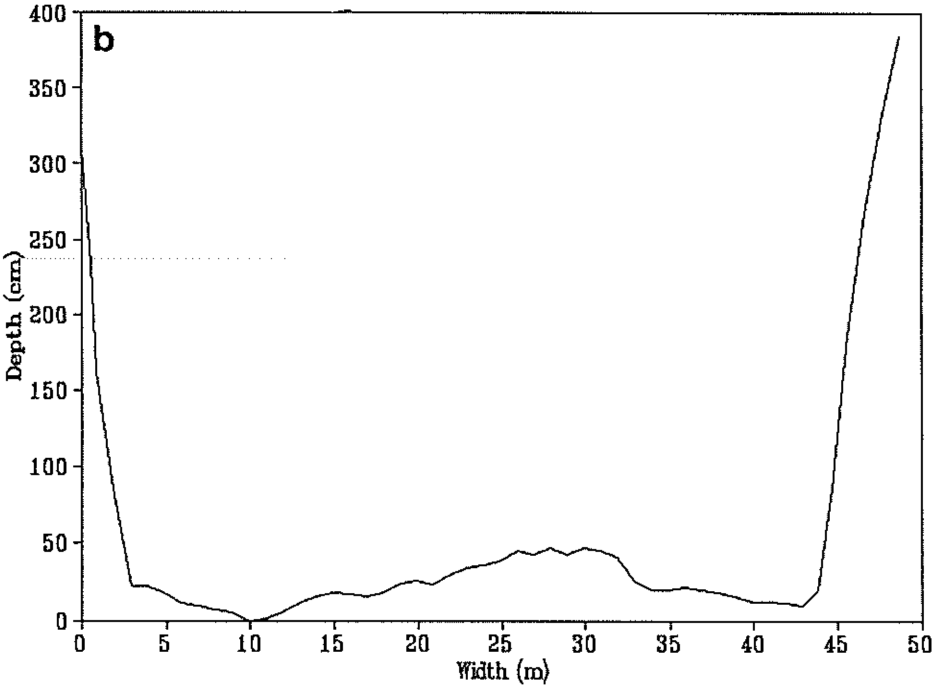


Figure 2.15 Cross-sectional profile of the channel of the Luvuvhu River at sample localities number 4 (Bobomenie) (a), and sample locality number 3 (Hapi) (b).

from the Luvuvhu River where flow reductions and consequent dewatering of marginal areas are possibly primary factors.

The now characteristic high suspensoid levels of the Luvuvhu River have also been instrumental in causing species declines, particularly *C. swierstrai*, *B. annectens* and *P. philander* which favour clear waters (section 2.3.2.3), as well as *B. trimaculatus*, *B. viviparus* and *M. brevianalis* which are reported to be intolerant of high suspensoid levels (Jackson 1961a; Pienaar 1978; Bruton *et al.* 1982; Kenmuir 1984). High suspensiod levels have also resulted in species declines in Nigeria (Udoidiong 1988), Sri Lanka (Senanayake and Moyle 1982) and Iran (Coad 1981). In these countries the effect of suspensoids is manifested primarily in silt and clay deposition on the substratum. This effect is also evident in the Luvuvhu River where, in the lower reaches, the substratum consists predominantly of fine silt and clay - in places in excess of one meter deep (*pers. obs.*). Reduced flow velocities have limited scouring and subsequent removal of this layer. Three declining species (*C. swierstrai*, *A. aeneofuscus*, *P. philander*) are known to favour gravel or sandy substrata (Crass 1964; Le Roux and Steyn 1968; Gaigher 1969, 1973, 1978; Pienaar 1978; Bruton and Kok 1980; Bruton *et al.* 1982) and the lack of such substrata may have been instrumental in causing their decline.

Letaba River

Although a statistically significant long-term increase in the severity of low flows could not be demonstrated in the Letaba River, the frequent incidence of extended low or zero flow conditions, (section 2.3.3.1), and the construction of impoundments within KNP to combat this (section 1.3.5), remain the most obvious reason for many of the observed changes in fish species distribution. Reduced seasonal flow has also been suggested by Chutter and Heath (1993) as the reason for low fish community diversity in the lower reaches of the Letaba River. The decline in the rapid-dwelling catlet species *C. pretoriae* and *C. swierstrai* can be readily explained by their dependence on perennial flow (Crass 1964; Pienaar 1978; Bruton *et al.* 1982). *Labeo congoro* are frequently recorded in strongly flowing water (section 2.3.2.2), particularly below rapids (Pienaar 1978). Extended low or zero flow conditions in the Letaba River (section 2.3.3.1) are likely to have contributed to this species decline in distribution.

Chutter and Heath (1993) concluded that the distribution of fish in the Letaba River could not be shown to be limited by any dam or weir. The decreased distribution of *H. vittatus* can, however, be attributed to the absence of fish ways on three instream impoundments constructed within the parks boundaries. *Hydrocynus vittatus* do not breed in KNP but rather migrate to the lowlands of Mocambique to spawn along the shallow, grass-covered fringes of lakes and small streams (Pienaar 1978). Instream impoundments would prevent recruitment of *H. vittatus*, which were not found upstream of impoundments not fitted with fish ways, into the upper reaches of the Letaba river in the KNP. Barriers created by large impoundments in the Olifants river in Mozambique (below the confluence of the Letaba and Olifants rivers) may also be responsible for the decline in the catadromous *A. marmorata*. The elvers of anguillid eels, such as *A. marmorata*, have been reported to overcome physical barriers, such as waterfalls and small impoundments, by climbing up moist rock surfaces adjacent to the barrier (Bruton *et al.* 1989; Skelton 1993). The barrier to migration created by large impoundments, however, is considered a major threat to these fish (Bruton *et al.* 1989). Reduction in the distribution of *H. vittatus* and *A. marmorata* in the Letaba River is consistent with the findings of Moyle and Nichols (1974), Coad (1981), Cadwallader (1986) and Elvira (1995) who have reported reductions in the distribution of migratory fish due to the physical barrier caused by impoundments.

The increased distribution of the pool-dwelling *B. toppini*, *S. intermedius*, *L. ruddi* and *B. paludinosus* in the Letaba River can be attributed to an increase in their favoured habitat, namely slow flowing or stationary waters (section 2.3.2.2) formed by the four instream impoundments on this river. This conclusion is consistent with observed changes in riverine fish communities in several countries, where species which favour lake-like habitats flourish in rivers following impoundment (Moyle and Leidy 1992).

High suspensoid levels in the Letaba River (section 2.3.3.3) and the consequent deposition of silt and clays in pools and dams have also been instrumental in causing species declines, as previously discussed for the Luvuvhu River. It is probable that high suspensoid concentrations have contributed to declines in the distribution of *C. swierstrai* and *B. annectens* which favour clear waters (section 2.3.2.3). The deposition of silt and clays may also have contributed to the decline in *C. swierstrai* and *A. aeneofuscus* which are known to favour gravel or sandy substrata (Crass 1964; Le Roux and Steyn 1968; Gaigher 1969, 1973, 1978; Pienaar 1978; Bruton and Kok 1980; Bruton *et al.* 1982).

Olifants River

The ten species of fish that have decreased distributions in the Olifants River have very varied physical habitat requirements (section 2.3.2.6) suggesting that flow conditions are not the prime reason for the observed changes in distribution. The increased distribution of *C. paratus*, which occurs primarily in strongly flowing rapids (section 2.3.2.1), and unchanged distribution of other flow dependant species (*C. pretoriae*, *C. swierstrai*) also indicates flow reductions have not had a direct effect on the distribution of fish.

Episodic pollution events, such as the release of silt laden water from the Palaborwa Dam in 1983, and consistently high pollution levels resulting largely from upstream mining and catchment development (section 1.3.6), are causes more consistent with such wide spread declines in species distribution. Pollution of rivers with domestic, agricultural and industrial effluents, and pesticides is arguably the most widely cited cause for declines in the distribution and abundance of fish, with effects reported from most continents (Coad 1981; Senanayake and Moyle 1982; Udoidiong 1988; Mrakovcic *et al.* 1995; Almaça 1995; Elvira 1995; Economidis 1995; Balik 1995). Chronic, sublethal pollution is more common, and often viewed as having a larger influence than pollution that causes big fish kills (Moyle and Leidy 1992). In the Olifants River both lethal and sublethal pollution occur (section 1.3.6), though their comparative effects on species distribution is unknown. Although the Olifants River remains perennial (section 2.3.3.1), reduced flows experienced during winter months, would be expected to compound any effects of pollution on fish (Moyle 1995).

Several fish species that are reported to favour clear waters (*C. swierstrai*, *P. philander*, *B. trimaculatus*, *B. viviparus*) (Jackson 1961a; Pienaar 1978; Bruton *et al.* 1982; Kenmuir 1984; section 2.3.2.3) have not undergone decreases in distribution. Consequently, high suspensoid levels in the Olifants River (section 2.3.3.3) do not appear to have had a substantial influence on the distribution of fish.

As discussed for the Letaba River above, barriers created by large impoundments in the Olifants river in Mozambique may have contributed to the decline in the catadromous eels *A. marmorata* and *A. mossambica*.

Sabie River

The Sabie River is the least perturbed of the major rivers of the KNP (sections 1.3.7, 2.3.3.1 and 2.3.3.3), and this is reflected in the comparatively small number of fish which have undergone a reduction in distribution over the 30 year period between fish surveys. Both *B. argenteus* and *A. uranoscopus* which were not recorded in this study (section 2.3.1) are primarily inhabitants of well-aerated waters of the colder upland streams, and are rarely found in the warmer waters below 400m elevation (Pienaar 1978). Both species can at best be regarded as occasional migrants to the lowveld regions of the Sabie River (Pienaar 1978), and little can be deduced from their not having been sampled in recent surveys.

Large impoundments constructed in Mocambique and not fitted with fish ways are, as discussed for the Letaba River above, thought to be responsible for the decline of *H. vittatus* (Gaigher 1978; Pienaar 1978) and *A. marmorata* in the Sabie River.

Reasons for the decline of *B. imberi* and *L. congoro* are unclear. In contrast, the increased abundance of aquatic plants, and in particular the water lettuce *Pistia stratiotes* (section 2.3.3.4) is probably responsible for the observed increase in many species which frequently occur in marginal areas (*B. annectens, B. eutaenia, B. trimaculatus, M. macrolepidotus* and *P. philander* - see section 2.3.2.1) and use floating vegetation for both feeding and defensive cover (Bell-Cross 1976; Bruton *et al.* 1982).

Crocodile River

Many of the reasons for fish distributional changes in the Crocodile River are similar to those discussed for the Letaba (flow regulation) and Sabie (increase in aquatic plants) rivers above. The severity of low flows in the Crocodile River, particularly during the 15 month (August 1982 to October 1983) filling phase of the Braam Raubenheimer Dam (section 2.3.3.2) has possibly resulted in the decline of the rapid-dwelling catlet species (*C. anoterus* and *C. pretoriae*), which are dependant on perenniality of flow (Crass 1964; Pienaar 1978; Bruton *et al.* 1982; Skelton 1983).

The three species newly recorded within the Crocodile River in the KNP (*A. brevis, B. paludinosus* and *T. sparrmanii*) as well as *S. intermedius* with increased distribution, all favour low flow conditions (section 2.3.2.2), and their increase in distribution can be attributed to past low flow conditions (section 2.3.3.1) and increased flow regulation (section 1.3.8). For these species, conditions in the KNP have become more favourable. Flow regulation may, however, have resulted in the decline of the previously scarce *L. ruddi* and *S. zambezensis* which favour deep pools with little or zero flow (section 2.3.2.2).

Reasons for the decline of *L. rosae* remain unclear. The difficulties associated with collecting large cyprinids in the Crocodile River have been discussed in section 2.2.1.2. Few large cyprinids were collected despite the frequent observation of large schools of *Labeo* species (*pers. obs.*). Decreased distribution of *L. rosae* is potentially a sampling artifact resulting from poor sampling conditions in deep pools in the Crocodile River.

Anguilla bengalensis is rare in KNP rivers, with only one specimen ever having been collected (Pienaar 1978). Little can be deduced from it not being collected in recent surveys in the Crocodile River.

The increased distribution of two marginal dwelling species in the Crocodile River (*B. radiatus*, *B. viviparus*) can be attributed to increases in floating plant cover (section 2.3.3.4) that has accompanied flow regulation and eutrophication in this river.

Biotic factors as determinants of fish species distribution in KNP rivers

The above evaluation of changes in the distribution of fish in KNP rivers has centred primarily on the influence of abiotic factors. Very little is known about the role that biotic factors (such as competition and predation) play in shaping fish community diversity, beside documented instances where introduced species result in the decline of indigenous populations (De Moor and Bruton 1988; Soulé 1991; Moyle and Leidy 1992; Allan and Flecker 1993).

The relative importance of abiotic forces and interactions between indigenous populations has been widely debated, with a number of similar but subtly different models emerging. One viewpoint suggests that local environments vary from harsh to benign, with a corresponding shift in the relative importance of abiotic and biotic forces (Peckarsky 1983). Other models (Connell 1978; Yodzis 1986) emphasise the importance of biological interactions where, in very constant environments, strong biological interactions permit only few competitively superior species to maintain populations. The patch dynamics model encompass aspects of the models mentioned above, though places more emphasis on the dispersal ability of organisms and a shifting mosaic of environmental conditions (Townsend 1989). Allan (1995) concluded that it is likely that none of these models is correct to the exclusion of the others. The strong influence of environmental variability on the structure of lotic communities, however, has been demonstrated in several studies (LeRoy Poff and Ward 1989; Jowett and Duncan 1990; LeRoy Poff and Allan 1995; Death and Winterbourn 1995). The observed correlations between environmental perturbations and fish diversity in KNP rivers is consistent with the suggestion of Allan (1995) that abiotic factors have strong, possibly overriding influences on community structure in rivers.

Interspecific competition, may, in some instances play a role in determining community structure in KNP rivers. For example, fish communities in rapids in the Luvuvhu river were invariably numerically dominated by *Glossogobius* spp. whereas in other rivers *Chiloglanis* species were abundant. In highly stochastic rivers such as the Luvuvhu, habitat generalists such as *Glossogobius* spp. (section 2.3.2.6) may be able to outcompete habitat specialists such as the *Chiloglanis* species, whereas in rivers with a more predictable flow régime *Chiloglanis* could hold the competitive advantage. A further example stems from a study of fish communities in the Sabie River during drought conditions (Pollard *et al.* 1993) where predation was thought to play a role in species extinctions in some isolated pools. Such extreme consequences of biotic interactions are, however, like the environmental conditions that precipitated them, likely to be transient. The role of interspecific competition and predation on the distribution of fish in KNP rivers remains to be assessed, though the high variability in abiotic environmental conditions suggests that these remain the predominant factors.

Cumulative effect of environmental change on fish distribution

Many of the environmental factors highlighted above as potential causes for fish distribution changes in KNP rivers (Figure 2.16) have been discussed in isolation from one another. The cumulative effect of environmental changes on fish has been suggested by Harris (1988) and Moyle and Williams (1990), with species rarely declining from one factor alone, but usually from the effects of several working in conjunction with one another. The complexity of cumulative effects can frequently hamper identification of the primary causes for species changes where several

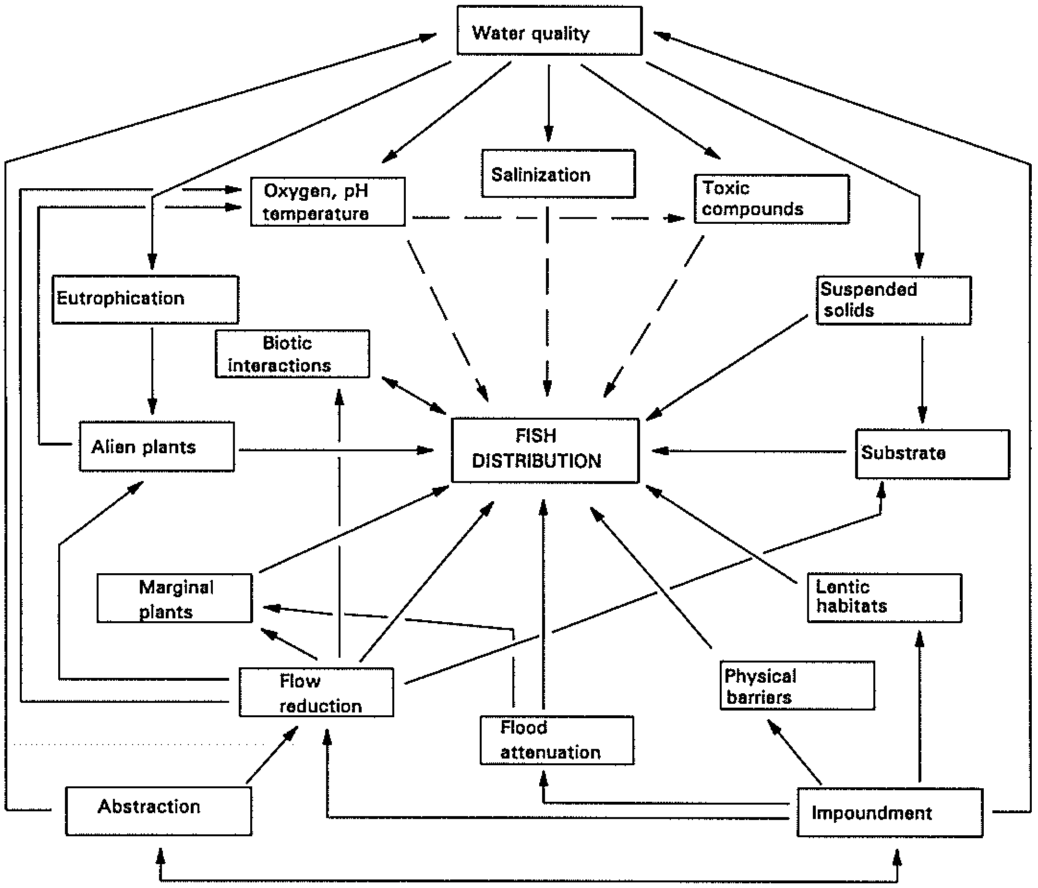


Figure 2.16 Conceptual plan of the major causes of change in the distribution of fish species in the major rivers of the Kruger National Park.

Stippled lines indicate suspected pathways.

perturbations are in force (Harris 1988). Such cumulative effects may be operative in KNP rivers where several perturbations are evident (Figure 2.16), though unfortunately little is known about the cumulative effects of environmental changes on fish communities, either in South Africa, or elsewhere in the world (Moyle and Leidy 1992). Improved understanding of the biological outcome of cumulative effects in KNP rivers is necessary to facilitate identification of the primary causes for species changes, and should be addressed in future research on the environmental tolerances of fish species.

2.3.4 Conservation status of fish communities in KNP rivers

The majority of the environmental changes that can be linked to changes in the distribution of fish species in KNP rivers have resulted from mans development of catchments, namely deterioration in water quality (Olifants and Crocodile); sustained high suspended solid concentrations (Luvuvhu and Letaba); episodic pollution events (Olifants); impoundments creating barriers to fish migration (Letaba, Olifants, Sabie) and changing lotic environments into lentic environments (Letaba); increased severity of low flows (Luvuvhu and Crocodile); and introduction of alien plant species (Sabie and Crocodile). With reference to operational goals outlined in the introduction to this chapter, the observed changes in the distribution of fish species brought about by man-induced environmental changes (section 2.3.3.5) indicate a decline in the conservation status of fish communities in all five major rivers in KNP as discussed below.

Change in the conservation status of fish communities was lowest in the Sabie River. Decreased distribution of the occasional migrants *B. argenteus* and *A. uranoscopus* did not constitute a decline in conservation status (rule viii - section 2.1). There is currently no evidence to suggest that the increased distribution of the several marginal habitat species (*B. annectens, B. eutaenia, B. paludinosus, B. trimaculatus, M. macrolepidotus* and *P. philander*) constitutes a threat to any other species or ecological processes in the Sabie River (rule vi - section 2.1). The decline in the distribution of *B. imberi*, *L. congoro* and *A. aeneofuscus* could not be linked to man induced environmental changes (section 2.3.3.5) (rule iv - section 2.1). The decline in only two fish species in the Sabie River (*H. vittatus, A. marmorata*) indicated a change in the conservation status of fish communities. The degree of change in the conservation status of fish communities in the Sabie River could thus be considered to be minor.

The second lowest degree of change in the conservation status of fish communities was recorded in the Crocodile River. The decline of *A. bengalensis* and *L. rosae* could not be linked to man induced environmental changes (section 2.3.3.5) (rule iv - section 2.1). *Acanthopagrus berda* is a marine species that occasionally occurs in freshwater systems (Skelton 1993). It can at best be considered an occasional migrant into the Crocodile River which is reflected in only one specimen ever being collected within the KNP (Pienaar 1978). That *A. berda* was not recorded in this study (1987-1989) did not constitute a change in the conservation status of fish communities (rule viii - section 2.1). In addition, there is currently no evidence to suggest that the increased distribution of four fish species (*B. radiatus*, *B. viviparus*, *B. paludinosus*, and *T. sparrmanii*) constitutes a threat to any other species or ecological processes in the Crocodile River (rule vi - section 2.1). *Chetia brevis*, however, has been deliberately introduced into impoundments in the Crocodile River catchment (Pienaar 1978), and the collection of this species at sample locality 35 indicated that it has successfully invaded the Crocodile River. The introduction of *C. brevis* can thus, despite its red-data species status (Skelton 1987), be viewed as contributing to the decline in the conservation status of fish communities in the Crocodile River (rule iii - section 2.1). Declines in the distribution of *C. pretoriae*, *C. anoterus*, *L. ruddi* and *S. zambezensis* in the Crocodile River have been linked to man-induced environmental changes (section 2.3.3.5) (rule i - section 2.1). Increased distribution of *S. intermedius* in the Crocodile river could pose a threat to other fish species. *Schilbe intermedius* is omnivorous (Skelton 1993) with adults having a large fish component in their diet (Pienaar 1978), hence an increase in distribution could increase predatory pressures on other fish species. Thus recorded distributional changes of six species contribute to the decline in the conservation status of fish communities in the Crocodile River which could be considered to be moderate.

The highest degree of change in the conservation status of fish communities were recorded in the rivers of the Limpopo system. The majority of species with increased distributions in the Letaba and Olifants rivers do not threaten other species or ecological processes (rule vi - section 2.1). Increased distribution of the omnivorous *S. intermedius* in the Letaba river, however, could as discussed for the Crocodile River above, pose a threat to other fish species. Declines in the distribution of fish species in the Olifants, Letaba and Luvuvhu rivers (with the exception of *C. leucas* in the Luvuvhu River), have been linked to man induced environmental changes (section 2.3.3.5) (rule i - section 2.1). The Bull shark *C. leucas* is a marine species (Skelton

1993), that has been recorded on only one occasion in the Luvuvhu River (U de V Pienaar *pers. comm*). This species can be regarded as an occasional migrant to the lowveld regions of the Luvuvhu River, and little can be deduced from its not having been sampled in recent surveys. Thus recorded distributional changes of eight fish species contribute to the decline in the conservation status of fish communities in the Letaba River, 10 fish species in the Olifants River, and 12 fish species in the Luvuvhu River. The degree of change in the conservation status of fish communities in the three rivers of the Limpopo system could be considered to be major.

Summary and conclusions

In this chapter, a framework for undertaking assessments of the conservation status of fish communities was proposed, and applied to fish in KNP rivers. In so doing, this study has increased the scientific knowledge of the environmental preferences of South African fish species, and quantified the effects of catchment and aquatic changes on the distribution of these species.

The proposed framework is based on established principles for monitoring, which is undertaken to measure the state of the environment and the extent to which it may have been altered (Constable 1991) and hence is orientated to specific targets or goals (Goldsmith 1991; Spellerberg 1991). The framework differs from similar proposals (Spellerberg 1991; Finlayson 1994) in that, rather than simply measuring environmental change, emphasis is placed on identifying the reason(s) for an altered environmental state. The objective of monitoring conservation status is to identify changes from a particular (usually pristine or near pristine) state, which necessitates that the distinction be made between natural and anthropogenic changes. This is particularly relevant in highly variable systems, such as southern African rivers (Alexander 1985; Braune 1985), where environmental variability is likely to have a strong influence on the distribution and abundance of biota (Jowett and Duncan 1990; LeRoy Poff and Allan 1995; Death and Winterbourn 1995).

Many assessments of the conservation status of freshwater fish are loosely based on the IUCN (1980b, 1986) red list categorisation of species (cf. Horwitz 1994; Mrakovcic *et al.* 1995; Rakaj and Flloko 1995; Elvira 1995; Changeux and Pont 1995) with species subjectively described as rare or endangered. Recent revision of the methodology of IUCN red list categorisation (IUCN 1994) has recognised the necessity for removing some of the subjectivity of assessments by quantifying changes, which is synonymous with the operational goals in the proposed framework of this study (Figure 2.3). The IUCN categorisation does not, however, require that the reasons for change be identified. Consequently, natural fluctuations in the abundances or distribution of organisms could, when taken into consideration on a precautionary basis, result in incorrect categorisation and hence lowered confidence in such assessments. The approach adopted in this study of attempting to distinguish between changes resulting from anthropogenic and natural environmental changes should provide a more accurate assessment of the conservation status of species.

Adhering to a logical framework cannot guarantee that a monitoring programme will meet management objectives, but will at least, provide a means of identifying the limits of a programme (Finlayson 1996). Several limits to the approach used in this study for assessing the conservation status of fish in KNP rivers could be identified. These are:

(i) Operational goals for this programme were, in the absence of guidance from managers or comparative studies, subjectively defined by the author. Goals could potentially be altered and improved through wider consultation between managers and scientists.

(ii) Understanding of the extent of natural fluctuations in the aquatic environment (both biotic and abiotic), and how these influence the distribution of fish species, is limited. Consequently assessments of the significance of recorded changes are frequently subjective (Kleynhans 1994). Further study of the environmental preferences of fish species, and responses to changes in the aquatic environment (both natural and anthropogenic) would assist in the removal of some of this subjectivity and facilitate future assessments.

(iii) Finally, no data exist on the distribution of fish in KNP rivers under pristine environmental conditions. Therefore it is not possible to distinguish change from a pristine state, but only from a set historical date. Furthermore, no historical data exists on several aspects of the diversity of communities (such as the relative abundance of species) and populations (age structures and physical condition). Consequently, measuring changes in these aspects of biotic diversity could not be addressed in the evaluation of conservation status of fish communities in KNP rivers. Attempts to overcome these limitations by identifying techniques which are appropriate for monitoring changes in the diversity of fish populations and communities form the basis of discussion in the following chapter.

CHAPTER 3

ESTABLISHING THE CONCEPTUAL AND QUANTITATIVE BASIS FOR MONITORING THE DIVERSITY OF FISH ASSEMBLAGES

3.1 INTRODUCTION

One of the primary goals of this study was to provide guide-lines on a program for monitoring the responses of fish assemblages in KNP rivers to environmental changes. Proposed frameworks for designing monitoring programs (Figures 2.1 to 2.3) have emphasized the importance of undertaking several information gathering and decision making processes (Spellerberg 1991; Hellawell 1992; Usher 1992; Finlayson 1996) before effective and cost-efficient monitoring can commence. These processes include :

(i) Identifying the problems or issues which make monitoring necessary.
(ii) Defining the monitoring objectives.
(iii) Defining what is to be monitored.
(iv) Identifying cost-effective methods of data collection and analyses which can be used to achieve the stated objective.
(v) Defining how the data will be interpreted.
(vi) Defining when monitoring will be terminated.

If these processes are not addressed before monitoring commences, a "monitoring" program would run the risk of becoming a directionless exercise in data collection, with either excessive, inadequate or irrelevant data being collected (Spellerberg 1991), and no predetermined degree of change or means of analysis identified by which to evaluate the significance of recorded changes (Finlayson 1996).

Motivation for the monitoring of fish assemblages in KNP rivers stemmed from concerns about the effects that catchment development has had on the quantity and quality of water and status of aquatic biota (Joubert 1985, 1986a, 1986b). These concerns were strong enough to result in repeated calls for monitoring actions (Ferrar 1989; Bruwer 1991c; Pollard *et al.* 1993). This study has highlighted that catchment development of major rivers flowing through the KNP (sections 1.3.4 to 1.3.8), and resultant water quality and quantity changes, have resulted in changes in the distribution of several fish species (section 2.3.3.5). These observed abiotic and biotic changes serve as further motivation for regular assessment of the effectiveness of conservation actions by determining the achievement of conservation objectives pertaining to the diversity of fish assemblages.

There is currently no official policy defining the objectives for monitoring fish assemblages in KNP river. The management policies of KNP are, however, currently under review, and will detail objectives for monitoring actions (L. Braack *pers. comm.*). The probable objective for monitoring biota in KNP rivers will be "to determine whether biodiversity has been impacted beyond limits of acceptable change, and whether human influence has played a significant role in this" (H. Biggs *pers. comm.*)[9]. As such, a monitoring program could provide a means of detecting incipient (usually undesirable) change in the diversity of fish assemblages to act as an early warning system of deterioration in the aquatic environment. The conceptual framework for biodiversity described by Noss (1990) will serve as the basis for defining measurable indicators (L. Braack *pers. comm.*).

In the context of a monitoring programme of fish assemblages in KNP rivers, defining what should be monitored, and how the data should be collected and analysed (steps iii to iv above) was problematic on two accounts, as described below:

Firstly the wording of existing National Parks Board conservation objectives, which can be paraphrased as "the maintenance of biotic diversity" (section 1.2.2.3), provide no indication of which aspects of biotic diversity should be monitored, what analytical methods should be used, or what degree of change in diversity is considered acceptable (Mentis 1984). The framework for selecting indicators for a biodiversity monitoring project suggested by Noss (1990, 1994) does provide some clarity, in that a large number of potential indicator variables are described. Such lists, however, provide a broad scale perspective to measuring changes in diversity, and tayloring to meet local requirements for cost-effective monitoring is essential (Noss 1990). Little guidance is provided on how to select indicators, other than the emphasis that indicators must fit the objectives for monitoring (Noss 1990). In the context of this study indicators should enable

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[9] H. Biggs, Manager: Biometry, Skukuza, Kruger National Park, South Africa.

assessment of change in the compositional, structural and functional components of fish assemblages.

The second difficulty was the lack of critical evaluation of analytical techniques for monitoring biotic diversity, which results in little guidance being available on which techniques are appropriate. Several texts exist which describe a variety of analytical alternatives for monitoring (Pielou 1975; Clarke 1986; Magurran 1988; Goldsmith 1991; Spellerberg 1991; Aubrecht *et al.* 1994) though provide little or no indication of the applicability of techniques for defining and testing of achievement of objectives pertaining to biotic diversity. Similarly, several accounts have been published which utilized a variety of techniques to describe changes in the diversity of fish assemblages (Bechtel and Copeland 1970; Leidy and Fiedler 1985; Udoidiong 1988; Penczak *et al.* 1995), though evaluation of which techniques are appropriate for monitoring are rare. Consequently, discussion of the applicability of analytical techniques utilised by authors can frequently be difficult (beyond listing which authors utilised which techniques).

The lack of monitoring guide-lines and critical assessment of analytical methods did, however, provide an opportunity to promote understanding of how to monitor diverse fish assemblages through assessment of methods commonly used to describe biotic diversity. Thus the objective of this chapter is to advance the science of monitoring diverse fish assemblages by identifying methods of data collection, analysis and interpretation that would be appropriate for assessing the achievement of conservation objectives (points iii to v above). Associated problems, and the approaches adopted to overcome these problems are introduced below. Deciding when monitoring should be terminated (point vi above) was not specifically tested using empirical data, though is addressed in the general discussion of this study.

With respect to defining what is to be monitored (question iii), the aspects of biotic diversity of fish assemblages which could practically be measured in a cost-effective monitoring programme have been reviewed in section 1.2.2.4, though for the purpose of clarity are also summarised here. Biodiversity consists of several frequently interrelated, aspects (Whittaker 1972, 1977; Peet 1974; Cody 1975; Noss 1990), namely the structural, compositional and functional attributes of genes, populations, communities and landscapes. As this study deals with the monitoring of fish assemblages the aspect of landscape or ecosystem diversity is not dealt with directly, beyond identification of landscape processes and disturbances which potentially influence the diversity of fish assemblages. Direct measurement of the structural diversity of communities and genetic diversity were considered beyond the scope of this study because of the complexity and expense of determinative methodologies (Mentis 1984; Noss 1990). This study thus emphasized the compositional and structural diversity of fish populations and communities.

The question of which analytical techniques to employ has been complicated by the wide range available, particularly indices for quantifying the diversity of communities (Whittaker 1977; Magurran 1988). It would be unrealistic to apply all available methods in a cost-effective monitoring programme, and rationalization by selection of a few analytical methods would be required (Finlayson 1996). The selected methods must fit the purpose of the monitoring programme (Hellawell 1992), namely the testing of the achievement of conservation objectives. Consequently the results must be interpretable and there must be clear operational goals to test the significance of changes (Spellerberg 1991; Finlayson 1996). In this study, choice of analytical methods was undertaken in two phases. Preliminary choices were made on the basis of the limitations and advantages of various techniques, as discussed in the literature (section 1.2.2.4), with the methods selected being:

(i) Population diversity
    - Length frequency distribution
    - Condition factors

(ii) Community diversity
    - Informal descriptions of species abundance changes
    - Diversity indices (Berger-Parker, log-series-α)
    - Fitting of abundance distribution models
    - Ordinations (ß-diversity)

Secondly, the use of selected analytical methods for quantifying biotic diversity was evaluated to determine how monitoring of fish assemblages in KNP rivers should be undertaken. Evaluation criteria used were whether:

(i) Results generated from the methodology were interpretable in that they provided a clear and plausible indication of change in the diversity of fish assemblages (Spellerberg 1991; Finlayson 1996).

(ii) Operational goals could be defined in such a way that they enabled clear and unambiguous assessment of the significance of change in biotic diversity, indicated by the non-achievement of a specified state or set of criteria (Goldsmith 1991; Finlayson 1996).

(iii) The method was cost-effective (Hinds 1984; Wolfe *et al.* 1987; Spellerberg 1991) in that understanding gained of change in the diversity of populations and communities outweighed the cost and effort involved in data collection and analysis.

Three approaches were used to evaluate the interpretability of survey results, depending on the availability of comparative data. Firstly, recorded changes in biotic diversity were compared to expected changes concluded from comparing changes in the aquatic environment with the environmental preferences of fish species (section 2.3.2). Secondly, informal descriptions of species abundance changes were used to describe directional changes in the diversity of fish assemblages between 1987 and 1989, which were in turn used as a yardstick against which the interpretability of results from methods of quantifying alpha diversity were evaluated. No such yardstick based on actual measurement and description of species abundances was available for the evaluation of measures of beta diversity because of an inability to subjectively describe beta diversity changes simply by viewing data sets. Therefore, the third approach entailed use of simulated data sets depicting hypothetical changes in the species composition of samples. The interpretability of results was thus undertaken by comparing indicated changes in beta diversity against expected results for samples of known species compositional changes.

The need for achievable, auditable goals in conservation has been emphasized by several environmental managers and scientists (Mentis 1989; Blackmore 1995; Centre for Water in the Environment 1996). Goals pertaining to the diversity of riverine systems in the KNP are currently being developed (L. Braack *pers. comm.*), and will likely be worded as "to ensure the intrinsic attributes and role of each river as a part of landscape diversity, in such a way as to allow natural functioning over space and time in structure, function and composition" (H. Biggs *pers. comm.*). To be of value such a goal must be both measurable and achievable (Richards 1986; Mentis 1989). Goals thus need to translated into operational terms which define the limits of acceptable change (Mentis 1984).

Operational goals pertaining to the diversity of fish assemblages in KNP rivers have never been defined, and few references could be located which indicate how this could be undertaken. "Species richness lines" and "maximum density lines" depicting the species richness and abundance as a function of catchment area, have been used in several studies (Fausch *et al.* 1984; Miller *et al.* 1988; Oberdorff and Hughes 1992) in an attempt to define expected species richness and abundance. Their primary failings, however, are that they will invariably have to be compiled using data from already degraded systems thereby biasing diversity estimates, and fail to distinguish between the effects of natural and anthropogenic disturbances. Data for the compilation of species richness and density lines for fish assemblages in KNP rivers is, in any event, not available. Such methods also fail to address several aspects of diversity, such as the relative abundance of species and the structural diversity of populations. The absence of suitable methods for defining operational goals necessitated the independent selection and application of three different approaches, as discussed below.

The first approach could probably be best described as being reliant on "basic biological principles" in that goals are based on established cause and effect relationships rather than on untested hypotheses or historical data. For example, a goal could be to not have declining populations, which are often characterised by a large proportion of old individuals (Odum 1971). Thus in an evaluation of the age distribution of a population, an operational goal would be that a large proportion of the population must consist of 0+ year-old individuals. Such an age distribution would indicate successful breeding and/or recruitment during the period under review.

The second approach used scientific theory on topics such as niche competition and resource partitioning (Whittaker 1970, 1972; May 1975), as a basis for predicting the abundance relationships of species under different environmental conditions. Thus the diversity abundance models which should theoretically best describe species abundance patterns in both environmentally perturbed and unperturbed rivers could be defined and tested.

The third approach entailed the use of comparisons of diversity measurements of one or more communities from rivers which are relatively pristine (for example the Sabie River - see section 1.3.7) and hence acceptable diversity, relative to heavily perturbed rivers (for example Letaba and Luvuvhu rivers - see sections 1.3.4 and 1.3.5) where biotic diversity would be expected to be unacceptably low.

A potential fourth means of goal determination would have been the use of historical data describing past diversity fluctuations under unperturbed environmental conditions. However, few data are available on the abundance of fish in unperturbed rivers (Cambray *et al.* 1989; Davies *et al.* 1993) and none are available for fish species in KNP rivers. Consequently in this study reliance was placed on the former three methods of goal determination.

Evaluation of the cost-effectiveness of analytical methods was, because of the absence of standardised procedures (Spellerberg 1991), essentially a subjective value judgement. Factors taken into consideration were the ease of data collection (for example sample size required to describe or quantify biotic diversity) and analysis in relation to the likely gains in understanding of the direction, extent and causes of change in the diversity of fish assemblages.

For each evaluation of an analytical method, it was necessary to firstly describe the changes that had occurred in the diversity of fish populations or communities, and secondly to compare these findings against either hypothesized, measured or hypothetical changes in diversity, to enable evaluation of the interpretability of results. The sequencing of descriptions of the diversity of fish assemblages in the text (informal descriptions of change in species abundances; length frequency distribution; α-diversity indices; α-diversity models; condition factors; ß-diversity ordinations), each with a separate results and discussion section, was intended to facilitate comparisons between descriptions of change in biotic diversity using different analytical techniques, and hence evaluations of the interpretability of results.

3.2 MATERIALS AND METHODS

3.2.1 Sampling of fish communities

Field techniques used to collect fish samples were described in section 2.2.1.2. The number of individuals of all species captured was recorded. The different sampling intensities used at different sites necessitated the use of catch per unit effort (CPUE) values for assessments of changes in the abundances of species and community diversity. Unit effort values were defined as 10 seine net pulls in deep pools, 60 minute electro-fishing in marginal areas, and 60 minute electo-fishing in rapids. Species abundance data was used to calculate diversity indices and abundance models (community composition diversity).

The fork length of all specimens was measured to the nearest millimetre with the specimen laid flat on a measuring board. Specimens less than 330g total wet body mass were weighed to the nearest 0.01g on a portable electronic balance (Sartorius Model PT200). Specimens heavier than 330g were weighed to the nearest 10g on a 25kg capacity spring balance. Fork length measurements were used to describe the length frequency distribution of populations, and both fork length and body mass were used to calculate the mean physical condition of populations (population structural diversity).

3.2.2 Descriptions of fish assemblage diversity

Analyses were undertaken to describe change in the diversity of fish populations (length frequency distribution; condition factors) and communities (alpha-diversity; beta-diversity). Both diversity indices and the fitting of frequency abundance models were used to define alpha-diversity of fish communities.

Several studies have illustrated that the diversity of biotic assemblages increases with sample size (Green 1979; Grieg-Smith 1983). Sample size can thus influence the ability to accurately define the compositional diversity of communities (Magurran 1988) and the length frequency distribution of fish populations (Lagler 1978). Consequently, analytical methods also included determination of minimum sample size for evaluation of the length frequency of populations and description of community diversity.

3.2.2.1 Length frequency distribution of fish populations

- *Minimum sample size needed to describe the length frequency of fish populations.*

Determination of the minimum sample size for description of the length frequency distribution of fish populations was undertaken using *L. rosae*, *M. acutidens* and *O. mossambicus* as test species. Three species were used to test the effect of body size on minimum sample size, with *L. rosae* representing a physically large species, *M. acutidens* a physically small species, and *O. mossambicus* a species of intermediate adult length. Both 5mm and 10mm length classes were used to describe the length frequency of *O. mossambicus* to test the effect of the size of the length classes used to describe the length frequency distribution of a species on minimum sample size.

The procedure used followed that of Mentis (1986) of establishing the dependence of replicate similarity on sample size. For each species a random number generator was used to select ten sets of N individuals. This was repeated for N = 25, 50, 100, 125, 150, 175, 200, 250, 300, 350, and 400. For each ten sets of N individuals, percentage sample similarity was calculated for each set with every other set, using the formula below, to produce a 10 x 10 similarity matrix.

$$PSjk = \frac{200 \mathop{E}\limits_{i-1}^{I} \min(Aij,Aik)}{\mathop{E}\limits_{i-1}^{I} (Aij + Aik)}$$

where I = summation over all samples I
Aij = abundances of samples i in sample j
Aik = abundances of samples i in sample k

For each similarity matrix the mean sample similarity was calculated, and plotted on a Number of Point-observations (N) versus Replicate Similarity (RS) graph. Due to the non-independence of data in the similarity matrices, the focus of attention was on mean similarity values rather than their variances. Minimum sample size was determined by subjectively assessing the highest value of N beyond which replicate similarity was no longer improved.

Measurement of length frequency distribution of fish populations

Length frequency distribution graphs of fish species, for which sample size from a river exceeded the calculated minimum, were constructed to enable evaluation of the structural diversity of populations. Modal lengths were described subjectively. Where possible, age classes were assigned to modal lengths by referring to available literature on the growth rate of fish. The occurrence and relative abundance of different age classes was used to describe the age structure of populations.

3.2.2.2. Description of fish community alpha-diversity using diversity indices

Minimum sample size needed to describe fish community alpha-diversity using diversity indices.

The pooled quadrat method (Pielou 1975) of calculating minimum sample size for accurately determining a mean (Grieg-Smith 1983; Gauch 1984) was used to determine sampling intensity required to quantify alpha-diversity of fish communities in KNP rivers. This method was selected because there is no assumption that species occurrences and sample locations are randomly distributed, in contrast to other methodologies which mostly entail a decision on sample size based on a desired confidence level, and hence are based on the assumption of randomised sample collection (Gauch 1984). This was necessary as sample localities used in this study were judgementally selected (section 2.2.1.1)

Diversity curves were constructed using five diversity indices (Margaleff, Shannon, Simpson, Berger-Parker, log-series-α), with index values calculated from the successive summing of N (number on individuals) and S (number of species) values from randomly ordered sampling units (seine net pull in deep pools; minutes electro-fishing in rapids and marginal areas). Diversity curves were subjectively assessed for the cessation of large oscillations, indicating the point where further observations would not greatly increase the accuracy of the mean, hence indicating minimum sample size (Grieg-Smith 1983).

Magurran (1988) has suggested that the construction of diversity curves be undertaken using data from the most diverse sites, where minimum sample size is likely to be highest. Therefore, data used for the construction of diversity curves were obtained from the intensively sampled, species rich communities in deep pools in the Letaba River, and marginal habitats and rapids in both the Sabie and Olifants rivers.

Formulae used for the calculation of diversity indices were as follows (formulae obtained from Magurran (1988) and Southwood (1980)):

(i) Margaleff diversity index (D_{Mg})

$D_{Mg} = (S-1)/\ln N$

where S = number of species
N = number of individuals

(ii) Shannon diversity index (H')

$H' = -\Sigma p_i \ln p_i$

where p_i = proportional abundance of the *i*th species = (n_i/N)

(iii) Log-series diversity index (α)

$$\alpha = \frac{N(1-x)}{x}$$

where x is a constant determined by iterating the term:
$S/N = [(1-x)/x][-\ln(1-x)]$
and S = number of species
N = number of individuals

(iv) Berger-Parker diversity index (d)

$d = N_{max}/N$

where N = total number of individuals

N_{max} = number of individuals in the most abundant species.

(v) Simpson diversity index (1/D)

$$D = \Sigma \frac{(n_i(n_i-1))}{(N(N-1))}$$

where n_i = number of individuals in the *i*th species

N = total number of individuals

The reciprocal of Simpson's index (1/D) was adopted so that, as with other indices, calculated index values increased with increasing diversity.

Alpha-diversity indices

A large variety of diversity indices have been proposed in the literature based on the proportional abundance of species (Southwood 1980). These indices are widely used as simple means of comparing community alpha-diversity (Bechtel and Copeland 1970; Gorman and Karr 1978; Udoidiong 1988; Penczak *et al.* 1995). Diversity indices can be divided into two categories, the first derived from information theory, which emphasize species richness, and the second classed as dominance indices which emphasize the relative abundance of species (Magurran 1988).

Alpha-diversity of fish communities in the KNP rivers in different surveys (Winter 1987, Summer 1987/88, Winter 1988, Winter 1989) was initially described using values of the number of species (S), number of individuals (expressed as CPUE), Margaleff, Shannon, Simpson Berger-Parker and log-series-α indices (using formulae detailed in section 3.2.2.2.), as well as the log-normal and Shannon evenness indices using the formulae described below (formulae obtained from Southwood (1980) and Magurran (1988)):

(i) Log-normal diversity index (Ln)

$$Ln = S^*/\sigma$$

where $\sigma = \sqrt{\Sigma(x-x^i)^2/S)}$
$S^* = S/(1-p_o)$

p_o is read off a table giving the area under a normal curve, and represents the unsampled species in the community, that is, species to the left of the veil line. To determine this value the value of Z_0 must be known:

where $Z_0 = (x_0-\mu_x)/\sqrt{V_x}$
$\mu_x = x^i - \Theta(x^i-x_0)$
$V_x = \sigma^2 + \Theta(x^i-x_0)^2$

Θ is read off Cohen's table for truncated log-normal using the value of y where:

$y = \sigma^2/(x^i-x_0)^2$
$x = \log_{10}$ of each species abundance
x^i = mean of species abundances ($x^i = \Sigma x/S$)
$x_0 = \log_{10}$ of upper boundary of zero abundance class
S = number of species

(ii) Shannon evenness (E)

$E = H'/\ln S$

where H' = Shannon diversity index
S = number of species

However, differences were observed in the magnitude and direction of community diversity change indicated by different indices which are theoretically supposed to emphasise the same aspects of alpha diversity. This highlighted the necessity for rationalisation of the number of indices used to explore changes in community diversity. Only indices, the theoretical properties of which are well known, were selected, and these included the log-series-α index as a measure of species richness, and the Berger-Parker index as a measure of dominance/evenness, together with measures of the total number of species and individuals sampled.

3.2.2.3 Description of fish community alpha-diversity using diversity models

Two methods of exploring the fit of community abundance data to the geometric-series, log-series, log-normal and broken-stick abundance distributions were undertaken - visual inspection of rank abundance plots (Whittaker 1965, 1972), and comparisons of observed and expected abundances using X^2tests (Magurran 1988). Two methods were used as each method, when used individually, has been criticised on its ability to provide a clear distinction between competing species abundance models (Magurran 1988). The chief criticism of rank abundance plots is that decisions as to the fit of competing models are subjective (Magurran 1988). Goodness of fit tests are criticised for invariably being carried out on only a small number of abundance classes, whereas the differences between models can lie in the way they allocate species between two or three classes (Hughes 1986). This drawback has resulted in certain workers having rejected the use of goodness of fit tests, and relying entirely on graphical inspection (Lambshead and Platt 1985; Hughes 1986). Although visual inspection of species abundance data, and in particular graphs of log abundance on rank, is frequently considered a valuable tool for interpretation of results (Southwood 1980), goodness of fit tests have also been retained in this study because, as Magurran (1988) points out, the best solution to the problem will in almost all cases be to interpret results using both methodologies.

Rank abundance plots

Whittaker (1965, 1972) has been one of the chief exponents of using rank abundance plots for exploring species abundance relationships. In this technique, a measure of species abundance is plotted against species sequence from the most abundant to the least abundant. Problems do however exist with deciding exactly how the data are presented, with the various types of plots highlighting aspects of the data which the ecologist may wish to emphasise (Magurran 1988). In general, investigators of the geometric-series distribution usually use straight rank/abundance plots (May 1975), whereas proponents of the log-series distribution tend to favour a frequency distribution in which numbers of species is plotted against number of individuals per species (Magurran 1988). A similar plot is used, but with the x axis on a log scale when the log-normal is chosen (Preston 1962), whereas when the broken-stick model is under investigation a rank/abundance plot in which the ranks but not the abundances are logged is generally adopted (King 1964). Whittaker (1972) considered a logarithmic scale of abundance to be the most useful, because when plotted in this way, the geometric distribution is linear whereas the log-series, log-normal and broken-stick are sigmoid though are progressively flatter (Figure 3.1), thus facilitating distinction of the different abundance distributions. Consequently, the log abundance method of data presentation (Whittaker 1972) was selected for this study as the objective was to identify which model best described abundance distribution data. Species abundance (logarithmic scale) from different rivers and surveys was plotted against species sequence from the most to the least abundant species. Visual comparison of the shape of the resultant curves against rank abundance plots illustrating the typical shape of four species abundance models (Figure 3.1) indicated the type of species-abundance relationship present, with the slope of the upper parts of the curves indicating the degree of numerical dominance.

Expected species abundances using abundance models

Calculation of the expected species abundances in different communities from different rivers and surveys, according to the geometric-series, log-series, log-normal and broken-stick abundance models, were undertaken following the procedures described by Magurran (1988). For all abundance models, observed species abundances were allocated to Log_2 abundance classes and hence expected abundances calculated for such classes. Upper boundaries of abundance classes used were 5, 10, 20, 40, 80, 160, 320, 640, 1280, 2560 and 5120 for communities in deep pools, and 4, 8, 16, 32, 64, 128, 256, 512, 1024 and 2048 for fish communities in rapids and marginal habitats. Larger size classes were used for fish communities in deep pools on account of the greater number of individuals sampled. Different sampling effort employed at different sample sites necessitated the use of catch per unit effort values, with species abundances of communities sampled in deep pool standardised to 10 seine net pulls, and in rapids and marginal habitats to 60 minutes electro-fishing. Formulae used for the calculation of expected abundances were as follows (formulae obtained from Magurran (1988)):

(i) Geometric-series.

$$n_i = NC_k k(1-k)^{i-1}$$

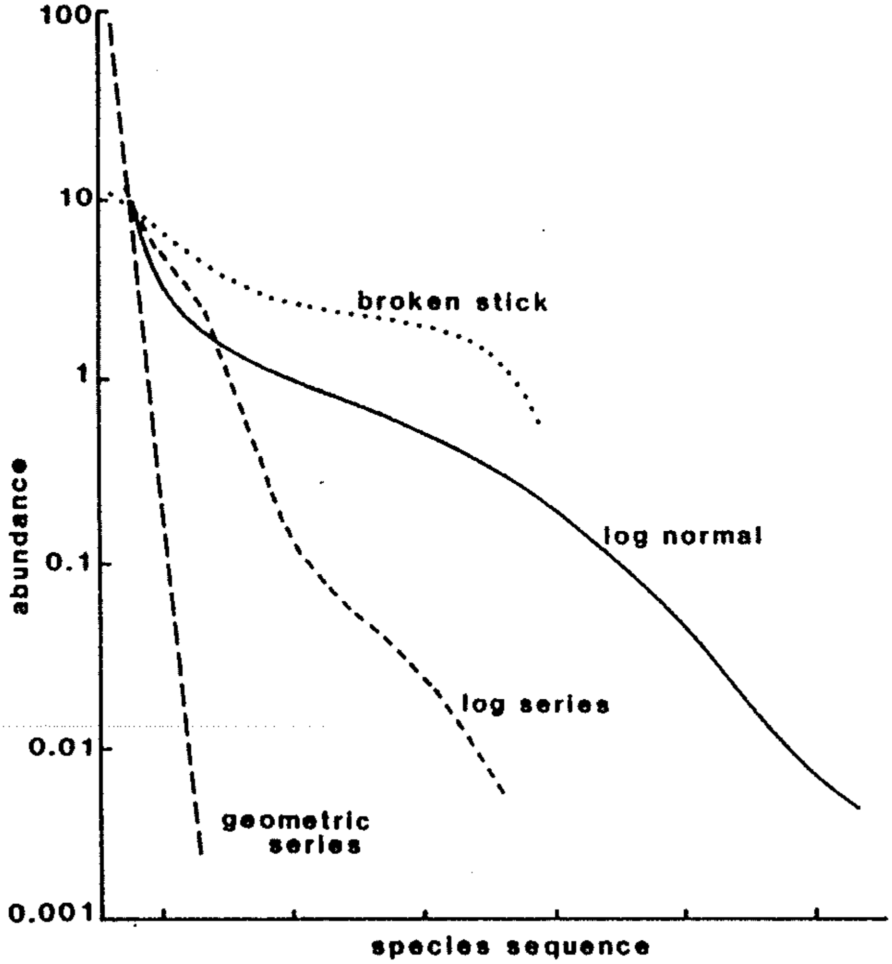

Figure 3.1 Rank abundance plots illustrating the typical shape of four species abundance models: geometric-series, log-series, log-normal and broken-stick (redrawn from Magurran 1988).

Where n_i = the number of individuals of the ith species
N = the total number of individuals
$C_k = [1-(1-k)^S]^{-1}$ constant where S = number of species
k = is equivalent to the available niche space or resource that each species occupies and is obtained from solving the problem:
$N_{min}/N = [k/(1-k)][(1-k)^S]/[1-(1-k)^S]$
where S = number of species

(ii) Log-series

αx, $\alpha x^2/2$, $\alpha x^3/3$ .... $\alpha x^n/n$ with αx being the number of species with one individual, $\alpha x^2/2$ the number of species with two individuals, $\alpha x^3/3$ the number of species with three individuals, etcetera.

Where x = constant, calculated by iterating the term:
$$S/N = [(1-x)/x][-\ln(1-x)]$$
Where S = total number of species
N = total number of individuals
$\alpha = [N(1-x)/x]$

(iii) Truncated log-normal

For the purpose of clarity, the calculations for determination of expected number of species under a truncated log-normal distribution are given in the order in which they were undertaken.

(a) Species abundances logged ($x = \log_{10} n_i$)
(b) Mean of log species abundances ($x^i = \Sigma x/S$) where S = total number of species
(c) Variance of log species abundances ($\sigma^2 = \Sigma(x-x^i)^2/S$)
(d) $y = \sigma^2/(x^i-x_o)^2$ where $x_o = \log 0.5$
(e) Cohen's (1961) table for the 'auxiliary estimation function' used to determine the value of Θ using value of y.
(f) $\mu_x = x^i-\Theta(x^i-x_o)$
(g) $V_x = \sigma^2+\Theta(x^i-x_o)^2$
(h) $z_o = (x_o-\mu_x)/\sqrt{V_x}$ Standard normal variate

(i) The standard normal variate z_o was used in conjunction with tables giving the area under a normal curve to find the value p_o which represents the species to the left of the veil line, that is, the unsampled species in the community.

(j) $S^* = S/(1-p_o)$ Total number of species in community

(k) Log_{10} of each upper class boundary (Log 0.5, Log 5, Log 10, Log 20, etcetera)

(l) Standardised form of each logged upper class boundary [logged upper class boundary value-μ_x]/$\sqrt{V_x}$

(m) Standardised form of logged upper class boundary values used in conjunction with tables giving the area under a normal curve to find the values p_o which multiplied by S^* give expected total number of species.

(n) Differences between successive totals provide expected number of species in each abundance class.

(iv) MacArthur's broken-stick

The number of species expected to have one individual, two individuals etcetera, was undertaken using the following formula:

$$S(n) = [S(S-1)/N](1-n/N)^{S-2}$$

Where $S(n)$ = number of species in abundance class with n individuals
S = total number of species
N = total number of individuals
n = number of individuals in abundance class

Significance of difference between the number of observed and expected species in different abundance classes was determined, for all abundance models, using the X^2 goodness of fit test. For each class, X^2 was calculated, where X^2 = (observed-expected)^2/expected, with classes-1 degrees of freedom for the geometric, log-series and broken-stick models, and classes-2 degrees of freedom for the log-normal model.

3.2.2.4 Physical condition of species

Several methods have been described and used in the literature to enumerate or display, and hence compare condition of fish. Brief descriptions of the more commonly used methods as well as reasons for their being considered unsuitable for use in this study are given below:

(i) The most widely used condition factor is possibly that proposed by Le Cren (1951) ($CF = M/cL^n$; M = mass, L = length, c and n = regression constants determined for the species under 'standard' conditions). Modifications of this allometric condition factor have been proposed (Schoonbee *et al.* 1972; Baird and Fourie 1978) entailing use of different c and n constants for different age groups. These indices, although eliminating the effect of length and correlated factors on condition, were rejected for use in this study as they do not enable direct comparison between groups where different c and n constants are applied. Thus comparison of condition of species from different surveys would not be possible unless the same constants were applied, which, in view of the observed variability in these constants in different survey years (Tables 3.1a to 3.1e), would negate the proposed benefits of the methodology.

(ii) Le Cren (1951) maintained that where it can be shown that the value n from the regression $\log M = \log c + n \log L$ is the same for two groups of fish, the value of "c" obtained from separate length-mass regressions calculated for each group would be a direct measure of their condition relative to each other. The variability of different "n" values computed for the different species in different years (Tables 3.1a to 3.1e) precluded the use of this methodology in this study.

(iii) Direct plotting of the length-mass regression has also been used as a means of displaying change in physical condition (White *et al.* 1984). This method was attempted in this study though was later rejected on the basis of the graphs being difficult to interpret, particularly when regression lines overlapped one another.

(iv) Kenmuir (1973) assessed condition in *H. vittatus* by calculating the mean mass of fish falling within selected length groups. This method was

Table 3.1a Regression analysis constants, from regression of fork length versus wet body mass, for fish collected in the Luvuvhu River during Winter 1987, 1988 and 1989 surveys.

	Winter 1987		Winter 1988		Winter 1989	
Species	Log c	n	Log c	n	Log c	n
Barbus afrohamiltoni	-5.27822	3.254058	-5.22331	3.247169	-	-
Barbus radiatus	-	-	-	-	-4.28345	2.647084
Barbus viviparus	-	-	-	-	-5.52801	3.418957
Brycinus imberi	-4.99085	3.119688	-5.74465	3.513562	-4.81770	3.022973
Chiloglanis paratus	-	-	-5.67561	3.215001	-5.37908	3.299362
Chiloglanis pretoriae	-	-	-	-	-4.80318	2.957519
Clarias gariepinus	-5.13171	3.007328	-4.44379	2.747942	-4.39152	2.668357
Glossogobius spp.	-4.92940	2.932848	-4.67226	2.790551	-5.05282	2.968290
Hydrocynus vittatus	-	-	-4.85310	3.008421	-4.97343	3.039435
Labeo cylindricus	-	-	-	-	-5.04613	3.107064
Labeo molybdinus	-	-	-	-	-5.01082	3.103699
Labeo rosae	-	-	-4.97163	3.101430	-4.79406	2.987930
Micralestes acutidens	-5.18827	3.205824	-4.96326	3.056041	-4.99078	3.074627
Oreochromis mossambicus	-4.76021	3.028725	-4.90605	3.091761	-4.84241	3.041478
Schilbe intermedius	-5.08328	3.048564	-5.43106	3.220748	-	-
Synodontis zambezensis	-	-	-4.33483	2.827920	-3.97556	2.595543
Tilapia rendalli	-4.52488	2.920772	-	-	-4.64246	2.975026

Table 3.1b Regression analysis constants, from regression of fork length versus wet body mass, for fish collected in the Letaba River during Winter 1987, 1988 and 1989 surveys.

	Winter 1987		Winter 1988		Winter 1989	
Species	Log c	n	Log c	n	Log c	n
Barbus afrohamiltoni	-4.94883	3.067939	-5.21496	3.225712	-5.14093	3.168392
Barbus marequensis	-	-	-	-	-5.28833	3.232325
Barbus radiatus	-4.87279	2.998415	-4.99702	3.075706	-5.00389	3.103193
Barbus toppini	-5.15557	3.135749	-4.82782	2.936911	-5.15062	3.138156
Barbus trimaculatus	-5.12380	3.127142	-5.23269	3.195225	-4.99194	3.063492
Barbus unitaeniatus	-5.05467	3.092431	-5.24340	3.186997	-4.82463	2.950400
Barbus viviparus	-	-	-4.73001	2.889678	-4.72151	2.885271
Brycinus imberi	-4.82595	3.006457	-5.35835	3.299939	-4.77622	2.993548
Chiloglanis paratus	-	-	-	-	-3.47261	2.148103
Clarias gariepinus	-5.43063	3.101586	-5.21976	3.015670	-	-
Glossogobius spp.	-	-	-4.87659	2.858284	-4.61350	2.709041
Hydrocynus vittatus	-4.55739	2.841183	-5.30439	3.196790	-	-
Labeo cylindricus	-5.02992	3.094184	-5.34842	3.261587	-5.20906	3.196075
Labeo molybdinus	-5.11279	3.134741	-5.31656	3.247867	-4.95692	3.073272
Labeo rosae	-4.94230	3.056003	-4.97491	3.067508	-4.90698	3.045268
Labeo ruddi	-4.93543	3.030132	-4.89684	3.014995	-4.88560	3.012843
Marcusenius macrolepidotus	-	-	-4.72283	2.898999	-4.22228	2.669126
Mesobola brevianalis	-3.96753	2.351283	-5.50069	3.273995	-4.71083	2.879223
Micralestes acutidens	-	-	-	-	-4.75675	2.930165
Oreochromis mossambicus	-4.79103	3.016752	-4.73219	2.987397	-4.74916	2.997918
Schilbe intermedius	-5.22958	3.094871	-5.21870	3.089982	-5.16919	3.055023
Tilapia rendalli	-4.98750	3.054709	-	-	-4.89993	3.108209

Table 3.1c Regression analysis constants, from regression of fork length versus wet body mass, for fish collected in the Olifants River during Winter 1987, 1988 and 1989 surveys.

	Winter 1987		Winter 1988		Winter 1989	
Species	Log c	n	Log c	n	Log c	n
Barbus marequensis	-5.12508	3.143892	-5.09768	3.141379	-5.00971	3.096160
Barbus paludinosus	-	-	-3.66587	2.298251	-	-
Barbus toppini	-	-	-5.61343	3.443224	-	-
Barbus trimaculatus	-	-	-5.31108	3.236070	-5.26846	3.217733
Barbus viviparus	-4.78250	2.926400	-4.53236	2.767104	-4.95095	3.038258
Chiloglanis paratus	-4.32318	2.693950	-4.48520	2.789791	-4.45975	2.772877
Chiloglanis pretoriae	-4.22442	2.663924	-	-	-4.91389	3.075438
Chiloglanis swierstrai	-	-	-	-	-5.85484	3.566905
Clarias gariepinus	-5.21147	3.004590	-5.21446	3.025701	-4.49334	2.723361
Labeo congoro	-	-	-5.51037	3.321236	-	-
Labeo cylindricus	-5.08061	3.131972	-4.83293	2.989228	-5.37314	3.278353
Labeo molybdinus	-4.98548	3.095055	-5.15092	3.178713	-5.14063	3.175068
Labeo rosae	-4.80006	2.990970	-5.11840	3.151763	-	-
Marcusenius macrolepidotus	-	-	-4.68797	2.899256	-	-
Oreochromis mossambicus	-4.79179	3.018700	-4.97375	3.109906	-4.89189	3.068594
Petrocephalus catostoma	-	-	-4.65302	2.892391	-	-
Synodontis zambezensis	-	-	-5.31548	3.313603	-	-

Table 3.1d Regression analysis constants, from regression of fork length versus wet body mass, for fish collected in the Sabie River during Winter 1987, 1988 and 1989 surveys.

	Winter 1987		Winter 1988		Winter 1989	
	Log c	n	Log c	n	Log c	n
Barbus afrohamoltoni	-	-	-	-	-4.79562	3.002630
Barbus annectens	-4.75542	2.940178	-4.68552	2.860000	-4.73000	2.910130
Barbus eutaenia	-	-	-	-	-4.97789	3.067029
Barbus marequensis	-4.97681	3.078139	-5.08879	3.143637	-5.16103	3.164812
Barbus radiatus	-4.92427	3.062658	-4.85888	2.991636	-4.91896	3.043882
Barbus trimaculatus	-5.09387	3.142569	-5.25633	3.215906	-5.14102	3.140475
Barbus unitaeniatus	-	-	-	-	-4.95116	3.020907
Barbus viviparus	-4.38152	2.699588	-4.59976	2.832636	-4.97152	3.032209
Brycinus imberi	-4.95844	3.086326	-5.08845	3.157555	-	-
Chiloglanis anoterus	-	-	-	-	-3.57052	2.214277
Chiloglanis paratus	-4.80238	2.982741	-4.83322	2.965195	-4.83754	2.965391
Chiloglanis swierstrai	-4.99167	3.016076	-5.57800	3.353865	-5.08363	3.017943
Glossogobius spp.	-	-	-	-	-4.54288	2.676195
Labeo cylindricus	-5.00798	3.105577	-5.13040	3.159656	-5.03253	2.957462
Labeo molybdinus	-5.11736	3.159819	-5.09790	3.149675	-5.11575	3.158062
Marcusenius macrolepidotus	-4.82568	2.956082	-4.49679	2.808620	-4.74637	2.908115
Mesobola brevianalis	-4.95942	2.946867	-5.31221	3.154581	-5.66715	3.342901
Micralestes acutidens	-4.72443	2.910722	-4.74629	2.905290	-5.03943	3.093579
Opsaridium zambezense	-5.65836	3.419032	-	-	-4.87309	2.922834
Oreochromis mossambicus	-5.02795	3.146810	-5.20699	3.233150	-4.92610	3.082339
Petrocephalus catostoma	-	-	-4.57843	2.873664	-4.81456	2.996039
Pseudocrenilabrus philander	-5.06320	3.134322	-5.20466	3.224047	-5.11591	3.157988
Serranochromis meridianus	-4.77342	2.922526	-5.33692	3.213446	-4.89504	2.988636
Tilapia rendalli	-5.03982	3.179934	-5.12147	3.217420	-5.06510	3.181431

Table 3.1e Regression analysis constants, from regression of fork length versus wet body mass, for fish collected in the Crocodile River during Winter 1987, 1988 and 1989 surveys.

	Winter 1987		Winter 1988		Winter 1989	
Species	Log c	n	Log c	n	Log c	n
Barbus marequensis	-5.02458	3.104593	-5.10630	3.146866	-5.15422	3.165190
Barbus paludinosus	-	-	-5.87405	3.544720	-	-
Barbus radiatus	-	-	-5.15640	3.201547	-	-
Barbus trimaculatus	-5.45549	3.311572	-5.01256	3.085618	-5.17939	3.175737
Barbus unitaeniatus	-5.05750	3.105326	-	-	-5.52142	3.372031
Barbus viviparus	-5.13515	3.159253	-4.91094	3.009586	-5.26183	3.246143
Chiloglanis paratus	-4.74974	2.891890	-4.20826	2.628525	-4.98690	3.074678
Chiloglanis swierstrai	-	-	-	-	-5.33380	3.215025
Clarias gariepinus	-	-	-5.27686	3.062836	-	-
Labeo cylindricus	-5.09106	3.143365	-5.06075	3.129760	-5.20967	3.198433
Labeo molybdinus	-	-	-	-	-5.11351	3.161602
Marcusenius macrolepidotus	-	-	-	-	-4.74438	2.935563
Mesobola brevianalis	-	-	-	-	-5.22216	3.136032
Mesobola brevianalis	-5.10363	3.089324	-	-	-	-
Micralestes acutidens	-4.95313	3.068563	-5.09740	3.132678	-5.23905	3.226430
Opsaridium zambezense	-	-	-4.99628	3.023036	-	-
Oreochromis mossambicus	-5.09682	3.181289	-5.19424	3.262137	-5.03728	3.158280
Pseudocrenilabrus philander	-5.09369	3.169300	-5.37439	3.313862	-5.23773	3.240926
Schilbe intermedius	-	-	-5.40071	3.247148	-4.95313	2.975963
Tilapia rendalli	-5.10809	3.218025	-5.00837	3.167949	-5.03127	3.185512

rejected in this study as difficulty was experienced for several species in identifying suitable length groups in which sufficient individuals were regularly collected for accurate analysis of mean mass.

To avoid some of the many pitfalls encountered when using condition factors (see points i to iv above), a method based on Fulton's condition factor (w/l^3; w = weight, l = length) (Fulton 1911, cited in Ricker 1975) was adopted. This method was selected as the standardization of regression constants enabled direct comparison of fish populations sampled in different rivers and surveys. An additional advantage of the method is that a condition factor could be calculated for all individuals in a population, thus enabling the calculation of confidence limits for mean population condition. Furthermore, population condition could also be assessed for species where sample size was small.

The following steps were followed in the calculation of this index:

(i) The length/mass relationship of populations was determined using the logarithmic form of the regression equation:

$$\text{Log } M = \text{Log } c + n (\text{Log } L)$$

where M = observed individual mass (grams),
L = observed individual fork length (mm)
c = regression constant
n = regression constant

(ii) The equation $M^i = cL^n$ was used to calculate the expected mass of all individuals using regression constants:

M^i = calculated individual mass (grams)
$c = 1xe^{-5}$
$n = 3$

Values for the regression constants were selected on the basis of their being similar to the calculated values for most species sampled (see point (i) above), and with a n-value of 3 describing isometric growth in fish (Le Cren 1951) ensuring 'realistic' expected mass values.

(iii) The constant M^i values were used as a basis for calculation of an index of condition for all specimens using the formula:

$$CF = M / M^i$$

Where M = observed individual mass (grams)
M^i = calculated individual mass (grams)
CF = condition index

(iv) The mean condition index value, and 95% confidence limits of the mean were calculated for all species where sample size per river, and per survey, was greater than 10 individuals.

3.2.2.5 Beta diversity

The ability to describe directional changes in the beta-diversity of fish communities using an ordination technique was explored using correspondence analysis (Greenacre 1989). Correspondence analysis was selected because, like the ordination techniques frequently used to describe changes in beta diversity (Mentis 1984; Gauch 1984; Pusey *et al.* 1993) it is also based on reciprocal averaging (Greenacre 1989; James and McCulloch 1990). The ability to interpret changes in the beta-diversity of community samples (see section 1.2.2.4) was assessed by visual inspection of the extent and direction of change within an ordination space of simulated samples of known beta diversity change.

Simulated data sets consisted of two sample types:

(i) Three samples per ordination representing three idealised communities, which, for the purpose of reality, were called deep pool community, marginal habitat community and rapid community. Each sample consisted of six species, three of which occurred exclusively in the sample (habitat specialists), two species which occurred in two samples (bi-habitat generalist), and one species which occurred in all three samples (multi-habitat generalist). For example, a idealised rapid community consisted of three species which occurred exclusively in rapids, one species which occurred in both rapids and deep pools, one species which occurred in both rapids and marginal areas, and one species which occurred in rapids, deep pools and marginal areas. Within the layout of the ordination database these samples were designated as being "illustrative" (Greenacre 1985) and were used to fix the scale of the ordination graphics.

(ii) Up to nine samples per ordination consisting of various combinations of habitat specialist, bi-habitat generalist and multi-habitat generalist species. Within the layout of the ordination database these samples were designated as being "supplementary" (Greenacre 1985) and were used to investigate the ability to interpret changes in the ß-diversity of communities by means of changes in the positioning of community samples within an ordination space.

Supplementary samples used consisted of a wide variety of combinations of species depicting the gain, or loss, of between one and nine species. The types of community change that were investigated were:

(i) The gain, or loss, of habitat specialists in equal or unequal frequencies.

(ii) The gain, or loss, of bi-habitat generalists in equal or unequal frequencies.

(iii) The gain, or loss, of multi-habitat generalists in equal or unequal frequencies.

(iv) The gain, or loss, of a habitat specialist simultaneous with the gain, or loss, of a bi-habitat generalist, in equal or unequal frequencies.

(v) The gain, or loss, of a habitat specialist simultaneous with the gain, or loss, of a multi-habitat generalist, in equal or unequal frequencies.

(vi) The gain, or loss, of a bi-habitat generalists simultaneous with the gain, or loss, of a multi-habitat generalist, in equal or unequal frequencies.

(vii) The gain, or loss, of a habitat specialist simultaneous with the gain, or loss, of bi-habitat and multi-habitat generalists, in equal or unequal frequencies.

All ordinations were run twice, firstly with equal weighting on all species, and secondly with weighting on species according to habitat specialization, where habitat specialists were weighted three, bi-habitat generalists weighted two, and multi-habitat generalists weighted one.

3.3 INFORMAL DESCRIPTIONS OF CHANGE IN THE ABUNDANCE OF FISH SPECIES (1987 to 1989)

Informal description of changes in the abundance of fish species is frequently employed as a means of defining the effect of environmental perturbations on fish communities (Kenmuir 1973; Bok 1979; Hamman 1980; Gaigher *et al.* 1981; Cambray 1984; Kenmuir 1984; White *et al.* 1984; Merron *et al.* 1985; Kinsolving and Bain 1993). In this section changes in the abundance of fish species in KNP rivers between 1987 and 1989 are described to achieve two objectives:

Firstly to evaluate the methodology as a means of describing the diversity of fish assemblages. This was undertaken by assessing whether results were interpretable in that plausible hypotheses of the causes for species changes could be generated based on recorded changes in the aquatic environment (sections 1.3.4 to 1.3.8, section 2.3.3) and the environmental preferences of fish species (section 2.3.2).

Secondly, to formulate hypotheses as to the nature of changes in the diversity of fish assemblages which could serve as a basis for evaluating the interpretability of alternative analytical methods used in subsequent sections of this chapter.

3.3.1 Results

Fish surveys revealed complex changes in the abundance of species in all KNP rivers (Tables 3.2 to 3.6). The abundance of several species increased substantially during the three year sample period, while some species declined in abundance. In general, more prominent changes in species abundance occurred in communities in deep pools, with the general trend being a reduction in abundance. Changes have been specific to each river, although more species underwent prominent changes in abundance in the Luvuvhu and Letaba rivers.

In the Luvuvhu River, reductions in the abundance of five species in deep pools were recorded (*Glossogobius* spp., *B. afrohamiltoni*, *C. gariepinus*, *O. mossambicus* and *T. rendalli*), whereas the abundance of one species (*L. rosae*) increased (Table 3.2). Fish were not sampled in rapids during 1987, as zero flow prevailed during the sample period. Rapids had, however, been re-colonised by typical rapid-dwelling species in 1988 (cf. *C. paratus*, *C. pretoriae*, *L. cylindricus*,

Table 3.2 Number of specimens (CPUE) captured in deep pools (number per 10 seine net pulls), rapids (number per 60 minutes electro-fishing) and marginal habitats (number per 60 minutes electro-fishing) in the Luvuvhu River during 1987, 1988 and 1989.

Species	Pools			Rapids			Marginal		
	1987	1988	1989	1987	1988	1989	1987	1988	1989
Anguilla marmorata	-	-	-	-	-	-	-	-	-
Anguilla mossambica	-	-	-	-	-	0.5	-	-	-
Barbus afrohamiltoni	19.4	3.1	-	-	-	-	-	4.9	-
Barbus annectens	-	-	-	-	-	-	-	-	-
Barbus eutaena	-	-	-	-	-	-	-	-	-
Barbus marequensis	-	-	-	-	-	1.0	0.2	-	3.0
Barbus paludinosus	-	-	-	-	-	-	-	-	-
Barbus radiatus	-	-	-	-	-	-	-	0.7	5.3
Barbus toppini	-	-	-	-	-	-	-	-	-
Barbus trimaculatus	-	-	-	-	-	-	-	-	-
Barbus unitaeniatus	-	-	-	-	-	-	-	-	-
Barbus viviparus	-	-	-	-	-	-	0.2	2.1	4.9
Brycinus imberi	3.7	8.4	9.6	-	0.5	-	0.5	-	-
Chetia brevis	-	-	-	-	-	-	-	-	-
Chiloglanis anoterus	-	-	-	-	-	-	-	-	-
Chiloglanis paratus	1.7	0.6	-	-	27.1	17.7	-	-	-
Chiloglanis pretoriae	-	-	-	-	1.0	5.2	-	-	-
Chiloglanis swierstrai	-	-	-	-	-	-	-	-	-
Clarias gariepinus	13.1	4.4	1.3	-	1.6	2.6	1.2	4.9	1.1
Glossogobius spp.	85.1	0.3	-	-	26.1	9.4	5.8	26.1	12.4
Hydrocynus vittatus	2.0	4.7	4.6	-	-	-	-	-	-
Labeo congoro	-	0.6	0.4	-	-	-	-	-	-
Labeo cylindricus	-	-	-	-	5.2	16.2	1.7	-	0.8
Labeo molybdinus	-	-	-	-	5.7	14.6	0.3	-	1.1
Labeo rosae	1.1	7.8	19.2	-	0.5	-	-	-	-
Labeo ruddi	-	0.6	-	-	-	-	0.3	-	-
Marcusenius macrolepidotus	-	-	-	-	1.0	0.5	0.2	1.4	0.4
Mesobola brevianalis	-	-	0.4	-	-	-	-	-	0.8
Micralestes acutidens	10.9	-	0.8	-	8.3	1.0	1.7	-	21.8
Opsaridium zambezense	-	-	-	-	-	-	-	-	-
Oreochromis mossambicus	53.7	13.8	7.9	-	1.0	-	13.3	3.5	2.3
Petrocephalus catostoma	-	-	-	-	1.6	2.1	0.2	0.7	-
Pseudocrenilabrus philander	-	-	-	-	-	-	-	-	-
Schilbe intermedius	14.6	79.1	1.3	-	-	-	-	1.4	0.8
Serranochromis meridianus	-	-	-	-	-	-	-	-	-
Synodontis zambezensis	0.3	24.4	13.8	-	-	-	-	-	-
Tilapia rendalli	13.4	1.3	-	-	-	2.1	13.3	0.7	4.1
Tilapia sparrmanii	-	-	-	-	-	-	-	-	-

Table 3.3 Number of specimens (CPUE) captured in deep pools (number per 10 seine net pulls), rapids (number per 60 minutes electro-fishing) and marginal habitats (number per 60 minutes electro-fishing) in the Letaba River during 1987, 1988 and 1989.

	Pools			Rapids			Marginal		
Species	1987	1988	1989	1987	1988	1989	1987	1988	1989
Anguilla marmorata	-	-	-	-	-	-	-	-	-
Anguilla mossambica	-	-	-	-	2.0	-	-	-	-
Barbus afrohamiltoni	1.7	7.3	27.1	2.0	-	-	34.0	6.0	39.7
Barbus annectens	-	-	-	-	-	-	-	-	-
Barbus eutaena	-	-	-	-	-	-	-	-	-
Barbus marequensis	3.9	0.9	4.1	2.0	-	50.0	-	1.5	3.7
Barbus paludinosus	-	-	-	-	-	-	0.7	1.5	-
Barbus radiatus	1.7	1.8	17.1	-	-	-	21.3	15.8	18.5
Barbus toppini	1323.9	705.9	183.5	-	-	-	-	3.8	75.7
Barbus trimaculatus	6.7	15.5	18.8	10.0	14.0	34.0	4.7	27.8	104.3
Barbus unitaeniatus	12.2	30.5	4.1	4.0	-	4.0	-	9.0	3.7
Barbus viviparus	11.7	22.3	23.5	-	2.0	4.0	-	39.8	28.6
Brycinus imberi	178.3	166.8	213.5	-	-	30.0	3.3	-	7.4
Chetia brevis	-	-	-	-	-	-	-	-	-
Chiloglanis anoterus	-	-	-	-	-	-	-	-	-
Chiloglanis paratus	-	-	-	-	-	46.0	-	0.8	-
Chiloglanis pretoriae	-	-	-	-	-	-	-	-	-
Chiloglanis swierstrai	-	-	-	-	-	-	-	-	-
Clarias gariepinus	22.8	6.8	0.6	-	4.0	4.0	2.7	9.8	2.8
Glossogobius spp.	0.6	1.8	49.4	-	34.0	-	0.7	19.5	15.7
Hydrocynus vittatus	8.3	11.4	3.5	-	-	-	-	-	-
Labeo congoro	-	-	-	-	-	-	-	-	-
Labeo cylindricus	1.7	1.4	4.1	34.0	-	14.0	8.7	14.3	24.9
Labeo molybdinus	6.7	-	2.4	16.0	-	14.0	6.0	27.0	4.6
Labeo rosae	436.1	33.6	22.9	8.0	-	2.0	9.3	48.0	1.8
Labeo ruddi	161.1	6.4	45.3	-	-	-	-	3.0	-
Marcusenius macrolepidotus	1.1	13.6	23.5	2.0	-	-	1.3	0.8	4.6
Mesobola brevianalis	7.2	185.0	294.7	-	-	36.0	0.7	5.3	2.8
Micralestes acutidens	-	-	14.7	-	-	2.0	-	-	-
Opsaridium zambezense	-	-	-	-	-	-	-	-	-
Oreochromis mossambicus	192.2	40.9	188.8	58.0	192.0	32.0	66.7	192.8	112.6
Petrocephalus catostoma	-	-	-	-	-	-	-	-	1.8
Pseudocrenilabrus philander	-	-	-	-	-	-	-	-	0.9
Schilbe intermedius	399.4	45.9	68.2	-	-	-	4.0	-	-
Serranochromis meridianus	-	-	-	-	-	-	-	-	-
Synodontis zambezensis	2.2	0.5	1.2	-	-	-	-	-	-
Tilapia rendalli	12.2	2.3	9.4	-	-	4.0	4.0	2.3	15.7
Tilapia sparrmanii	-	-	-	-	-	-	-	-	-

Table 3.4 Number of specimens (CPUE) captured in deep pools (number per 10 seine net pulls), rapids (number per 60 minutes electro-fishing) and marginal habitats (number per 60 minutes electro-fishing) in the Olifants River during 1987, 1988 and 1989.

	Pools			Rapids			Marginal		
Species	1987	1988	1989	1987	1988	1989	1987	1988	1989
Anguilla marmorata	-	-	-	-	-	-	-	-	-
Anguilla mossambica	-	-	-	-	-	-	-	-	-
Barbus afrohamiltoni	-	-	-	-	-	-	-	-	-
Barbus annectens	-	-	-	-	-	-	-	-	-
Barbus eutaena	-	-	-	-	-	-	-	-	-
Barbus marequensis	55.4	-	23.8	12.4	41.9	102.2	6.4	9.8	64.0
Barbus paludinosus	-	-	-	-	-	-	0.7	3.8	-
Barbus radiatus	-	-	-	-	-	0.3	2.1	-	-
Barbus toppini	-	-	-	-	-	-	0.7	9.8	-
Barbus trimaculatus	-	-	23.8	0.4	-	2.9	2.8	46.5	12.4
Barbus unitaeniatus	-	-	-	-	-	-	-	-	-
Barbus viviparus	-	-	-	-	0.8	9.4	7.1	24.4	28.9
Brycinus imberi	-	-	-	0.2	-	-	-	-	-
Chetia brevis	-	-	-	-	-	-	-	-	-
Chiloglanis anoterus	-	-	-	-	-	-	-	-	-
Chiloglanis paratus	-	-	-	25.2	8.4	15.6	-	3.4	1.3
Chiloglanis pretoriae	-	-	-	2.3	-	6.8	-	-	-
Chiloglanis swierstrai	1.5	-	-	-	0.3	13.9	3.5	-	-
Clarias gariepinus	3.1	-	-	0.2	1.4	1.9	6.4	6.8	13.8
Glossogobius spp.	0.8	-	-	-	0.3	0.3	0.7	-	0.4
Hydrocynus vittatus	1.5	-	-	-	0.6	0.3	-	-	-
Labeo congoro	2.3	-	-	-	4.5	-	-	-	-
Labeo cylindricus	-	-	-	7.9	2.8	3.9	7.1	0.8	0.4
Labeo molybdinus	1.5	-	-	30.0	26.5	50.3	6.4	8.6	4.4
Labeo rosae	236.9	-	7.5	-	0.3	-	-	6.4	-
Labeo ruddi	8.5	-	1.3	-	-	-	-	-	0.4
Marcusenius macrolepidotus	-	-	-	-	-	-	-	21.8	2.2
Mesobola brevianalis	-	-	-	-	-	-	-	-	0.4
Micralestes acutidens	-	-	-	-	-	-	-	-	-
Opsaridium zambezense	-	-	-	-	-	-	-	-	-
Oreochromis mossambicus	27.7	4.0	12.5	1.9	7.3	0.6	104.5	20.3	70.2
Petrocephalus catostoma	-	-	-	-	-	-	-	5.6	-
Pseudocrenilabrus philander	-	-	-	-	-	-	0.7	-	0.9
Schilbe intermedius	3.1	-	-	-	-	-	-	0.4	-
Serranochromis meridianus	-	-	-	-	-	-	-	-	-
Synodontis zambezensis	-	35.0	-	-	0.3	3.2	-	2.6	-
Tilapia rendalli	0.8	-	-	-	0.3	0.6	-	-	-
Tilapia sparrmanii	-	-	-	-	-	-	-	-	-

Table 3.5 Number of specimens (CPUE) captured in deep pools (number per 10 seine net pulls), rapids (number per 60 minutes electro-fishing) and marginal habitats (number per 60 minutes electro-fishing) in the Sabie River during 1987, 1988 and 1989.

	Pools			Rapids			Marginal		
Species	1987	1988	1989	1987	1988	1989	1987	1988	1989
Anguilla marmorata	-	-	-	-	-	-	-	-	-
Anguilla mossambica	-	-	-	0.9	-	0.4	-	0.2	0.2
Barbus afrohamiltoni	-	2.2	-	-	-	2.4	0.3	-	3.9
Barbus annectens	5.7	-	-	-	-	1.2	2.9	34.2	5.8
Barbus eutaena	-	-	-	-	-	2.8	0.5	1.2	1.8
Barbus marequensis	20.0	-	16.2	15.1	21.7	53.6	2.7	2.0	0.5
Barbus paludinosus	-	-	0.8	-	-	-	-	0.2	-
Barbus radiatus	0.7	-	-	-	-	-	2.6	13.0	6.6
Barbus toppini	-	-	-	-	-	-	0.3	0.4	-
Barbus trimaculatus	0.7	-	-	0.4	1.1	1.2	1.6	22.6	9.7
Barbus unitaeniatus	-	-	-	-	-	0.4	-	0.2	1.3
Barbus viviparus	95.7	2.8	16.9	1.3	1.7	12.4	4.0	45.4	23.8
Brycinus imberi	35.0	18.9	-	-	-	-	0.2	-	-
Chetia brevis	-	-	-	-	-	-	-	-	-
Chiloglanis anoterus	-	-	-	3.1	5.1	5.2	-	0.2	-
Chiloglanis paratus	-	-	-	22.2	15.4	6.4	0.3	-	-
Chiloglanis pretoriae	-	-	-	0.9	-	-	-	-	-
Chiloglanis swierstrai	-	-	-	-	17.7	-	3.4	1.8	7.8
Clarias gariepinus	-	-	13.8	-	-	0.4	0.3	1.4	1.0
Glossogobius spp.	2.9	-	7.7	0.4	0.6	-	0.3	0.6	6.0
Hydrocynus vittatus	-	-	-	-	-	0.4	-	-	-
Labeo congoro	0.7	-	-	-	-	-	-	-	-
Labeo cylindricus	1.4	-	-	11.1	8.6	-	1.4	3.4	0.2
Labeo molybdinus	0.7	1.1	0.8	3.1	8.0	12.4	1.4	1.6	0.5
Labeo rosae	5.7	1.1	-	-	-	-	-	-	0.2
Labeo ruddi	-	-	-	-	-	-	-	-	-
Marcusenius macrolepidotus	-	-	-	0.4	0.6	3.2	4.2	5.6	1.8
Mesobola brevianalis	39.3	36.7	13.8	-	-	-	-	0.4	2.9
Micralestes acutidens	1945.7	350.6	238.5	2.2	1.7	2.0	11.5	2.8	13.9
Opsaridium zambezense	30.0	0.6	10.8	-	-	2.4	0.3	-	0.5
Oreochromis mossambicus	5.7	1.1	6.9	2.7	-	1.2	4.2	17.2	15.1
Petrocephalus catostoma	-	0.6	-	-	-	-	0.6	3.8	7.3
Pseudocrenilabrus philander	0.7	0.6	0.8	-	-	0.4	7.5	6.0	7.9
Schilbe intermedius	-	2.2	0.8	0.4	-	-	0.5	1.0	0.2
Serranochromis meridianus	1.4	-	1.5	0.4	-	1.2	2.7	3.2	7.9
Synodontis zambezensis	-	-	-	-	-	-	-	-	-
Tilapia rendalli	14.3	0.6	1.5	3.1	-	1.2	6.2	4.6	5.0
Tilapia sparrmanii	-	-	-	-	-	-	-	-	-

Table 3.6 Number of specimens (CPUE) captured in deep pools (number per 10 seine net pulls), rapids (number per 60 minutes electro-fishing) and marginal habitats (number per 60 minutes electro-fishing) in the Crocodile River during 1987, 1988 and 1989.

	Pools			Rapids			Marginal		
Species	1987	1988	1989	1987	1988	1989	1987	1988	1989
Anguilla marmorata	-	-	-	-	0.7	0.6	-	-	-
Anguilla mossambica	-	-	-	-	-	-	-	-	0.2
Barbus afrohamiltoni	-	-	-	-	-	-	-	0.2	-
Barbus annectens	-	-	-	-	-	-	-	-	-
Barbus eutaena	-	-	-	-	-	0.6	-	-	0.5
Barbus marequensis	230.0	20.0	40.0	15.8	22.0	28.6	2.3	5.3	22.2
Barbus paludinosus	-	-	-	-	-	-	0.2	2.3	0.5
Barbus radiatus	-	-	-	-	-	-	-	4.8	1.3
Barbus toppini	-	-	-	-	-	-	-	1.5	1.0
Barbus trimaculatus	-	-	-	-	0.7	2.3	3.1	2.3	2.8
Barbus unitaeniatus	-	-	-	-	-	-	2.2	0.7	5.2
Barbus viviparus	-	1.7	-	-	0.7	9.7	5.6	12.0	48.3
Brycinus imberi	-	-	-	-	-	-	-	0.7	-
Chetia brevis	-	-	-	-	-	-	-	-	0.2
Chiloglanis anoterus	-	-	-	-	-	-	-	-	-
Chiloglanis paratus	-	-	-	27.8	31.3	80.0	-	0.3	1.3
Chiloglanis pretoriae	-	-	-	-	-	-	-	-	-
Chiloglanis swierstrai	-	-	-	0.8	2.0	38.3	-	-	-
Clarias gariepinus	-	-	-	-	-	-	0.8	2.5	2.5
Glossogobius spp.	-	-	-	0.8	0.7	0.6	0.2	0.2	0.7
Hydrocynus vittatus	-	-	-	-	0.7	-	-	-	-
Labeo congoro	-	-	-	-	1.3	-	0.2	0.3	0.5
Labeo cylindricus	4.0	-	-	7.5	18.7	9.1	0.5	0.3	1.0
Labeo molybdinus	-	-	-	-	4.7	4.0	-	-	2.0
Labeo rosae	2.0	-	-	-	-	-	-	0.2	-
Labeo ruddi	-	-	-	-	-	-	-	-	-
Marcusenius macrolepidotus	-	-	-	-	-	-	0.5	0.8	2.0
Mesobola brevianalis	204.0	6.7	35.0	-	-	0.6	-	0.2	6.7
Micralestes acutidens	186.0	15.0	3.3	-	0.7	2.9	5.0	7.7	9.7
Opsaridium zambezense	4.0	20.0	3.3	-	-	-	-	-	0.2
Oreochromis mossambicus	4.0	3.3	-	-	1.3	-	4.8	6.7	8.0
Petrocephalus catostoma	-	-	-	-	-	-	-	0.2	0.2
Pseudocrenilabrus philander	-	-	1.7	-	0.7	-	5.8	11.7	15.2
Schilbe intermedius	-	-	-	-	-	-	-	3.3	2.8
Serranochromis meridianus	-	-	-	-	-	-	-	-	-
Synodontis zambezensis	-	-	-	-	-	-	-	-	-
Tilapia rendalli	4.0	-	-	-	-	-	5.6	6.2	7.2
Tilapia sparrmanii	-	-	-	-	-	0.6	-	-	0.3

L. molybdinus). No prominent changes occurred in the abundances of fish in marginal areas.

In the Letaba River, both declines and increases in the abundances of species occurred. Four species in deep pools (*S. intermedius, L. rosae, L. ruddi, B. toppini*) declined in abundance, particularly in 1988 (Table 3.3). Conversely, *M. brevianalis* increased in abundance in successive sample years. Fish communities in rapids were characterised by the predominance of species more commonly recorded in slow flowing water (*O. mossambicus, Glossogobius* spp.), particularly in 1987 and 1988. *Chiloglanis paratus* was recorded in rapids only in 1989, which, along with an increase in the number of *B. marequensis* in this year, indicated an increase in the abundance of species which occur predominantly in fast flowing water. Abundance of most species in marginal areas was variable, though the abundance of *B. trimaculatus* increased in successive sample years.

Relatively few changes in the abundance of fish species were recorded in the Olifants River. Fewer *L. rosae* were sampled in deep pools in 1989 than in 1987 (Table 3.4). However, deep pools in the Olifants River were possibly undersampled due to difficulties experienced with operating the sampling apparatus (particularly in 1988). Thus, descriptions of species abundances in pools may not accurately reflect community composition. The abundance of *B. marequensis* increased in both rapids and marginal areas. In all sample years, fish communities in rapids were found to be numerically dominated by typical rapid-dwelling species (section 2.3.2.1) (*C. paratus, L. molybdinus* and *B. marequensis*).

Few substantial changes in the abundance of fish species were recorded in the Sabie River. Only two species (*M. acutidens* and *B. viviparus*) underwent substantial declines in abundance in deep pools (Table 3.5). In rapids, the abundance of one species (*B. marequensis*) increased in successive sample periods. Four species which occur infrequently in strongly flowing water (*T. rendalli, S. meridianus, O. mossambicus, C. gariepinus*) were recorded in rapids in low abundances in 1987 and 1989, though were absent in 1988 (Table 3.5), indicating a decline in diversity. No substantial changes occurred in the abundances of any species in marginal areas, though the abundance of most species increased slightly in 1988 and 1989.

In the Crocodile River, both declines and increases in the abundance of species were recorded. The abundance of three species in pools (*B. marequensis, M. acutidens, M. brevianalis*) declined in 1988 (Table 3.6). Deep pools in the Crocodile River were possibly undersampled due to difficulties experienced with operating the sampling apparatus, with large cyprinids, and in particular *Labeo* species, being under-represented in catch returns. Large shoals of *Labeo* species were observed from low flying aircraft (*pers. obs.*) yet relatively few of these species were collected during the fish sampling programme. Thus, descriptions of species abundances in pools given here possibly do not accurately reflect community composition. Substantial increases occurred in the abundance of *C. paratus* and *C. swierstrai* in rapids, and *B. viviparus* in marginal areas, and small increases occurred in the abundances of most species in marginal areas in both 1988 and 1989 (Table 3.6), indicating increased diversity of these communities.

Overall, the type of changes in diversity over the three year sample period where:

(i) Diversity of pool-dwelling communities declined.

(ii) Diversity of rapid-dwelling communities either increased (Luvuvhu and Letaba rivers) or remain unaltered.

(iii) Diversity of marginal area-dwelling communities either increased slightly or remained unaltered.

(iv) Largest changes in community diversity occurred in 1988.

(v) Changes in community diversity were greatest in the Luvuvhu and Letaba rivers.

3.3.2 Discussion

Hypotheses of causes for observed community changes

Recorded changes in the abundance of fish species could result from both sampling variability as well as species responses to changes in environmental conditions (Royce 1972, 1984; Gulland 1977, 1985; Zalewski and Cowx 1990).

Evaluation of the interpretability of results was based largely on the plausibility of hypotheses on the causes for species abundance changes.

A standardised sampling programme was adopted in all surveys, and only in deep pools in the Olifants and Crocodile rivers was sampling efficiency reduced in 1988 due to high water levels. Thus most recorded changes in species abundance were likely to have been real, and the consequence of environmental changes, rather than a result of sampling variability.

No substantial changes in water quality, nor episodic pollution events were recorded during the three year sample period (section 2.3.3.3). Fish community changes resulting from water quality deterioration would be expected to have been specific to each river, and to have negatively affected a variety of fish species in different habitats. The similarity of short-term changes in species abundance in all five rivers (reduction of species abundances in pools, and increases in rapids and marginal areas) indicated that most changes are unlikely to have been a consequence of declines in water quality.

Changes did occur in hydraulic conditions in all rivers during the three year sample period, with large magnitude floods in all rivers in 1988, as well as in 1989 in the Sabie and Crocodile rivers (sections 1.3.4 to 1.3.8). Furthermore, in the Letaba River, there was a reduction in the duration of zero flow conditions in 1988 (section 1.3.5), and in the Luvuvhu River, perenniality of flow was restored in 1988 and 1989 (section 1.3.4). Changes in the flow patterns is one of the primary environmental disturbances in lotic systems (Ward and Stanford 1983; Resh *et al.* 1988; Poff and Ward 1989) and can significantly influence the distribution and abundance of fish (Moyle and Nichols 1974; Stanford and Ward 1986; Scudder 1989; Moyle *et al.* 1992; Merron *et al.* 1993; Moyle 1995). Changes in hydraulic conditions in KNP rivers are thus likely the primary cause of observed changes in the abundance of fish.

The effect of changing flow patterns on the abundance of fish has also been demonstrated in the Pongolo River (KwaZulu/Natal) (White *et al.* 1984; Merron *et al.* 1985) which has a similar fish fauna to KNP rivers (Bruton and Kok 1980). Increases in flow in the Pongolo River caused a decline in the abundance of *O. mossambicus*, *G. giuris* and *B. afrohamiltoni*, and increases in the abundance of *S. intermedius*, *H. vittatus*, *C. gariepinus*, *B. imberi* and *B. toppini* (White *et al.* 1984;

Merron *et al.* 1985). Several of the community changes observed in the Pongolo River were mirrored in the Luvuvhu River in 1988 and 1989 after increases in the volume and duration of flow in these years. One notable exception, however, was the absence of *B. toppini* in the Luvuvhu River. *Barbus toppini* is commonly recorded in slow flowing pools (Gaigher 1973; Pienaar 1978; section 2.3.2.1) confirmed by its abundance in the Letaba River. Its absence, along with several other small minnow species (section 2.3.1), from pools in the Luvuvhu River can possibly be ascribed, in part, to the abundance of predatory species (*B. imberi*, *C. gariepinus*, *S. intermedius*, *Glossogobius* spp., *H. vittatus*) in this river.

The abundance of *B. afrohamiltoni* in both the Pongolo River during drought years (White *et al.* 1984) and the Luvuvhu River during 1987, and its decline in abundance in both systems during wetter years, can be ascribed to its non-flood dependant spawning (Kok 1980; White *et al.* 1984) and its tolerance of low-flow conditions. Similar reasons could be given for the observed decline of *Glossogobius* spp. in the Luvuvhu River, which, in view of its marine origins (Bruton *et al.* 1982), is unlikely to be a flood-dependant spawner, a point illustrated by the ability of *G. giuris* to breed in isolated impoundments (Hecht 1982). It could be expected that *B. afrohamiltoni* and *Glossogobius* spp. would increase in abundance during extensive periods of low flow, though would loose their reproductive advantage, and hence decline in abundance once flow conditions improved.

Increases in the abundances of rapid-dwelling species in the Letaba River, coupled with declines in *L. ruddi, S. intermedius, L. rosae* and *B. toppini*, which favour pools with little or zero flow (section 2.3.2.2), indicated changes in fish communities in response to increased volume and duration of flow in 1988 and 1989 (section 1.3.5). Similarly, increases in the abundance of *M. brevianalis*, which favour slow flowing waters (Skelton 1993; section 2.3.2.2), can be attributed to a reduction in the duration of zero flow conditions in 1988 and 1989.

Increases in the abundances of rapid- and marginal area-dwelling species in the Olifants, Sabie and Crocodile rivers most likely resulted from flow increases in these rivers (sections 1.3.6 to 1.3.8). However, the reason for the decline in abundance of *M. acutidens* in the Sabie River, and both *M. acutidens* and *M. brevianalis* in the Crocodile River is unknown. It is speculated that since both species occur predominantly in slow flowing waters (section 2.3.2.2), large magnitude flood events in the Sabie and Crocodile rivers in both 1988 and 1989 (sections 1.3.7 and 1.3.8) resulted in the observed declines.

Based on the above discussion it can be concluded that changes in hydraulic conditions have been largely responsible for changes in the abundance of several fish species in KNP rivers during 1988 and 1989. Although Weeks (1991) found that the structure of fish communities in the Sabie-Sand system at altitudes higher than 400m amsl was influenced primarily by summer water temperature, it is hypothesized that the structure of fish communities in the low altitude (<400m amsl) portions of Mpumalanga are primarily flow dominated.

The effect of changes in flow on aquatic biota have been extensively studied (Niemi *et al.* 1990; Yount and Niemi 1990) though emphasis has previously been primarily on the effects of flow reductions rather than the effects of flood events. Press disturbances (Niemi *et al.* 1990; Yount and Neimi 1990) such as flow regulation, have been found to be especially detrimental to stenoscopic fish species (Poff and Ward 1989) and in particular species that are highly specialised for lotic environments (Petts 1984). Pusey *et al.* (1993) have questioned the role that high discharge events play in structuring fish communities in Australian river systems. It is evident from the data presented here, however, that flood events do influence community structure in rivers in the lowveld region of South Africa. Increases in the magnitude and duration of flow in highly regulated systems (for example Luvuvhu and Letaba river) can result in increased distribution and abundance of stenoscopic fish species and declines in species which favour lentic conditions. Flood events in rivers with a more natural flow régime (for example Sabie and Olifants rivers), however, appear to have minor effects on the abundance of fish. Regular surveillance of the abundance of fish could thus serve as a basis for monitoring the effects of both decreases and increases in flow of rivers.

Informal descriptions of species abundances as a means of evaluating the achievement of conservation objectives.

Informal descriptions of changes in the abundances of fish species are frequently used to describe change in the diversity of fish communities (Hamman 1980; Gaigher *et al.* 1981; Kenmuir 1984). The method enables identification of species undergoing substantial changes in abundance and, through an understanding of the environmental requirements of species, an indication of the probable causes for community changes. However, problems do exist with this methodology as a means of assessing the achievement of conservation objectives. Decisions as to which changes are relevant are subjective, based entirely on the perceptions of the observer. In studies of highly dynamic or species rich communities such as those in KNP rivers, there may be a tendency to overlook less obvious changes, with concentration either on very abundant species, or species for which the reasons for change are readily apparent. These types of situations can result in a loss of information, and hence poorer understanding of community dynamics. Furthermore, the significance of species abundance changes (in terms of conservation objectives) cannot be evaluated as there are no operational goals which define acceptable abundance ranges for different species (see section 3.1). The natural dynamism of fish communities in most rivers (Finlayson 1994; Allan 1995) including those of South Africa (Cambray *et al.* 1989) is poorly understood, making it possible only to illustrate trends of change rather than to rigourously test for the achievement of an objective. Clearly, alternative methods of data analysis are required to enable assessment of the significance of change in the diversity of fish communities, and for this purpose the analysis of species abundance data using diversity indices and abundance models are evaluated in subsequent sections of this chapter.

Southwood (1980) has emphasised that it is important, and invariably informative, for ecologists undertaking community studies to undertake informal investigations of their data before proceeding with complex analyses. Such investigations can frequently provide a rough indication of the nature and extent of change in community diversity. The analyses undertaken in this chapter proved useful in this context as they enabled the formulation of broad hypotheses of the type of change in diversity that occurred over the three year sample period. These hypotheses (section 3.3.1) are used in the following sections of this chapter as a yardstick to gauge the interpretability of described changes in community diversity using quantitative analytical methods.

3.4 LENGTH FREQUENCY DISTRIBUTION OF FISH POPULATIONS

The use of length frequencies to graphically illustrate the structural diversity of fish populations was first used by Petersen (1892, cited in Ricker 1975). Since this time length frequency data have commonly been used to assess recruitment, survival and mortality of, in particular, commercially exploited fish species (Nikolskii 1969; Ricker 1975; Nielsen and Johnson 1983). Such assessments generally require detailed knowledge of age and growth, breeding biology, and vulnerability of different age classes to sampling (Cushing 1981; Everhart and Youngs 1981; Pauly 1984; Royce 1984; Gulland 1985), data frequently not available for freshwater fish that are not commercially exploited.

Consequently, when this method of population analysis is used in the study of species of ecological rather than commercial interest, reliance is usually placed on subjective extrapolation of age classes from length frequency (Ricker 1975). The relative abundance of different age classes is used to gauge the potential effects of environmental disturbances on population status. Such analyses are based on the theory that rapidly expanding populations will contain a large proportion of young individuals, a stationary population a more even distribution of age classes, and a declining population a large proportion of old individuals (Odum 1971).

Despite the potential for inaccurately describing the abundance of different age classes that can result from subjective extrapolation of age from length, evaluation of length frequency histograms remains a popular means of evaluating the structural diversity of fish populations, both in South Africa (Cambray 1984; White *et al.* 1984; Merron *et al.* 1985; Schramm 1993; van Zyl *et al.* 1995) and elsewhere in the world (Kenmuir 1973, 1984; Drake and Taylor 1996; Yamamoto and Nakano 1996; Kjellman and Hudd 1996). The objective of this section is to evaluate the applicability of using length frequency distributions to assess the structural diversity of fish populations of the relatively poorly researched fish communities in KNP rivers. This was undertaken by:

(i) Describing changes (1987-1989) in the age structure of species for which sufficient data on growth were available to define age from length.

(ii) Evaluating the interpretability of changes in age structure by comparison with changes in diversity concluded from informal descriptions of species abundances (section 3.3.1), and expected changes from comparisons of changes in the aquatic environment with the environmental preferences of fish species (section 2.3.2).

No reference could be found on the minimum sample size required to describe the inherent variability in the length frequency distribution of fish populations, other than the suggestion by Lagler (1978) that sample size should be large enough for normal distribution curves to be evident. Therefore, the issue of minimum sample size has also been addressed below to ensure that, within this study, evaluation of change in length frequency distribution is undertaken only for those species for which sample size was large enough to support research conclusions.

3.4.1 Results and discussion

3.4.1.1 Minimum sample size for description of the length frequency distribution of fish populations

For all three species analysed (*L. rosae*, *M. acutidens*, *O. mossambicus*) there was an initial rapid increase in the percentage similarity (indicating the similarity of 10 randomly selected samples, see section 3.2.2.1), with this increase becoming more gradual with increasing sample size (Figure 3.2a to 3.2d). The sample size at which inflection of these replicate similarity (RS) curves commenced differed between species. For *L. rosae*, and *O. mossambicus* measured in 10mm length classes, inflection commenced at a sample size of approximately 100 individuals (Figures 3.2b and 3.2d). However, for *M. acutidens*, and *O. mossambicus* measured in 5mm length classes, levelling off of the RS curve only commenced at a sample size of approximately 150 individuals (Figures 3.2a and 3.2c). Thus, the smaller the length class intervals used to describe the length frequency distribution of a species, the larger the required minimum sample size. A minimum sample size of 150 individuals would be appropriate for both small (*M. acutidens*) and large (*L. rosae*) species. Although a minimum sample size of 150 may be slightly larger than that calculated for when large (>5mm) length class intervals are used in length frequency histograms (viz. *L. rosae*, *O. mossambicus*), to err conservatively in this case would seem reasonable.

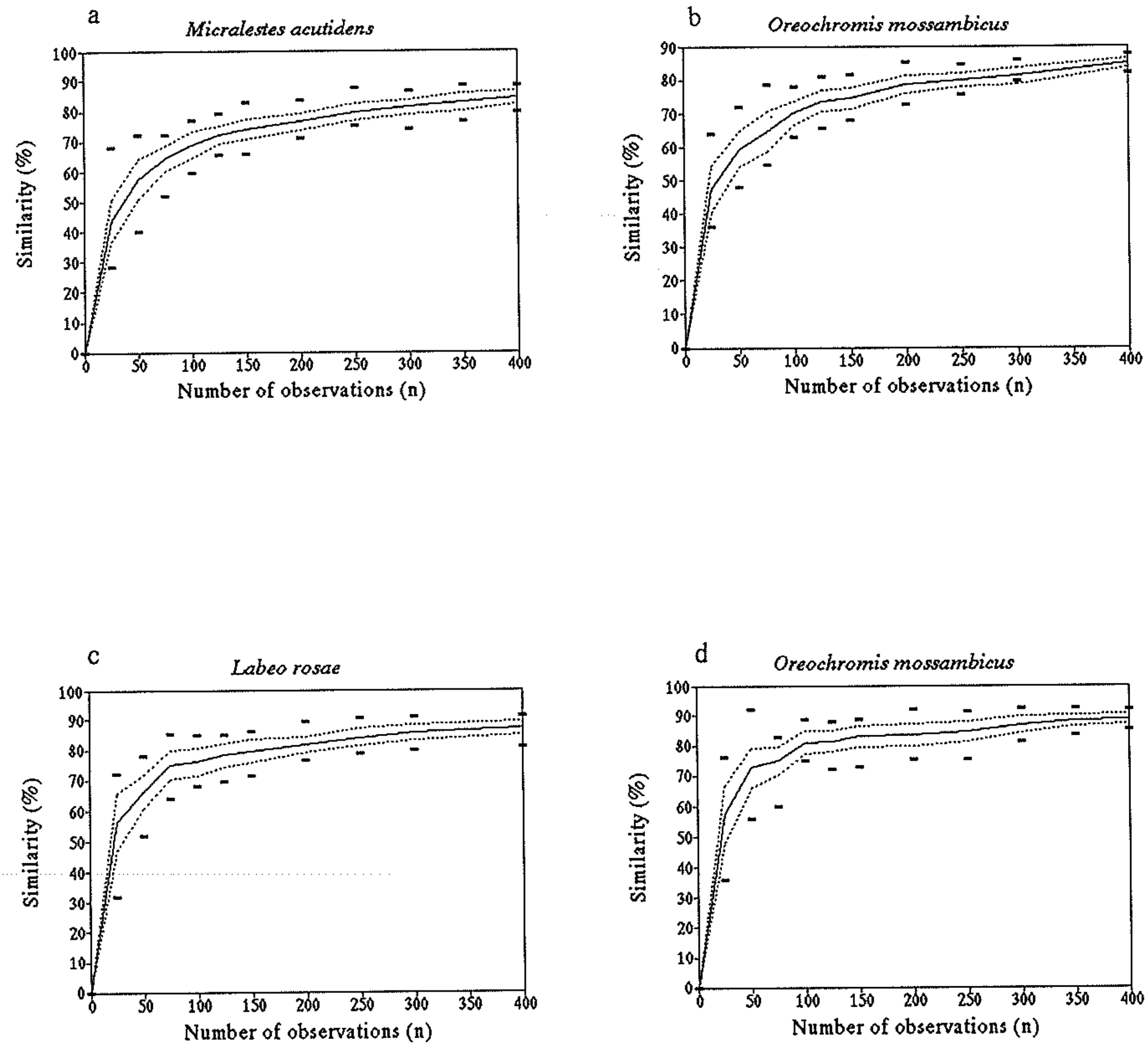

Figure 3.2 Plots of the mean percentage similarity (solid lines), 95% confidence limits (dotted lines) and maximum and minimum values (dashes) of the length frequency distribution with increasing sample size for (a) *Micralestes acutidens* (1mm length classes), (b) *Labeo rosae* (10mm length classes), (c) *Oreochromis mossambicus* (5mm length classes) and (d) *Oreochromis mossambicus* (10mm length classes).

For *M. acutidens*, there was an increase from mean RS = 74.07% (std. dev. = 3.239) to mean RS = 81.19% (std. dev. = 2.513) for sample sizes of 150 to 300 individuals. Thus a doubling in sample size was accompanied by only a 7.12% increase in mean RS. Similar results were obtained for both *L. rosae* and *O. mossambicus*, with a doubling of the sample size from 150 to 300 individuals resulting in a 5.23% (*L. rosae*), 3.86% (*O. mossambicus* measured in 10mm size length classes) and 6.66% (*O. mossambicus* measured in 5mm size length classes) increase in mean RS. Consequently, for all three species there was a relatively small increase in mean RS, and hence a small increase in the accuracy of results, for sample sizes larger than 150 individuals. Thus, there is little advantage in sampling more than 150 individuals when describing the length frequency of a population.

The recommendation of a minimum sample size of 150 individuals to describe the length frequency of fish populations indicated that this type of analysis could be conducted on only a few species sampled in these surveys. Species for which sufficient individuals (>150 individuals) were collected in most sample years were *B. imberi*, *L. rosae* and *O. mossambicus* in the Letaba River, *B. marequensis* and *L. molybdinus* in the Olifants River, and *B. viviparus* and *M. acutidens* in the Sabie River.

3.4.1.2 Length frequency distribution of selected fish species

Analysis of length frequency distribution was confined to those species for which a minimum sample size of 150-plus individuals (see Section 3.4.1.1) were collected in more than one sample year.

Length frequency distribution of Brycinus imberi *in the Letaba River*

The length frequency distribution of *B. imberi* in the Letaba River in winter 1987 was bimodal (Figure 3.3a), with modes at 66-70 and 101-105mm fork length (FL). Catches from 1988 were essentially unimodal (Figure 3.3b), with the mode at 96-100mm FL, though small peaks occurring at 81-85 and 116-120mm FL could also be distinguished. Catches from 1989 showed a unimodal length frequency distribution (Figure 3.3c), with the mode at 56-60mm FL.

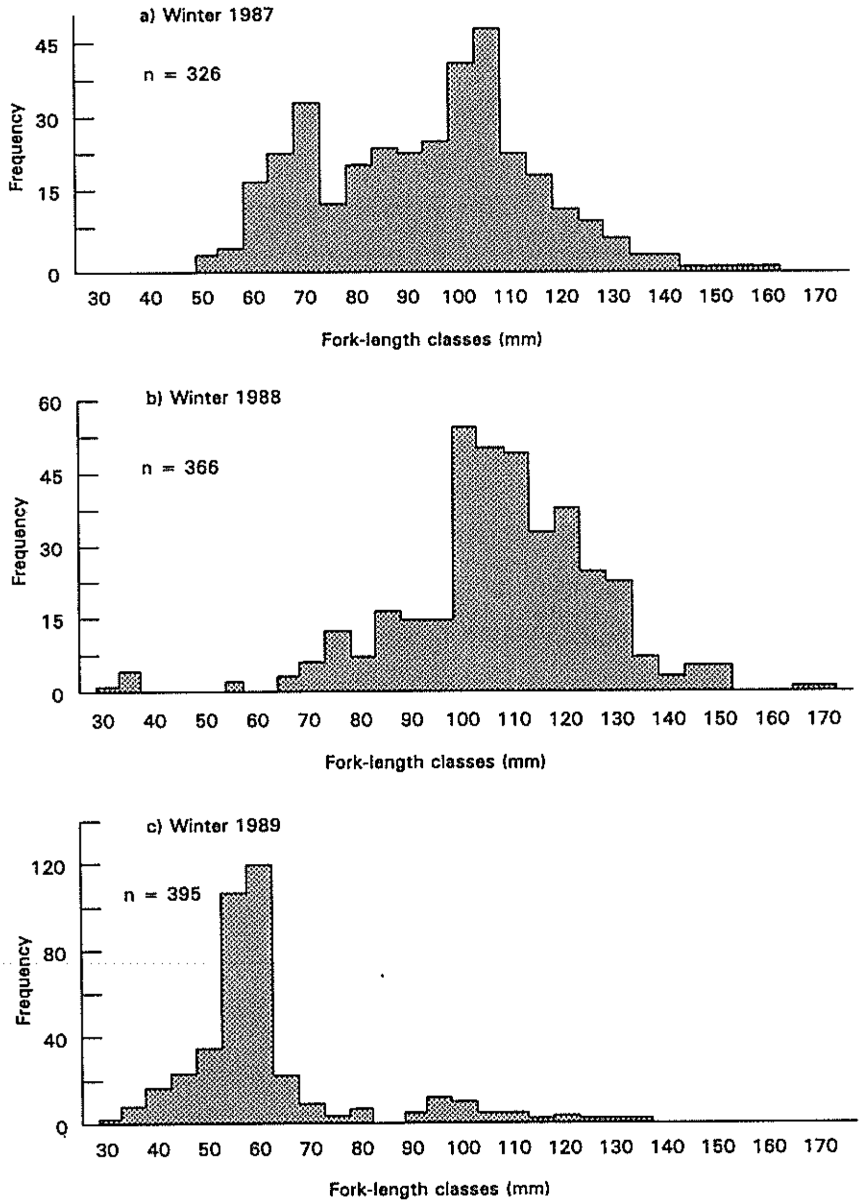

Figure 3.3 Length frequency distribution of *Brycinus imberi* in the Letaba River sampled in the winter 1987 (a), winter 1988 (b) and winter 1989 (c) sample periods.

Brycinus imberi populations have been calculated to attain mean fork lengths of 68mm within their first growth season in Lake Kariba (Zimbabwe) (Balon 1971), 92mm in the Pongolo River (South Africa) (Kok 1980), and 101mm in Lake McIlwaine (Zimbabwe) (Marshall and Van der Heiden 1977). All original length values given by Balon (1971), Kok (1980) and Marshall and van der Heiden (1977) were converted from standard length (SL) to fork length using the formula $FL = 2.265 + 1.117 (SL)$ calculated for populations in KNP rivers. By their second season of growth, the average FL of *B. imberi* populations was between 132mm (Balon 1971) and 136mm (Marshall and Van der Heiden 1977), with three-year-old fish averaging between 148mm (Balon 1971), and 181mm (Marshall and Van der Heiden 1977).

Assuming growth of *B. imberi* in the Letaba River was similar to those recorded in other southern African waterbodies, at least three age classes were recorded in the 1987 survey, with both one- and two-year-olds being abundant. In 1988, however, the bulk of the population was made up of two-year-old fish, whereas in 1989 individuals in their first growth season predominated. Fry (<35mm FL) collected in 1988 and 1989 where approximately three months old (based on Kok's (1980) growth estimates), and this indicated extended spawning of this summer flood breeder (Kok 1980; Bruton *et al.* 1982) in these years. Extended spawning in 1988 and 1989, and the predominance of one-year-old fish in 1989 may have been a consequence of improved hydraulic conditions in the Letaba River in these years (section 1.3.5). The low abundance of one-year-olds in 1988, however, remains unexplained.

Successful recruitment in all sample years confirmed the finding that the abundance of *B. imberi* in the Letaba River did not alter substantially between 1987 and 1989 (section 3.3.1). A good understanding of the growth of *B. imberi* coupled with easily identifiable length-for-age classes allowed for plausible descriptions of the age structure and recruitment of this species. Differential growth rates and wide length-for-age ranges of adult fish (Kok 1980), however, hampered the identification of age classes of fish older than three years.

Length frequency distribution of Labeo rosae *in the Letaba River*

Sufficient individuals of *Labeo rosae* for reliable length frequency analysis (>150 individuals; section 3.4.1.1) were collected only in the winter samples of 1987

(Figure 3.4a) and 1988 (Figure 3.4c). Length frequency distributions from the summer 1987/88 and winter 1989 samples have, however, also been included (Figures 3.4b and 3.4d) as they illustrate the occurrence of juveniles (<65mm SL (Kok 1980)) and fry in these periods.

Catches in winter 1987 were bimodal (Figure 3.4a) with modes at 61-70mm and 81-90mm FL. In winter 1988 the length frequency distribution was unimodal (Figure 3.4c), with the mode at 81-90mm FL. Very little is known about the growth rates for *L. rosae*. Kok (1980), however, in an investigation of the length frequency distribution of *L. rosae* in the Pongolo system, extrapolated from data on the growth of *Labeo altivelis* Peters, 1852, which is closely related to *L. rosae* (Jubb, cited *pers. comm.* in Kok 1980). Mean lengths for consecutive growth seasons of *L. altivelis* in Lake Kariba were found by Balon (1974) to be 79, 129, 192, 242, 282, 294, 365, 381 and 400mm SL. Assuming the growth rate of *L. rosae* in the Letaba River was comparable to that of *L. altivelis* in Lake Kariba, Figures 3.4a and 3.4c illustrate that *L. rosae* sampled in winter 1987 and 1988 consisted of up to four year classes, with the bulk of individuals being one year old. The bimodality of Figure 3.4a is possibly an artifact of sampling as both modes fall within the range of the one-year-old length-for-age class, or alternatively illustrates two cohorts within this class.

Analysis of length frequency distribution of *L. rosae* illustrated that successful recruitment occurred in the period 1986 to 1988. *Labeo rosae* is a summer spawner (Kok 1980) and is capable of breeding throughout the summer period. The occurrence of juveniles in 1989 (Figure 3.4d) though not in winter 1988 (Figure 3.4c), despite successful breeding in summer 1987/88 (Figure 3.4b), demonstrated either delayed or protracted breeding in 1989. The reason for this could, as discussed for *B. imberi* above, be related to altered hydraulics in the Letaba River in these years.

Study of the length-frequency distribution of *L. rosae* did enable evaluation of the success of recruitment in populations. However, limited understanding of the growth of *L. rosae*, coupled with the obscuring of size peaks for fish larger than 110mm FL (approximately second growth season) by wide ranges of length-for-age classes, limits the usefulness of this methodology for monitoring age distribution.

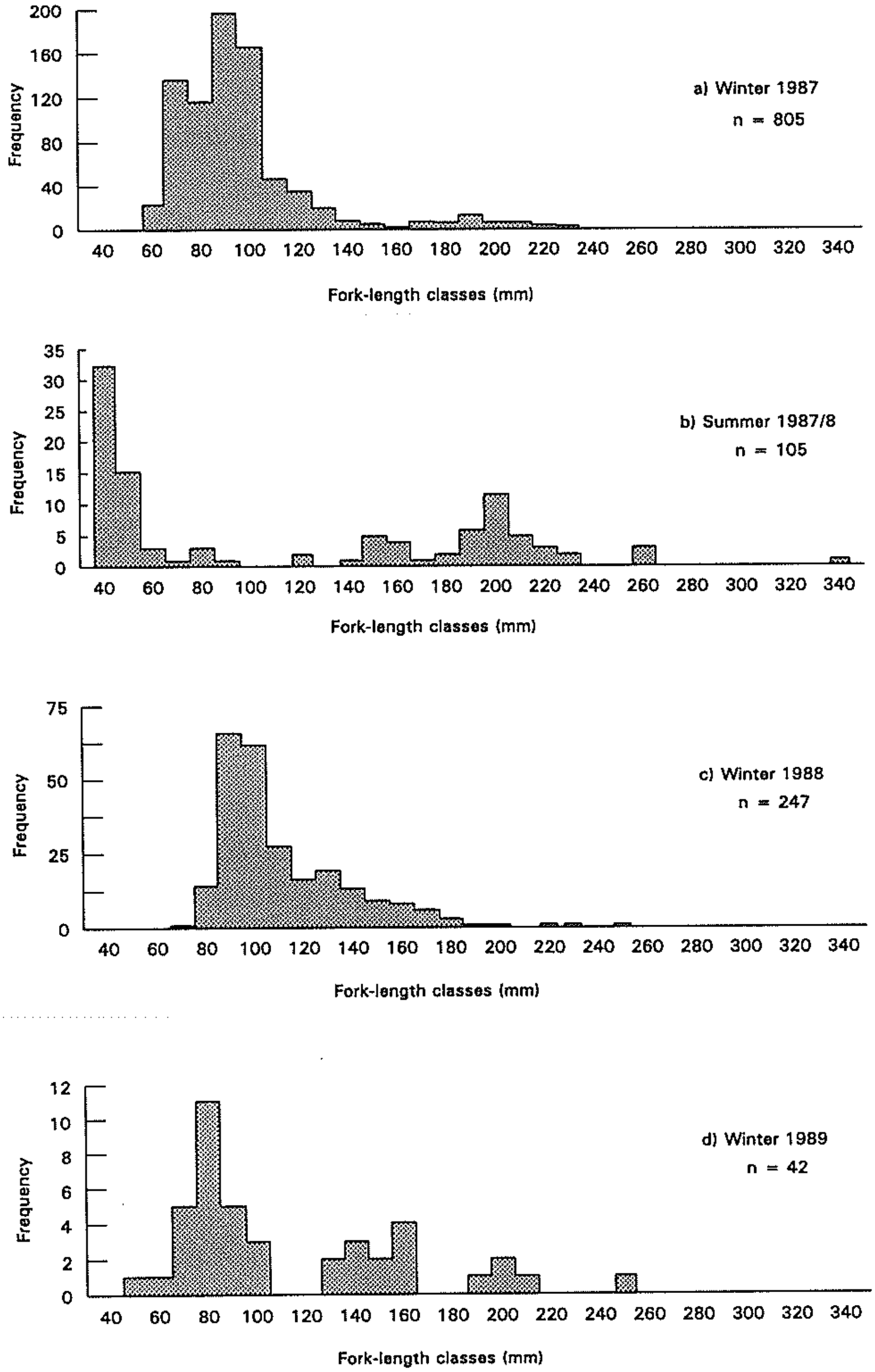

Figure 3.4 Length frequency distribution of *Labeo rosae* in the Letaba River sampled in the winter 1987 (a), summer 1987/88 (b), winter 1988 (c) and winter 1989 (d) sample periods.

Length frequency distribution of Oreochromis mossambicus *in the Letaba River*

Length frequency distribution of *Oreochromis mossambicus* in the Letaba River were polymodal in all sample years, with the modes at 31-40, 81-90, 141-150 and 210-210mm FL in the 1987 sample (Figure 3.5a), 21-30, 61-70, 121-130 and 161-170mm FL in the 1988 sample (Figure 3.5b), and 41-50, 91-100, 121-130, and 161-170mm FL in the 1989 sample (Figure 3.5c). The breeding season of *O. mossambicus* extends over most of the year (Kok 1980), with multiple spawning being common (Bruton and Allanson 1974). Thus recruitment could have occurred throughout the year, which hampered the distinction of age classes from length frequency data.

The distinction of age classes from length frequency data is further complicated by the finding that the growth rate of *O. mossambicus* varies widely in different southern African waterbodies (Table 3.7). Studies of the performance of *O. mossambicus* in aquacultural practices and in feeding trials have shown growth rates to be largely dependant on environmental conditions (Vaas and Hofstede 1952; Shell 1966). Stunting of the older age classes of *O. mossambicus* has also been recorded in southern Africa (Bruton and Allanson 1974), which Bowen (1976) attributed to lack of sufficient food in the preferred habitat. The consequence of this variability in the growth rate of *O. mossambicus* is that there is no basis on which accurate age for length extrapolation could be undertaken for populations in KNP rivers.

A further complication to the interpretation of length frequency graphs for *O. mossambicus* was the finding that the growth rates of males and females can differ substantially (Du Toit *et al.* 1972; Bruton and Allanson 1974; Batchelor 1974; Potgieter 1974; Hecht 1980a), with males growing faster than females. Differential growth rates of sexes would necessitate the compilation of separate length frequency graphs for different sexes for accurate assessment of age-for-length frequency.

In view of the variability in growth patterns implied from cited literature, no estimate of age has been attempted for *O. mossambicus* in the Letaba River. The best interpretation of length frequency graphs for *O. mossambicus* in the Letaba River would be that in all years a variety of different length and hence age classes were recorded, and that in all years the majority of individuals were small,

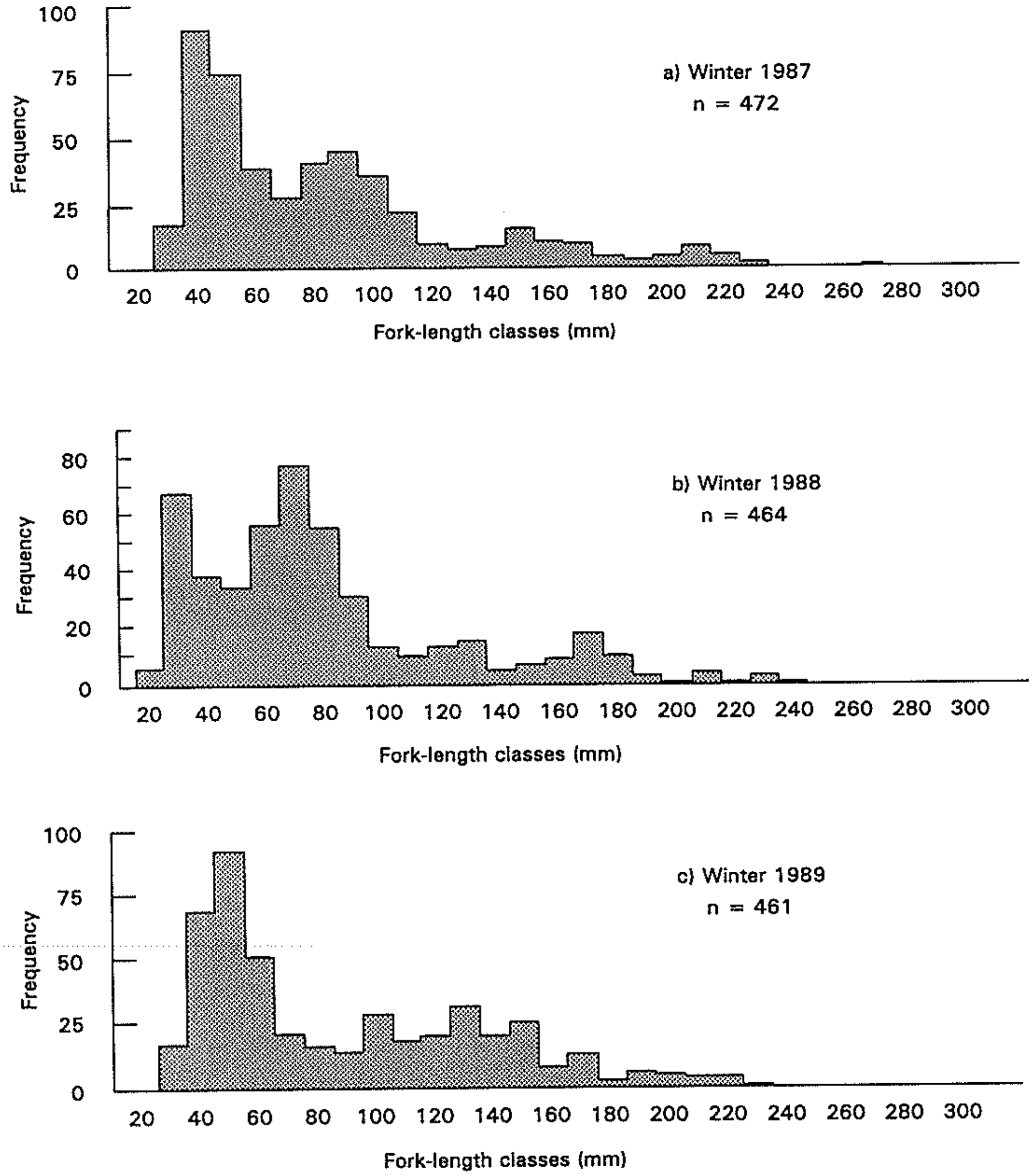

Figure 3.5 Length frequency distribution of *Oreochromis mossambicus* in the Letaba River sampled in the winter 1987 (a), winter 1988 (b) and winter 1989 (c) sample periods.

Table 3.7 Growth of *Oreochromis mossambicus* in various water bodies in southern Africa. All lengths are expressed as TL with original values given by Bruton and Allanson (1974), Hecht (1980a) and Krupka (1974) being converted from SL to TL using the formula TL = 18.417 + 1.212(SL) after Kok (1980). Values from Le Roux (1961) were read from growth curves and converted from inches to millimetres (M = male; F = Female).

Locality	Reference	Fork Length (mm) at age (years)									
		Sex	1	2	3	4	5	6	7	8	9
Njelele dam	Le Roux (1961)	M&F	127	191	229	254	275	285	302	-	-
Lake Funduzi	Le Roux (1961)	M&F	81	104	135	165	193	229	254	279	-
Albasini dam	Le Roux (1961)	M&F	84	127	173	203	241	299	-	-	-
Rust de Winter dam	Le Roux (1961)	M&F	86	149	211	254	287	-	-	-	-
Loskop dam	Le Roux (1961)	M&F	102	188	254	302	325	353	381	-	-
Sheyo-lo-ngubu dam	Le Roux (1961)	M&F	127	201	249	254	299	323	-	-	-
Hartebeespoortdam	Le Roux (1961)	M&F	97	170	229	274	305	-	-	-	-
Loskopdam	Du Toit *et al.* (1972)	M&F	113	203	263	312	328	343	350	359	-
Dorndraaidam	Batchelor (1974)	M&F	134	216	251	279	293	312	-	-	-
Inkomati-Limpopo river	Potgieter (1974)	M	162	224	269	301	329	361	384	403	418
Inkomati-Limpopo river	Potgieter (1974)	F	162	214	247	273	292	306	327	343	-
Luphephe/Nwanedzi	Hecht (1980a)	M&F	159	224	168	296	314	326	334	340	342
Lake Sibaya	Bruton & Allanson (1974)	M	121	169	198	233	245	254	-	-	-
Lake Sibaya	Bruton & Allanson (1974)	F	119	155	181	197	220	-	-	-	-
De Hoop Vlei	Van Rensberg (1966)	M&F	132	235	290	-	-	-	-	-	-
Zeekoei Vlei	Van Rensberg (1966)	M&F	120	195	250	-	-	-	-	-	-
Lake Kariba	Krupka (1974)	M&F	85	130	172	214	-	-	-	-	-

possibly in their first season of growth. Successful recruitment in all sample years confirmed the finding that the abundance of *O. mossambicus* in the Letaba River did not alter substantially between 1987 and 1989 (section 3.3.1).

Length frequency distribution of Barbus marequensis *in the Olifants River*

The length frequency distributions of *Barbus marequensis* in the Olifants River were polymodal in 1987 and 1988, with the modes at 21-30, 101-120, 161-170, and 241-250mm FL in the 1987 sample (Figure 3.6a); 31-40, 111-120 and 191-200mm FL in the 1988 sample (Figure 3.6b); and bimodal in the 1989 sample with modes at 41-50 and 91-100mm FL (Figure 3.6c). No data on growth rates on *B. marequensis* could be found in the literature. This lack of data, coupled with inconsistencies in modal lengths in different sample years, resulted in it not being possible to accurately assess the age of *B. marequensis* at different modal lengths.

Barbus marequensis is a summer flood breeder (Bruton *et al.* 1982), thus the left-hand modal groups of Figures 3.6a to 3.6c (<70mm FL), possibly consisted predominantly of individuals in their first season. However, the length span of individuals in their first season is unknown, thus limiting assessment of recruitment. The majority of individuals collected in 1988 and 1989 were less than 70mm FL indicating either more successful recruitment in these years and/or delayed breeding. This conclusion was consistent with the observation that *B. marequensis* increased in abundance in the Olifants River in 1988 and 1989 (section 3.3.1).

Study of the length-frequency distribution of *B. marequensis* does enable evaluation of the success of recruitment in populations. However, the absence of data on the growth of *B. marequensis* limits the usefulness of this methodology for monitoring change in the age distribution of this species.

Length frequency distribution of Labeo molybdinus *in the Olifants River*

Length frequency distribution of *Labeo molybdinus* in the Olifants River showed an almost consistent unimodal distribution in all sample years, with the modes at 131-140mm FL in 1987 (Figure 3.7a), 71-80mm FL in 1988 (Figure 3.7b), and 121-130mm FL in 1989 (Figure 3.7c). Unimodality implies that lengths-for-ages of *L. molybdinus* must range so widely as to obscure the separation of size peaks.

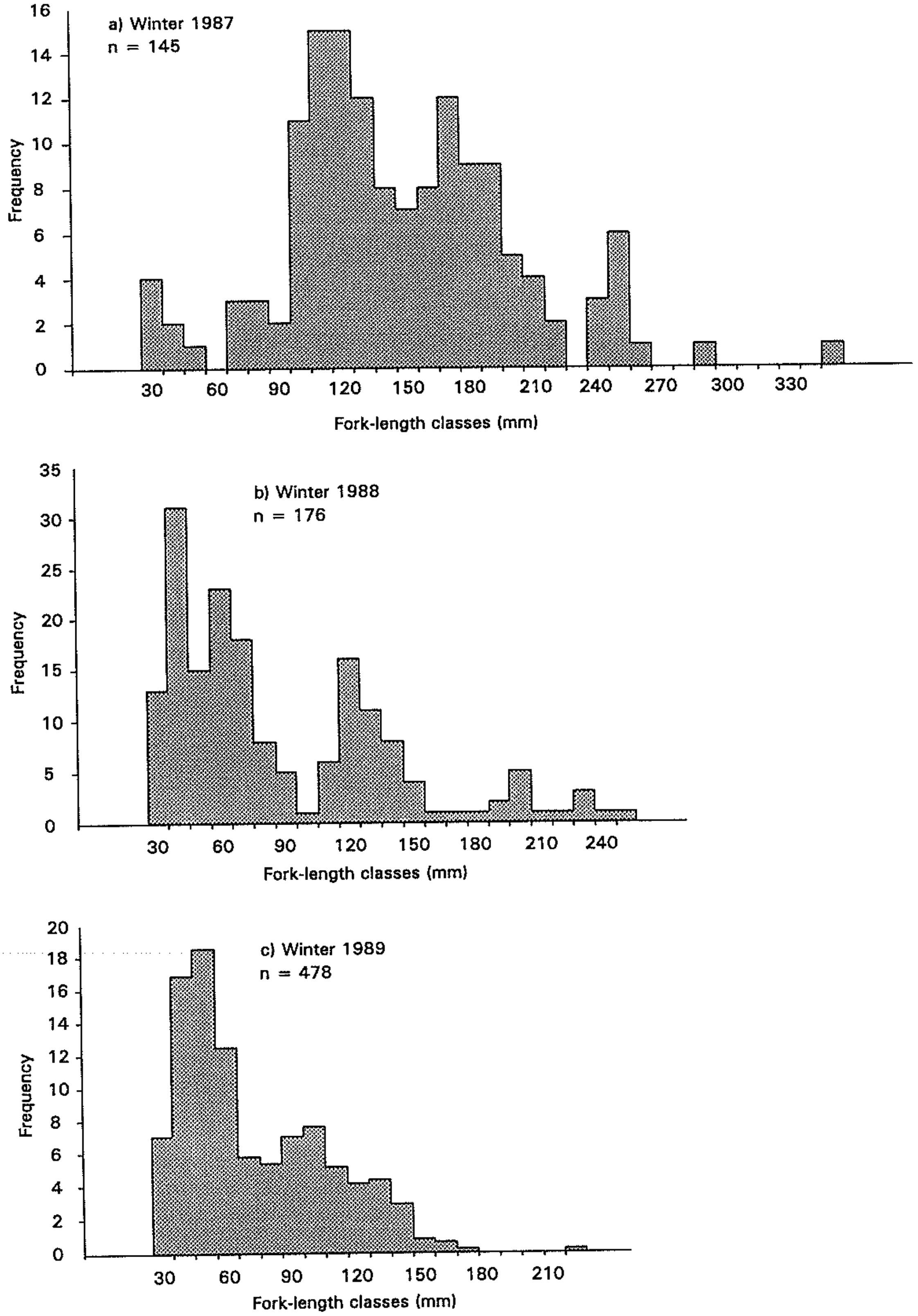

Figure 3.6 Length frequency distribution of *Barbus marequensis* in the Olifants River sampled in the winter 1987 (a), winter 1988 (b) and winter 1989 (c) sample periods.

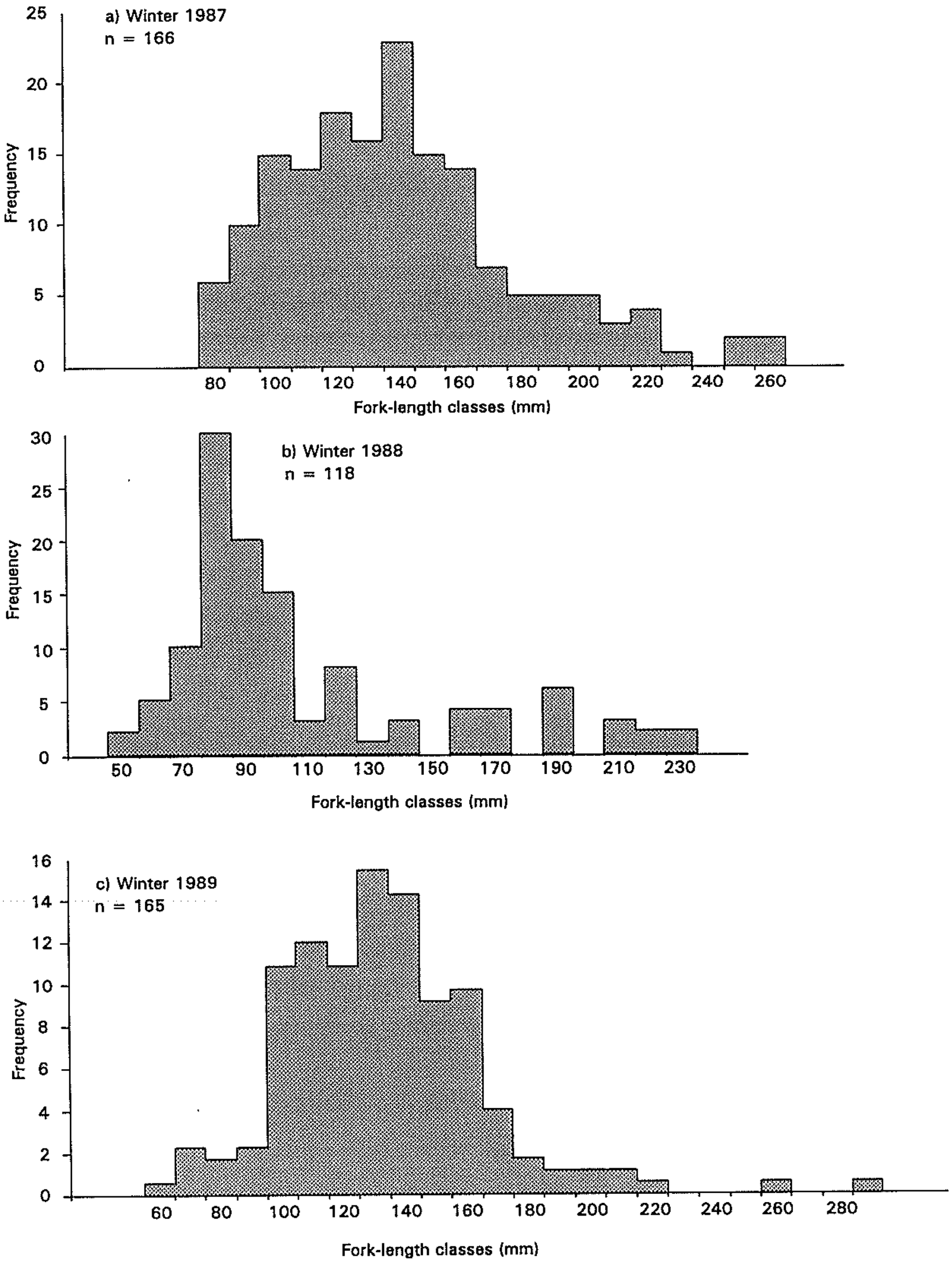

Figure 3.7 Length frequency distribution of *Labeo molybdinus* in the Olifants River sampled in the winter 1987 (a), winter 1988 (b) and winter 1989 (c) sample periods.

Furthermore, no data on growth rates on *L. molybdinus* could be found in the literature, hence accurate assessment of age at different modal lengths was not possible.

Length frequency distribution of Barbus viviparus *in the Sabie River*

Length frequency distributions of *Barbus viviparus* in the Sabie River were unimodal in 1987 (Figure 3.8a) with the mode at 41-42mm FL, whereas catches from 1988 and 1989 were bimodal with modes at 27-28 and 37-38mm FL in 1988 (Figure 3.8b) and 29-30 and 45-46mm FL in 1989 (Figure 3.8c). No data on growth rates on *B. viviparus* could be found in the literature, hence accurate assessment of age at different modal lengths was not possible. *Barbus viviparus* breeds during summer (Bruton *et al.* 1982), and the abundance of smaller specimens (<30mm FL) in the winter 1988 and 1989 samples indicated either more successful recruitment and/or delayed breeding, which may have been a consequence of improved hydraulic conditions in these years (section 1.3.7).

Length frequency distribution of Micralestes acutidens *in the Sabie River*

Several size peaks in the length frequency distributions of *Micralestes acutidens* in the Sabie River were observed from catches undertaken in winter months (Figures 3.9a, 3.9c and 3.9d), however, no clear polymodality of length frequency distribution was evident. Catches from the summer 1987/88 sample were unimodal, with the mode at 55-56mm FL (Figure 3.9b).

Micralestes acutidens is a summer breeder (Bruton *et al.* 1982) yet the smaller fish did not form a distinctive peak in the summer 1987/88 (Figure 3.9b) catches. This implied that juvenile *M. acutidens* grow rapidly to adult size, and that the lengths-for-ages must range so widely as to obscure the separation of size peaks. These data thus have little value for assessment of growth, breeding and recruitment of this species.

Summarising discussion and conclusions

Assessments of change in the length frequency distribution of populations are undertaken primarily to illustrate changes in the age-class structure in response to environmental factors which influence natality and mortality (Ricker 1975). The

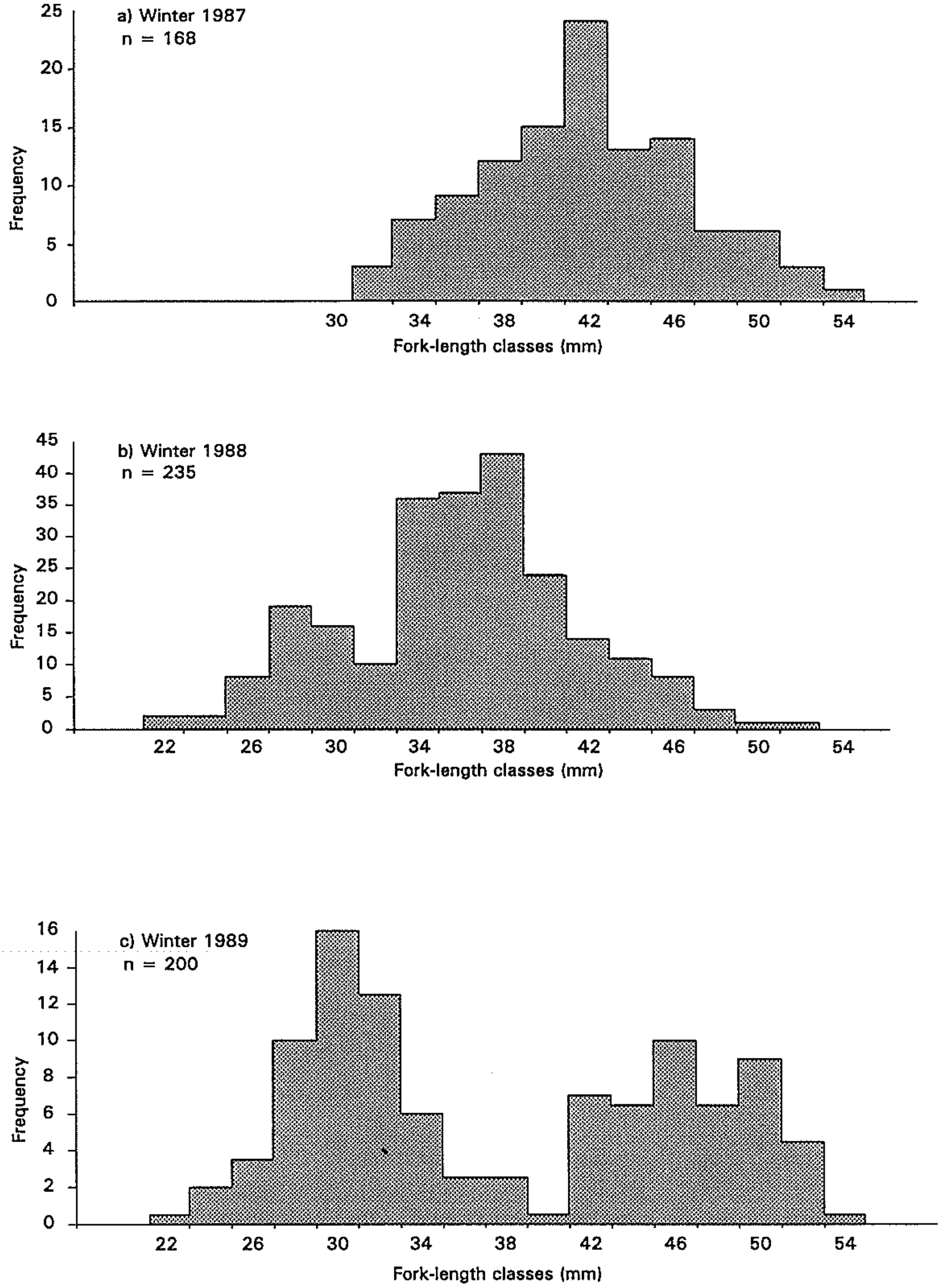

Figure 3.8 Length frequency distribution of *Barbus viviparus* in the Sabie River sampled in the winter 1987 (a), winter 1988 (b) and winter 1989 (c) sample periods.

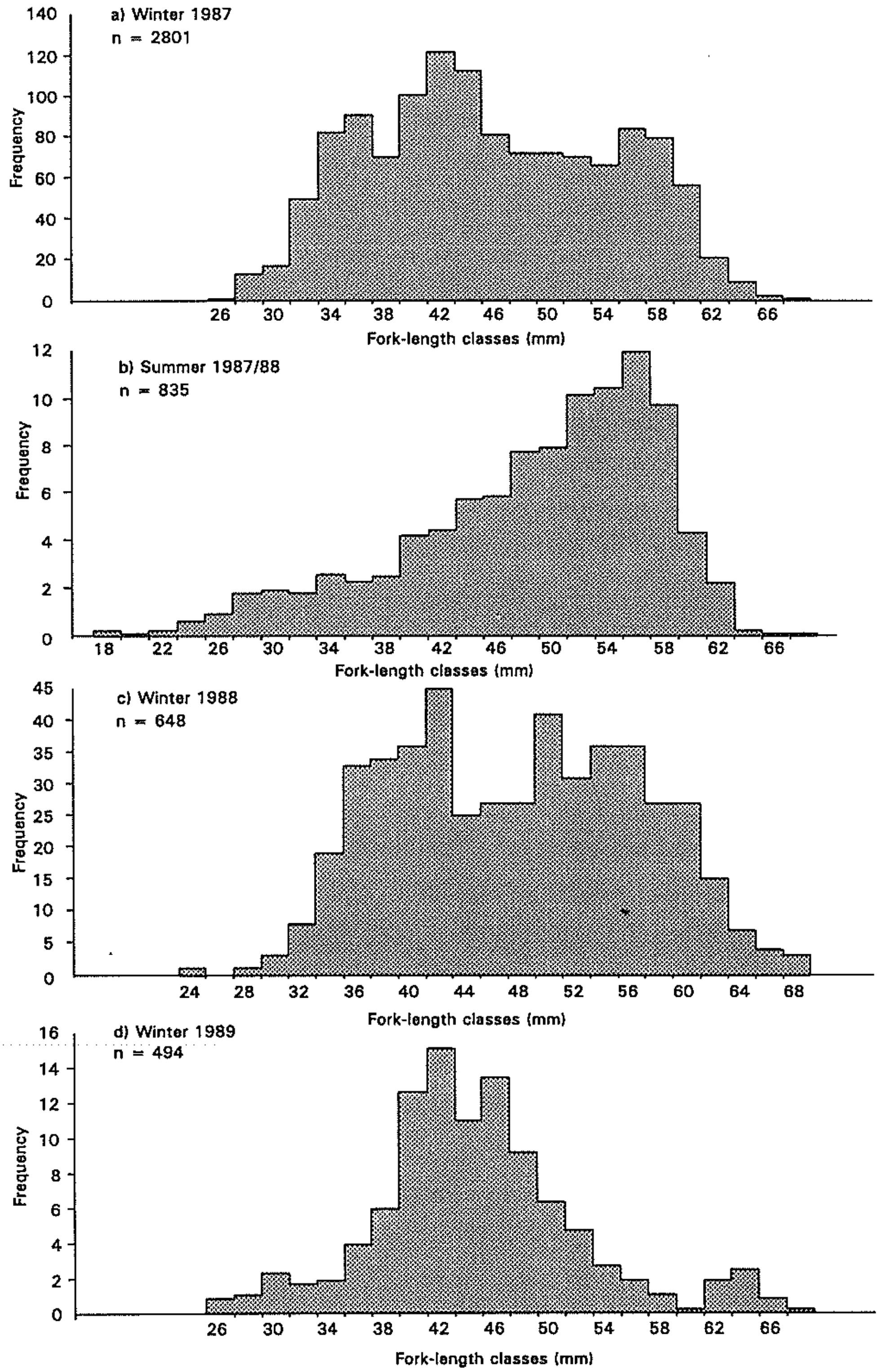

Figure 3.9 Length frequency distribution of *Micralestes acutidens* in the Sabie River sampled in the winter 1987 (a), summer 1987/88 (b), winter 1988 (c) and winter 1989 (d) sample periods.

above discussion, however, has emphasized several shortcomings with regard to evaluating the length frequency distribution of populations from diverse, though relatively poorly researched, fish communities. These are:

(i) Insufficient knowledge on the growth of the majority of species which severely limited accurate interpretation of length frequency distribution graphs.

(ii) Wide lengths-for-ages ranges of several species obscured the separation of size peaks. Even when sampling conditions were ideal and representative samples obtained, length frequency abundances normally failed to give reliable estimates of lengths at various ages beyond those attained by the end of the second or third growing season. This trend was confirmed by observations of Lagler (1978). A requirement for effective assessment of the age structure of populations from morphometric data is that species are long-lived and slow growing so that different age classes can be sampled and identified (Butler *et al.* 1971; Buikema *et al.* 1982). However, many of the smaller fish species in KNP rivers, such as the minnows (*Barbus* spp.), *M. acutidens* and *M. brevianalis* are short-lived and grow rapidly to adult size (Skelton 1993). Reliable interpretation of length frequency distribution graphs of short-lived species, and species with wide length-for age ranges was frequently not possible.

(iii) Large numbers of specimens were required to reliably illustrate the length frequency distribution of a species (section 3.4.1.1). Large sample sizes meant that length-frequency analyses are not possible for the majority of species unless extraordinary efforts are made to collect sufficient specimens. A requirement for effective assessment of the age structure of populations is that specimens are both abundant and easy to sample (Butler *et al.* 1971; Buikema *et al.* 1982). The collection of sufficient specimens for all except the most abundant species would entail extensive time and financial commitment, thus reducing the cost-efficiency of monitoring.

Successful recruitment of five fish species (*B. imberi, L. rosae, O. mossambicus, B. marequensis, B viviparus*) in KNP rivers, particularly in 1988 and 1989, was illustrated in this study by the abundance of individuals calculated to be in their first growth period. These findings differ, in some respects, from changes in community diversity concluded from informal assessments of species abundances (section 3.3). Declines in the abundances of species could be expected to reflect low recruitment success. Declines in the abundance of *L. rosae* in the Letaba River, and *B. viviparus* in the Sabie River, however, were recorded (section 3.3.1) despite successful recruitment. Alternatively, successful recruitment of *B. marequensis* in the Olifants River did accompany an increase in abundance (section 3.3.1). Similarly, successful recruitment of *O. mossambicus* and *B. imberi* in the Letaba river accompanied little change in the abundances of these species (Table 3.3). Assessment of age distribution from length-frequency graphs does not appear to consistently mirror population size, with successful recruitment and high abundance of individuals in their first growth period still apparent in some numerically declining populations.

The shortcomings highlighted above suggest that assessment of the length-frequency of most fish populations in KNP rivers would not, with current knowledge and resources, be a viable, cost-effective monitoring approach. Texts which promote the use of length frequency assessments deal primarily with the study of single, commercially exploited populations, for the purpose of fisheries yield assessments (Rounsefell and Everhart 1953; Laeuastu 1965; Nikolskii 1969; Steele 1977; Gulland 1977, 1985; Cushing 1981; Everhart and Youngs 1981; Nielsen and Johnson 1983; Pauly 1984; Bell 1986; Saila and Recksiek 1988). The growth of such species are usually well researched, thus facilitating interpretation of length frequency graphs. Relatively few age and growth studies have been done on southern African freshwater fish (Skelton 1993), particularly species of little commercial interest. Such studies should form part of future research on KNP fish to facilitate use of length frequency assessments as a means of evaluating the structural diversity of fish populations.

3.5 ALPHA-DIVERSITY INDICES AS MEASURES OF CHANGE IN THE DIVERSITY OF FISH COMMUNITIES.

The limitations of largely descriptive methods of defining change in the diversity of fish assemblages (sections 3.3 and 3.4) indicated the necessity for more rigourous analytical methods, whereby the direction, degree and significance of diversity changes could be assessed. For this purpose alpha-diversity indices have been widely used in community studies in an attempt to simplify complex relationships between the number of species and individuals, and in doing so, describe community diversity with a single number (Dearden 1978; Magurran 1988).

The usefulness of indices for evaluating change in the diversity of communities has been debated in the literature almost since their inception (Hurlbert 1971; Peet 1974; Usher 1983; Wolda 1983). Diversity indices are considered by several authors to be informative (Peet 1974; Usher 1983; Wolda 1983; Magurran 1988), and having an important role in environmental assessments. Conversely, several authors (Whittaker 1972; May 1975; Southwood 1980; Karr 1981; Grieg-Smith 1983; Gotmark *et al.* 1986; Gadagker 1989) have questioned the value of diversity indices to enhance understanding of the dynamics of communities. Despite these criticisms, diversity indices continue (as pointed out in section 1.2.2.4) to be widely used in ecological studies.

The opposing opinions on the value of diversity indices to facilitate understanding of the dynamics of communities indicated the necessity for evaluation of the usefulness of their application to monitor diversity of fish communities in KNP rivers. The objective of this section is to undertake such an evaluation, with the value of diversity indices based on:

(i) The interpretability of diversity index results

(ii) The ability to define operational goals couched in terms of index values.

A vast array of alpha-diversity indices have been described in the literature, which differ with respect to the aspects of biotic diversity emphasized (species richness or dominance), wide usage in environmental studies, ease of calculation, and sensitivity to sample size (Magurran 1988). Time constraints precluded an evaluation of the usefulness of all diversity indices to describe fish community diversity changes in this study. Indices selected for evaluation were those which either enjoy wide usage and/or which have been described as providing a valuable measure in assessment of the diversity of communities (Magurran 1988). These are the Simpson, Shannon, Margaleff, Berger-Parker and log-series-α indices. In the modern era of ready access to computer technology, the ease of calculation was considered to be of little consequence in selecting indices for monitoring changes in the diversity of fish communities in KNP rivers. The sensitivity of different indices to sample size, however, and hence the question of what constitutes an appropriate sample size for reliable use of different diversity indices also had to be addressed.

Numerous biological studies have illustrated that the number of species sampled increases with sample size (Green 1979). The number of species sampled can, in turn, influence calculated values of alpha-diversity indices (Magurran 1988), particularly indices which emphasize species richness. Although an extensive literature exists on methodologies to determine minimum sampling intensity in plant community ecology (Green 1979; Grieg-Smith 1983), no references could be located where these have been applied in ichthyological studies. It appears as if most ichthyologists take what Magurran (1988) calls "the pragmatic approach" in determining sampling intensity, and sample until either time or money runs out, or alternatively, until they intuitively feel that they have adequately described community diversity. The danger of this approach is that where sample sizes are small, doubt will always exist about the accuracy of results. Sampling must be appropriate in intensity and breadth to support research conclusions, but likewise, should not occupy large amounts of time and resources beyond those required to reach the research objectives (Gauch 1984). Therefore the issue of minimum sample size has also been addressed below in order to:

(i) Ensure that within this study, evaluations of the usefulness of diversity indices to assess changes in the diversity of KNP fish communities was undertaken only using indices for which sample size was sufficiently large to support research conclusions.

(ii) Assess cost-efficiency of describing community diversity using diversity indices, based on required sampling intensity (number of samples).

3.5.1 Results and discussion

3.5.1.1 Minimum sampling intensity for describing alpha-diversity of fish communities

Species richness (S) of fish communities in deep pools in the Letaba River in 1988 stabilised at a sampling intensity of 18 seine net pulls (Figure 3.10a). No rapid inflection occurred in the species richness plot of the 1989 data (Figure 3.10b), though a decrease in slope did occur for a sampling intensity of greater than 14 seine net pulls. Inflection of diversity plots for the Simpson, Margaleff, Shannon, Berger-Parker and log-series-α indices occurred at approximately 14 seine net pulls in both sample years, indicating this to be the minimum sampling intensity on which diversity estimates should be based.

A minimum sampling intensity of 14 seine net pulls is suggested in spite of the species richness plot from the 1988 data set levelling off at 18 seine net pulls, as the increase from a mean S = 19 to mean S = 20 for sample sizes of 14 and 21 pulls respectively, represented only a 5% increase in information for a 33% increase in sampling effort. There is thus little advantage in a sampling intensity of greater than 14 seine net pulls when describing the diversity of fish communities in deep pools.

Minimum sampling intensity required for determination of diversity of rapid-dwelling communities differed for the Sabie and Olifants rivers. Inflection of the species richness plot derived from Sabie River data occurred after 60 sampling units (minutes electro-fishing) (Figure 3.11a), compared to a sampling intensity of approximately 110 sampling units in the Olifants River (Figure 3.11b). No marked inflection of diversity plots were apparent for indices which emphasize species richness (log-series-α and Margaleff) from samples collected in rapids in the Sabie River. Inflection of the diversity plots using indices which emphasize dominance (Berger-Parker, Simpson, Shannon), however, occurred at a sampling intensity of approximately 80 minutes (Figure 3.11a).

In contrast, in the Olifants River, despite a lower maximum species richness in comparison to the Sabie River (Olifants = 16, Sabie = 19), a higher minimum sampling intensity was indicated by the inflection of the diversity plots at a

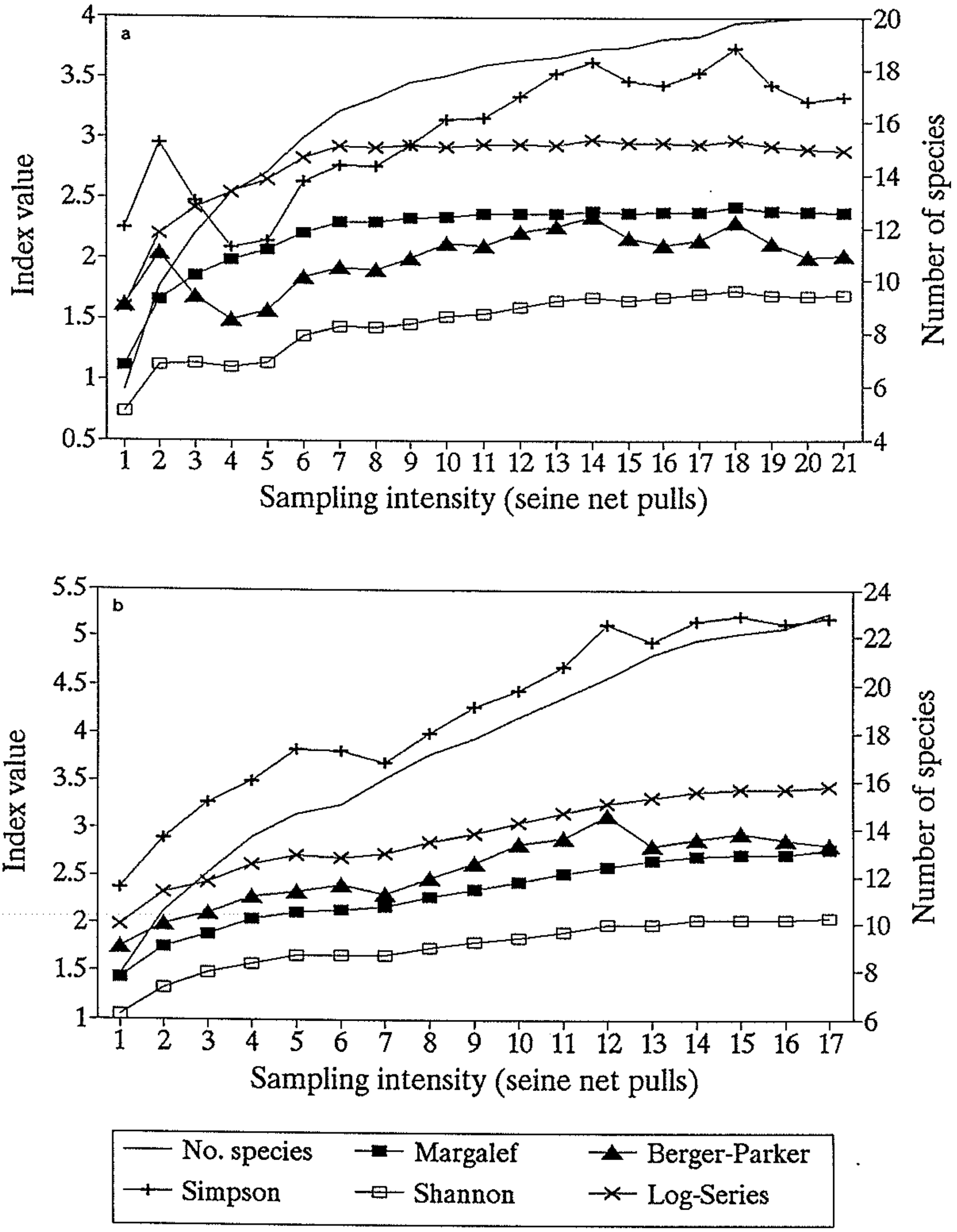

Figure 3.10 The number of fish species sampled (species richness), and alpha-diversity index values for increasing sampling intensity of fish communities sampled in deep pools in the Letaba River during 1988 (a) and 1989 (b).

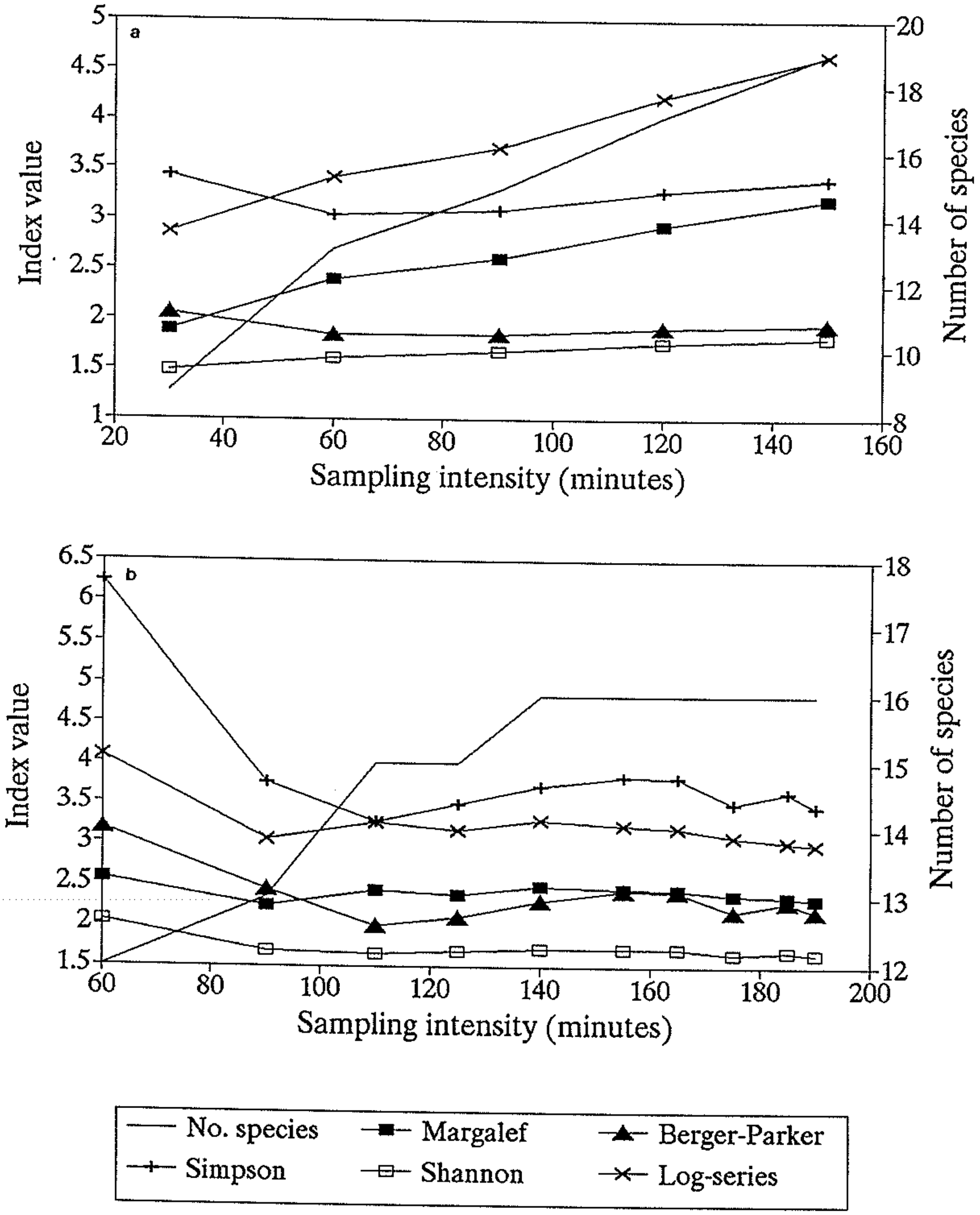

Figure 3.11 The number of fish species sampled (species richness), and alpha-diversity index values for increasing sampling intensity of fish communities sampled in rapids in the Sabie River (a) and Olifants River (b).

sampling intensity of approximately 110 minutes (Figure 3.11b). One hundred and ten minutes thus appears to be the minimum sampling intensity for describing diversity of rapid-dwelling fish communities.

Minimum sampling intensity required for determination of diversity of fish communities in marginal areas differed for the Sabie and Olifants rivers. Inflection of the species richness plots for communities in the Olifants River commenced at 105 sampling units (minutes electro-fishing) (Figure 3.12a), compared to 300 sampling units for the Sabie River (Figure 3.12b). In both rivers, the inflection of diversity plots using indices which emphasize dominance (Simpson and Berger-Parker) occurred at higher sampling intensities than diversity curves for indices emphasizing species richness (Figures 3.12a and 3.12b), indicating a necessity for a higher sampling intensity for the measurement of this community attribute. For the relatively species rich communities of the Sabie River, inflection of diversity plots occurred at a sampling intensity of 180 or less minutes, whereas in the relatively species poor communities of the Olifants River, inflection commenced at a sampling intensity of 120 or less minutes. Thus in the species rich communities of the Sabie River (and possibly the Crocodile River), a minimum sampling intensity of 180 minutes would be required to describe the diversity of fish communities in marginal areas, whereas in the species poorer rivers of the Limpopo system, a sampling intensity of 120 minutes would seem likely to be sufficient.

Adequacy of sampling intensities used in this study

Sampling intensity used in this study was, for some communities, below the calculated minimum for describing community diversity using alpha-diversity indices. These were deep pool-dwelling communities in the Olifants and Crocodile rivers, rapid-dwelling communities in the Letaba and Crocodile rivers, and marginal area-dwelling communities in the Letaba River. In addition, sampling intensity in marginal area-dwelling communities in the Olifants River in 1987 and Luvuvhu River in 1988, as well as rapid-dwelling communities in the Sabie River in 1988 were slightly below the recommended minima. As pointed out by Crovello (1970 cited in Gauch 1984), designing a sampling procedure frequently involves the making of subjective *a priori* decisions about basic parameters such as sampling intensity which, with hindsight, may be found to be inadequate. To negate the influence of undersampled communities, in subsequent sections of this

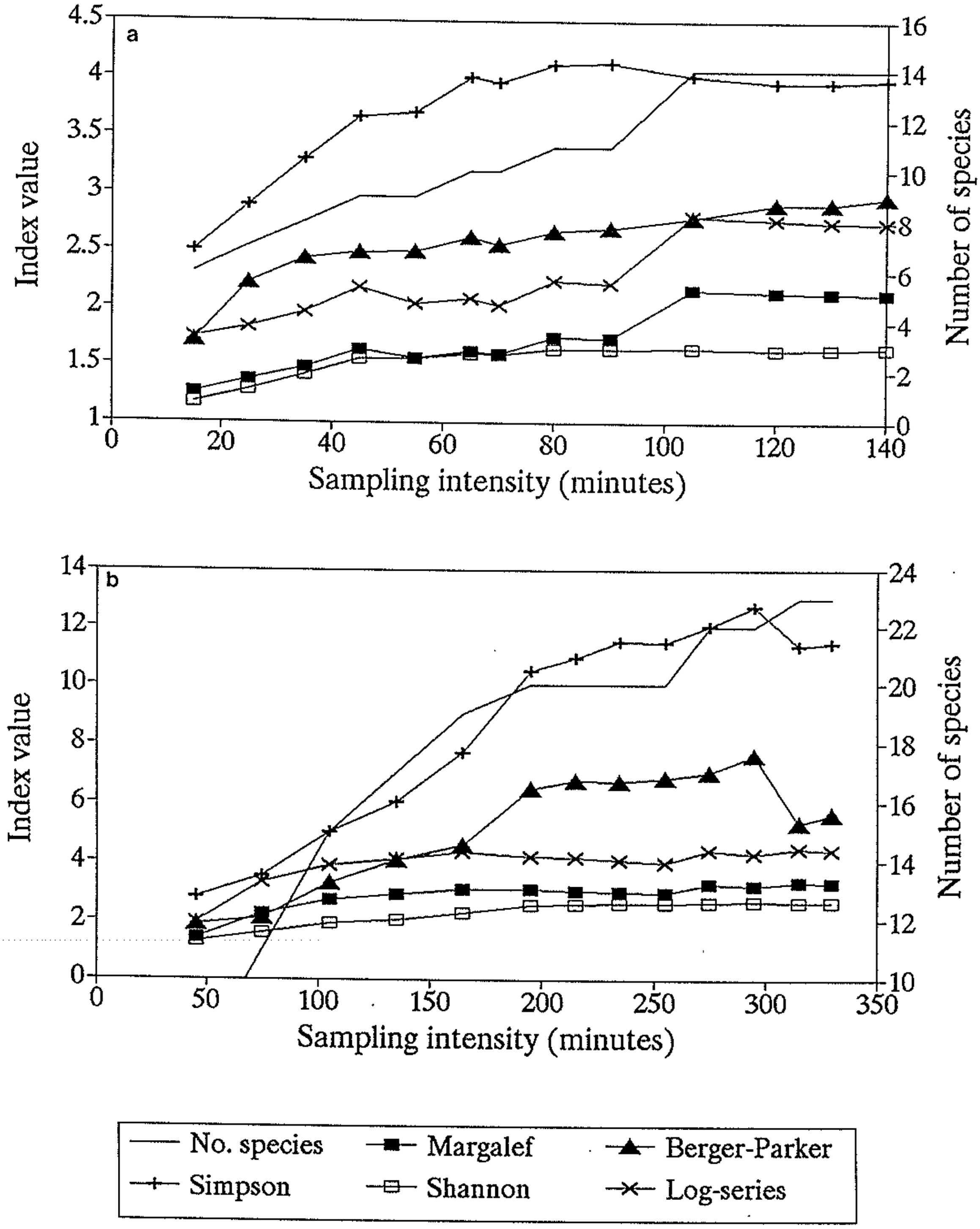

Figure 3.12 The number of fish species sampled (species richness), and alpha-diversity index values for increasing sampling intensity of fish communities sampled in marginal habitats in the Olifants River (a) and Sabie River (b).

chapter use has been made only of diversity indices which have been shown to be less sensitive to sample size, namely the log-series-α and Berger-Parker indices (Bullock 1971a; Kempton and Taylor 1974; May 1975; Taylor *et al.* 1976; Taylor 1978).

3.5.1.2 Cost-efficiency of monitoring programme using diversity indices

The calculated minimum sampling intensities necessary to describe the diversity of fish communities using indices are high (see above). The ease with which sampling could be undertaken at the calculated intensities in KNP rivers varied between rivers. Access to large portions of some rivers (particularly the Luvuvhu, Olifants, Crocodile rivers) was difficult due to the absence of roads and/or dense riparian vegetation. Consequently, the availability of sample localities where sampling apparatus could be safely and efficiently operated was limited. Difficulties associated with obtaining sufficient samples in some rivers (for example, rapids in the Letaba and Crocodile rivers, deep pools in the Olifants and Crocodile rivers) without extraordinary effort, would reduce the cost-efficiency of a monitoring programme in which alpha-diversity indices are used to describe change in the diversity of fish communities.

3.5.1.3 Interpretability of diversity index results

Determination of change in fish community alpha-diversity was undertaken by inspection of graphic plots of the number of species and individuals sampled (CPUE), and the log-series-α and Berger-Parker indices (Figures 3.13a to 3.13l). The log-series-α index provided a measure of alpha-diversity with an emphasis on species richness, whereas the Berger-Parker index emphasized species dominance (Magurran 1988). An increase in the log-series-α index value indicated an increase in diversity, whilst a decrease in the index value indicated a decrease in diversity. To facilitate interpretability, the inverse of the Berger-Parker index was used. Consequently, an increase in the index value indicated an increase in evenness (high evenness, which occurs when species are equal or virtually equal in abundance, is conventionally equated with high diversity (Magurran 1988)), whilst a decrease in the index value indicated an increase in dominance, and thus decrease in diversity.

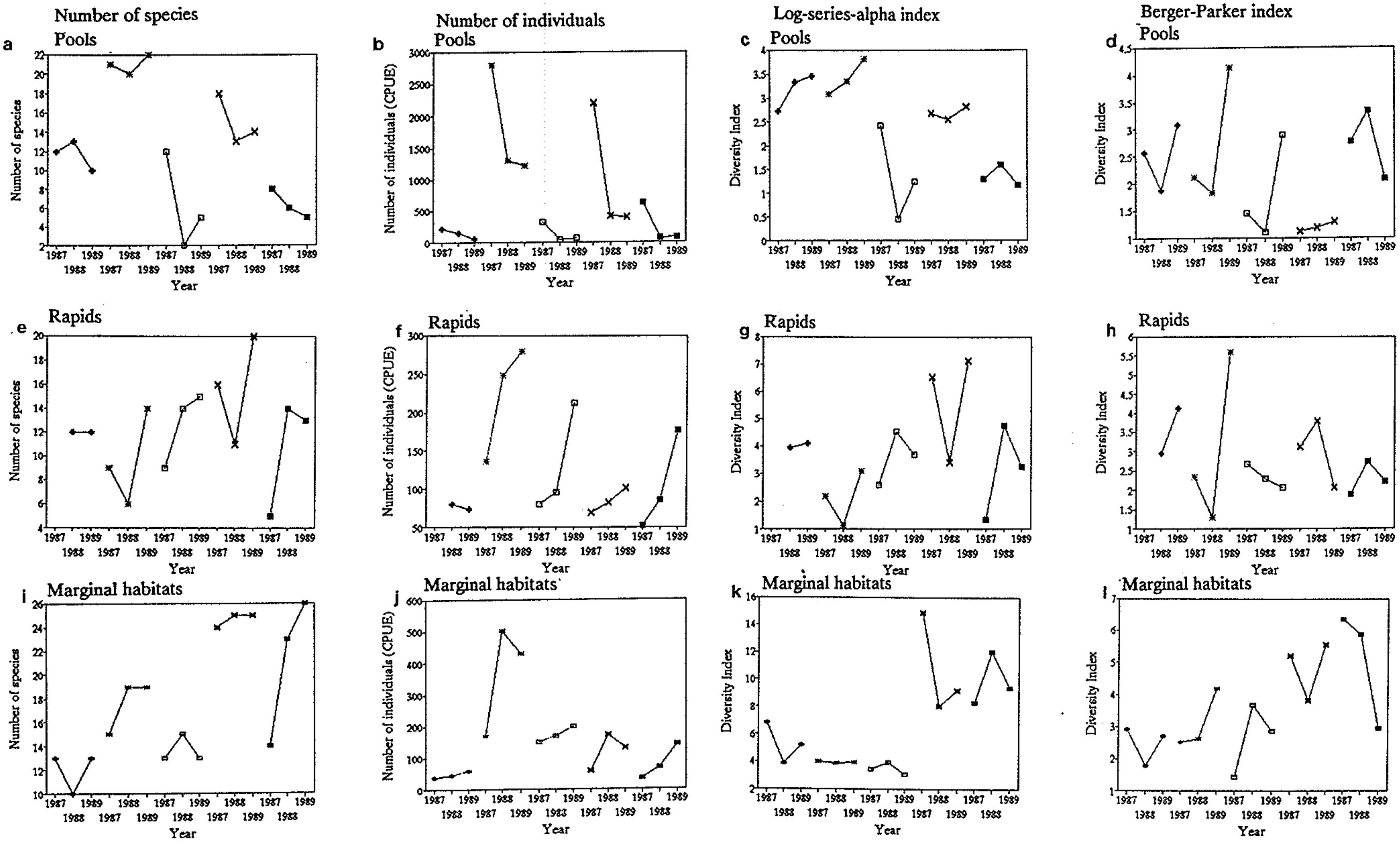

Figure 3.13 Species richness (a, e, i), number of individuals sampled (b, f, j), and index values for the log-series-alpha (c, g, k) and Berger-Parker (d, h, l) indices for fish communities in the Luvuvhu (plus), Letaba (star), Olifants (open square), Sabie (cross) and Crocodile (closed square) rivers. Abundance values expressed as CPUE, with sampling effort being ten seine net pulls in deep pools, and 60 minutes electro-fishing in rapids and marginal habitats.

The objective of describing changes in the diversity of fish communities using diversity indices was to enable evaluation of the interpretability of results by comparing indicated diversity changes with diversity changes concluded from informal assessments of species abundances (see section 3.3.1). As previously discussed (section 3.3.1) these changes incorporated decreases in the diversity of pool dwelling communities and increases or unchanged diversity in rapid and marginal area-dwelling communities, with the larges changes in diversity having occurred in 1988, notably in the Luvuvhu and Letaba rivers.

Instances where indices support previous diversity assessments.

In all KNP rivers, the number of individuals recorded in deep pools in the 1988 survey period was less than in 1987, with further declines in 1989 also recorded in the Luvuvhu, and Letaba rivers (Figure 3.13b). The largest declines in the number of individuals recorded in deep pools occurred in the Letaba and Sabie rivers. Declines in species richness of deep pool communities were also recorded in all rivers in 1988, with the exception of the Luvuvhu (Figures 3.13a). In addition, substantial decreases in the evenness of pool-dwelling communities in the Luvuvhu and Letaba rivers were recorded during 1988 (Figure 3.13d). These changes conformed with previously concluded declines in the diversity of pool-dwelling communities, large diversity changes in 1988, and notably large changes in the diversity of fish communities in the Letaba River (section 3.3.1).

Increases in the abundance of both rapid (Figure 3.13f) and marginal area-dwelling species (Figure 3.13j) were recorded in the Letaba, Olifants, Sabie and Crocodile rivers in 1988. In most rivers, this increase continued in 1989. Furthermore, increases in evenness were recorded in rapid-dwelling communities in the Sabie and Crocodile rivers in 1988 (Figure 3.13h), and marginal area communities in the Olifants River (Figure 3.13l). These changes conformed with previously (section 3.3.1) concluded increases in the diversity of rapid- and marginal area-dwelling communities.

Instances where indices and previous diversity assessments produced different results.

In all fish communities, log-series-α index values (Figures 3.13c, 3.13g and 3.13k) were strongly influenced by changes in species richness (Figures 3.13a, 3.13e, and

3.13i), with increases in diversity indicated in deep pool communities in the Luvuvhu and Letaba rivers, and a substantial decline in the diversity of marginal area-dwelling communities in the Sabie River during 1988. Decreases in evenness, and hence diversity, were also indicated in rapid-dwelling communities in the Letaba River in 1988 (Figure 3.13h), as well as marginal area-dwelling communities in the Luvuvhu, Sabie and Crocodile rivers (Figure 3.13l). These changes did not support previous (section 3.3.1) conclusions of decreasing diversity in pool-dwelling communities and increasing or unchanged diversity of rapid- and marginal area-dwelling communities.

In summary, similar trends of change in the diversity of fish communities in different rivers were consistently indicated only by changes in the abundances (CPUE) of individuals. These similarities were not reflected by either the log-series and Berger-Parker indices or species richness values. Changes in community diversity indicated by the abundances of individuals largely conformed with changes in fish community diversity previously concluded from informal studies of species abundances. The majority of community changes indicated using diversity indices, however, did not support previously concluded diversity changes.

Reasons for the frequent failure of indices to describe changes in community diversity.

Two potential explanations can be given for the large number of inconsistencies found between changes in community diversity using diversity indices and changes concluded from informal studies of species abundances. These are:

(i) Inaccurate conclusions of the direction and extent of changes in the diversity of fish communities as a consequence of the imprecise nature (section 3.3.1) of using informal studies of change in the species richness and abundance to define changes in biotic diversity.

(ii) An inability to accurately and consistently interpret the direction and extent, and hence desirability, of changes in biotic diversity using diversity indices.

Conclusions of the direction and extent of changes in the diversity of fish communities using informal studies of change in the species richness and abundance were motivated in section 3.3.1, and are assumed to be reasonably correct. Consequently, in this discussion emphasis is placed the ability of diversity indices to consistently indicate the direction and degree of biotic change.

To determine why diversity indices did not consistently indicate the direction and extent, and hence desirability, of changes in the diversity of fish communities, it is necessary to firstly establish what would constitute a desirable or undesirable change. In terms of the conservation objective to "maintain biotic diversity" (Mentis 1984), it is suggested that the occurrence of a greater number of indigenous fish species and individuals within a river would be a more desirable state than fewer species and individuals. Diversity indices, however, did not consistently indicate a change either towards or away from this desired state, and the latter situation (fewer species and individuals) in some instances (for example pool-dwelling communities in the Letaba and Crocodile rivers in 1988) resulted in a higher diversity index value than the former situation (greater number of species and individuals). The reason for this inconsistency is that indices which emphasize species richness are essentially a measure of the number of species in a defined sampling unit (Magurran 1988), and as such depict the ratio between the number of individuals and the number of species (Kempton and Taylor 1974; Taylor *et al.* 1976). Consequently, as pointed out by James and Rathbun (1981), different combinations of species richness and abundance can potentially produce the same index value. Although this limitation of diversity indices was not illustrated in this study, several other inconsistencies with respect to the ability of diversity indices to indicate the desirability of biotic changes were readily apparent. For example, declines in both the number of species and individuals sampled resulted in either an increase (for example, pool-dwelling community, Crocodile River, 1988) or decrease (for example, pool-dwelling community, Olifants River, 1988) in the index value. Alternatively, an increase in the abundance of both the number of species and individuals sampled could also result in either an increase (for example, rapid-dwelling community, Crocodile River, 1988) or decrease (for example, marginal-dwelling community, Sabie River, 1988) in the index value. Inconsistent directional changes in index values to changes in the number of species and individuals clearly limit their usefulness within a monitoring programme where the objective is to ascertain the desirability of changes in community diversity.

Interpreting changes in diversity index values

Problems also arose with interpreting the desirability of community changes when using diversity indices, such as the log-series-α, which afford equal weighting to all species by virtue of the algorithm being based solely on the parameters S (total number of species) and N (total number of individuals) (section 3.2.2.2). Two examples from this study can be used to illustrate that interpreting the desirability of community changes when using diversity indices cannot be effectively done without recourse to biological information. It was not readily apparent whether observed increases in log-series-α index values (for example in rapids in the Crocodile River in 1988) indicated a desirable process, or alternatively if declines in diversity (for example in rapids in the Sabie River in 1988) indicated an undesirable change in community diversity. The reasons for this statement become apparent when the species abundance changes in rapid communities which resulted in the observed diversity index changes are investigated, as discussed below.

The substantial increase in the diversity of rapid dwelling communities in the Crocodile River in 1988 was primarily a result of an increase in the number of species sampled. However, the additional species that were sampled were *A. mossambica*, *B. trimaculatus*, *B. viviparus*, *Glossogobius* spp., *H. vittatus*, *L. congoro*, *M. acutidens*, *O. mossambicus* and *P. philander*, none of which commonly occur in rapids (section 2.3.2.1). Alternatively, the recorded decline in diversity in rapids in the Sabie River in 1988 was primarily a consequence of *S. intermedius*, *T. rendalli*, *S. meridianus*, *A. mossambica* and *C. swierstrai* not being sampled. None of these species occur predominantly in rapids (section 2.3.2.1). Thus the question remains as to whether the invasion of a rapid by species which occur predominantly in other geomorphological features (as described above for the Crocodile River), resulting in an increase in species richness and community diversity, would constitute a desirable change. The reverse situation is also applicable with the question being whether the loss from rapids of species which occur predominantly in other geomorphological features (as described above for the Sabie River), and subsequent decline in species richness and diversity, indicates an undesirable change in the rapid community. It is suggested that the answer to both of these questions would be the affirmative. The reason for this being that although the species in question are not usually abundant in rapids, they would, even under pristine flow conditions, be expected to, on occasions, occur in rapids. They thus form a natural component of the rapid community. Diversity indices typically ignore the species composition of sampled communities (Karr 1981; Noss 1990), and the consequent equal weighting afforded to all species can result in the magnitude of the recorded change over-emphasizing the importance of the event.

3.5.1.4 Determination of operational goals for index values

In terms of the definition of monitoring given by Mentis (1984), monitoring is undertaken in order to test the hypothesis of no change from a set point or set of limits. This implies that before monitoring can commence, these limits or operational goals need to be known and clearly stated (Spellerberg 1991; Finlayson 1996).

Operational goals in terms of index values should reflect natural variation in species/abundance ratios and the proportional abundance of species (Spellerberg 1991). However, current understanding of the extremes of natural community fluxes is limited (Ferrar 1989), and thus how these translate into diversity index values is unknown. Consequently, diversity indices which reflect the proportional abundance of species cannot at present be used to monitor change in community diversity with the purpose of testing the achievement of conservation goals.

The only goal that could realistically be quantified is that of total species richness, defined as the number of species occurring in all geomorphological features (see Table 2.8). It is reasonable to assume that, for the purpose of conservation, the desired goal would be to retain a full species complement. Testing for the achievement of such a goal, however, would provide no additional ecological insights beyond those that could be obtained from assessment of species distribution changes (Chapter 2) and informal comparison of the abundance of species (section 3.3).

3.5.2 Summary and conclusions

The use of alpha-diversity indices to describe the diversity of fish communities, although easily achieved, entailed several practical and interpretive problems. Minimum sampling intensities necessary to describe the diversity of fish communities using indices are high (section 3.5.1.1), thus reducing the cost-efficiency of a monitoring programme in which diversity indices are employed as an analytical tool. Dissimilarities in the direction of change indicated by different indices (Spellerberg 1991) can create confusion about the type of change occurring, thus lowering confidence in the accuracy of interpretations of data sets. Difficulties also exist with evaluating the desirability of recorded changes, and it is not possible, with current knowledge, to confidently define and hence test for the achievement of conservation goals.

Diversity indices, and in particular the Shannon Index, have previously been used in studies of the diversity of fish assemblages (Udoidiong 1988; Silva 1995; Verbitskii 1996). Their reliability for enumerating the diversity of fish assemblages, however, appears to have not previously been assessed. The suite of problems associated with the use of alpha-diversity highlighted by this study lends support to the conclusions of Whittaker (1972), May (1975), Southwood (1980), Grieg-Smith (1983) and Gotmark *et al.* (1986) that diversity indices are of limited value for advancing understanding of the dynamics of communities. It is concluded that alpha-diversity indices should not be used in a monitoring programme of fish communities in KNP rivers.

The inability of alpha-diversity indices to illustrate the direction, extent, and desirability of changes in the diversity of fish communities stemmed largely from their simplicity. The identity of the component species is irrelevant (Karr 1981) with all species being afforded equal weighting. This simplicity frequently results in a loss of community information (James and Rathbun 1981; Noss 1990). One of the primary advantages of species abundance models, however, is that they incorporate all of the information of species abundances, and consequently are considered to provide a more complete mathematical description of species abundance data (Magurran 1988). Consequently the use of species abundance models as measures of change in the diversity of fish communities were considered as a potentially useful analytical tool to pursue, and are evaluated in the following section of this chapter.

3.6 SPECIES ABUNDANCE MODELS AS MEASURES OF FISH COMMUNITY CHANGE

Study of the species-abundance relationships in communities has led to the development of several species abundance models, of which the geometric-series, log-series, log-normal and broken-stick models are widely recognised (Magurran 1988). The use of species abundance models as a basis for examining the diversity of communities has been advocated by several authors (May 1975; Southwood 1980; Magurran 1988). Community diversity is described by referring to the model which provides the closest fit to the observed pattern of species abundances (Magurran 1988).

In this study, the suitability of species abundance models for monitoring change in the diversity of fish communities is evaluated, based on:

(i) The interpretability of species abundance model results by comparison with diversity changes concluded from informal assessments of species abundances (section 3.3.1)

(ii) The ability to define operational goals couched in terms of the fit of species abundance models.

3.6.1 Results and discussion

3.6.1.1 Interpretability of species abundance models

Assessment of the interpretability of species abundance model results necessitated translation of fish community diversity changes previously concluded from informal studies of the abundance of fish species (section 3.3.1) into terms of the fit of different abundance models. Based on the theoretical properties of the different species abundance models (section 1.2.2.4), it is expected that a decline in the diversity of pool-dwelling communities would be indicated by change in the fit of species abundance models in the direction of broken-stick to log-normal, to log-series, to geometric-series. Conversely, the diversity of rapid and marginal area-dwelling communities would remain unchanged or increase slightly, indicated by a change in the fit of species abundance models in the direction of geometric-series to log-series to log-normal to broken-stick. Furthermore, the largest changes in the diversity of fish communities would occur in 1988, and notably in the Luvuvhu and Letaba rivers (section 3.3.1).

Instances where species abundance models and informal assessments of species abundances produced similar results.

Increases in the diversity of fish communities in successive sample years, illustrated by the fit of abundance models and the shape of rank abundance plots, were indicated in rapid-dwelling communities in the Olifants River (1987 = log-series; 1988 = log-series; 1989 = log-series/log-normal) (Figure 3.14h; Table 3.9) and Crocodile River (1987 = geometric-series; 1988 = log-series; 1989 = log-series) (Figure 3.14n; Table 3.9). Similar increases in diversity were indicated in marginal area-dwelling communities in the Olifants River (1987 = log-series; 1988 = broken-stick; 1989 = log-series/log-normal) (Figure 3.14j; Table 3.10) and Crocodile River (1987 = log-series; 1988 = log-series; 1989 = log-series/log-normal) (Figure 3.14o; Table 3.10). Relatively minor changes in diversity were indicated in rapid-dwelling communities in the Luvuvhu River (geometric-series in all sample years) and Sabie River (log-normal in all sample years) (Figures 3.14b and 3.14k; Table 3.9), as well as marginal area-dwelling communities in the Luvuvhu River (geometric-series in all sample years though with log-series becoming a better fit with time), Letaba River (log-series in all sample years) and Sabie River (log-normal in all sample years) (Figures 3.14c, 3.14e and 3.14l; Table 3.10). These changes conformed with prior conclusions of minor changes in diversity of rapid and marginal area-dwelling communities, with the largest diversity changes occurring in 1988 (section 3.3.1).

Deep pool communities in the Sabie River underwent, as predicted (section 3.3.1), a decline in diversity in 1988, with the log-normal distribution providing the best fit in 1987 and 1989 (Figure 3.14j), and species abundances being best described by the log-series distribution in 1988.

Instances where species abundance models and informal assessments of species abundances produced different results.

Some changes in the diversity of fish communities indicated using diversity models did not support changes in fish community diversity previously concluded

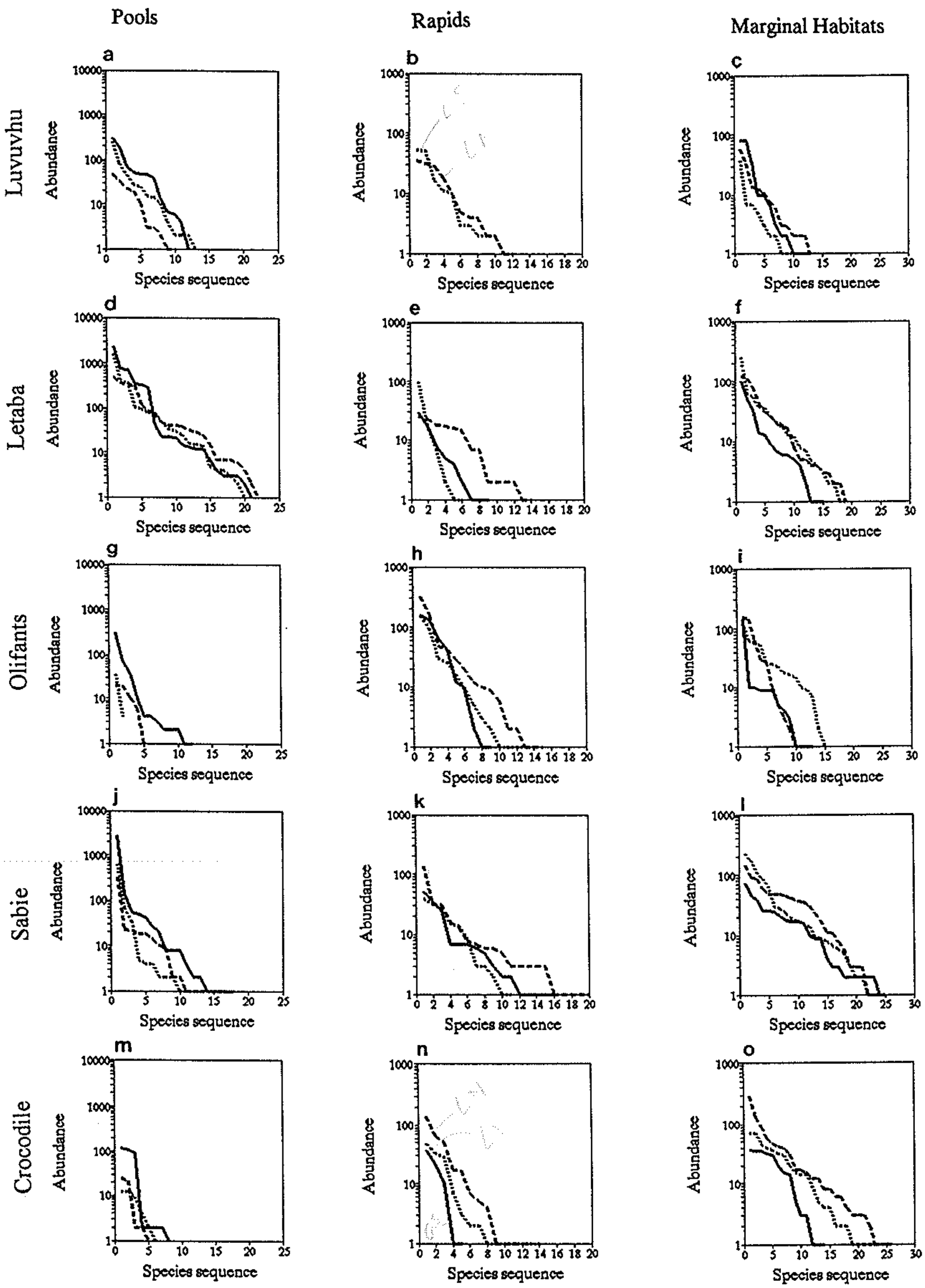

Figure 3.14 Rank abundance plots for fish communities in deep pools, rapids and marginal habitats in the Luvuvhu (a, b, c), Letaba (d, e, f), Olifants (g, h, i) Sabie (j, k, l) and Crocodile (m, n, o) rivers. Fish communities sampled in 1987 indicated by solid lines, 1988 by dotted lines, and 1989 by dashed lines.

Table 3.8 Chi-squared test results for the fit of observed fish species abundance's from deep pools in the Luvuvhu, Letaba, Olifants and Sabie rivers to species abundance's predicted by the geometric-series, log-series, log-normal and broken-stick abundance models.

		1987			1988			1989		
River	Model	X^2	df	Prob	X^2	df	Prob	X^2	df	Prob
Luvuvhu	Geometric series	1.90	3	>50%	0.64	4	>90%	0.00	2	>99%
	Log series	3.29	3	>10%	0.35	4	>98%	0.42	2	>80%
	Log normal	3.44	2	>10%	0.19	3	>98%	0.35	1	>50%
	Broken stick	10.72	3	>1%	7.38	4	>10%	0.28	2	>98%
Letaba	Geometric series	7.33	5	>10%	2.64	5	>70%	2.04	5	>80%
	Log series	2.07	6	>90%	2.03	6	>90%	4.33	5	>50%
	Log normal	9.48	5	>5%	2.69	5	>70%	3.71	4	>10%
	Broken stick	81.29	5	<0.1%	24.54	5	<0.1%	27.15	5	<0.1%
Olifants	Geometric series	3.47	3	>10%						
	Log series	3.72	4	>10%						
	Log normal	1.57	3	>60%						
	Broken stick	125.07	4	<0.1%						
Sabie	Geometric series	24.20	9	>0.1%	7.05	4	>10%	13.00	4	>0.1%
	Log series	2.92	7	>70%	7.98	6	>10%	6.19	5	>10%
	Log normal	4.46	8	>80%	11.51	5	>2.5%	5.64	4	>10%
	Broken stick	222.52	9	<0.1%	57.52	4	<0.1%	32.80	4	<0.1%

Table 3.9 Chi-squared test results for the fit of observed fish species abundance's from rapids in the Luvuvhu, Olifants and Sabie rivers to species abundance's predicted by the geometric-series, log-series, log-normal and broken-stick abundance models.

		1987			1988			1989		
River	Model	X^2	df	Prob	X^2	df	Prob	X^2	df	Prob
Luvuvhu	Geometric series				0.05	3	>90%	2.00	5	>80%
	Log series				5.97	4	>10%	4.92	5	>10%
	Log normal				3.75	3	>10%	2.50	4	>60%
	Broken stick				24.43	4	<0.1%	5.55	5	>10%
Olifants	Geometric series	2.25	4	>60%	7.50	6	>10%	6.5	7	>10%
	Log series	1.03	5	>95%	1.64	6	>95%	1.95	7	>95%
	Log normal	.94	4	>90%	2.40	5	>70%	1.16	6	>98%
	Broken stick	8.81	4	>5%	42.36	6	<0.1%	22.17	7	>0.1%
Sabie	Geometric series	2.67	4	>60%	2.50	5	>70%	4.58	4	>10%
	Log series	3.33	4	>50%	3.48	5	>60%	20.00	6	>0.1%
	Log normal	.85	3	>80%	1.32	4	>80%	18.54	5	>0.1%
	Broken stick	4.22	4	>10%	2.68	5	>70%	8.99	4	>5.0%
Crocodile	Geometric series				41.50	4	<0.1%	2.17	5	>80%
	Log series				2.87	5	>70%	1.73	5	>80%
	Log normal				6.01	4	>10%	2.41	4	>60%
	Broken stick				29.93	5	<0.1%	16.96	5	>0.1%

Table 3.10 Chi-squared test results for the fit of observed fish species abundance's from marginal areas in the Luvuvhu, Letaba, Olifants, Sabie and Crocodile rivers to species abundance's predicted by the geometric-series, log-series, log-normal and broken-stick abundance models.

		1987			1988			1989		
River	Model	X^2	df	Prob	X^2	df	Prob	X^2	df	Prob
Luvuvhu	Geometric series	1.55	3	>60%	4.70	3	>10%	0.83	5	>95%
	Log series	4.17	4	>10%	2.12	4	>70%	2.20	5	>80%
	Log normal	3.57	3	>10%	9.12	3	>3%	0.91	4	>90%
	Broken stick	46.13	4	<0.1%	101.65	4	<0.1%	3.54	5	>60%
Letaba	Geometric series	.64	4	>95%	3.33	5	>60%	0.67	5	>98%
	Log series	1.17	5	>90%	2.11	6	>90%	1.51	5	>90%
	Log normal	1.03	4	>80%	1.36	5	>90%	1.68	4	>70%
	Broken stick	54.03	5	<0.1%	11.32	6	>5%	12.97	5	>1%
Olifants	Geometric series	3.83	3	>10%	7.30	5	>10%	4.50	7	>70%
	Log series	1.71	4	>70%	13.59	5	>1%	1.46	7	>98%
	Log normal	10.41	3	>1%	2.11	4	>70%	1.42	6	>95%
	Broken stick	8.04	3	>3%	1.15	5	>90%	33.42	7	<0.1%
Sabie	Geometric series	1.00	5	>95%	3.33	6	>70%	4.37	6	>60%
	Log series	4.72	5	>10%	5.82	7	>50%	11.10	6	>5%
	Log normal	3.02	4	>50%	4.04	6	>60%	4.63	5	>10%
	Broken stick	5.31	5	>10%	60.67	7	<0.1%	14.78	6	>3%
Crocodile	Geometric series				1.50	4	>80%	4.38	6	>60%
	Log series				1.49	4	>80%	3.73	6	>70%
	Log normal				2.71	3	>10%	3.81	5	>50%
	Broken stick				8.03	4	>5%	18.65	6	>0.1%

from informal studies of species abundances (section 3.3.1). For example, the abundance of rapid-dwelling species in the Letaba River approached a log-series distribution in 1987, though degraded into a classic geometric-series distribution in 1988 (Figure 3.14e), which did not concur with previously concluded minor changes or increases in diversity of rapid dwelling communities (section 3.3.1).

Species abundances in deep pool communities in the Luvuvhu River approached a geometric distribution in 1987 and 1989 (Figure 3.14a), with abundances being described by both log-series and log-normal distributions in 1988 (Table 3.8). Consequently, the abundance models for pool communities in the Luvuvhu river did not, as concluded (section 3.3.1), indicate a decline in diversity over time, despite successive reductions in species richness (Figure 3.14a) (indicated by the progressive movement of rank abundance plots towards the graph origin). Similarly, species abundances in deep pools in the Letaba River approached a log-series distribution in all years (Figure 3.14d; Table 3.8) which did not indicate a decline in diversity over time, as previously concluded (section 3.3.1). Finally, abundance models did not indicate greater diversity changes in fish communities in the Luvuvhu and Letaba rivers compared to the Olifants, Sabie and Crocodile rivers.

Deep pool communities in the Olifants (Figure 3.14g) and Crocodile (Figure 3.14m) rivers were inadequately sampled for meaningful interpretation of species abundance data.

In summary, there were three instances where changes in community diversity indicated by species abundance models differed from informal assessments of changes in species abundances. However, in the majority of communities and rivers, diversity changes indicated by the two methods were similar. This suggests that abundance models could potentially provide interpretable results on change in the diversity of fish communities in the majority of cases. To further test this conclusion, an alternative evaluation approach was used. This entailed comparison of recorded changes in the aquatic environment with changes in fish community diversity, in order to define plausible hypotheses of cause and effect.

Comparisons between environmental and diversity changes.

In large species-rich communities, species abundances usually approach a log-normal distribution (Magurran 1988) whereas the geometric-series pattern of species abundance is found primarily in species poor communities, occurring under a harsh environmental régime (May 1981). Several studies have demonstrated that stressed communities undergo reductions in diversity (Schafer 1973; Rosenberg 1976; Wu 1982) and can shift from a log-normal distribution to the less equitable log-series or geometric-series distribution (May 1981). Knowledge of the extent of environmental stress on fish communities resulting from anthropogenic modifications to the physical, chemical and biological environment could thus potentially provide insight into the environmental processes governing the diversity of communities.

Fish community diversity was highest in the Sabie River, where species abundances in deep pool communities approached a log-normal distribution in two of the three sample years (1987 and 1989) (Figure 3.14j), and rapid-dwelling communities conformed to a log-normal distribution in all sample years (Figure 3.14k, Table 3.9). Chi-squared tests indicated that species abundances in marginal areas in the Sabie River were described by the geometric-series in all sample years (Table 3.10), due largely to the absence of abundant species, particularly in the 1987 and 1989 samples. The shape of rank abundance plots (Figure 3.14l), however, indicated that for the middle and lower species abundance classes, marginal area-dwelling communities in the Sabie River were best described by a log-normal distribution in all sample years. In terms of anthropogenic modifications to the physical, chemical and biological environment, the Sabie River, with comparatively low severity of past low flow conditions (section 2.3.3.2), minor long-term changes in water quality (section 2.3.3.3), relatively low incidence of episodic pollution events (section 1.3.7), and moderate infestations of alien aquatic plants (section 2.3.3.4), could be considered to be the least perturbed of KNP rivers. Diverse fish communities have undoubtedly persisted in the Sabie River by virtue of low levels of anthropogenic modifications to the physical, chemical and biological environment.

In contrast, the diversity in fish communities was lowest in the Luvuvhu River, with deep pool communities approaching a geometric distribution in two of the three sample years (1987 and 1989) (Figure 3.14a), and both rapid and marginal area-dwelling communities approaching a geometric-series distribution in all sample years (Figures 3.14b and 3.14c; Table 3.9). Diversity of fish communities in the Letaba River, although variable, most frequently approached a log-series distribution in the majority of sample years (Tables 3.8, 3.9 and 3.10) and hence is intermediate to the Luvuvhu and Sabie rivers. The severity of low flow conditions in the Luvuvhu and Letaba rivers (section 2.3.3.2), coupled with deteriorations in water quality (sections 1.3.4; 1.3.5; 2.3.3.3) and long-term reductions in the abundance and distribution of emergent aquatic plants (section 2.3.3.4), indicate that the Luvuvhu and Letaba rivers are the most highly perturbed of KNP rivers. The low diversity of fish communities in the Luvuvhu, and to a lesser extent, Letaba river can be readily explained by the high levels of anthropogenic modifications of the physical, chemical and biological environment, and in particular, recent increases in the severity of low flows (section 2.3.3.2).

Diversity of fish communities in the Olifants and Crocodile rivers, similar to the Letaba River, most frequently approached a log-series distribution in the majority of sample years (Tables 3.8, 3.9 and 3.10) and hence were intermediate to the Luvuvhu and Sabie rivers. The severity of past low flows in the Olifants River has been comparatively low (section 2.3.3.2) and both decreases and increases in the abundance of emergent aquatic plants have been recorded (section 2.3.3.4). Substantial deterioration in water quality has, however, been recorded (section 2.3.3.3) which, coupled with periodic episodic pollution events (section 1.3.6), suggests a level of environmental perturbation intermediate to the Sabie and Luvuvhu rivers. A similar, intermediate ranking of environmental perturbation could be assigned to the Crocodile River, with comparatively low severity of past low flows (section 2.3.3.2), moderate changes in water quality (section 2.3.3.3), and high infestations of alien aquatic plants (section 2.3.3.4). The observation that the diversity of fish communities in the Olifants and Crocodile rivers were, for the most part, intermediate to the Luvuvhu (geometric-series) and Sabie (log-series) rivers, can be readily explained by the moderate levels of anthropogenic modifications of the aquatic environment.

In summary, changes in the aquatic environment in KNP rivers correlated with the fit of species abundance models, with fish community diversity being low in highly perturbed rivers, high community diversity in relatively pristine rivers, and intermediate community diversity in rivers with intermediate levels of environmental disturbance. Recorded historic changes in the aquatic environment of KNP rivers can thus provide plausible explanations for the diversity of fish communities in KNP rivers indicated by the fit of species abundance models. This conforms with the findings of Schafer (1973), Rosenberg (1976), May (1981) and Wu (1982) who hypothesized a correlation between community diversity, measured as the fit of species abundance models, and environmental disturbance. It is concluded that the fit of diversity models to fish species abundance data can provide interpretable results on change in the diversity of fish communities.

3.6.1.2 Determination of operational goals for species abundance models

One of the primary advantages of the use of species abundance models to monitor change in the diversity of fish communities is that realistic operational goals (Mentis 1984) can be set. Theoretically, the operational goal for all communities should be that species abundances should approach a broken-stick distribution, as this would reflect maximal uniformity of species abundance. The point in question, however, is whether this goal would be realistic for diverse fish communities in KNP rivers.

The broken-stick model has been used successfully to describe species abundances in fish communities of taxonomically related species (King 1964). Furthermore, it was observed in this study that fish communities in marginal areas in the Olifants River in 1988 were described by the broken-stick distribution. Thus the broken-stick distribution is biologically realistic. However, there are three arguments, based on consideration of the theoretical properties of the various distribution models, as well as tests with field data, that can be used to suggest that a log-normal distribution would be a more appropriate goal than the broken-stick distribution.

Firstly, most studies of the diversity of equilibrium communities in unperturbed environments have revealed that species abundances are log-normally distributed (May 1975; 1981). Species abundances in stable communities which are not described by a log-normal distribution, are generally described by the log-series (Taylor 1978; Kempton and Wedderburn 1978; Shaw *et al.* 1983), rather than by a broken-stick distribution. Small sample sizes can result in rare species not being collected, and hence log-normally distributed species abundances being truncated (Preston 1948) which can be virtually indistinguishable from a log-series species abundance distribution (Magurran 1988). The undersampling of rare species is frequently viewed as the reason for the diversity of some unperturbed, equilibrium communities being described by the log-series rather than the log-normal distribution (Magurran 1988). There is no evidence in the literature, however, to suggest that the broken-stick distribution is appropriate to most communities, and similarly, there is no evidence to suggest that species abundances of fish communities would not follow the general rule of being log-normally distributed.

Secondly, the broken-stick distribution is most frequently observed in communities consisting predominantly of taxonomically related species (Magurran 1988). Fish communities in KNP rivers, however, contain representatives of nine different families (Anguillidae, Mormyridae, Characidae, Cyprinidae, Schilbeidae, Mochokidae, Cichlidae, Sparidae, Gobiidae). These communities are taxonomically diverse. Thus, theoretically a broken-stick distribution would be inappropriate.

The third argument in favour of a log-normal distribution as an appropriate operational goal for species abundances stems from the results of this study. Working on the premise that the Sabie River is the least perturbed of the five rivers studied (sections 1.3.7, 2.3.3.5 and 3.6.1.1) it is argued that species abundances observed in this river would most closely approach that expected under natural conditions. Only in the Sabie River were species abundances consistently normally distributed.

There is no evidence to suggest that the diversity of fish communities would, under pristine environmental conditions, differ substantially between the different KNP rivers studied. All rivers have a similar species composition (section 3.3.1), history of perenniallity of flow, and chemical composition (sections 1.3.4 to 1.3.8). Consequently, it would be reasonable to expect similarity in fish community diversity in the different KNP rivers under natural conditions. Thus, it is concluded that a log-normal species abundance would be the most appropriate operational goal for fish communities in all major rivers in the KNP. Although several communities described in this study approach a log-series or geometric-series distribution, these deviations from the ideal (log-normal) can readily be explained by recorded environmental changes and habitat perturbations (section 3.6.1.1) which could have driven these communities towards a less equitable species distribution.

3.6.1.3 General discussion and conclusions

Although species abundance models have been used to describe the diversity in a wide range of biota, including plant (Whittaker 1965), insect (Kempton and Taylor 1978; Taylor 1978; Wells 1992) and birds communities (MacArthur 1960), only one reference could be located which describe their use to define the diversity of fish communities (King 1964). The majority of studies which have utilised abundance models, however, have centred primarily on understanding the allocation of environmental resources between species (Whittaker 1972; Pielou 1975; May 1975, 1981; Sugihara 1980; Ugland and Gray 1982), with few critical assessments, based on empirical studies, of the ability of abundance models to discriminate between changed environmental conditions. Kempton and Taylor (1974) and Taylor *et al.* (1976) have, however, demonstrated that in some terrestrial insect communities, abundance models, and in particular the slope of the log-series curve, can be used to discriminate between diversities in areas where the environment had been known to have changed. Similarly, Schafer (1973), Rosenberg (1976) and Wu (1982) have demonstrated that species abundance models can be used to determine the effects of water pollution on aquatic invertebrate communities. The findings of this study indicate that the fit of abundance models could also be used to describe the effect of environmental changes on the diversity of riverine fish communities, and as such provide a useful means of data analysis within a monitoring programme.

A further advantage to using abundance models is that, in accordance with the requirements of monitoring (Hellawell 1978, 1992; Mentis 1984; Smith 1985) realistic operational goals can be set. It was concluded that a log-normal pattern of species abundance is the most appropriate operational goal for fish communities in KNP rivers, which conforms with the observation of Sugihara (1980) that the log-normal abundance pattern is displayed by the majority of communities studied by ecologists.

The usefulness of species abundance models to provide information on the diversity of fish communities was, however, reduced by several shortcomings. These were:

(i) Neither visual inspection of rank abundance plots or comparisons of observed and expected abundances using X^2 tests provided an ideal means of exploring the fit abundance models to species abundance data (Magurran 1988), necessitating the employment of both methodologies (see section 3.2.2.3). Problems arose where the different analytical methodologies yielded different results (for example see marginal area-dwelling communities in the Sabie River where X^2 tests indicated that species abundances were best described by the geometric-series, yet the shape of rank abundance plots indicated that species abundances were best described by a log-normal distribution) making it difficult to confidently describe community diversity.

(ii) Some data sets may be described equally well by more than one abundance model, particularly the log-series and the log-normal models where the log-normal is truncated (Shaw *et al.* 1983). In such situations it may be difficult to decide which model provides the best fit to a data set, thus hampering interpretation of the significance of directional change in community diversity.

(iii) If the data to which a log-normal distribution is fitted is derived from a finite sample, a portion of the normal curve to the left of the origin (representing the rare and undersampled species) will be obscured (Magurran 1988). This could result, as described in point (ii) above, in difficulty in distinguishing between the fit of the log-normal and log-series abundance models. Only in large data collections, covering wide geographic areas, will a full log-normal curve be apparent (Magurran 1988). Although minimum sampling intensity required to reliably distinguish between the fit of abundance models was not addressed in this study, this is likely to be substantial. The necessity for a large, though undefined, sample size would reduce the cost-efficiency of a monitoring programme, and necessitate the making of subjective decisions about when sample sizes are large enough.

Potential difficulties in distinguishing between the fit of the log-normal and log-series distributions described in points (i) and (ii) above, although hampering interpretation of the significance of directional change in community diversity where sample sizes are small, would not influence assessment of the achievement of the operational goal of normally distributed species abundances. Consequently, it is concluded that the fit of diversity models to fish species abundance data could provide an informative means of describing the diversity of fish communities in KNP rivers for the purpose of evaluating the achievement of conservation objectives. Sample sizes used in this study were sufficiently large to enable distinction between the fit of different abundance models and consequently could be used as a guide in future monitoring exercises. Sample sizes used in this study, however, were high, indicating the need to investigate alternate, potentially more cost-efficient, means of describing change in fish communities. To this end an assessment of the utility of condition factors as a means of monitoring change in fish communities is evaluated in the following section of this chapter.

3.7 CONDITION FACTORS AS MEASURES OF COMMUNITY CHANGE

The analysis of length-mass data of fish is usually directed towards one or both of two different objectives (Le Cren 1951). Firstly, describing mathematically the relationship between mass and length so that one can be converted into the other, and secondly, to enable measurement of the variation of the expected mass for length of either individuals or groups to provide a measure of fatness or general 'well-being'. This measure of fatness is generally described as a coefficient of condition, ponderal index, or condition factor (Le Cren 1951). The implication being that the heavier a fish is at a given length, the larger the factor, and hence the better its physical condition (Ricker 1975).

Several studies have used indices of condition to assess the effects of environmental stresses in fish populations in southern Africa (Schoonbee *et al.* 1972; Kenmuir 1973; Marshall and Van der Heiden 1977; Baird and Fourie 1978). In this section, an index of condition has been calculated for several fish species in different rivers to facilitate assessment of this methodology as a means of monitoring change in fish communities.

3.7.1 Results

Decline in the diversity of fish communities in KNP rivers has been observed to coincide with unfavourable environmental conditions (section 3.6.1.1). Therefore, it is hypothesized that decline in the physical condition of fish should accompany a decline in community diversity, and inversely an increase in physical condition should accompany an increase in community diversity. This hypothesis, and hence the interpretability of indices of physical condition of fish, was tested by comparing recorded changes in condition of fish species frequently recorded in the same geomorphological feature (section 2.3.2.1) with diversity changes concluded from both informal studies of species abundances (section 3.3.1), and the fit of species-abundance models (section 3.6.1.1).

If a correlation should exist between the physical condition of fish species and community diversity, expected changes in condition over the study period would include decreases in the condition of pool-dwelling species; increases or unchanged condition in rapid and marginal area-dwelling species; and large changes in condition in 1988, particularly in the Luvuvhu and Letaba rivers.

3.7.1.1 Condition of fish species in the Luvuvhu River

The condition of the majority of fish species abundant in pools in the Luvuvhu River declined over the sample period of 1987 to 1989. A significant decline in condition of *Glossogobius* spp. ($t=11.202$ $p<0.0001$) and *O. mossambicus* ($t=8.267$ $p<0.0001$) occurred between 1987 and 1989 (Figures 3.15o and 3.15x). The condition of *M. acutidens* showed a downward trend over this same period, though declines in 1989 were not significant ($t=0.911$ $p>0.05$) (Figure 3.15w). A downward trend was also indicated by *B. afrohamiltoni* in 1988 (Figure 3.15a), and significant declines were recorded for *S. zambezensis* ($t=8.307$ $p<0.0001$), *L. rosae* ($t=7.006$ $p<0.0001$) and *H. vittatus* ($t=4.257$ $p<0.0001$) in 1989 (Figures 3.15aa, 3.15s and 3.15p). Insufficient specimens of the latter three species were collected in 1987 to enable comparison of change in condition over the period 1987 to 1988. A significant decline in the condition of *C. gariepinus* ($t=6.628$ $p<0.0001$) was recorded in 1988, though condition increased again in 1989 (Figure 3.15m). The condition of only two pool-dwelling species, *B. imberi* ($t=3.564$ $p<0.005$) and *S. intermedius* ($t=11.191$ $p<0.0001$), showed increases over the sample period (Figure 3.15i and 3.15n), however, condition of *B. imberi* declined in 1989 to a level similar to that recorded in 1987. The decline in condition of most deep-pool specialists in the Luvuvhu River concurred with observations of declines in the diversity of this community concluded from informal studies of species abundances (section 3.3.1).

Sufficient specimens for analysis of condition of the rapid-dwelling *C. paratus* and *L. molybdinus* were collected only in 1988 and 1989. Direction of change in condition differed in these two species, with that of *L. molybdinus* increasing in 1989 (Figure 3.15r), whereas a decline was recorded for *C. paratus* (Figure 3.15j). Both changes, however, were not significant. Insignificant changes in condition of fish species in rapids in the Luvuvhu River concurred with previous conclusions of minor changes in diversity of these communities (section 3.3.1).

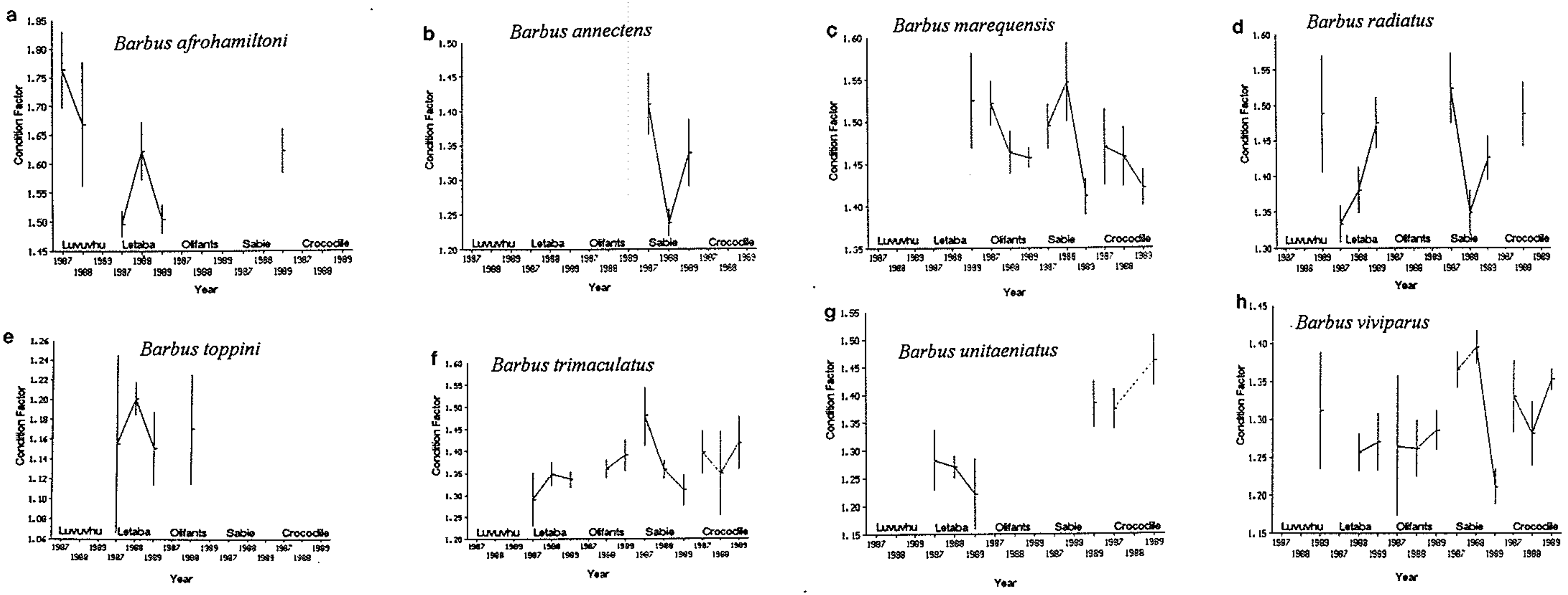

Figure 3.15 Condition factor analysis in successive sample years (1987 to 1989) of twenty eight abundant fish in KNP rivers, showing the mean and 95% confidence limits.

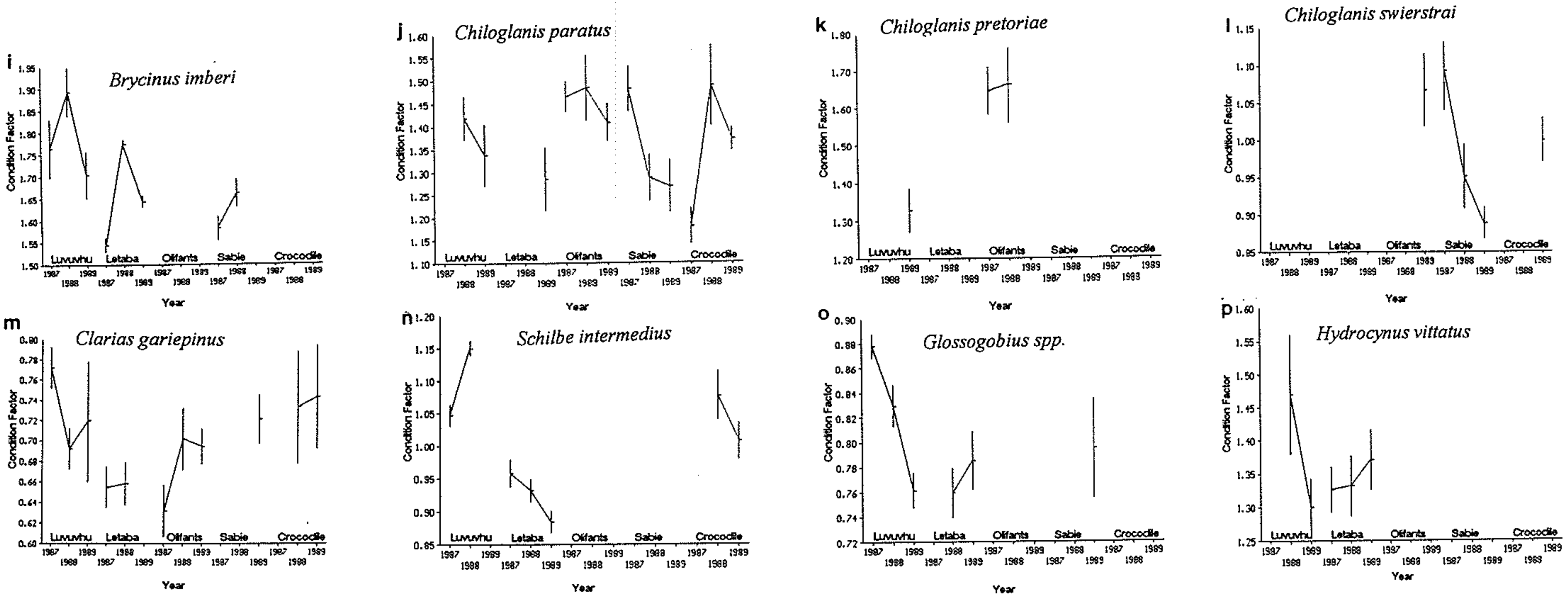

Figure 3.15 Continued

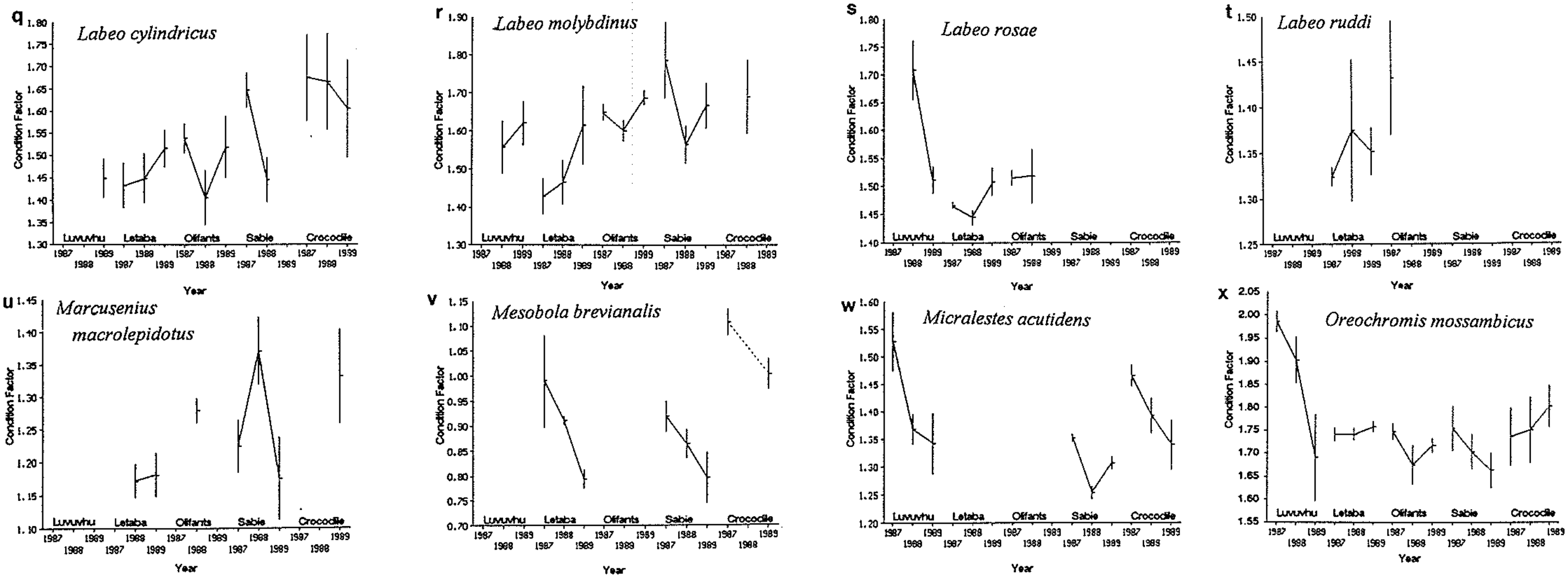

Figure 3.15 Continued

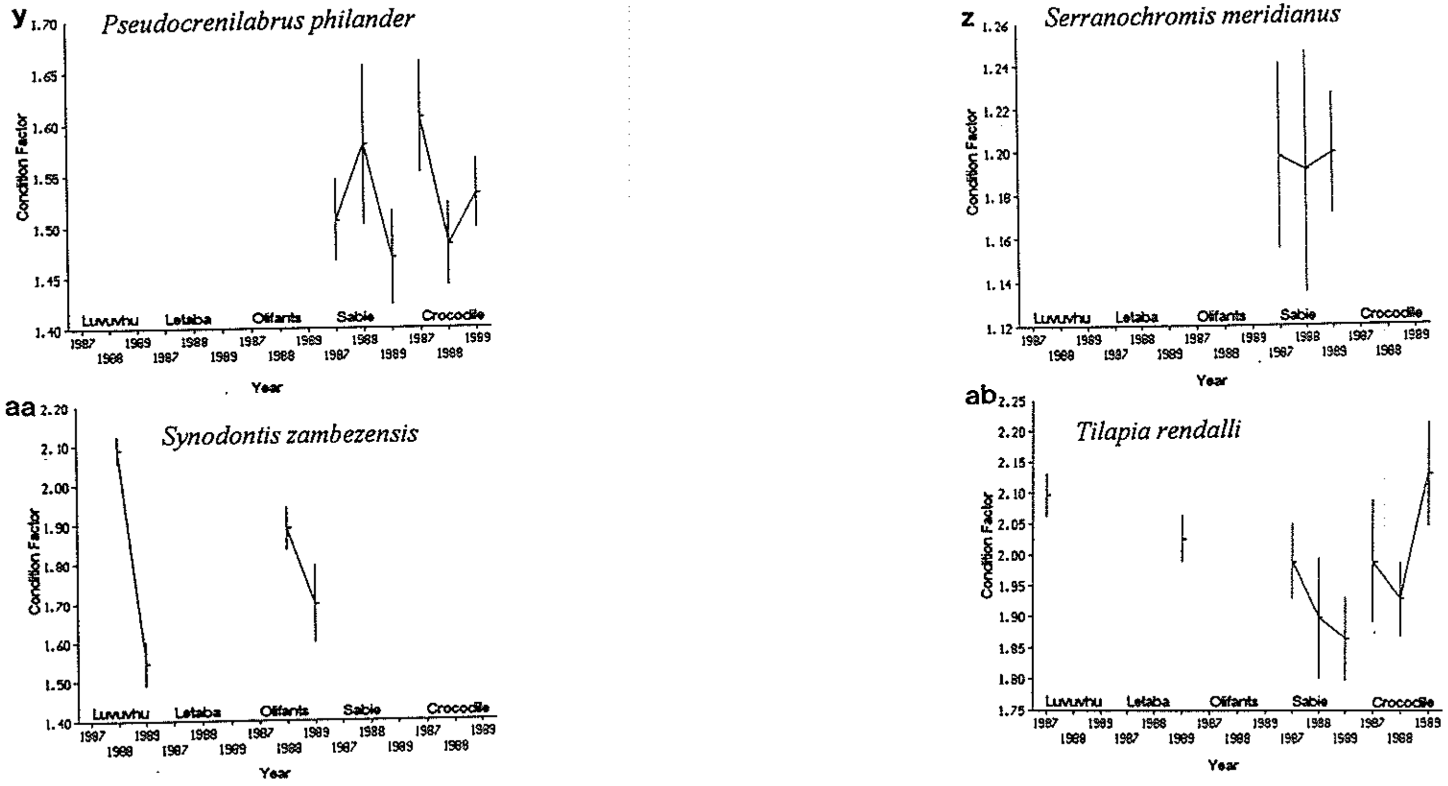

Figure 3.15 Continued

3.7.1.2 Condition of fish species in the Letaba River

Four different trends of change in condition were observed for species abundant in pools in the Letaba River. Firstly, significant increases in the condition of three species, *B. afrohamiltoni* (t=7.091 p<0.0001), *B. imberi* (t=21.347 p<0.0001) and *B. toppini* (t=4.141 p<0.0001) in 1988 where followed by declines in 1989 (Figures 3.15a, 3.15i and 3.15e). The opposite trend was displayed by *L. rosae*, with a decline in condition in 1988 (t=11.639 p<0.0001), followed by a significant increase in 1989 (t=10.026 p<0.0001) (Figure 3.15s). The third response entailed a decline in condition in both 1988 and 1989, displayed by *M. brevianalis* (t=6.159 p<0.0001) and *S. intermedius* (t=7.210 p<0.0001) (Figures 3.15v and 3.15n). Lastly, the physical condition of *O. mossambicus*, *L. ruddi* and *H. vittatus* remained relatively unchanged over the three year sample period (Figures 3.15x, 3.15t and 3.15p). The variability of changes in condition observed in pool-dwelling species in the Letaba River made it impossible to draw conclusions about directional changes in pool-dwellers as a group. This observation differed from previously concluded declines in the diversity of pool-dwelling communities in the Letaba River (section 3.3.1).

Condition of the rapid-dwelling species *L. cylindricus* and *L. molybdinus* showed an upward trend in 1988 and 1989 (Figures 3.15q and 3.15r), with the condition of *L. molybdinus* in 1989 being significantly higher (t=5.224 p<0.0001) than that recorded in 1987. The increase in condition of rapid-dwelling species in the Letaba River concurred with observations of increased diversity in this community from both informal study of species abundances (section 3.3.1) and the fit of species-abundance models (section 3.6.1.1). Changed environmental conditions (probably increased flow) resulted in an increase in the abundance and condition of typical rapid-dwelling species, and concurrent declines in the abundance of species not typically abundant in rapids (section 2.3.2.1). This decline in 'non-rapid-dwelling' species resulted in the observed decline in community diversity in 1988, with subsequent increases in diversity in 1989 as rapid-dwelling species predominated.

Condition of the marginal area-dwelling species *B. radiatus* showed an upward trend, with condition in 1989 being significantly higher (t=7.779 p<0.0001) than that of previous years (Figure 3.15d). Four species which are abundant in marginal areas (*B. unitaeniatus*, *B. trimaculatus*, *B. viviparus* and *M. macrolepidotus*), however, did not show any significant ($p>0.05$) change in condition over the three year sample period (Figures 3.15g, 3.15f, 3.15h and 3.15u). Insignificant changes in condition of most species in marginal areas in the Letaba River concurred with observations of minor changes in diversity of these communities previously concluded from comparisons of species abundances (section 3.3.1), as well as from the fit of species abundance models (section 3.6.1.1).

3.7.1.3 Condition of fish species in the Olifants River

Inconsistent changes in physical condition were recorded for the majority of fish species in different communities in the Olifants River.

Of species abundant in deep pools, a decline in condition was recorded for *S. zambezensis* in 1989 ($t=5.384$ $p<0.0001$), an increase for *C. gariepinus* in 1988 ($t=5.137$ $p<0.0001$), whereas the condition of *O. mossambicus* ($t=0.804$ $p>0.1$) and *L. rosae* ($t=3.069$ $p>0.01$) remained relatively unaltered.

Significant declines in condition of the predominantly rapid-dwelling species *L. cylindricus* ($t=5.348$ $p<0.0001$), as well as *B. marequensis* ($t=4.726$ $p<0.0001$), which has frequently been recorded in rapids (section 2.3.2.1), occurred in 1988 (Figures 3.15q and 3.15c). The condition of *L. molybdinus*, however, increased significantly in 1989 ($t=7.7421$ $p<0.0001$) (Figure 3.15r), with an upward trend also recorded for *L. cylindricus* ($t=3.062$ $p<0.01$) in this year. The condition of *C. paratus* ($t=0.999$ $p>0.1$) and *C. pretoriae* (0.356 $p>0.5$), however, remained relatively unaltered during the three year sample period (Figures 3.15j and 3.15k).

No significant changes were recorded in the condition of species occurring predominantly in marginal areas.

Most recorded changes in the condition of deep pool and rapid dwelling fish in the Olifants River differed from previously concluded directional changes in the diversity of fish communities based on informal studies of species abundances (section 3.3.1). Insignificant changes in condition of marginal area-dwelling species, however, conformed with observations of minor changes in community diversity concluded from both comparisons of species abundances (section 3.3.1) and the fit of species abundance models (section 3.6.1.1).

3.7.1.4 Condition of fish species in the Sabie River

Several fish species in the Sabie River showed similar changes in condition, with declines in condition recorded for several pool- and rapid-dwelling species. Of species abundant in pools, significant declines in condition were recorded for *O. mossambicus* (t=2.711 p<0.01) and *M. acutidens* (t=32.429 p<0.0001) in 1988, and *M. brevianalis* in both 1988 (t=9.099 p<0.0001) and 1989 (t=7.573 p<0.0001) (Figures 3.15x, 3.15w and 3.15v). The opposite trend, however, was observed for only *B. imberi*, with an increase in condition (t=5.976 p<0.0001) occurring in 1988 (Figure 3.15i). Most rapid-dwelling species in the Sabie River also showed similar changes in condition, with significant declines recorded in *L. molybdinus* (t=3.957 p<0.0001), *L. cylindricus*,(t=6.736 p<0.0001) *C. swierstrai* (t=6.385 p<0.0001) and *C. paratus* (t=7.278 p<0.0001) in 1988 (Figures 3.15r, 3.15q, 3.15l and 3.15j). This downward trend was continued in 1989 for *C. swierstrai* (t=7.606 p<0.0001). A significant decline in the condition of *B. marequensis* (t=7.007 p<0.0001), a species frequently recorded in rapids (section 2.3.2.1), was also recorded in 1989 (Figure 3.15c). Declines in the condition of deep pool-dwelling species in the Sabie River concurred with the changes in diversity previously concluded from comparisons of species abundances (section 3.3.1). Observation of widespread declines in physical condition of rapid-dwelling species, however, differed from prior conclusions based on both comparisons of species abundances (section 3.3.1), as well as the fit of species abundance models (section 3.6.1.1), where insignificant changes or small increases in community diversity were indicated.

Change in the condition of species occurring predominantly in marginal areas in the Sabie River was variable. Significant declines in condition were recorded for *B. radiatus* (t=6.600 p<0.0001), *B. trimaculatus* (t=5.669 p<0.0001) and *B. annectens* (t=5.670 p<0.0001) in 1988 (Figures 3.15d, 3.15f and 3.15b). A further decline in 1989 was recorded for *B. trimaculatus* (t=4.628 p<0.0001), whereas the condition of *B. radiatus* (t=8.629 p<0.0001) and *B. annectens* (t=8.629 p<0.0001) increased significantly in this year. Increases in condition in 1988 were recorded for *B. viviparus* (t=5.077 p<0.0001), *P. philander* (t=4.349 p<0.001) and *M. macrolepidotus* (t=5.888 p<0.0001), with subsequent declines in 1989 for all three species (Figures 3.15h, 3.15y and 3.15u). Inconsistent changes in condition of marginal area-dwelling species made it impossible to draw conclusions about directional changes of these species as a group. These observations differed from conclusions based on both comparisons of species abundances (section 3.3.1), as well as the fit of species abundance models (section 3.6.1.1), where insignificant changes or small increases in the diversity of marginal area-dwelling communities in the Sabie River were indicated.

3.7.1.5 Condition of fish species in the Crocodile River

Condition of the predominantly pool-dwelling species *M. acutidens*, *M. brevianalis* and *S. intermedius* underwent a significant ($p<0.01$) decline in most sample years (Figures 3.15w, 3.15v and 3.15n). Condition of *O. mossambicus* and *C. gariepinus*, however, remained relatively unaltered (Figures 3.15x and 3.15m), whereas a significant increase in the condition of *T. rendalli* ($t=5.479$ $p<0.0001$) was recorded for 1989 (Figure 3.15ab). Declines in the condition of several pool-dwelling species in the Crocodile River concurred with the decline in diversity concluded from comparisons of species abundances (section 3.3.1). Similarly, insignificant or small increases in diversity predicted for rapid-dwelling species (section 2.3.2.6) were confirmed by insignificant changes in the condition of most species abundant in rapids in the Crocodile River, with the condition of only *C. paratus* increasing substantially ($t=5.730$ $p<0.0001$) in 1988, followed by a significant decline ($t=5.621$ $p<0.0001$) in 1989 (Figure 3.15j).

The pattern of change in condition of the marginal area-dwelling species *B. viviparus* and *P. philander* were similar (Figures 3.15h and 3.15y), with significant ($p<0.01$) declines in condition in 1988, followed by increases in 1989. A similar trend was indicated by *B. trimaculatus* (Figure 3.15f) though changes were not significant. Change in the condition of species abundant in marginal areas in the Crocodile River thus did not concur with previous conclusions of either small increases (section 3.3.1) or nominal change (section 3.6.1.1) in community diversity.

3.7.1.6 Comparisons of the condition of fish in relatively pristine and perturbed rivers.

The condition of fish species in the Sabie river, the least perturbed of KNP rivers (sections 1.3.7, 2.3.3.5 and 3.6.1.1) were, for most species, within the range of, and frequently lower than, the condition of fish species in other KNP rivers (for example Luvuvhu River) where man-induced changes in the aquatic environment have been substantial (Figure 3.15). Thus, although fish community diversity differs between KNP rivers (highest in the Sabie River and lowest in the Luvuvhu River - see section 3.6.1.1) it would not be possible to conclude these differences in community diversity from comparisons of condition factors alone. There appears to be little correlation between the diversity of a fish community and the condition of species from which that community is comprised.

3.7.1.6 Summary

Of the fifteen fish communities used in this evaluation (three communities in each of five rivers), changes in the condition of species in only eight communities (pool-dwelling communities in the Luvuvhu, Sabie and Crocodile rivers; rapid-dwelling communities in the Luvuvhu, Letaba and Crocodile rivers; marginal area-dwelling communities in the Letaba and Olifants rivers) concurred with changes in diversity concluded using both informal studies of species abundances (section 3.3.1) and the fit of species abundance models (section 3.6.1.1). In six communities (pool-dwelling communities in the Letaba and Olifants rivers; rapid-dwelling communities in the Olifants and Sabie rivers; marginal area-dwelling communities in the Sabie and Crocodile rivers), changes in the condition of species differed from previous conclusions of change in community diversity. In one community (marginal area-dwelling communities in the Luvuvhu River) evaluation was impossible due to too few specimens having been collected. Furthermore, there was no indication, as concluded from informal studies of species abundances (section 3.3.1), that changes in the physical condition of fish populations in the Luvuvhu and Letaba was greater than in other KNP rivers studied, or that changes in the physical condition of fish populations was greater in 1988 than in other sample years. Consequently, comparisons of changes in condition of fish species in KNP rivers with diversity changes concluded from informal studies of species abundances and the fit of species-abundance models, failed to indicate the ability of condition factors to consistently provide interpretable information about changes in the diversity of fish communities.

3.7.2 Discussion

As with most methods for monitoring fish assemblages, there has been little critical comment in the literature of the applicability of using condition factor to monitor the effects of changing environmental conditions. Some early authors have emphasized that it is frequently difficult to identify reasons for recorded changes in condition (Le Cren 1951; Ricker 1975) because a variety of intrinsic (for example, age, sex, maturity and racial variation in morphometrics) and extrinsic (for example, food availability and degree of parasitization) factors can influence the length mass relationship of fish.

Interpretive difficulties can be exacerbated by the bias inherent in most fish sampling methods. Large specimens, in particular, are often under-represented in catch returns because they are frequently successful at avoiding capture with both electro-fishing (Vibert 1967; Penczak and Jakubowski 1990; Cowx and Lamarque 1990) and seine netting (Kok 1980, section 2.2.1.2). The length mass relationship can differ significantly in different age classes (Ricker 1975), with older and larger individuals frequently having a higher body length/mass ratio. Thus sampling bias could frequently result in underestimation of the mean condition of a fish population.

Attempts have been made to overcome the effect of body size on condition by calculating separate condition values for different length classes of a species (Schoonbee *et al.* 1972; Kenmuir 1973; Baird and Fourie 1978). Such an approach may be practical in the study of an individual population. However, where the objective is, as in this study, to investigate changes in condition in a large number of species, the high sampling effort that would be required to collect sufficient specimens of a range of length classes for each species would render this analytical approach impractical for the monitoring of diverse communities.

Despite the difficulties associated with interpreting condition values, they have been used by several authors to assess the effects of environmental conditions of both freshwater (Schoonbee *et al.* 1972; Kenmuir 1973; Marshall and Van der Heiden 1977; Baird and Fourie 1978) and estuarine (Whitfield 1982) fish populations, as well as amphibians (Davis 1989 cited in Noss 1990). White *et al.* (1984) have recorded decreases in the body length-mass relationship of several southern African fish species in response to deteriorating or unfavourable environmental conditions, and Kenmuir (1973) recorded increases in condition under favourable environmental conditions. Thus theoretically, change in the physical condition of fish species should provide an index whereby the effect of changing environmental conditions can be monitored (Karr 1981). The findings of this study, however, indicate that condition factors of fish from diverse communities cannot consistently provide interpretable information about the effects of environmental changes on fish, either within or between rivers. The unreliable performance of condition factors in community assessments has also been highlighted by their omission from methods for defining the integrity of fish communities (Karr *et al.* 1987). The importance of retaining a measure of physical condition in integrity assessment has been recognised (Miller *et al.* 1988) though length-mass ratios as a measure of condition have been discarded in favour of indirect measures such as the proportion of individuals with damaged fins or heavy parasitic loads (Karr 1981; Karr *et al.* 1987; Miller *et al.* 1988; Oberdorff and Hughes 1992).

3.7.3 Summary and conclusions

Correlations between the condition of several southern African fish populations and environmental conditions (White *et al.* 1984; Kenmuir 1973; Whitfield 1982) suggested that condition factors could potentially provide a cost-effective means of describing change in the diversity of fish communities. For several fish communities in KNP rivers, different changes in condition were determined for different species, making it difficult to formulate conclusions about changes in a community as a whole. Furthermore, comparisons of changes in condition of fish species in KNP rivers with diversity changes concluded from informal studies of species abundances and the fit of species-abundance models indicated that condition factors did not consistently provide interpretable information about changes in the diversity of fish communities. Difficulties associated with interpreting diversity highlighted by Le Cren (1951) and Ricker (1975) cannot easily be overcome in a cost-effective monitoring programme of diverse communities. Consequently, it is concluded that condition factors are of limited value for describing the diversity of fish communities in KNP rivers for the purpose of evaluating the achievement of conservation objectives.

3.8 BETA-DIVERSITY OF FISH COMMUNITIES

Beta-diversity is defined as the rate at which species are replaced along habitat gradients or amongst different communities in a landscape (Whittaker 1972; Cody 1975). As suggested by this definition, there are two approaches to studying beta-diversity. The first entails investigation of the rate of turnover of species along an environmental gradient (Wilson and Mohler 1983), and the second is to compare the degree to which the species composition of samples, habitats or communities differ (Southwood 1980). The fewer species that the different communities or gradient positions share, the higher the beta-diversity will be (Magurran 1988). As the aim of a monitoring programme of fish assemblages in KNP rivers is to provide means of detecting changes in the diversity of fish communities (section 3.1), it is the second of these two approaches to estimating beta-diversity which is of relevance to this study.

Two methods of analysis have been used to study change in beta-diversity:

(i) Indices which provide a measure of sample similarity or dissimilarity (Southwood 1980; Spellerberg 1991).

(ii) The ordination of species abundance data, with some intrinsic measure of heterogeneity (for example standard deviation units in the case of Detrended Correspondence Analysis) (Gauch 1984) used to provide a measure of diversity.

A large number of both quantitative (incorporating information on both species richness and abundances) and qualitative (incorporating information only on species richness) beta-diversity indices and similarity coefficients exist. Several have been tested by Bullock (1971b), Wolda (1981), and Wilson and Shmida (1984). All have their weaknesses and strengths, and none provide an ideal, universal measure of the difference in diversity between samples. Several of the problems associated with the use of indices to measure change in the alpha-diversity of fish communities (sections 3.5.1.3; 3.5.1.4) would also be applicable to the measurement of beta-diversity. Prominent in this regard are the difficulties associated with defining operational goals whereby the significance of changes in the species composition of samples could be evaluated.

Understanding of natural fluctuations in the abundances of fish species in KNP rivers is so vague that operational goals could be accurately defined only in terms of the species composition of communities. Consequently, measurement of the similarity of samples to operational goals could only be undertaken using qualitative beta-diversity indices and similarity coefficients. Such measures, however, are simplistic, as all species count equally in the equation, irrespective of whether they are abundant or rare (Magurran 1988). This limitation, combined with the observation that fish communities in KNP rivers comprise both habitat specialist (confined to one community) and habitat generalist species (occur in more than one community) (section 2.3.2.6), would make it difficult to distinguish between the loss or gain of habitat specialist (indicating an undesirable change in community diversity) and habitat generalist species (desirability of change dependant on species involved). Thus substantial changes in the diversity of communities could occur which, in certain circumstances, would not be conveyed in an index or similarity value. Consequently, evaluation of the significance (in terms of conservation objectives) of community changes indicated using qualitative beta-diversity indices would necessitate close inspection of the raw data.

The limitations of qualitative beta-diversity indices described above indicated that few insights into the dynamics of fish communities would be gained beyond those which could be gleaned from informal investigations of changes in the species composition of communities. Consequently no attempt was made to formally evaluate their suitability for monitoring changes in the beta-diversity of fish communities in KNP rivers. Emphasis rather was placed on assessing the utility of multivariate analyses as a means of describing and evaluating the significance of change in the beta-diversity of fish communities.

Multivariate analyses are traditionally used to investigate the overall similarity of samples and to identify major groupings (Gauch 1984). Magurran (1988) maintains that these methods do not give any direct measure of beta-diversity *per se*. Gauch's (1984) observation that, with Detrended Correspondence Analysis (DCA), species turnover can be measured in terms of standard deviation (the unit of scaling of axes in DCA), however, indicates that ordination may indeed provide some measure of the heterogeneity of community samples. Luff *et al.* (1989), for example, have used DCA to ordinate species of ground beetles from different localities, with the relative distances between the centroids of different habitat groups used as a measure of similarity. The use of such measures of heterogeneity to monitor change in the diversity of communities over time could prove difficult, as within an ordination, useful information on community diversity could be conveyed along secondary, tertiary, and subsequent ordination axes (Gauch 1984). Thus more than one value would be required to define the diversity of a community. The use of several values (one for each ordination axis) would more likely confuse rather than improve understanding of community changes.

Multivariate analyses are generally not used to test the hypothesis of no departure from goals, though Mentis (1984) has proposed a method of analysis using correspondence analysis whereby this could be achieved. This method, in which the scale of the ordination axes are standardised by using dummy samples (Walker 1987), is based on the premise that the significance of changes in community samples can be measured by the extent of their directional change within an ordination space. This hypothesis was tested in this study using simulated data sets, depicting hypothetical changes in the species composition of samples (section 3.2.2.5). Ordination results were thus compared against expected results for samples of known species compositional changes. Correspondence analysis was chosen as the method of ordination as the algorithm on which it is based, reciprocal averaging, has been found to be effective and robust for analysis of data sets of intermediate heterogeneity (Gauch 1984). Furthermore, the use of multivariate analyses to assess changes in beta diversity of fish communities have also been based on reciprocal averaging (Pusey *et al.* 1993).

3.8.1 Results and discussion

To assist descriptions of the ability to distinguish changes in the beta-diversity of fish communities using ordination analyses it is necessary to reemphasize the variability in the environmental preferences of fish species in KNP rivers, as described in section 2.3.2. Three types of fish species were identified based on their frequency of occurrence under different environmental conditions (section 2.3.2.6). These are:

(i) Habitat specialists which occurred predominantly in one geomorphological feature (rapids, pools or marginal areas).

(ii) Habitat generalists which frequently occurred in two geomorphological features (referred to below as a bi-habitat generalist).

(iii) Habitat generalists which frequently occurred in a number of different geomorphological features (referred to below as a multi-habitat generalist).

Of the seven processes of change in the species composition of fish communities investigated using ordination analyses (section 3.2.2.5), the movement of sample plots within an ordination space enabled recognition of change resulting from (Figure 3.16):

(i) The gain or loss of bi-habitat generalists.

(ii) The gain or loss of multi-habitat generalists.

(iii) The gain or loss of bi-habitat generalists simultaneously with the gain or loss of multi-habitat generalists.

(iv) The gain or loss of habitat specialists simultaneously with the gain or loss of bi-habitat and multi-habitat generalists.

Using correspondence analysis it was, however, not possible to distinguish changes in the species composition of a sample resulting from:

(v) The gain or loss of different habitat specialist species if they occurred in, or disappeared from, a sample in equal frequencies.

(vi) The gain or loss of a habitat specialist if it occurred simultaneously with the gain, or loss, of a bi-habitat generalist which occurs naturally in the same geomorphological feature as the habitat specialist.

(vii) The gain or loss of a habitat specialist if it occurred simultaneously with the gain, or loss, of a multi-habitat generalist.

For scenarios (v), (vi) and (vii) above, samples both with and without the described changes in species composition plotted in identical positions within an ordination diagram. In the case of scenarios (vi) and (vii), however, the inability to

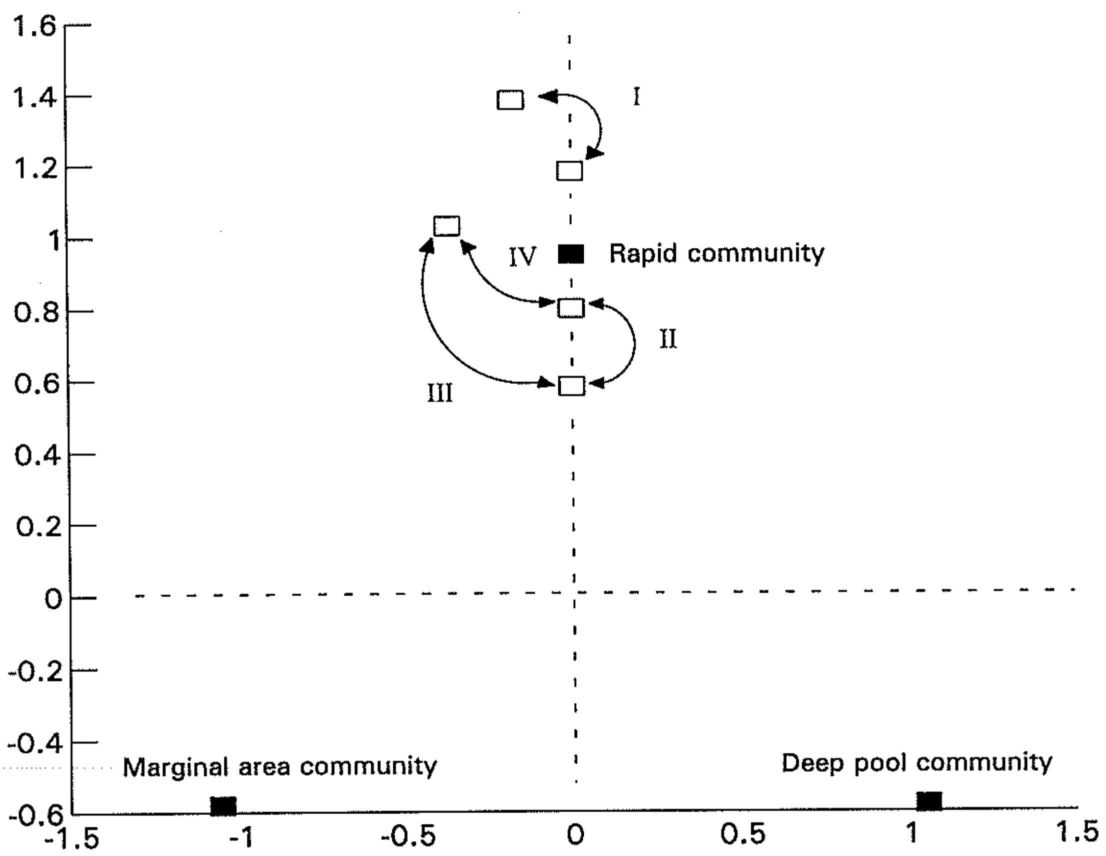

Figure 3.16 Ordination display of changes in the beta-diversity of hypothetical samples indicating changes in the position of a sample within the ordination space with (I) the gain (or loss) of bi-habitat generalists, (II) the gain (or loss) of multi-habitat generalists, (III) the gain (or loss) of bi-habitat generalists simultaneously with the gain (or loss) of multi-habitat generalists, and (IV) the gain (or loss) of habitat specialists simultaneously with the gain (or loss) of bi-habitat and multi-habitat generalists.

distinguish changes in the species composition of a sample applied only where habitat specialists and habitat generalists were equally abundant in a sample. The weighting of species did not alter the ability to distinguish the effect of the above changes in species composition on diversity.

A further difficulty noted with the visual assessment of ordination diagrams was the close orientation of different samples within an ordination space, despite such samples having substantially different species compositions. For example, a sample with a basic species composition characteristic of a rapid-dwelling community, but with the addition of a pool specialist species, would plot very close within an ordination space to a second sample with the same basic rapid-dwelling species composition but with the addition of a further two pool/rapid-habitat generalist species rather than the pool-dwelling specialist (Figure 3.17). The species composition of the first of these samples would represent a deviation from a typical rapid-dwelling community, whereas the second sample would not, yet it would be difficult to identify the deviation from visual inspection of the ordination diagram. Distinction between such samples could be partially improved by the weighting of species (Figure 3.18) though the degree of improvement would depend on the weighting scores assigned and the number of species changes involved. The greater the difference in weighting scores for different species, and lower the number of species changes, the greater the improvement in distinguishing between changes in species composition.

The consequence of the difficulties experienced with identifying some types of species compositional change and interpreting ordination displays (described above) is that fish communities could undergo substantial changes in diversity and/or gain atypical species, and these changes could be masked by the gain or loss of naturally occurring habitat generalists. Consequently, one could only interpret the significance of observed community changes, or identify significant changes that are not displayed within an ordination by intensive study of the raw data on which the ordinations are based. The findings of this evaluation is thus in contrast with studies such as Pusey *et al.* (1993) and Arthington and Pusey (1994) where ordination of fish community data is assumed to provide readily interpretable information on changes in community diversity. Similarly, the use of ordination techniques to measure community heterogeneity, typically using measures of standard deviation (Gauch 1984; Mentis 1984) may suggest changes

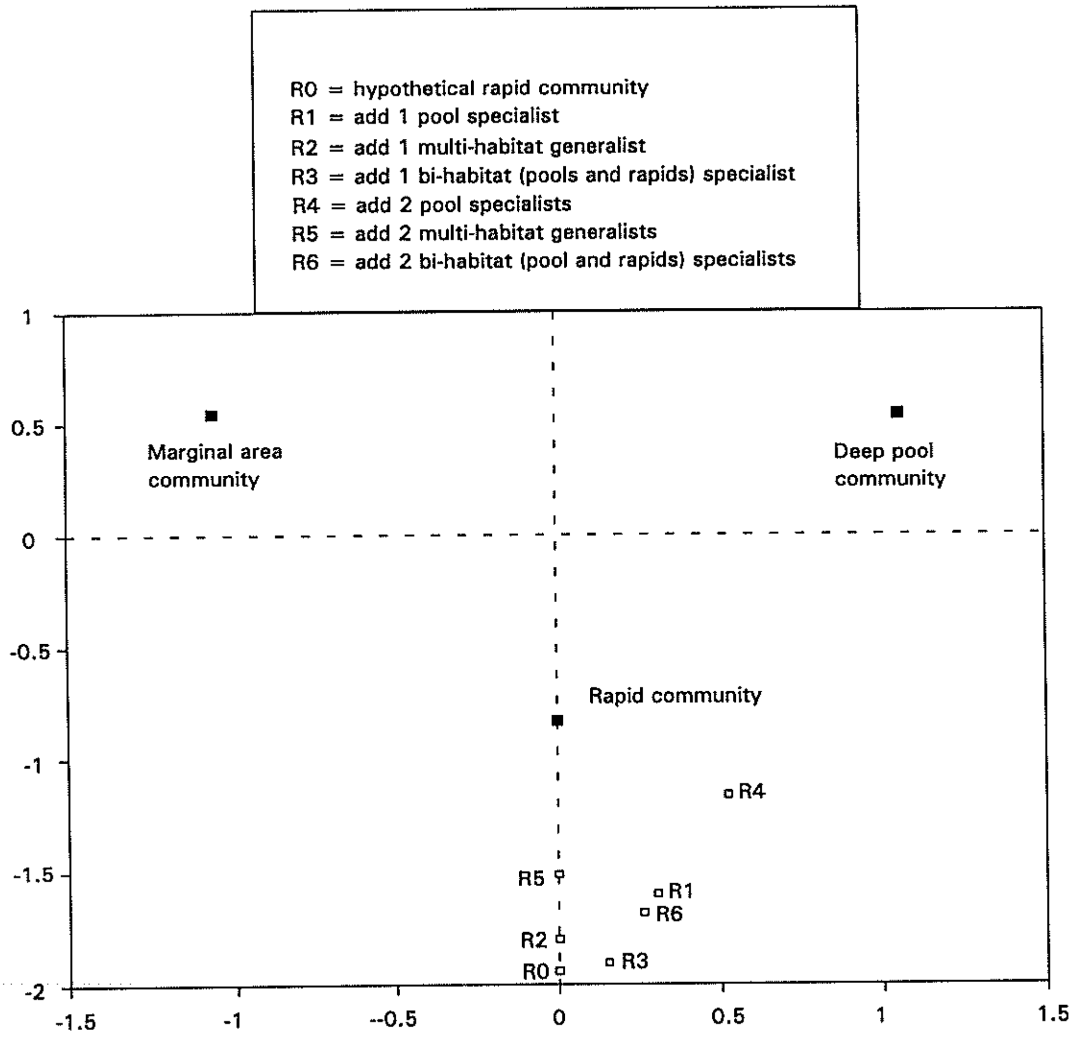

Figure 3.17 Ordination display of changes in the beta-diversity of a hypothetical sample with the addition of different combinations of habitat generalist and habitat specialist species. Equal weighting on all species. Open squares = samples; closed squares = idealized communities.

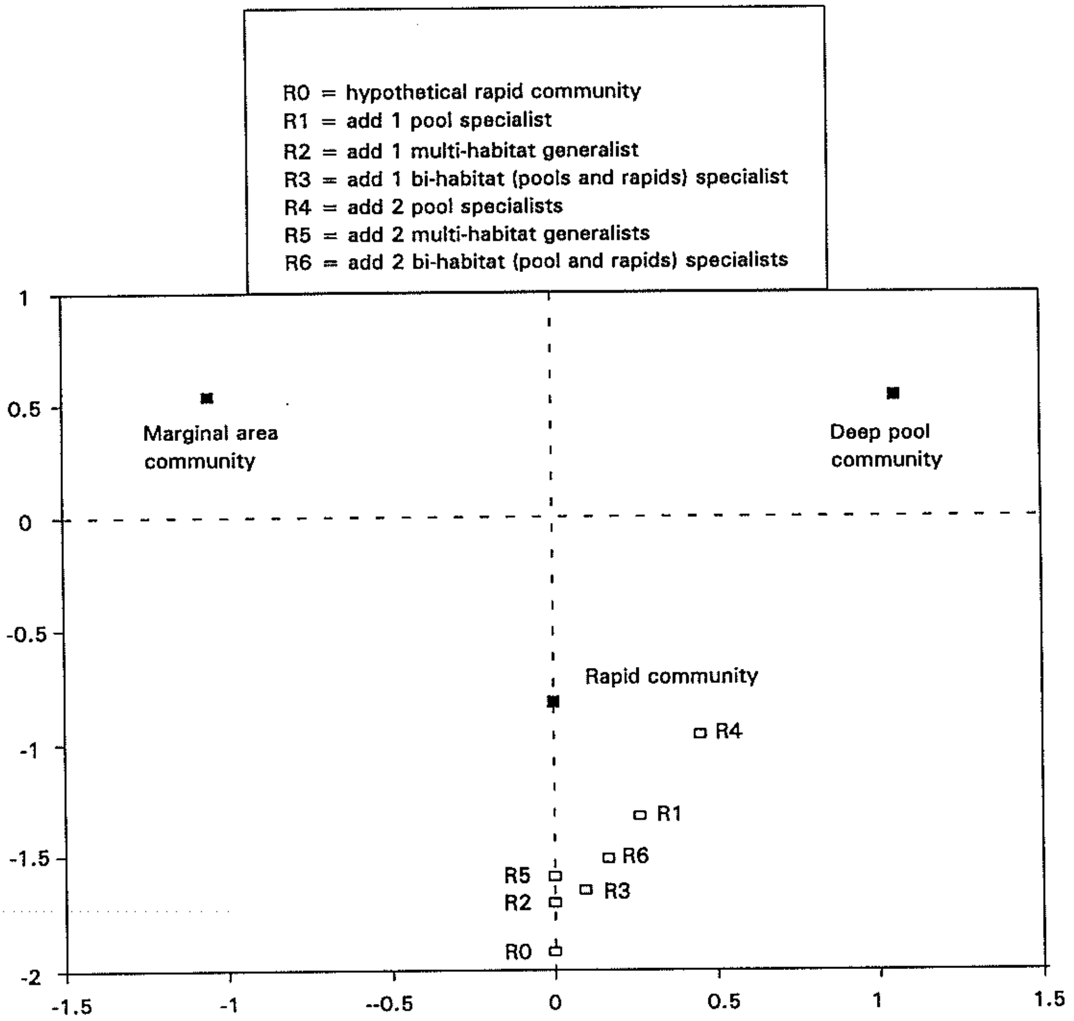

Figure 3.18 Ordination display of changes in the beta-diversity of a hypothetical sample with the addition of different combinations of habitat generalist and habitat specialist species. Weighting on species, where habitat specialists = 3, bi-habitat generalists = 2, multi-habitat generalists = 1. Open squares = samples; closed squares = idealized communities.

in the species composition of communities, though is unlikely to provide insight into the acceptability of such changes.

In summary, comparison of observed and expected results revealed several shortcomings in the effectiveness of correspondence analysis to illustrate changes in the species composition of a sample. It must be questioned whether there is much to be gained by employing this analytical technique to monitor changes in the diversity of fish communities in KNP rivers, as few ecological insights would be gained beyond those which could be gleaned from informal comparison of the abundance of species.

3.9 SUMMARY AND CONCLUSIONS

The importance of planning monitoring programs, including the identification of methods of data collection, analyses, and interpretation, has been emphasized by several authors (Spellerberg 1991; Hellawell 1992; Usher 1992; Finlayson 1996). A variety of analytical methods exists which could be used to quantify the diversity of fish assemblages at both the population and community level of organization (Noss 1990). Little guidance exists, however, on which methods can provide interpretable information on the achievement of conservation objectives. This issue was addressed in this study, with the evaluation of six commonly used analytical methods.

Deciding which methodology would be appropriate for monitoring change in the diversity of fish assemblages in KNP rivers was problematic, as none provided an all-embracing means of testing the significance of change in diversity from predefined goals. Furthermore, the evaluation of analytical methods was, in many cases, inconclusive, as it was of necessity based largely on comparison of the findings of one method against those of an alternative, imperfect method. Despite these difficulties it was necessary to be pragmatic and identify those analytical methods which would best serve as a means of testing the achievement of the conservation goals of the KNP.

Of all the analytical methods evaluated, the one which came closest to filling the criteria of providing interpretable information (Hellawell 1992) which could be used to assess the achievement of conservation goals (Finlayson 1996) was the fitting of species abundance models (section 3.6). Consequently, this method should, along with informal investigations of the abundance of species (section 3.3), provide the basis for assessing the significance and direction of change in the diversity of KNP fish communities. Alternative analytical methods, such as diversity indices, physical condition measures, and measures of community beta-diversity using ordinations, were unable to consistently provide interpretable information for assessment of the direction, extent and significance of diversity changes. Thus, these methods are not suitable for the monitoring of diverse fish communities in the KNP. The importance of monitoring biotic diversity at a variety of scales (Noss 1990) suggests the need for future work on the growth of fish species occurring in KNP rivers to enable assessments of the structure of selected populations.

CHAPTER 4

MONITORING FISH ASSEMBLAGES : SUMMARISING DISCUSSION AND CONCLUSIONS

This chapter comprises a description of how monitoring of diverse fish assemblages, to assess the achievement of conservation objectives, should be undertaken in KNP rivers. Topics discussed include why monitoring should be undertaken, which indicators of diversity change should be used, methods and frequency of sampling, and when monitoring should be terminated. The paucity of published accounts of similar studies frequently makes comparisons difficult. A brief discussion is also given of how some of the findings of this study could aid in the adapting of established measures of the integrity of fish communities for use in KNP rivers.

4.1 WHY MONITORING OF FISH ASSEMBLAGES IN KNP RIVERS SHOULD BE UNDERTAKEN

Nett decreases in the distribution of fish species brought about by man-induced environmental changes indicated declines in the conservation status of fish communities in all KNP rivers (section 2.3.4). The degree of change was lowest in the Sabie River (two species changes) and highest in the Luvuvhu River (twelve species changes). The Crocodile, Letaba and Olifants rivers fell between these two extremes with six, eight and ten species changes, respectively. The fit of alpha-diversity models to species abundance data indicated similar long-term changes in the conservation status of fish communities with community diversity being highest in the Sabie River (log-normal distribution in most sample years), lowest in the Luvuvhu River (geometric series distribution in most sample years), and intermediate in the Letaba, Olifants and Crocodile rivers (log-series distribution in most sample years) (section 3.6.1). Thus concluded declines in the diversity of fish communities in KNP rivers using different study approaches were similar.

Substantial declines in the diversity and status of fish communities in KNP rivers suggest that prior conservation actions (for example national park proclamation, negotiation of limited water rights in the Crocodile, Sabie and Olifants rivers, construction of impoundments in the Letaba River - Chapter 1) have not been effective in eliminating undesirable changes in the distribution and abundances of fish species. Declines in the diversity and conservation status of fish communities have occurred despite conservation actions because all major rivers in the KNP are only small components of much larger aquatic systems (section 1.3.4 to 1.3.8). Land-use changes in river catchments outside the boundaries of the KNP (sections 1.3.4 to 1.3.8) influence the dynamics of aquatic systems within KNP (sections 2.3.3.5; 3.3.2 and 3.6.1.1), with conservation authorities having little control over these processes. This difficulty with providing effective protection of freshwater biota in formal conservation areas has also been noted by Sheldon (1988) and Davies *et al.* (1993).

Encouraging signs that a more holistic approach to water management will be adopted in the future stems from the recognition of the natural environment as a legitimate water user (Department of Water Affairs and Forestry 1992), and encouragement of the participation of conservation bodies in decision making regarding flow allocations to river systems in conservation areas. Determination of the quantitative and qualitative water requirements of KNP rivers through the Kruger National Park Rivers Research Programme (Breen *et al.* 1994) should facilitate identification of appropriate management actions. The necessity for refinement of management actions taken to limit undesirable changes in KNP fish assemblages needs to be periodically assessed through study of the effects of environmental changes on fish assemblages. A key component of such a study programme would be the monitoring of change in the diversity of fish assemblages to assess the achievement of conservation goals.

4.2 GUIDE-LINES ON A COST-EFFECTIVE MONITORING PROGRAMME

The necessity for thorough planning of monitoring programmes has been emphasized by several authors (Hellawell 1992; Usher 1992; Roberts 1992), with decisions being taken before monitoring commences on the purpose for monitoring, what should be monitored, and methods of data collection and analysis. The purpose for monitoring fish assemblages in KNP rivers was addressed in the introduction to Chapter 3, and entailed determination whether diversity has been impacted beyond limits of acceptable change, and whether human influence has played a significant role in this. Deciding what must be monitored, and how data should be analysed, necessitated consideration of both the theoretical aspects of the spatial and temporal variability of fish assemblages, and the practical limitations of analytical techniques, as discussed below.

4.2.1 Hierarchical characterization of biotic diversity

Several environmental changes in KNP rivers were described. These included long-term changes resulting from mans development of catchment basins (for example increases in the severity of low flows and deterioration in water quality), as well as shorter-term, primarily natural changes (for example seasonal flood events). Both types of environmental changes could be expected to effect the distribution and abundance of fish species (Calow and Petts 1992), though the temporal and spatial scales of such effects may differ. The manner in which these scales could differ can be inferred from hypotheses of habitat sensitivity formulated by Frissell *et al.* (1986), who argued the existence of a continuum of habitat sensitivity to environmental disturbances (see section 1.2.2.2). In the same manner that the response time and sensitivity of environmental units (microhabitats, habitats, reaches, rivers) differ with respect to magnitude and duration of environmental disturbances (Naiman *et al.* 1992), so could different levels of biotic organisation (sub-organism, organism, population, communities, ecosystem) vary in their sensitivity and response to environmental disturbances (Noss 1990).

Hierarchy theory suggests that lower levels of biotic organisation, such as the physiology of individuals (sub-organism level) would be the most sensitive to environmental disturbances, potentially being influenced by both small and large magnitude, and both short-term and long-term disturbances (Allen & Star 1982; O'Neill *et al.* 1986). Higher levels of biotic organisation, such as the diversity of communities, however, would be less susceptible to environmental disturbances, being influenced essentially only by large scale and/or long-duration environmental disturbances (Burton *et al.* 1992). Noss (1990) provides a simple analogy of these processes by describing ecosystems as consisting of "small balls" (lower levels of organization) within "larger balls" (higher level of organization). Small scale disturbances could cause the small balls to roll around inside the larger ball, though if a large scale disturbance causes the big ball to roll downhill, the small balls inside it will roll downhill also.

Differing sensitivity of levels of biotic organisation to environmental changes could profoundly influence the scale of biotic measurement, and hence type of data collected within a monitoring programme. Carrying the ideas of hierarchical theory through into the monitoring of fish assemblages, it could be argued that monitoring changes in the lower orders of biotic organisation (length frequency distributions as an indicator of reproductive competency; physical condition of individuals), which could be expected to respond to both small and large scale environmental stresses (Noss 1990), would provide greater sensitivity to environmental changes. Lower order indicators could thus, in circumstances of small scale or incipient environmental changes, provide warning that the biota have been exposed to unfavourable environmental conditions before the system becomes totally compromised, thus providing warning of the necessity for corrective management actions. Greater sensitivity, however, would also mean that difficulty could be experienced with distinguishing between biotic changes resulting from the continuing natural fluctuations in river ecosystems (Allan 1995), and anthropogenic disturbances. Monitoring lower order changes could be important as they provide the mechanistic basis for higher order patterns (Noss 1990) and hence provide a basis for understanding higher order diversity changes.

Monitoring of change in higher orders of biotic organisation (distribution of species; diversity of communities) would provide an indication that substantial biotic change had already occurred. Such changes are more likely to be the result of long-term and/or extensive (usually anthropogenic) changes in the aquatic environment (Noss 1990). A drawback to the monitoring of change in higher orders of biotic organisation could be that by the time significant biotic changes have been detected, the appropriate time for implementation of corrective management actions may already have passed and a new stable state already reached. Furthermore, environmental conditions may have changed such that the reasons for the biotic changes may no longer be readily apparent.

The hierarchy concept thus suggests that the monitoring of biological diversity should be undertaken at multiple levels or organization and at multiple spatial scales (Frissell *et al.* 1986; Noss 1990). This would provide the best mix of sensitivity to environmental changes, and clarity on changes in the attributes of biotic assemblages that are considered by river managers to be of importance (viz. biotic diversity). The importance of integrating measures from multiple levels of biotic organization in assessments of the integrity of fish communities has also been emphasized by Miller *et al.* (1988).

Indicators of change in biotic diversity

Seven methods for analysing change in the diversity of both high and low orders of organization of fish assemblages have been discussed in this study (species distribution, informal descriptions of change in species abundances, length frequency distributions of populations, alpha-diversity indices, frequency abundance models, physical condition of individuals, beta-diversity), all of which where found to have various strengths and weaknesses. It was necessary, however, to decided which of these methodologies conveyed useful information about fish community change, and hence which should be adopted in a monitoring programme to identify and assess the significance of change in fish assemblages in KNP rivers. The time span of the data series recorded in this study was inadequate to enable identification of the similarity of trends of community change indicated by different analytical methods. Thus, boosting of confidence in the accuracy of the descriptive capabilities of different methodologies by this means was possibly premature. Furthermore correlation between community and environmental changes using different analytical methodologies, in some instances, gave conflicting results (for example differences in diversity changes indicated by condition factors (section 3.7) and the fit of diversity models (section 3.6)). This in itself was not unexpected as the different analytical methodologies assessed emphasized different aspects of biotic diversity (Magurran 1988), which need not necessarily alter in similar ways in response to particular environmental changes (Noss 1990). It was concluded that the prudent approach to the dilemma of recommending appropriate analytical methodologies would be to advocate the utilisation of those methodologies which have both theoretically, and in this study, shown to provide reliable means of indicating change in the diversity of fish assemblages.

Consequently it is recommended that analysis of fish community change should always commence with an informal investigation of changes in the abundances of species. With knowledge of the habitat requirements of species, such investigations could possibly provide the first indications of failure in the functioning aquatic systems, and reveal probable causes for biotic changes. Such investigations should also incorporate assessment of change in the distribution of species. Formal analyses of changes in the diversity of fish communities should, however, be based primarily on determination of the fit of observed species abundances to the MacArthur broken-stick, log-normal, log-series and geometric-series abundance distribution models, with the goal being that species abundances are log-normally distributed. Assessment of the fit of abundance distributions should be undertaken by both comparison of observed and expected abundances, and visual inspection of the shape of rank abundance plots.

Evaluations of analytical methods undertaken in this study revealed that monitoring of low orders of biotic organisation of fish (length frequency distributions of populations; physical condition of individuals) could yield disappointing results. Poor understanding of the biology of freshwater fish in many countries (Davies *et al.* 1993; Campbell 1994) as well as limitations of the methods *per se* (Le Cren 1951; Ricker 1975; Royce 1984; Gulland 1985) can hamper evaluation of the significance of, and causes for recorded changes. The desirability of incorporation measures of low orders of biotic organisation into a monitoring programme have been discussed above. There is clearly a need for further study of these aspects of biological monitoring to develop interpretive capabilities. In particular the reproductive biology and growth of fish species in KNP rivers should be addressed in future research programmes.

Monitoring in relation to likely KNP management policy changes

The management policies of KNP are currently under review (L. Braack *pers. comm.*), with future policies likely to emphasize the need for cost-efficient monitoring programs to test the achievement of operational goals (limits of acceptable change). This will represent a significant advancement from the current mission statement (section 1.2.2.3), with recognition of the necessity for predetermined goals, in particular, bringing KNP's management policies in line with modern thinking on planning for conservation (Centre for Water in the Environment 1996) and monitoring (Hellawell 1978, 1992; Goldsmith 1991; Finlayson 1996). The need for predetermined operational goals and cost-efficiency in the monitoring of fish assemblages has been emphasized throughout this study.

A further probable policy change of relevance to environmental monitoring is the adoption of Noss's (1990) conceptual framework for biodiversity as a basis for defining measurable indicators (see section 1.2.2.4). The monitoring approaches outlined in this study deal mainly with the structure and composition of fish communities and populations. Assessments of the length frequency distribution of species would (if implemented for selected species following growth studies - see section 3.4) address structural aspects at the population level of organization, whereas the dispersion of species will address compositional aspects of populations across landscapes. Alternatively the fitting of species abundance models, and informal investigations of species abundances will address structural and compositional aspects at the community level of organization.

Aspects of Noss's (1990) conceptual framework not directly addressed in this study are the functional components of populations and communities. These include the abiotic (climatic, geologic, hydraulic) and biotic (ecological, evolutionary) processes that generate biodiversity (Noss 1994). Broad principles relating to the functional diversity of tropical freshwater fish communities have been discussed by Lowe-McConnell (1975). Study of the functional diversity of KNP fish assemblages, however, should enjoy high priority in future research initiatives to facilitate identification of processes influencing the distribution and abundance of species. Although the relative importance of abiotic and biotic processes in shaping fish community diversity in KNP rivers (or any other southern African river) remains to be formally investigated, observed correlations between environmental perturbations and fish community diversity in KNP rivers (section 3.6.1.1) and other rivers in the world (LeRoy Poff and Ward 1989; Jowett and Duncan 1990; LeRoy Poff and Allan 1995; Death and Winterbourn 1995) suggest that abiotic factors have strong, possibly overriding influences on community diversity in rivers. Assessment of the functional components of Noss's (1990) biodiversity hierarchy should thus emphasize the effect of abiotic process on the diversity of fish assemblages.

The results of this study have highlighted the necessity for the continuous collection of environmental data (sections 2.3.3), and a thorough understanding of the environmental requirements of species (section 2.3.2) to enable the formulation of hypotheses on the causes for change in biotic diversity. The necessity of environmental data when addressing complex biodiversity issues has also been highlighted by Schanberger (1988) and Noss (1990). This and other studies (Karr and Dudley 1981; Hortle and Lake 1983; Cadwallader 1986; Stanford and Ward 1986; Moyle and Williams 1990; Moyle and Leidy 1992; Penczak *et al.* 1995; Moyle 1995) have emphasized the effects of flow variation, water quality, and aspects of habitat structure (distribution of aquatic plants;

substrate type) on the diversity of fish assemblages. Surveillance of these environmental variables should continue to be undertaken in conjunction with monitoring of fish assemblages in KNP rivers.

4.2.2 Methods of fish collection

Numerous methods of sampling fish communities have been employed in southern African rivers, of which the most frequently used are gill nets, seine nets, traps, poisons, long lines and electro-fishing. The different types of fish sampling gear vary with respect to the capture probability of different fish species (Ricker 1975), as well as the size (Cross and Scott 1975; Bohlin and Sundstrom 1977) and fatness (Le Cren 1951) of individuals.

No one sampling method will prove equally efficient in sampling all fish species or all sizes of individuals. Thus the catch composition from any sampling programme will be biased depending on the sampling methods employed. The ability to reliably detect changes in the diversity of fish assemblages is dependant on keeping this bias constant. Sampling methods employed in a monitoring programme of fish assemblages in KNP rivers should thus be constant. Sampling methods employed in this study were seine netting in deep pools, and electro-fishing in marginal areas and rapids (section 2.2.1.1), as these had been used in previous studies of fish communities in KNP rivers (Pienaar 1968, 1978; Gaigher 1969). Seine netting and electro-fishing should thus be the sampling methods of choice in future monitoring programmes.

Temporal activity differences of fish within rivers, particularly in relation to seasonal changes in flow (Lowe-McConnell 1975; Merron *et al.* 1985), necessitates that the time of year in which sampling is undertaken remains constant to reduce sampling bias. Highly seasonal, summer rainfall patterns (section 1.3.3) suggest higher variability in flow volumes in summer months, whereas flow during winter is more likely to consistently be low. Thus short-term flow changes which influence fish migrations are likely to be less erratic during winter. Furthermore, sampling in high rainfall summer months in KNP rivers was found to be less effective than winter sampling, with reduced efficiency of seine net operation and collection of electro-narcotisized specimens in fast flowing, turbid waters (section 2.2). Sampling in low-flow winter months is indicated both to increase sampling efficiency and reduce sampling bias related to temporal activity differences of fish.

One of the problems associated with measurements of the diversity of communities is knowing what sample size to adopt (Magurran 1988). Sampling intensity values given in sections 3.4.1.1 and 3.5.1.1 can serve as guide-lines for future monitoring programmes in that they represent minimum viable sample sizes for description of the length frequency of populations and diversity of fish communities in KNP rivers. Thus the minimum sample size for the description of the length frequency distribution of a fish population is 150 individuals. For the description of the diversity of fish communities effective sampling intensity must be equivalent to, or greater than, 14 seine net pulls in pools, 110 minutes electro-fishing in rapids and 120 minutes electro-fishing in marginal areas in rivers of the Limpopo system, and 180 minutes electro-fishing in both rapids and marginal areas in rivers of the Inkomati system.

Comparisons of the number of species and individuals should only be undertaken between data sets where sampling intensity is constant. In situations where sample sizes are unequal the use of catch per unit effort values can be used to reduce all samples to a standard size (Ricker 1975).

4.2.3 Selection of sample localities

The choice of where to sample fish in KNP rivers is limited by the availability of access routes. The lack of roads results in large portions of KNP rivers being, in practical terms, inaccessible to field workers encumbered with bulky sampling equipment. Consequently, the random, stratified random, or regular placement of sample localities is not practically possible. The desirability of incorporating a random element into sample site selection has been emphasized by several workers (Southwood 1980; Grieg-Smith 1983; Gauch 1984) without which inferential statistical tests are invalid (Hurlbert 1984).

The judgemental positioning of sample localities in KNP rivers is unavoidable. Monitoring should thus be undertaken with the understanding that results are for descriptive purposes only (Gauch 1984), which is adequate for the purpose of monitoring as discussed in this study. Sample localities should span the length of rivers in KNP to enable description of the distribution of fish species throughout the KNP. As the sites used in this study were positioned along the length of rivers; readily accessible from established roads; suitable for the effective operation of fish sampling apparatus; and covered a wide variety of geomorphological features, it is suggested that future field exercises should at least include these sites. It is also suggested that future monitoring should include sampling in instream impoundments in KNP rivers to assess their role as refugia, particularly during low flow years.

4.2.4 Frequency of sampling

The question of how frequently evaluation of the diversity of fish assemblages in KNP rivers should be undertaken was not specifically addressed in this study. The methods of data analysis proposed above for future monitoring exercises, however, address primarily the higher orders of biotic organisation (species distribution; community diversity), changes in which are essentially long-term in nature (Noss 1990; Burton *et al.* 1992). Similarly, changes in the aquatic environment concluded to have resulted in recorded changes in the distribution of fish species (section 2.3.3.5) and diversity of communities (sections 3.6.1.1), were, with the exception of episodic pollution, essentially long-term in nature (viz. increased severity of low flows, decline in water quality, distribution and abundance of aquatic plants, river impoundment). Thus a relatively long sampling interval should provide adequate resolution of changes in the diversity of fish communities. As it is not possible to justify sampling intervals longer than the time duration of this study, it is suggested that surveys of the distribution and abundance of fish species should initially be undertaken once every three years. As monitoring continues it should be possible to periodically re-assess the optimum frequency of sampling to ensure that understanding gained of the dynamics of fish communities justifies the expenditure of resources on data collection and analysis (Spellerberg 1991; Finlayson 1996).

Monitoring of changes in the reproductive competency of fish (which address low orders of biotic organization and hence should yield information on proximal changes in environment (Allen & Star 1982; O'Neill *et al.* 1986)), however, should be undertaken more frequently, with the survey of selected species being undertaken at no longer than two year intervals.

4.2.5 Termination of monitoring

As part of the planning for any monitoring programme there should be rules for stopping (Usher 1992). Without knowing when sufficient data has been collected, or whether the monitoring programme is still relevant, there is always the danger of diminishing scientific returns for the resources invested. Most proposed frameworks for monitoring indicate that regular reviews should be an integral part of monitoring activities (Spellerberg 1991; Hellawell 1992; Finlayson 1996). Considerable resources would need to be invested in monitoring fish communities in KNP rivers, and knowing when to stop monitoring is important to ensure that these resources could not be better expended elsewhere.

There are two types of rules for stopping that can be built into the plans for any monitoring programme (Usher 1992), these being:

(i) The terminal kind rule, where a criterion is satisfied then the monitoring stops.

(ii) The review kind rule, where provision is made for periodic review of the programme, with decisions on programme termination being based on a cost-benefit comparison of the resources devoted to, and the benefits derived from the programme.

Definition of an end-point for monitoring fish communities in KNP rivers is difficult as the processes resulting in the non-achievement of conservation objectives, namely agricultural, industrial and urban development in river catchments (sections 1.3.4 to 1.3.8) are on-going. Thus, although the achievement of conservation objectives may be demonstrated (for example in the Sabie River, see section 3.6.1.1) this need not imply the necessity for terminating monitoring. Catchment development will continue (sections 1.3.4 to 1.3.8), which in KNP rivers has been demonstrated to result in undesirable changes in the diversity of fish assemblages (sections 2.3.3.5; 3.3.1 and 3.6.1.1). A terminal type stopping rule such as 'when the defined conservation objectives have been achieved' would be appropriate for monitoring KNP fish communities only where it could simultaneously be demonstrated that anthropogenic modifications to the aquatic environment have been sufficiently reduced so that detrimental effects on the diversity of fish assemblages are minimal.

A review type stopping rule appears to be a more appropriate means of deciding when to terminate monitoring of fish assemblages in KNP rivers. A cost-benefit comparison should be undertaken periodically (for example, after every field sampling programme). In this way the understanding gained about changes in fish communities, which can be used to define or motivate conservation actions, are weighed up against both the resources expended, and the potential conservation successes that could be achieved by utilising these resources on alternative conservation endeavours.

4.3 RECENT CONCEPTS IN MONITORING FISH ASSEMBLAGES: BIOTIC INTEGRITY

A developing fish community based evaluation scheme for lotic systems in North America is the Index of Biotic Integrity (IBI) (Karr 1981; Miller *et al.* 1988; Steedman 1988; Plafkin *et al.* 1989; Fausch *et al.* 1990) which incorporates primarily compositional components of fish communities to assess the environmental health of rivers (Karr 1981; Kleynhans 1994). The IBI is viewed by several authors as an alternative to long-standing diversity measures, such as diversity indices, as a means of assessing the status of fish assemblages (Karr 1981; Plafkin *et al.* 1989). Attributes evaluated include fish species richness, indicator taxa, species and trophic guild relative abundances, the incidence of hybridization, and condition. These criteria are assessed by evaluating different metrics (Karr 1981; Fausch *et al.* 1990). IBI has also been applied in France (Orberdorff and Hughes 1992), and equivalent procedures are being developed in Australia (Arthington and Pusey 1994) and South Africa (N. Kleynhans *pers. comm.*)[10].

Adaptation of IBI for use in South Africa will require major revision of the metrics in order to reflect local fish assemblage structure and river functioning. Some of the results from this study may be useful in developing appropriate metrics. For example, descriptions of change in the distribution of fish species (section 2.3.1) resulting from anthropogenic modification of rivers (section 2.3.3.5) could serve as a basis for identifying indicator species (for example, *B. annectens*, *O. zambezense*, *H. vittatus*) or groups (for example, barbs and catlets).

The findings of this study also support aspects of the trophic metrics of IBI which assumes an increase in the proportion of omnivores, and a decrease in insectivores and top carnivores with increasing environmental degradation (Karr 1981; Fausch *et al.* 1990; Orberdorff and Hughes 1992). Perturbed rivers in the KNP (Letaba and Luvuvhu) support a higher proportion of omnivorous species (for example *B. imberi*, *O. mossambicus*, *S. intermedius*) and lower proportion of insectivorous

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species (for example most small *Barbus* species, *Chiloglanis* spp., *M. acutidens* and *M. brevianalis*) than relatively less perturbed systems (Sabie River) (Tables 3.2 to 3.6). There is little indication, however, that river degradation in KNP has resulted in a decrease in piscivorous species (for example *Anguilla* spp. and *H. vittatus*), with a low proportion of this trophic guild having been recorded in all river systems (Tables 3.2 to 3.6). Thus the percentage of omnivores and insectivores may prove to be informative metrics in an IBI assessment of KNP river health, though a metric based on the proportion of top carnivores is unlikely to convey useful information.

Most variants of the IBI incorporate measures of both species richness and the number of individuals (Karr 1981; Steedman 1988; Miller *et al.* 1988; Plafkin *et al.* 1989; Fausch *et al.* 1990; Orberdorff and Hughes 1992). While the total number of individuals collected was found to be a reasonably reliable measure of the diversity of different fish communities in KNP rivers (section 3.5.1.3), the total number of specimens collected in different geomorphological features was found to be poorly correlated with river degradation. If an IBI assessment is to be applied separately to different fish communities in KNP rivers, developers of the procedure should carefully evaluate the value of retaining the 'species richness' metrics for assessment, whereas retention of a measure of number of individuals is indicated.

The question may well be asked whether IBI will or should replace the more traditional diversity measures discussed in this study. To answer this question it is necessary to discuss some of the limitations of IBI and the likelihood of these limitations being overcome.

One of the primary difficulties associated with the use of IBI is the determination of a baseline defining fish species abundances resulting from natural disturbances (Plafkin *et al.* 1989). This is likely to be a significant hurdle in the development of IBI for South African rivers, and in particular rivers in KNP, where such data does not exist. Consequently it is not possible to specify precise quantitative criteria for IBI metrics. Karr's (1981) statement that the circumvention of this problem is a primary challenge to biologists in the development of IBI, is as valid today as when he wrote it in 1981. Species richness lines and maximum density lines have been used in some studies to determine metric scores (Fausch *et al.* 1984; Miller *et al.* 1988; Oberdorff and Hughes 1992). Limitations of this approach have been discussed in the introduction to Chapter 3, and include the frequent necessity to use data from already degraded systems thereby biasing metric boundaries, and failure to distinguish between the effects of natural and anthropogenic disturbances.

Several other limitations of the IBI can be identified. Although the combination of metrics in IBI is designed to integrate attributes from several levels of ecosystem organization (Karr 1981), some aspects of biodiversity (Noss 1990) such as the structural diversity of populations are not directly addressed. This deficiency, combined with the equal weighting and coarse grading of various metrics could result in subtle changes in species composition, diversity, and functional organization of fish assemblages being overlooked. Fausch *et al.* (1990) has also emphasized that, unlike earlier bio-assessment methods, such as diversity indices and abundance models, the statistical properties of the IBI have not yet been studied. The IBI in its current state of development is a promising, though incomplete and largely untested monitoring approach.

If an IBI applicable to fish assemblages in KNP rivers is successfully developed, and tested, it would likely provide a valuable means of early detection of deleterious effects of anthropogenic changes to the aquatic environment. It would help focus attention on species or groups of special interest, which would be an improvement on aspects of the informal assessment of species abundances discussed in section 3.3. A disadvantage of this component of IBI, however, is that changes in the abundances of species or groups not specifically targeted could not be reflected in IBI scores.

IBI could also be a useful means of translating complex ecological processes into values meaningful to decision makers and the general public (Karr 1981; Miller *et al.* 1988). As Karr (1981) points out, however, IBI should serve only as an exploratory assessment of water resource quality. Where environmental degradation use is suggested, a more complete monitoring program can be implemented. Changes in the distribution and abundance of fish in the major rivers in KNP resulting from anthropogenic modification of water resource quality, as illustrated in this and other studies (Pollard *et al.* 1993; Chutter and Heath 1993) suggest that the time for a "more complete" monitoring program, which includes the search for causative agents, is overdue.

4.4 SUMMARY AND CONCLUSIONS

The above discussion briefly outlines an environmental monitoring strategy to investigate changes in the diversity of fish assemblages in KNP rivers. The measurement of biotic diversity has application in environmental monitoring in that it provides an index of ecosystem well-being (Magurran 1988). This application is based on the assumption that adverse changes in the environment will be reflected in a reduction in biotic diversity (Kempton and Taylor 1974; Taylor *et al.* 1976). The monitoring of fish assemblages in KNP rivers, and aspects of their environment, will provide opportunities for improving understanding of the effect of both natural and man-induced environmental changes on the functioning of riverine ecosystems. Unfortunately there is no panacea with respect to methodologies used to evaluate change in biotic diversity. Consequently, a variety of analytical methods would need to be employed to ensure confidence in the accuracy of measured biotic changes as discussed above. Ultimately, the use of a number of methods to assess change in the diversity of fish assemblages at different scales is of little consequence, and even desirable (Noss 1990), so long as the properties of the different methodologies are understood, and resources are not wasted on repetitive data analysis. As pointed out by Magurran (1988), diversity measures are valuable, but are only a means to an end. The end being that ecologists are able to formulate hypotheses which assist in the understanding and sensible management of the natural world.

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