DEFINING FLOWS TO PROTECT INSTREAM BIOTA:

A CRITIQUE OF THE INSTREAM FLOW INCREMENTAL METHODOLOGY AND THE DEVELOPMENT OF A HIERARCHICAL HABITAT-BASED APPROACH, USING THE PENNANT-TAILED CATLET, *Chiloglanis anoterus* IN THE MARITE RIVER, SOUTH AFRICA.

Sharon Raé Pollard

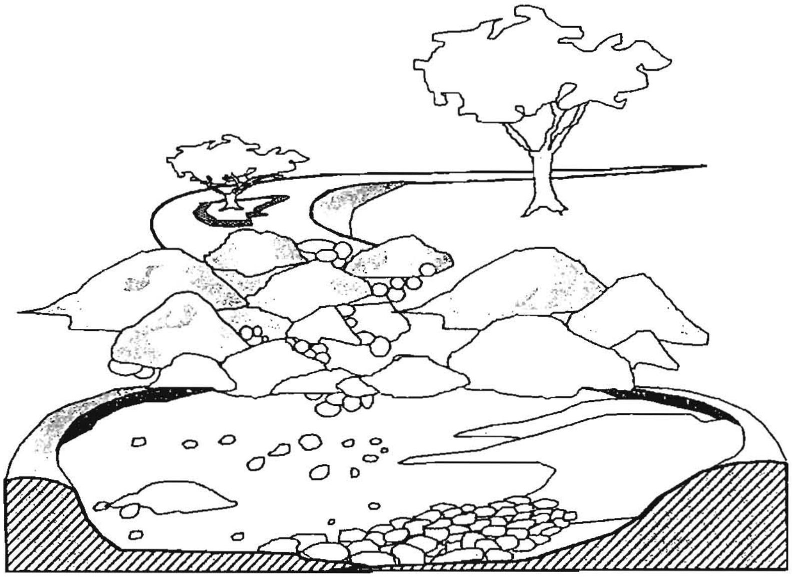
Thesis presented for the degree of

DOCTOR OF PHILOSOPHY

in the Department of Zoology

UNIVERSITY OF CAPE TOWN

December, 2000



Defining flows to protect instream biota: A critique of the Instream Flow Incremental Methodology and the development of a hierarchical habitat-based approach, using the pennant-tailed catlet, *Chiloglanis anoterus* in the Marite River, South Africa.

Sharon Raé Pollard

December 2000

Abstract

This thesis focusses on two approaches to determining Instream Flow Requirements (IFR) for regulated rivers, specifically in the sub-tropical eastern region of South Africa using a flow-sensitive fish species, the pennant-tailed catlet, *Chiloglanis anoterus*.

In response to the diminishing and altered flow regimes of rivers, and the ecological consequences, a range of methodologies has evolved that attempt to quantify IFRs for rivers. One group of methods that attempts to do this are known as habitat-assessment approaches. They focus specifically on understanding how changes in river flow affect the quantity of physical instream habitat. The most widely used of these is the Instream Flow Incremental Methodology (IFIM) and it's associated computer packages, PHABSIM II.

More recently, South Africa has also turned its attention of ways to defining IFRs. Given IFIM's prominence internationally, it was considered as one potential methodology. Nonetheless, its applicability to local conditions required testing. At the same time, the easterly-flowing rivers were under increasing development pressure, providing a particular immediacy to find appropriate means to define IFRs. Thus, my research was designed to assess the downstream effects of the Injaka Dam on the physical habitat of a flow-sensitive fish species of the Marite River. Specifically, it aimed to test the local applicability of IFIM, based on the microhabitat requirements of *C. anoterus*, and to explore an alternative approach if it were found to be unsuitable. *Microhabitat* is described on the basis of three hydraulic variables: depth, velocity and Channel Index (substratum and cover).

Standard IFIM approaches were used to describe the microhabitat requirements of this species. These involved the development of use and preference microhabitat curves for three lifestages: early juveniles, late juveniles and adults, at a number of discharges. This information was used to compute the total available habitat via PHABSIM II. These data were also tested to elucidate differences in seasonal, site and lifestage use of microhabitat. Many of the results appeared to have little biological rationale. Hence, approaches to describing the microhabitat availability (specifically the use of transects to describe habitat conditions at a site), and mathematical effects of this on the development of preference indices were interrogated.

Based on my findings, I concluded that IFIM was largely inappropriate for use locally. This conclusion was based principally on concerns regarding the approach to defining habitat availability and the approach to site selection. Specifically I pointed to a number of key factors that contributed to this conclusion: (i) the lack of a clear geomorphological classification which defined the spatial relationship between habitat features in rivers (and the processes that govern them); (ii) the means by which availability is quantified (transect approaches) and described (univariate curves of microhabitat) and, (iii) the failure to incorporate evolving conceptual models.

Consequently I developed and proposed the use of an alternative approach formulated as the Geomorphological - Biotope Assessment, or GBA. This approach is based on a locally-developed, hierarchical classification system for bedrock/ alluvial rivers that holds, as it smallest scale of habitat, the biotope. *Biotopes* are spatially distinct instream environments characterised by their flow and substratum types, which hence preserve their spatial reference. Such a classification system allows the smallest scale of habitat to be linked to the catchment scale and thus provides a framework for extrapolating site-specific results up to the scale of the study river. The central tenet is that the geomorphology provides the physical template on which biotope availability, as a function of flow, is superimposed.

Based on the GBA, the habitat availability (as biotopes) for the target fish species, was described. This involved delineating channel types that occur in the Marite River, and selecting sites to represent them. At each of the five sites, habitat was described on the basis of key geomorphological features, or geomorphic units. Maps of these provided the physical template on which the distribution and extent of biotopes were mapped at four different discharges. The data analyses focussed specifically on biotope characteristics of Pool and Rapid geomorphic units. These were described and tested to explore differences between Rapids and Pools, and differences within geomorphic units at different discharges. Each geomorphic unit displayed a distinct biotope assemblage, which changed as a function of flow. However, the overall characteristics of each type of geomorphic unit, such as numbers, diversity and density, did not change as flow varied.

Estimates of habitat availability at each flow were then demonstrated by extrapolating biotope information at the scale of the geomorphic units up to channel type and then for the river. Furthermore, a framework for describing biotope use was given and tested, and approaches to extrapolating these results up to the scale of the river, demonstrated. Finally, recommendations for future research directions were also provided.

ACKNOWLEDGEMENTS

In thinking through all the people that had assisted me, the overwhelming theme was one of collaboration and multidisciplinarity. I can only remember vaguely as a thing of the past the difficulties of talking at cross-purposes between ecologists, engineers, geomorphologists and hydrologists.

Foremost my thanks goes to my supervisors, Dr. Jackie King and Prof. Bryan Davies (Freshwater Research Unit, University of Cape Town). Jackie spent many days with me trying to understand PHABSIM, and finally getting it right, and producing together with Rebecca Tharme the manual on PHABSIM. Both Prof. Davies and Dr. King gave invaluable editorial comments - my sincere thanks to them for persisting in their support. Dr. Paul Skelton (JLB Smith Institute, Grahamstown) also took on the role of "unofficial" supervision in the early part of the work on fish. I am indebted to Mr. Bill Rowlston (Department of Water Affairs & Forestry) without whose persistence and good humour with PHABSIM none of the earlier results would have been possible.

At a later stage, three people were key in helping formulate and refine my ideas on new approaches to describing habitat. They were Dr. Andre van Niekerk (University of the Witswatersrand), a dear friend who has sadly passed away, Dr. George Heritage (Department of Geography, University of Salford) and Prof. Kate Rowntree (Department of Geography, Rhodes University). Dr. Heritage in particular, contributed many days to field visits whilst here from the UK. My sincere thanks - without them, I certainly would not have developed a different view of rivers.

I am indebted to various institutions for funding this work. The early work was supported through the Foundation for Research and Development (FRD) Special Programme on South African River Systems, awarded to Prof. B.R. Davies and Dr. J. O'Keeffe (Institute for Water Research, Rhodes University). Additional support was also provided through a collaborative project, the Pre-impoundment Study of the Sabie-Sand Rivers (under the Kruger Park Rivers Research Programme), funded through the Water Research Commission. The Claude Harris Leon Foundation and the Association for Water & Rural Development has assisted in various ways over the last three years.

Then to my dear friends, Dr. Harry Biggs (Scientific Services, Kruger National Park) and his family for his tenacity through endless conceptual discussions and gymnastics - thanks for being there through all of this. My field assistants not only helped in the field but were good friends. Thanks to Victor Makunhane who still says he would prefer to be working in rivers, Kenneth Muchocho who now works in the Kruger Park, and to Rael Mashego and Simon Mdaka.

Dr. Jim Cambray (JLB Smith Institute, Grahamstown) very kindly offered assistance with some of the work on the reproductive ecology of fish, and Prof. June Juritz (Department of Statistical Sciences), from the University of Cape Town, provided statistical support. Thanks also to Ninham Shand Consultants (Cape Town), for assistance with the hydrological analyses.

Mr. And Mrs. Schweiser offered us food and accommodation on numerous field trips. The Mckenzie family very kindly provided field accommodation for two years. Mr. Alex Durr allowed access to the river from his property.

An entire team of people made up of DWAF staff and colleagues helped with collecting the macrohabitat data and lightened the field trips considerably. They included Jay O'Keeffe and Desmond Weeks (Institute for Water Research) of Rhodes University, Andrew Birkhead of the University of Witwatersrand and Rebecca Tharme from the University of Cape Town. My thanks for setting up all those tape measures. Andre Fourie specifically was very supportive and readily went into areas of rivers that were perhaps less than safe.

Many thanks to James Hargreaves (Health Services Development Unit/ London School of Tropical Medicine) who, in the last months, persisted in getting me to "ask the right questions". He comes from a different discipline- the health sciences, and is a good example of how interdisciplinary discussion can work. Thanks are also due to Rhian Evans and Wayne Twine (University of the Witwatersrand) for editorial comments and the numerous friends for their support throughout. Not last, sincere thanks Kevin Mitchell (Wits Rural Facility) for his support throughout the last two years, and many late nights helping with the final version. For those I may not have mentioned, my thanks to you.

Summary

Chapter 1 Introduction

In Chapter 1, the conceptual framework and motivation for this thesis was provided. Initially, the major theories that govern lotic systems were reviewed. This was followed by a discussion on the downstream effects of impoundments, which can be broadly categorised as hydrological, sedimentological, chemical, morphological, thermal and biotic. Coupled with this was a focussed discussion on river regulation in South Africa where, with almost all major river systems impounded, similar deleterious effects are apparent. Globally, these impacts have pointed to the need for mitigatory measures, an important component of which is the determination of the Instream Flow Requirements (IFR) of rivers. A number of approaches have been developed internationally to quantify these. Most notably, the habitat-assessment approaches such as the Instream Flow Incremental Methodology (IFIM) and its associated computer package, PHABSIM, have gained prominence. Given its wide-scale use, IFIM was also being considered as a means to determine IFRs for South African rivers in general, but its applicability required testing. At the same time, the increasing development pressures on the rivers of the eastern region of the country focussed attention on finding appropriate means to define IFRs, particularly for the Sabie River system.

Thus, my research was designed to assess the downstream effects of the Injaka Dam on the physical habitat of a flow-sensitive fish species of the Marite River. This river is the site of the Injaka Dam which is currently under construction.

The aim and objectives of this thesis were:

Aim: To assess the potential downstream effects of the proposed Injaka Dam on the physical habitat of a flow-sensitive fish species of the Marite River, a sub-tropical southern African system, with particular emphasis on the hydraulic modifications associated with low-flow conditions.

Objectives:

1. To test the applicability of a quantitative, habitat-assessment approach, namely IFIM, with a view to exploring its potential use as a contribution to recommending IFRs in the local, geographic context. The sub-objectives were:
    a. to quantify the hydraulic microhabitat requirements of the adult, and possibly other life-history stages, of a target species, as required by the IFIM;

a. to describe microhabitat changes of the target species as a function of discharge and;

c. to evaluate the possibility of setting IFRs based on this approach.

2. To explore alternative habitat-assessment approaches to determine IFRs.

The chapter closed with a description of the terms describing *habitat*, and an outline of the thesis format (see summary of Chapter 2).

Chapter 2 Overview of the Instream Flow Incremental Methodology (IFIM) and PHABSIM

Chapter 2 provided an overview of the rationale and steps of IFIM and its computer package, PHABSIM. The IFIM process is said to evaluate the effects of incremental changes in streamflow on macrohabitat, and physical microhabitat, described as follows:

- *Macrohabitat* includes water quality and temperature and secondarily, geology, slope, elevation, water yields and sediment and chemical yields.
- *Microhabitat* comprises the physical variables of depth, velocity, substratum and cover at the location that an organism was sighted, or captured.

The objective of IFIM and PHABSIM is to develop a habitat versus flow relationship that is quantitatively defensible. The final output is a quantitative description of the availability of physical microhabitat, known as the Weighted Usable Area, or WUA, for selected species over a range of discharges.

Essentially, the main steps of IFIM include: (i) setting the objectives (Chapter 1), (ii) defining the study area (Chapter 3), (iii) scoping (assessing catchment equilibrium and macrohabitat conditions; Chapter 4), (iv) site selection (Chapter 4) for the monitoring of macrohabitat (Chapter 5) and microhabitat (Chapter 8), (v) target species selection (Chapter 6), (vi) defining the physical habitat and biological inputs for PHABSIM (Chapter 8), (vii) running PHABSIM, and computing the available microhabitat, known as Weighted Usable Area (WUA), for different river discharges (Chapter 9). Although not formally part of IFIM, the constraints of the limited ecological data resulted in additional research on the reproductive ecology of the target species (Chapter 7).

Chapter 3 The Marite River Catchment and study area

An overview of the biophysical parameters, available water resources and land-use patterns of the Marite River Catchment, in which the study area is located, was outlined in Chapter 3. Reference was also made to major hydrological changes that have typified the region, as well as current and potential water shortages and planned water-resource developments.

The key attributes of the Marite are that, together with the Sand River, it is the most significant tributary of the Sabie River, which is the only perennial system that flows eastwards through the Kruger National Park in South Africa to Moçambique. Increasing pressures on the water resources have resulted in declining flows and consequently, the Injaka Dam is currently under construction on the Marite River.

Chapter 4 The assessment of catchment equilibrium and macrohabitat conditions, and the selection of PHABSIM II study sites

In Chapter 4, the concepts of catchment equilibrium, macrohabitat, and site selection were described and assessed, through their application to the Marite River. The assessment of catchment equilibrium is undertaken in order to verify that stream conditions will not change substantially in the future. Describing the macrohabitat conditions allows one to delimit macrohabitat zones and to select sites. Site selection is critical in that conditions at a site are considered representative of a predetermined section of the river and hence, theoretically, can be extrapolated to the entire study area.

I concluded that the Marite River was in equilibrium with no major changes anticipated. Due to a lack of guidelines and paucity of data, however, this conclusion was based mainly on professional judgement. The Marite River appeared to comprise one macrohabitat zone, with a potential second zone in the lower reaches. Based on IFIM guidelines, three sites were selected in the study area. These were described and the protocol for site selection was discussed. The chapter closed with an assessment of this step. Overall, the assessment of catchment equilibrium and macrohabitat conditions is difficult to implement and, as a precursor to site selection, requires refinement within IFIM.

Chapter 5 Monitoring macrohabitat conditions and the collection of hydraulic calibration data

This chapter described (i) the macrohabitat conditions of the Marite River over the IFIM study period and (ii) the collection of hydraulic calibration data for use in PHABSIM. Additionally, a severe drought provided the opportunity to document the physical and chemical characteristics of extreme low-flows.

In general, stable water quality and temperature conditions characterised this study until the height of the drought. No marked longitudinal differences existed in most of the variables, supporting the preliminary assessment that the study area comprises one macrohabitat zone.

The hydraulic calibration data included: (i) the placement and description of transect profiles across major habitat, or hydraulic, features at each site; (ii) measurements of hydraulic variables along each transect; (iii) velocity readings across the transects and; (iv) measurements of the water surface elevations of each transect, on three occasions, in order to derive a stage-discharge relationship. Although the procedures for the collection of calibration data are relatively well documented, problems were encountered in the placement of transects, particularly across multiple channels.

Chapter 6 Fish of the Marite River and the selection of an indicator species

Quantifying the instream flow requirements of the entire community is beyond the scope of most studies and warmwater streams, with high species and habitat diversity, pose additional challenges. Thus, the rationale has been to use a *target* or *indicator* species as a surrogate measure of the flow requirements of the community. Given their importance, and their limitations, this is a critical, but frequently neglected step in IFIM. Accordingly, the terms *target* species (chosen for predetermined reasons), and *indicator* species (chosen according to objective criteria) were distinguished. In this chapter, I argued that target species approach is inappropriate for use in South Africa which subscribes to an ecosystem approach to IFRs. The use of guilds was discussed but was not applied since it carries its own liabilities.

Guidelines for the selection of an indicator species were then developed and applied to the fish species of the Marite River. The final indicator species selected was *Chiloglanis anoterus*, the pennant-tailed catlet. Adults of this species were described as restricted to riffles or rapids and intolerant of low-flow conditions. Nothing was known about habitat requirements of other lifestages.

The chapter concluded with discussions on the relationship between flow and different habitat types, and on those habitat types that are considered to be potentially vulnerable to flow reductions. This is poorly understood in South Africa and requires further research.

Chapter 7 The reproductive biology of *Chiloglanis anoterus*

Although not a conventional step within IFIM, aspects of the reproductive biology of the target species, *C. anoterus* were examined for two reasons:

- to describe their major reproductive attributes, so as to better assess and validate the predictions generated by PHABSIM and;
- to describe the size delimitation between various lifestages, so as to develop SI curves for each lifestage.

My results indicated that *C. anoterus* exhibit a protracted spawning season from October to March. They are multiple spawners and produce three to four batches of large, slightly adhesive eggs in a season. Fecundity was linearly related to length, with a 50 mm (SL) female shedding about 20 eggs per batch. In the Marite, sexual differentiation was achieved in this species at 39 mm (SL), a shorter standard length than previous estimates from other rivers. This length delimited juvenile and adult lifestages.

These findings were then discussed in relation to the flow-related variables that may be important in the reproductive cycle for this species, and flow and temperature were implicated as key determinants. These were then evaluated in terms of the potential modifications to the flow regime of the Marite River.

Chapter 8 The use of hydraulic microhabitat by *Chiloglanis anoterus*

Chapter 8 focussed specifically on a description of microhabitat use by *C. anoterus* in accordance with IFIM protocols. It had two objectives.

1. To produce a description of microhabitat use in the format required by PHABSIM (SI curves).
2. To test the following hypotheses:
    - The indicator species, *C. anoterus* does not select particular microhabitat conditions.
    - Microhabitat availability does not differ significantly between sites, at a specific time.
    - Microhabitat use by *C. anoterus* does not differ between sites, at a specific time.
    - Microhabitat use does not differ significantly between juvenile and adult *C. anoterus.*
    - Microhabitat use by *C. anoterus* does not exhibit a seasonal variation.

A brief overview of the conceptual basis of SI curves, and the collection and manipulation of data needed to produce these curves, was given. Composite and seasonal SI curves for the hydraulic variables of depth, velocity and substratum were produced for three lifestages (early and late juveniles, and adults) of *C. anoterus.* Habitat use through the 1992 drought was also considered.

These results indicated that:

- Juvenile and adult *C. anoterus* select a specific range of depths and velocities.
- Microhabitat availability differed between sites in about half the cases tested.
- Adult *C. anoterus* use different microhabitats at each site.
- Differences in microhabitat use between juveniles and adults were only partially demonstrated.
- Seasonal differences in microhabitat use by adults were evident for all three hydraulic variables.

A critique of the competency of SI curves to represent microhabitat use followed. In summary:

- the use of preference indices was refuted, since their accuracy is conditional on accurate measurements of habitat availability, which is unlikely in reality. I demonstrated the implications of incorrect measurements of availability on the mathematical behaviour of the SI models. Moreover, ambiguities in their interpretation were also shown.

- The use of composite SI models obscures the heterogeneous nature of habitat use.
- My data indicated that the assumption that the three hydraulic variables operate independently to create suitable habitat for *C. anoterus,* is unlikely.

Given these reservations, I concluded that the use of SI curves can only offer a broad characterisation of microhabitat use, and that preference indices have been insufficiently interrogated in IFIM studies.

Chapter 9 Microhabitat availability for *Chiloglanis anoterus* as calculated by PHABSIM II

This chapter tested, and assessed, the application of PHABSIM II to the Marite River to determine the amount of suitable habitat for juvenile and adult *C. anoterus.* The chapter opened with a synopsis of the theory of hydraulic and habitat simulation, and the simulation routines used in this research. Ultimately, only one site (Site 3) was modelled due to the constraints encountered in modelling complex multiple channels at one site (Site 1), and inadequate representation of the primary habitat of *C. anoterus* at the other (Site 2).

The stage-discharge relationship for each of the transects, produced by the hydraulic simulation, were found to be hydraulically robust between 0.02 and 3.4 $m^3 s^{-1}$. This defined the range of flows simulated. Estimates of the total habitat (WUBA) indicated a sharp decline in habitat between 0.026 and 0.5 $m^3 s^{-1}$. Rapids, the primary habitat of *C. anoterus,* contributed an estimated 13% to 23% of the site area.

Finally, the following concerns were raised in relation to PHABSIM: (i) the inability of PHABSIM to model complex channel morphologies, rapids, pools and backwaters which occur in the Marite River; (ii) the use of transects (which assumes habitat homogeneity between them), to describe habitat availability and; (iii) the interpretation of the outputs of PHABSIM. These issues were elaborated in Chapters 10 to 13.

Chapter 10 An assessment of IFIM & PHABSIM and the conceptual basis for an alternative habitat-assessment approach

Generally, IFIM/ PHABSIM was considered to be unsuitable as a potential habitat-assessment approach for the Marite River. Consequently, this chapter summarised the main critiques and provided a conceptual framework and protocol for a proposed alternative.

Firstly, a major criticism of IFIM, which suggests that there is a relationship between habitat and standing stocks, was addressed. Three factors emerged from the literature: (i) Physical habitat may only influence abundance under specific circumstances, (ii) Physical habitat comprises a more complex array of variables than those nominated in IFIM and, (iii) IFIM does not take into account biological processes.

This was followed by a summary assessment of IFIM and PHABSIM based on the preceding research, as follows:

1. IFIM and PHABSIM were recognised for its contribution to assessments of IFRs. Nonetheless, key limitations hampered its use for the Marite River.
2. The weaknesses of assessing channel equilibrium and site selection were ascribed to poor guidelines and definitions and the failure to recognise the spatial relations between habitat features.
3. The use of transects was questioned on conceptual grounds.
4. Target or indicator species selection receives insufficient attention in IFIM and the available guidelines reflect the fisheries concerns that predominate in the US.
5. Preference indices were considered to be insufficiently robust to represent habitat selection and their use was strongly refuted.
6. The use of univariate SI curves was considered to have little biological basis.
7. The use of PHABSIM II to compute total microhabitat was problematic in complex channel morphologies, rapids, pools and backwaters. Notably, the interpretation of the outputs requires resolution.

I suggested that these constraints arise from (i) the omission of a morphological classification system for rivers and (ii) IFIM's failure to incorporate evolving conceptual models. Classification systems allow for an examination of geomorphic patterns that can be linked causally to physical factors regulating instream characteristics and were, thus, my central focus for the remaining chapters.

The development of classification systems in South Africa was traced, and the use of a bottom-up *agglomerative hierarchical classification system* (van Niekerk *et al.* 1995), which classifies the mixed alluvial/ bedrock rivers of the lowveld, was proposed. Essentially, this holds that **geomorphic units** combine to form **channel types**, which comprise **reaches, macro-reaches**, **zones**, and the **river** comprises all the zones and riparian margins and lies within the **catchment**. Added to this are **biotopes**, which are the smallest scale of physical habitat (Wadeson 1994).

A framework for an alternative approach: the Geomorphological-Biotope Assessment

Based on this classification, I proposed an alternative habitat-assessment approach, formulated as the Geomorpholgical - Biotope Assessment (GBA). In essence, the GBA is an approach to understanding and describing the distribution and abundance of physical habitat based on a locally-appropriate, hierarchical classification system for rivers. It draws on the themes of scale and pattern, integrated through the key concepts of patches (habitat) and patch dynamics (habitat changes and interactions). The GBA recognises the smallest scale of habitat as the biotope which, as a patch, has spatial dimension and reference. Technically, the main steps are not unlike those of IFIM but their main differences are discussed. The central tenet is that *the geomorphology provides the physical template on which biotope availability, as a function of flow, is superimposed.* The themes of heterogeneity, pattern and scale, and concepts of patch dynamics and landscape ecology underscore this tenet, which are also discussed.

Chapter 11 An alternative approach to determining the availability of hydraulic biotopes in the Marite River

Using the GBA, this chapter aimed to quantify the availability of biotopes, and their spatial and temporal attributes. The three objectives were:

1. To describe the channel types of the Marite River, and their assemblages of geomorphological units.
2. To describe the biotope availability of pool and rapid geomorphic units on a spatial and temporal scale.
3. To develop a framework for extrapolating site-specific (i.e. channel type) information on biotope availability, up to the study area.

This involved: (1) A geomorphological assessment of the channel types and their associated geomorphic units, of the Marite River. The geomorphic units were mapped and this comprised the geomorphic template. (2) A biotope assessment, which recorded the distribution of biotopes within these geomorphic units at four discharges. The major biotope characteristics were then analysed at the scale of geomorphic units. The major findings can be summarised as follows:

Channel types and geomorphic units of the Marite River

The Marite River study area comprises five channel types: Alluvial Single Thread (AST), Mixed Single Thread (MST), Mixed Pool Rapid (MPR), Mixed Anastomosing (MAN) and Bedrock Anastomosing (BAN) Two channel types, AST and BAN, were excluded in the IFIM site selection. The GBA recorded 25 types of geomorphic units in the Marite River. Generally, the highest diversity and number of biotopes occurred in rapids, followed by pools.

Biotope availability in pools and rapids

1. Geomorphic units have a characteristic biotope assemblage or fingerprint.
2. Generally, the biotopes of pools were larger, and more numerous and diverse than Rapids. Rapids, on the other hand, exhibit higher densities of biotopes.
3. Discharge exerts its major influence on the internal biotope make-up at low discharges, but not on the overall characteristics of numbers, diversity and density.
4. The exception to this is in the size of biotopes in rapids which decline dramatically at the lowest discharge measured. This pointed to the following key attributes of rapids:

- As discharge decreases, the reduction in the total wetted area of Rapids is more marked (41%) than that of pools (~15%).
- The biotope assemblage varies as a function of flow.

5. Habitat availability is better understood as the *assemblage of biotope types.*

The chapter concluded with a focus on geomorphic units as the scale to describe habitat which, I argued, is more objective than the transects of PHABSIM. Moreover, this spatial scale potentially provides the key to understanding habitat attributes (numbers, diversity, size and density, and spatial reference). The description of habitat as biotopes, as opposed to cells between transects, supports such an approach. Finally, a framework for extrapolation, together with recommendations for further refinement, was provided.

Chapter 12 Making the ecological link in the GBA - a framework for determining biotope use

A framework for the development of biotope-use models, commensurate with those of biotope availability, was outlined and demonstrated, using data for *C. anoterus.* The purpose was:

1. to demonstrate an approach to linking biotope use models with those of availability and;
2. to compare the utility of the outputs for adult *C. anoterus* from PHABSIM and the GBA.

Data were analysed at the spatial scale of geomorphic units. Two outputs were derived (i) composite-biotope profiles of biotope use (i.e. for the study area) for all three lifestages, and (ii) biotope use profiles at the scale of channel type.

The potential outputs on habitat-use within the GBA were then discussed. I suggested that the GBA offers advantages over IFIM which relates to two spatial scales, as follows.

1. The focus on *geomorphic units* to describe habitat use by *C. anoterus* revealed that:

- the three lifestages occurred in different proportions in each type of geomorphic-unit, where they used distinct assemblages of biotopes and which varied internally as discharge changed.
- Early juveniles use multiple geomorphic units.
- The composite and site-specific profiles of biotope availability and use differ due to the different assemblages of geomorphic units comprising the different channel types.
- Despite the restriction of *C. anoterus* adults to Rapids, the biotopes that they use were also found in other geomorphic units.

2. Representing biotope use as an *assemblage of biotope types* allows habitat characteristics to be explored. Furthermore, in addition to general descriptions of habitat loss or gain, understanding the spatial and temporal attributes of habitat may be equally important in habitat assessments.

Lastly, these findings were discussed in relation to the conventional (IFIM) descriptions of habitat. I contended that whilst the composite output might provide an overview of biotope availability and use, there were shortcomings associated with aggregating data. Moreover, the need for complimentary ecological data within habitat-assessment approaches was emphasized.

Chapter 13 Conclusions: an appraisal of the Geomorphological-Biotope Assessment and the Instream Flow Incremental Methodology and the future of habitat assessments

Chapter 13 concluded with an integrated, comparative appraisal of the IFIM/ PHABSIM and GBA approaches and recommendations for future research needs. The preceding discussions regarding the problems of IFIM, and their resolution in the GBA, were integrated around two themes: (a) the spatial reference of habitat features and mechanisms that control the architecture, distribution and abundance of biotopes and, (b) the conceptual approach that circumscribes the inputs and outputs of habitat availability. Discussions around these themes reviewed the benefits of a classification system for rivers, and of characterising habitat availability and use as assemblages of biotopes, in contrast to the disaggregated curves of IFIM. It was suggested that both of these allow researchers to capture environmental variability, for which a range of analytical tools has recently emerged.

As an alternative habitat-assessment approach, I suggested that the GBA requires testing in the following areas:

1. Links to broader approaches.
2. Temporal considerations and the use of the GBA in high flows.
3. Capturing heterogeneity.
4. Complimentary ecological data.
5. Resolution on the link between habitat availability and habitat use.
6. Interdisciplinary approaches focussing on geomorphological and hydraulic characterisation of rivers, data transferability, and the incorporation of the GBA into formal simulation.
7. Investigating long-term channel change.

The chapter concluded with a discussion on the future of habitat assessments and their contributions to defining instream flows. Ultimately I suggested that, as tools in evolution, their real strength can be measured in their conceptual adaptability and potential for evolution, and our ability to recognise this.

Table of Contents

PART I

Chapter 1 **Introduction**

Chapter 2 **Overview of the Instream Flow Incremental Methodology (IFIM) and PHABSIM**

PART II

Chapter 3 **The Marite River catchment and study area**

PART III

Chapter 4 **The assessment of catchment equilibrium and macrohabitat conditions, and the selection of PHABSIM II study sites**

Chapter 5 **Monitoring macrohabitat conditions and the collection of hydraulic calibration data**

Chapter 6 **Fish of the Marite River and the selection of an indicator species**

Chapter 7 **The reproductive biology of *Chiloglanis anoterus***

Chapter 8 **The use of hydraulic microhabitat by *Chiloglanis anoterus***

Chapter 9 **Microhabitat availability for *Chiloglanis anoterus* as calculated by PHABSIM II**

PART IV

Chapter 10 An assessment of IFIM & PHABSIM and the conceptual basis for an alternative habitat-assessment approach

LIST OF FIGURES

Figure captions are abbreviated

LIST OF PLATES

Plate captions are abbreviated

LIST OF TABLES

Table captions are abbreviated.

LIST OF APPENDICES

PART I

Background concepts, motivation and approach

1

Introduction

1.1 INTRODUCTION

South Africa is a water scarce country, and current predictions are that demand will outstrip water availability in the next ten to fifteen years (DWA(1) 1986). Two factors have interacted to produce such a stark and precarious picture: the aridity of the region, and it's socio-economic and political history.

Turning to the first of these, southern Africa lies within the drought belt of the Southern Hemisphere and, with an average rainfall of 497 mm, falls well below the global average of 860 mm (DWA, 1986; Figure 1.1a). Furthermore, potential evaporation rates are high (Figure 1.1b), and many parts of the country are often in water deficit (Alexander 1985). Indeed, South Africa has one of the lowest rainfall to runoff conversions globally of 8.6% compared to 9.8% in Australia and 67% in Canada (Figure 1.2). This figure illustrates all too well the highly variable rainfall- runoff regimes of the country, leading Davies *et al.* (1993) to coin the phrase "predictably unpredictable" in reference to their flow regimes. This also appropriately describes the cyclical nature of drought that periodically plagues the country (Tyson 1986). Water is often the limiting factor for development (O'Keeffe *et al.* 1989a) and, in fact, water is possibly South Africa's most limited and limiting resource (Davies & Day 1998).

A combination of socio-economic and political factors superimposed on these major physical constraints has exacerbated the effects of resource scarcity. These factors historically included large disparities in access to water within, and between, sectoral groups and a tariffing system that did not reflect the resource limitations. Political interests were evidenced in the previous water policy that endorsed agricultural priorities over other sectors, principally through heavy subsidies, as well as a duplication of institutional bodies tasked with the allocation and management of water. This backdrop provided little incentive for the "wise use of water" by consumer groups.

Added to these factors, South Africa supports a burgeoning population (2.7% growth per annum, World Bank 1980), with the current 42 million people comprised largely of rural poor. Although the situation has improved in the last five years, there are still an estimated 7 million people with no access to potable water supplies and between 16 and 18 million who have no water-borne sewerage (Mr. Muller, Director General, Community Water Supply, Department of Water Affairs & Forestry (DWAF), *pers. comm.*). With just over 1200 m^3 of water available for each person per annum, South Africa now sits on the threshold of qualifying for the internationally-used definition of "water stress", with already less water per person than her arid neighbours, Namibia and Botswana (DWAF 1997). Despite this, the past government of

---

[1] Department of Water Affairs, South Africa. Later the competency of this department was expanded to include forestry, and was renamed the Department of Water Affairs and Forestry.

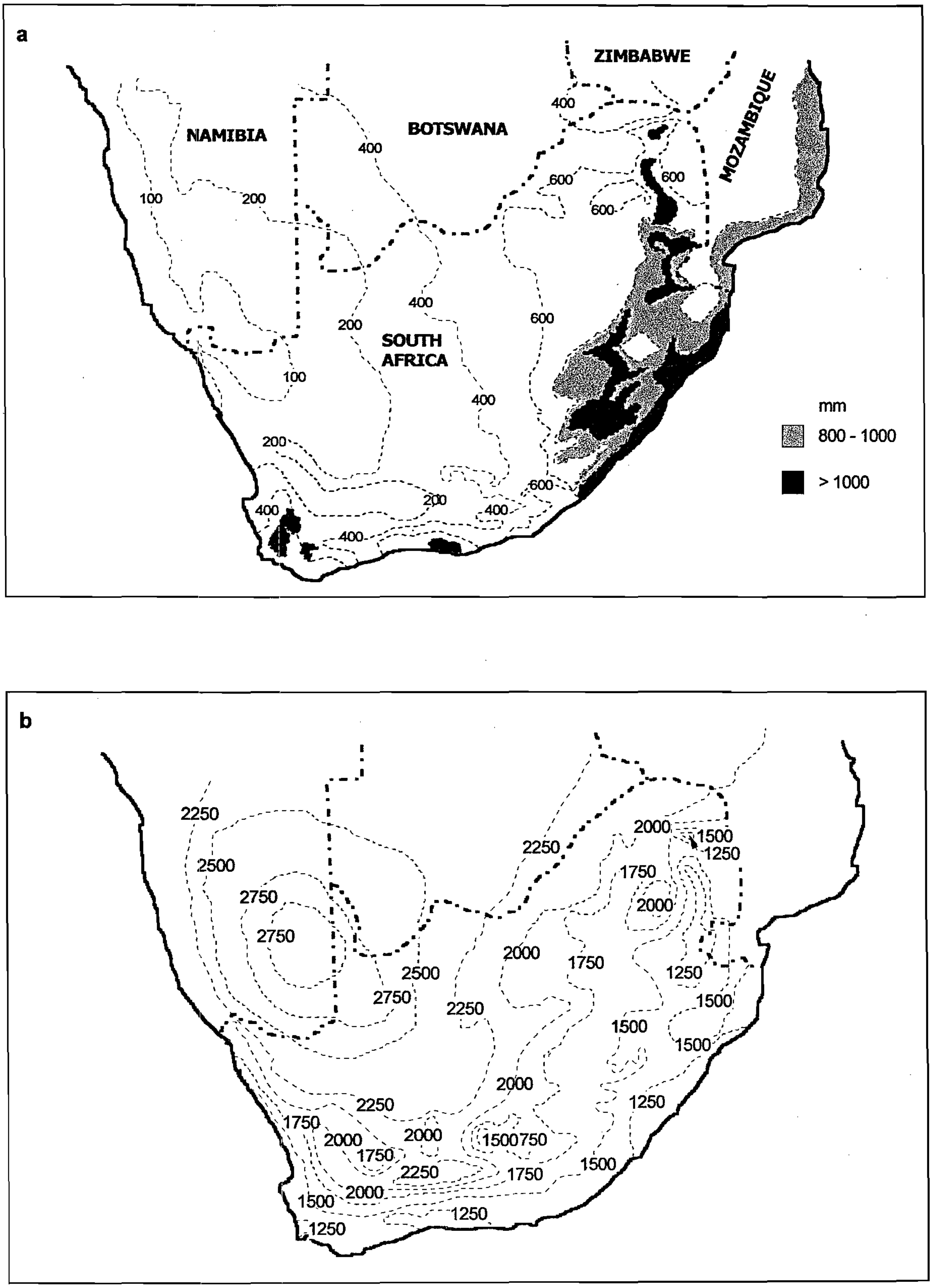


Figure 1.1 (a) Rainfall isohyets (average mm a^{-1}) and, (b) iseovaps (average mm a^{-1}) for southern Africa indicating the high evaporation rates that characterise most of the region (after Davies & Day 1998, modified from DWAF 1986).

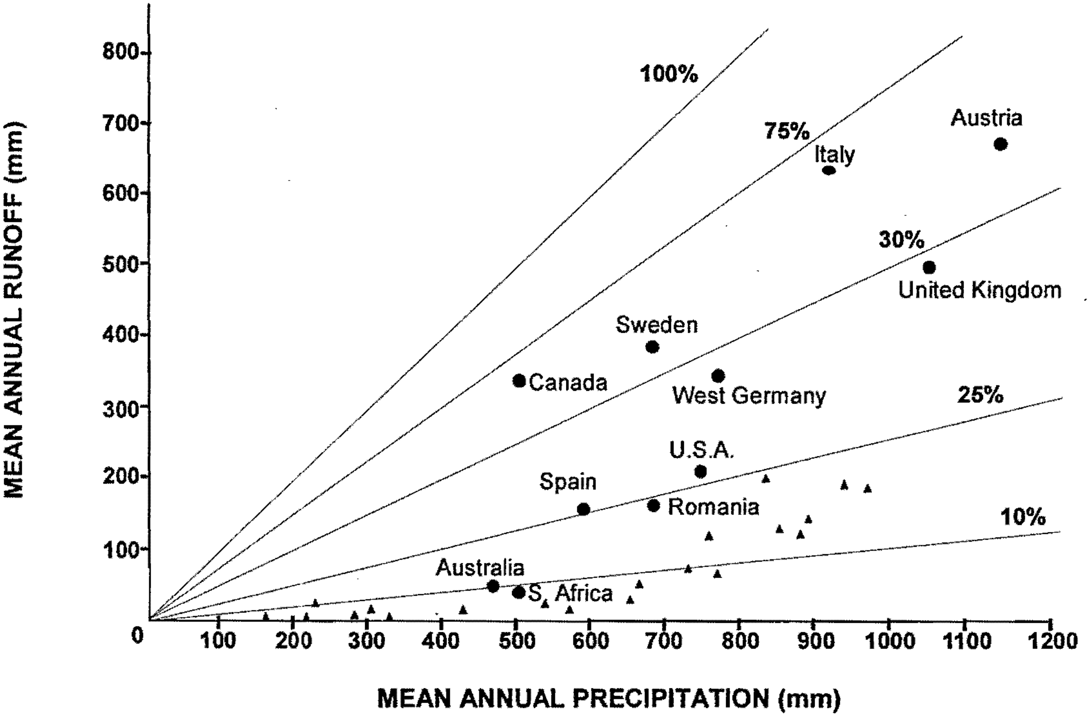


Figure 1.2 The relationship between mean annual runoff (MAR) and mean annual precipitation (MAP) for selected countries in the Northern and Southern Hemispheres (circles), including South Africa. Twenty individual South African river basins (triangles) are superimposed on the diagram (from Davies & Day *et al.* 1995, modified from Alexander 1985).

South Africa did little to address this critical issue in any cohesive way, particularly in terms of appropriate water conservation and management measures. In most cases, and not unlike the global trend at the time, engineering solutions were sought to mitigate declining water resources.

The recent political changes in South Africa have provided a climate conducive to redressing past disparities, and opened the arena for the consideration, and implementation, of scientific recommendations pertaining to the maintenance of the resource base. The massive reorientation in the management and conservation of water is underwritten in the constitution (Republic of South Africa (RSA) 1996), the White Paper on National Water Policy (RSA 1997) and the new Water Act (RSA 1998). In a fundamental departure from previous policy, equal status is given to *water for the environment* (or for the resource base itself) and for *domestic needs*. Together, these two priorities constitute what is known as the "Reserve", to which there is a statutory allocation requirement prior to any other sector. The implications are far-reaching in that the Reserve has to be quantified for all river systems.

The technical solution to the country's resource constraints has meant that most medium-sized, and many small river systems have been impounded (Davies & Day 1998). There are now 519 dams(2)

---

[2] The term *dam*, used principally in South Africa and Australia, is synonymous with the terms *reservoir* or *impoundment*.

greater than 50 000 m^3 capacity, which collectively are capable of storing some 50% of the country's mean annual runoff (MAR; DWA 1986). Where demand has exceeded supply, numerous inter-basin water transfer schemes (IBT) have been built or planned (Walmsley & Davies 1991; Davies *et al.* 1992). Currently, IBTs in South Africa divert some 1.63 x 10^9 m^3 of water per annum and carry associated ecological costs (Petitjean & Davies 1988; Davies *et al.* 1992; Davies *et al.* 2000). Yet, even in the face of substantial manipulations of river flows in South Africa, only the last decade has seen a recognition for both the need to provide water for the maintenance of river systems, as well as for assessments of the ecological impacts of human activities (DWA 1997).

With such scenarios of anthropogenic disturbance now common not only in South Africa, but on a global scale (McCully 1996), the proliferation of literature documenting the associated ecological consequences bears testimony to the increasing awareness and concerns of these effects (see Sections 1.2). One of the challenges facing the scientific community has been to determine the effects of modified flow regimes on the riverine ecosystems and, from these data, to recommend flow regimes for regulated rivers that safeguard the fundamental ecological functioning and sustainability of the system. These ***instream flow requirements*** (IFR)(3) need to be quantified in terms of the magnitude, duration, timing and frequency of different flows. This type of guidance is urgently required in South Africa and recently, such initiatives have received increasing support from the DWAF (King & Tharme 1994).

Indeed, this background contextualises the principal motivation for the major focus of this thesis, which essentially aims to explore approaches to the assessment of IFRs through research on a sub-tropical river in the eastern region of South Africa. First, this chapter describes the major conceptual frameworks of lotic-system functioning that guide such research and against which the effects of disturbance, such as river regulation, can be tested. This is followed by an overview of the documented impacts of impoundments on the receiving river reaches. This is particularly pertinent given that the global applicability of current paradigms, particularly to dryland systems, is under scrutiny (Williams 1988). Thereafter, the development of IFR assessments and relevant research in South Africa is discussed. Finally the aim of this research and the evolution of the approaches taken, is detailed.

1.2 REVIEW OF CONCEPTS RELATING TO THE ECOLOGICAL FUNCTIONING OF LOTIC SYSTEMS

Several conceptual models, and mutually supportive research themes, have emerged from studies in the field of lotic systems which have substantially contributed to an understanding of lotic-ecosystem functioning (e.g. Hynes 1970, 1975; Ward & Stanford 1979;1983a,b; Vannote *et al.* 1980; Winterbourn *et al.* 1981; Newbold *et al.* 1982; Fisher 1983; Cummins *et al.* 1984; Minshall *et al.* 1985; Junk *et al.* 1989; Naiman & Décamps 1990; Fisher & Grimm 1991; Stanford & Ward 1992).

More than three decades ago, studies on the classification systems of rivers, most notably the work of Professor Noel Hynes (1975), drew attention to their wider, catchment context. The earliest ecological

---

[3] Alternative terms used include *ecological flow requirements* or *environmental water allocations*.

classifications of rivers were based on the longitudinal zonation patterns of fish distribution (Illies & Botosaneanu 1963, *in* Ward 1986; Hynes 1970; Hynes 1975). The seminal work of Hynes pointed to the *ecological connectivity* in riverine systems, and described how rivers manifest the catchment, or valley, characteristics that they drain. He thus drew attention to the connectivity between terrestrial and aquatic systems as an important direction for future predictions about the structure and function of river systems. Early work by Harrison & Elsworth (1958) on river zonation represented the first South African initiative to describe the longitudinal physical characteristics of rivers, and to relate these to the biological structure of the river. Based primarily on the river profile, Harrison & Elsworth described six zones from source to floodplain for the Great Berg River, and later compared these zones to other South African and European rivers (Harrison 1965). The zonal delineation of rivers provided the model against which future work, particularly that of describing pre- and post-disturbance characteristics, could be documented or tested.

In contrast, later workers (Vannote *et al.* 1980; Newbold *et al.* 1982; Ward & Stanford 1983b) subscribed to the view that downstream changes were not zonal, but rather progressed along a resource trajectory down the river. The seminal work by Vannote *et al.* (1980), that of the *River Continuum Concept* (RCC; reviewed by Cummins *et al.* 1984; Minshall *et al.* 1985), recognised and embodied the continuous, unidirectional and lotic nature of change in rivers. Developed in temperate North America, the authors used the RCC to describe the gradual downstream changes in fauna and flora, driven principally by physical and chemical changes, from the headwaters to the lower reaches. They postulated that these changes occur in a predictable manner and classified reaches of the river primarily according to changes in the input of energy and the corresponding changes in the ratio of production-to-respiration down the system.

The RCC held that, due to the characteristically high-gradient, narrow, shaded and fast-flowing nature of the headwaters, organisms rely principally on allochthonous input rather than instream photosynthesis, classifying these upper reaches as *heterotrophic* (P:R<1). With progressive distance downstream, the gradient decreases and the river widens to allow sufficient sunlight for photosynthesis to dominate as the major form of energy production (P:R>1). With the biota relying on autochthonous energy, these middle reaches are *autotrophic.* In the slower-flowing lower reaches, the system reverts to heterotrophy, as the organic matter processed upstream settles out and is processed by bacteria in the sediments (P:R<1). The size of particulate matter down the length of the river also changes, with coarse particulate organic matter (CPOM) dominating the upper reaches and giving way to fine particulate organic matter (FPOM) in the middle reaches, that finally settles out in the lower reaches. Associated with this are different invertebrate feeding groups, with "shredders" dominating the upper reaches, "collectors" the lower reaches, and a combination thereof, the intermediate reaches. Fisher (1983) took the concept of a continuum further, postulating that communities exhibit a longitudinal ecological succession with each successive community influenced by their spatial predecessor.

The global applicability of the RCC has come under scrutiny (Williams 1988), with a number of authors suggesting that such rigid characteristics do not typify many areas, such as Australian ephemeral streams and the brown waters of Canada (Winterbourn *et al.* 1981; Barmuta & Lake 1982; Statzner &

Higler 1985; 1986). Typically, these systems are characterised by unpredictable climates, steep gradients, low allochthonous input and retention, and consequently low levels of CPOM (Allanson *et al.* 1990). The opposing model of Winterbourn *et al.* (1981) developed from work in New Zealand, contends that river systems are driven by stochastic events such as catastrophic climatic phenomena and are inhabited by unstructured, opportunistic biota which increase in the favourable, more stable periods. O'Keeffe *et al.* (1990) postulated that the Winterbourn *et al.* model, may be more applicable to South African rivers but this remains largely untested (see discussion in Section 1.3).

Additionally, research pointed to large floodplain rivers as another system in which the RCC and nutrient spiralling (see later) had little significance in that these rivers derive most of their biomass from within the floodplain itself. They are dominated by processes of lateral exchange between the floodplain and the river channel, and nutrient cycling within the floodplain. These concepts are embodied in the *Flood Pulse Concept* of Junk *et al.* (1989) which holds that the biota of floodplain rivers are determined principally by the hydrological regime in that the biota are adapted to the conspicuous aquatic and terrestrial phases. As waters rise, biota colonise the floodplain, taking advantage of increased food and spawning opportunities. Flood pulses, without which the production of the system is drastically reduced, are regarded as essential components of these fluvial systems (Bayley 1991; Petts & Maddock 1994).

Whether or not researchers subscribe to the postulate that changes are clinal or zonal, Ward (1986) highlighted the key concept underlying both of these views when he stated that "the fact remains that there are important upstream-downstream linkages". Whilst this may now seem obvious, only recently has the importance of this relationship been appreciated in relation to impoundments and their influence on the systems that they span (e.g. Stanford & Ward 1992). That is, the repercussions of a disturbance may be indirectly evidenced in components of the catchment far in excess of those initially, and directly, impacted on. Thus, the case for *ecological connectivity* in riverine systems, so eloquently put forward by Hynes in 1975, was proving to be more critical than possibly even he had originally anticipated. Further work, such as that on riparian and hyporheic influences, the source and fate of nutrients down the river course, the geomorphological determination of habitat and the importance of hydraulic conditions, as well as the flux of material between landscape patches, has provided substantive support for this unifying hypothesis.

The riparian zone plays an integral role in structural and functional characteristics of aquatic systems (as embodied in the RCC), acting as a source of allochthonous debris. This contributes to the source of reduced carbon compounds that fuel the energy requirements of biota (Cummins *et al.* 1984). The riparian component also acts as a buffer zone, both by playing a regulatory control on instream photosynthesis (Cummins 1992), and by dampening temperature extremes (e.g. Pollard *et al.* 1996). Further, root development and tree-falls influence channel structure and pattern (Cummins *et al.* 1984), stabilise stream banks, and filter nutrients and sediments moving downstream (Stanford & Ward 1984).

The longitudinal dependence of downstream reaches on a certain amount of upstream inefficiency is embodied in the *Nutrient Spiralling Hypothesis* which states that resources do not flow continuously down the river but are stored and released periodically with downstream progression (Newbold *et al.* 1982). This concept accounts for the fate of plant nutrients from dissolved to particulate states, as they are transferred downstream. For example, nutrients, taken up for metabolism by biota and ultimately released by excretion or decomposition after death, are thought to be transported in a helical fashion downstream, with the spiral length providing an index of nutrient turnover. Nonetheless, as pointed out by Davies & Day (1998), this hypothesis is thought to oversimplify the behaviour of nutrients in rivers.

In this regard, for example, Stanford & Ward (1988) demonstrated a vertical component in lotic-system functioning by their work on nutrient dynamics and spatial interactions between the gravel-bed of the Flathead River (Montana) and its *hyporheos.* The potential role of the hyporheic zone in nutrient retention and release in the form of nutrient-laden foams in western Cape rivers, has suggested that the concept of nutrient spiralling may not fully explain the source and fate of nutrients in rivers. As such, the term *nutrient cycling* may be more appropriate in describing the closed-recycling loops within the hyporheos (Davies *et al.* 1995).

Many organisms are controlled by the hydrodynamic nature of the fluvial environment and Statzner *et al.* (1988) reviewed the complex *hydraulic conditions* which influence the distribution of biota. The morphologies of benthic animals reflect adaptations which allow them to exploit specific hydraulic conditions (e.g. Statzner 1981). There are two major implications of this work. Firstly, the more complex the hydraulic environment the more likely it is to support a diverse fauna. Secondly, Statzner *et al.* suggest that certain hydraulic variables, particularly Reynolds Velocity and the Froude number, can be used to predict the distribution of biota. Much of the work on fish distribution and assemblages points to habitat diversity as a primary determinant of community structure and function (e.g. Gorman & Karr 1978; Angermeier & Karr 1983; Moyle & Vondracek 1985). In support of the gradual nature of biotic change embodied in the RCC, Schlosser (1987) developed a conceptual model describing the variation in fish-community structure along a gradient of increasing *habitat heterogeneity.* He thereby implicated physical variability, governed by the geomorphology, as a primary determinant of fish-community structure in rivers (see discussions on the geomorphological control of habitat abundance and spatial distribution, or heterogeneity, in Chapters 10 and 13).

Pickett & White (1985) articulated the view that catchments are ecosystems that comprise a mosaic of terrestrial *patches*, interconnected by a network of rivers, and this concept has been further developed by others (e.g. Wiens *et al.* 1985; Pringle *et al.* 1988; Townsend 1989; Wiens *et al.* 1993; see review in Chapter 10). The *Ecotone Concept* (Naiman & Décamps 1990) describes functionally interconnected patches that comprise the riverine landscape, and the fluxes and transformations of materials occurring within patch boundaries. More recently, Stanford & Ward (1992) have taken the concept of linkages further, proposing a *holistic* conceptual framework in which rivers are viewed as four-dimensional environments (lateral, longitudinal, vertical and temporal), that are intimately interlinked, and the integrity of which is dependent on the balance between these components.

With regard to disturbance, if the river is viewed as a continuum, then changes in flow, such as those caused by a reservoir, will uncouple components of the continuum described above and create a discontinuity. An early theoretical context on the effects of disturbance on instream biota was formulated by Connell (1978) in the *Intermediate Disturbance Hypothesis* (IDC), which holds that species richness will be lowest where a system is exposed to extremes in disturbance (either constant or erratic conditions) and highest when disturbance is intermediate in intensity. As a corollary to the RCC, together with the IDH, Ward & Stanford (1983b) developed the *Serial Discontinuity Concept* (SDC), which provides a theoretical framework for examining the effects of impoundments. The SDC proposes that the longitudinal location of an impoundment, and the depth from which releases are made from the impoundment, will determine the extent and types of downstream effects. Inherent in the SDC, is the tenet that interruptions to the continuum cause shifts in the abiotic and biotic variables which recover at some unknown distance (discontinuity distance) from the perturbation. This recovery or "reset" distance (*sensu* O'Keeffe *et al.* 1990), is considered to be influenced by factors such as the position and size of the dam, with lower-reach larger dams exhibiting much greater recovery distances (O'Keeffe *et al.* 1990).

A number of conceptual models exist to explain community structure and the effects of disturbance in rivers. For example, Bain & Boltz (1989) reviewed research on warmwater fish and invertebrate communities, and suggested that consistent patterns of community-level responses to regulation can be identified. They postulated, for example, that the biota of near-shore and mid-stream habitats, are more susceptible to fluctuating stream flows, and ascribed this to the high degree of variability in the availability of these specific habitats as flow varies. Schlosser (1990a) postulated that the life-history characteristics of headwater fish, which reflect the greater environmental variability of this river zone, confer the ability to recover more rapidly from severe anthropogenic disturbance than downstream fish communities. These are just two examples from numerous hypotheses submitted to explain the relationship between community-structure and disturbance which will be discussed throughout this thesis.

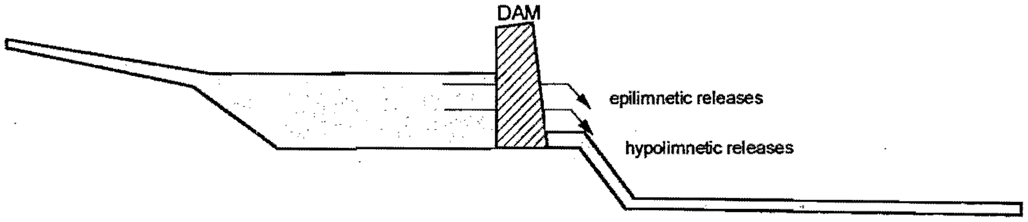
However, the overall effect of disturbance is complex and most likely embodied in the aforementioned concept of river systems as multi-dimensional environments (Ward & Stanford 1989; Stanford & Ward 1992). If, as they suggest, river basins comprise four, interconnected components, then the effect of human disturbance is to uncouple the ecological processes linking these components, thus disrupting the balance between them (Stanford & Ward 1992). Stanford & Ward use the collapse of the fisheries in Flathead Lake as a case study, and elegantly illustrate the cascade effect of disturbance on ecosystem components. With this concept in mind, it is appropriate to review the effects of regulation on rivers.

1.3 OVERVIEW OF THE DOWNSTREAM EFFECTS OF IMPOUNDMENTS

The literature detailing the effects of man's activities on aquatic systems indicates the complex and multifarious nature of these. Broadly, these include catchment changes; pollution and; regulation of the flow regime, by activities such as abstraction, inter-basin transfers, and the creation of discontinuities in the form of impoundments. As background to this thesis, the following discussion will focus specifically on the consequences of impoundments on the receiving reaches. Comprehensive reviews are presented in Neel (1963); Ward & Stanford (1979); Lillehammer & Saltveit (1984); Petts (1984) and Davies & Walker (1986). Johnson *et al.* (1995) specifically addressed the effects of man's activities on large river systems. Ward & Stanford (1989) also provide an excellent overview of human influence on river systems and further, advocate a holistic approach to understanding anthropogenic disturbance (Stanford

& Ward 1992). Both Fred Pearce (1992) and Patrick McCully (1996) offer popular global accounts of the consequences and politics of large dams.

Impoundments are one form of stream regulation, the anthropogenic control of discharge, which has profoundly influenced virtually all of the world's major rivers (Ward & Stanford 1979). Southern Africa is no exception with impoundments accounting for the major perturbations to riverine systems (Allanson *et al.* 1990). Each impounded system exhibits some unique responses (Ward & Stanford 1984), leading to calls for impoundment-specific ecological assessments. These differential responses reflect a host of interrelated influences such as (i) the function of the impoundment (Ward 1982), (ii) position of the impoundment along the longitudinal stream profile, (iii) basin geochemistry, (iv) terrestrial biome characteristics, (v) operational variables (Ward & Stanford 1984), and (vi) basin geomorphology. Nonetheless, generalised responses do occur (Figure 1.3), and can be broadly categorised as hydrological, physical, geomorphological, chemical and thermal changes, and the consequent biological responses (e.g. Ward 1982; Ward & Stanford 1987; 1989).



1. INCOMING WATER QUALITY

a. Precipitation chemistry
b. Basin geochemistry
c. Basin geomorphology
d. Terrestrial vegetation
e. Climatic conditions
f. Anthropogenic impacts

2. LIMNOLOGICAL PHENOMENA

a. Morphometric parameters
b. Retention time
c. Impoundment age
d. Impoundment position
e. Turbidity currents
f. Drawdown extent
g. Thermal stratification
h. Chemical stratification
i. Edaphic factors
j. Biological processes

3. OPERATIONAL VARIABLES

a. Discharge patterns
b. Release depths

4. STREAM, FLOODPLAIN AND ESTUARINE ENVIRONMENT

a. Flow regime
b. Sediment loads
c. Substratum type
d. Thermal regime
(a–d) Channel morphology → Physical habitat
e. Ground water
f. Nutrient levels
g. Water clarity
h. Lentic plankton
i. Dissolved salts
j. Dissolved gases
k. Organic detritus

5. BIOLOGICAL EFFECTS

OFFSTREAM
a. Riparian vegetation

INSTREAM
b. Aquatic vegetation
c. Invertebrates
d. Fish
e. Ecological diversity
f. Distribution
g. Abundance
h. Biotic productivity
i. Life- cycle phenomena
j. Biotic interactions
k. Trophic structure
l. Migratory movements

Figure 1.3 Major factors and phenomena (1-3) influencing the receiving reaches of rivers below impoundments (4), and some of the resultant effects (5) on the biota (modified from Ward *et al.* 1984; Davies & Day 1998).

- ***Hydrological responses***

The damming of a river results in a hydrodynamic disequilibrium in the downstream reach, reflected primarily in changes in the flow regime and sediment loads, and their interactions (Petts 1984; see also Figure 4.1). The flow regime of the receiving reaches may exhibit a suite of changes which include increased flow constancy; short-term flow fluctuations; a reduction in, and protraction of low-flow periods; a shift or reversal in seasonality; reduced mean annual discharge; reductions in the magnitude and frequency of flood events; and changes in the recurrence intervals of specific-magnitude floods (for example Ward 1976a; Stanford & Ward 1986). For example, seasonal reversals of flow regime now characterise sections of the Murray-Darling in Australia where, as a result of irrigation releases, summer-high flows have replaced winter-highs (Walker 1979). Moreover, the magnitude of average annual floods of the Murray River has been reduced by more than 50% (Maheshwari *et al.* 1995).

- ***Changes in the suspended particles***

Since large impoundments act as settling basins, they generally reduce downstream sediment loads and turbidity in comparison to pre-impoundment levels (Ward 1982; Gilvear 1987). However, an increase in downstream sedimentation can accompany construction activities (Ward & Stanford 1979), as well as the periodic flushing of sediments from the reservoir (Gray & Ward 1982). The downstream recovery of pre-impoundment sediment loads is largely a function of the tributaries, which add sediment to the main river (Petts 1984; Ward 1987). The most notable example of a reduction in sediment loads is seen on the River Nile which, prior to the construction of the Aswan High Dam, used to carry an annual silt load of some 60-180 million tons to the Mediterranean (Mancy 1979). Farmers now have to fertilise fields that were previously fertilised by silt deposition of the annual floods (Ramadan 1979).

Likewise, the transport of organic detritus downstream is disrupted by dams, which in turn significantly alters the energy base, and hence trophic structure of the system (Vannote *et al.* 1980). For example, with a truncation of detrital food availability by impoundment in a Rocky Mountain stream, Ward (1987) documented a pronounced reduction in the abundance of downstream detritivorous shredders.

- ***Changes in the channel morphology***

As a result of a disruption of the discharge-sediment relationship downstream of impoundments, the channel geomorphology alters as the system moves towards a new equilibrium (see Figure 4.1). As flows change, so too does the dynamic between sediment loads and channel morphology, and hence the distribution and architecture of the physical habitat. Channel degradation is the predominant process impacting on the morphology of the receiving reaches due to the release of silt-deficient waters (Leopold *et al.* 1964; Simons 1979). This may be limited by eventual armouring of the bed, with a layer of particles too large to be transported. Other possible responses include changes in channel pattern, width, cross-sectional area, bed roughness, sinuosity, gradient and lateral movements of the channel (Petts 1980; Bain *et al.* 1988; Olofin 1988). On the other hand, bed stability and reduced scouring is associated with flow moderation (Biggs 1982) and is largely implicated in the encroachment of riparian vegetation, and establishment of algal communities (Ward 1987).

Rather surprisingly, few of the earlier discussions on the effects of impoundments specifically coupled changes in channel morphology to changes in the physical habitat of biota, although these links have received far more explicit treatment in the last two decades (e.g. Peters 1982; Schlosser 1987; Bain & Boltz 1989; Ward & Stanford 1989; Neves & Angermeier 1990; Stanford & Ward 1992; King & Tharme 1994; van Niekerk *et al.* 1995; Wadeson & Rowntree 1994, and see late discussions on biotic responses). This topic is addressed in more depth in Chapters 10 to 13.

- ***Chemical responses***

Stream regulation may modify patterns in the river chemistry (Soltero *et al.* 1973), by disrupting the natural water quality and temperature gradients (Hauer & Stanford 1982; Ward & Stanford 1983b; Ward 1987), or seasonal characteristics (Neel 1963), or by dampening the variability which may characterise upstream reaches (Soltero *et al.* 1973; Crisp 1985). The internal dynamics of physical, chemical and in particular, biological processes within the dam basin, influence the chemical quality of the water that is released (Hannan 1979). These, in turn, are a function of the trophic status of the reservoir coupled to the retention time, release depth and other factors (Ward 1982).

Since the lower stratum of an impoundment is the primary site for decomposition, changes in downstream chemistry are particularly evident in hypolimnetic releases, which are associated with an elevation of carbon dioxide levels, and decrease in oxygen and pH (Hannan 1979). Further, these cold waters are often nutrient-rich, since organic matter synthesised within the impoundment and in the influent, settles to the bottom of the reservoir, and acts as a nutrient trap (Odum 1971; Spence & Hynes 1971a,b; Soltero *et al.* 1973). Anoxic conditions have been documented below some eutrophic, deep-release reservoirs (Neel 1963; Davies 1979; Crisp 1985), although oxygen depletion is not always associated with deep releases and its effects can be mitigated by the type of outlet valve used (Neel 1963).

Additional studies have documented an increase in downstream total dissolved solids (Ward 1976b), salinity (Neel 1963) and minerals, all trapped in the impoundment and released into the receiving reaches (Conner & Maughan 1984; Crisp *et al.* 1984). Notably, the salinisation of floodplains has been documented, where the truncation of floods result in flows that fail to provide the dilution effects of flooding (Davies 1979).

- ***Thermal responses***

The extent to which impoundments modify lotic temperatures depends not only on the characteristics and operation of the reservoir, but also on the position of the impoundment along the river (Ward & Stanford 1982). Disruptions in the natural thermal regime cause thermal discontinuities, including delayed seasonal minima and maxima (Ward 1974), dampened seasonal ranges (Neel 1963; Byren & Davies 1989); and/or diurnal constancy (Ward 1974; Armitage 1979; Stanford & Ward 1986), all of which have biological implications (Ward & Stanford 1987).

The most severe and wide-ranging thermal modifications have been documented below hypolimnetic releases from impoundments in temperate zones (Ward & Stanford 1982), often resulting in conditions of diel and seasonal constancy (Hannan & Young 1974; Ward 1976), winter-warm and summer-cool temperatures and alterations in the seasonal temperature patterns (Armitage 1979). For example, annual temperature ranges in the Colorado River below Glen Canyon Dam have decreased in their range from 0-29.5 °C to 6-15 °C (Stanford & Ward 1986). Reduced discharge, on the other hand, is frequently associated with increased summer temperatures and decreased winter temperatures (Ward & Stanford 1987). The rate of thermal recovery may take tens, or even hundreds, of kilometres and is a function of, amongst other factors, the thermic slope and discharge downstream of the dam (Ward 1982).

- ***Biotic responses***

The composition, distribution and abundance of stream biota are predicated on the influence of, and interaction between, six primary factors, which include the energy source, water quality, temperature, flow regime, physical habitat structure and biotic interactions (Karr & Dudley 1981). Biotic responses to regulation are manifest in a number of ways that reflect the complex interrelationship between some, or all, of the above factors. Further, these act in concert with physiological, morphological and behavioural traits of lotic species (Stalnaker 1981). The range of responses reported in the literature reflects this complexity, and precludes making generalisations regarding biotic responses. Nonetheless, the following synopsis highlights some of the changes in the functional and structural attributes of biota and the reasons advanced for these modifications.

Disturbance is recognised as an important factor in shaping the structure and interaction of communities (for example, predator- prey relationships) and is reviewed by Minshall (1988) and Resh *et al.* (1988; see also Fisher & Grimm 1991). The biological effects of disturbance are often exacerbated in conditions of low- or no-flow (often associated with impoundments), during which organisms are forced into conditions of deteriorating habitat quality due to desiccation, organic decomposition, loss of refuge from predation and reduced food availability (Lowe-McConnell 1987a; Welcomme 1989; Chapman & Kramer 1991a,b; Pollard *et al.* 1996).

Perturbations induced by river impoundments have markedly changed species composition, diversity and increased extinction rates of fish and invertebrates (e.g. Minckley & Deacon 1968; Ward 1976a; Armitage 1979, Décamps *et al.* 1979; Walker 1979; Northcote *et al.* 1985; Ward 1987; Russell & Rogers 1989). If, as suggested by Schlosser & Ebel (1989) from their work in a stream of the Mississippi catchment, the nature of the hydrological regime plays a major role in the colonisation and abundance by invertebrates and fish, then a disruption of the flow regime (and associated variables) would disrupt these processes. Research findings certainly appear to corroborate this thesis. For example, many zoobenthos species have been eliminated below impoundments on the Gunnison River as a result of summer-cold, stabilised flows (Stanford & Ward 1984; Hauer *et al.* 1989). Many fish and invertebrates have very specific flow-regime requirements and large flow fluctuations can greatly affect community composition (Ward & Stanford 1989). In many cases, the altered conditions have favoured the establishment of different species or communities. In Britain, for instance, river regulation has negatively affected the reproduction and recruitment of specialist rheophilic and limnophilic species and resulted in an increase in generalist species (Copp 1990). The consequence of attenuated floods, stabilised channel beds and decreased temperature ranges, has been the replacement of the native squawfish *(Ptychoceilus luciues)* by the alien rainbow trout (*Salmo gairdineri)* as the top carnivore of the Colorado River (Stanford & Ward 1986). They concluded that fish species exhibit a differential response to flow fluctuations governed by the habitat that they use. Similarly, Bain *et al.* (1988) submitted that the abundance of both small species, and early life-history stages, of fish which inhabit river margins, declined dramatically due to artificial streamflow fluctuations. Temperature changes have been ascribed a major role in determining changes in the diversity, abundance and species distribution of aquatic invertebrates below impoundments (Vannote & Sweeney 1980; Ward & Stanford 1982; Ward 1987). This was evident in the reduction of species abundance (by more than 95%), and distribution (by between 35 and 90%) of trichopterans in the Gunnison River due to disruptions in the thermal regime (Hauer & Stanford 1982). Spence & Hynes (1971b) attributed the absence of four cyprinid fish species downstream of a reservoir to the release of cold, hypolimnetic waters.

Decreases in fish abundances have been attributed to the flushing effects of aseasonal floods on young-of-the-year (Harvey 1987); stranding (Bain *et al.* 1988), loss of habitat (e.g. Stanford & Ward 1984) and/or increased vulnerability to predation (Schlosser 1987). Flood cycles in floodplains play a vitally important role in the release of nutrients accumulated during the dry period, as well as providing conditions for fish reproduction, growth and feeding (Welcomme 1979; Goulding 1980; Pringle *et al.* 1988). Attenuation of these floods has reduced recruitment and survival as a consequence of impeding these life-cycle processes (e.g. Heeg & Breen 1982; Sheppe 1985; Stanford & Ward 1992). Similarly, dams can influence growth and survival in that they pose an obvious barrier to the longitudinal migration of fish (Welcomme 1979; Décamps *et al.* 1979). This plays an important role in the ecology of riverine fish in terms of breeding, feeding and overwintering (Nikolsky 1963). Additionally, thermal modifications due to flow constancy, flood attenuation and the seasonal reversal in flows have all been implicated in reduced recruitment - largely as a result of the effects on environmental cues on biological processes such as timing of spawning (Ward & Stanford 1979).

In contrast, an increase in the density of some fauna, frequently pest species, has been documented below impoundments (reviewed in Ward 1982). It is suggested that this is due to the increased bed stability and the release of organic-rich waters from bottom-release reservoirs, which may augment productivity. Surface releases on the other hand, may also enrich downstream waters through the introduction of large quantities of zooplankton (Ward 1976a). Stream regulation also generally imparts conditions that favour an increase in some species of attached aquatic plants (bryophytes and algae) and submerged angiosperms (Spence & Hynes 1971a; Ward 1976b). Frequently, conditions associated with attenuation of the pre-impoundment hydrological variability favour the establishment of exotic or pest species. Stands of Kariba weed (*Salvinia molesta*) in Southern African rivers, and the replacement of diverse simuliid communities by a blood-feeding pest of livestock, *Simulium chutteri* in the Orange and Vaal rivers, pay testimony to this (Davies & Day 1998).

The attenuation of floods has also borne severe consequences for riparian communities. As noted initially by Cummins *et al.* (1984), and later by others (see Dodge 1989; Stanford & Ward 1992) riparian corridors are inseparable from the biological characteristics in the channel, and influence bank stability, sediment routing, channel morphology, the contribution of organic matter, light and temperature regimes, as well as cover for fish and invertebrates. Changes in the riparian zone are seen when the natural flooding that maintains the riparian systems in an early successional stage, is suppressed by regulation, thus enabling non-riparian species to invade (Stanford & Ward 1986). Such is the case along the banks of the Gunnison River, which has seen massive invasions of the old river floodplain by grasses, sedges, willow species and salt cedar as a result of the complete attenuation of spring floods by regulation (Stanford & Ward 1984). Carter & Rogers (1989) have documented reed-bed colonisation by woody riparian vegetation, due to changes in channel morphology that have accompanied reduced flows in the Sabie River, South Africa.

Changes in trophic structure of riverine communities have been noted with the truncation of downstream movement of detritus by impoundments (Ward 1987), as well as the alteration to the abundance and composition of the epilithion. In turn, fish survival which may depend on invertebrate availability as a food source (Schlosser 1990a), may be effected. Dufford *et al.* (1985) documented a dramatic increase in algal biomass below the dams, believed to be due to nutrient loading, high water clarity and relatively stable flows and temperature. This shift in biomass would be likely to affect zoobenthos that rely on algae as a food source.

The relationship both between physical habitat and flow, and physical habitat and populations, as well as the consequences of regulation on habitat, both spatially and temporally, have been the focus of intensive research efforts and have evoked considerable debate (Orth & Maughan 1982; 1983; 1986; Mathur *et al.* 1985a,b; Scott & Shirvell 1985; Shirvell 1986; 1989; Orth 1987; Bain & Boltz 1989). These contentions are discussed in detail in Chapters 9 and 10. In short, changes in the flow regime, such as those associated with impoundments, effect changes in the distribution and abundance of physical habitat, and hence for the biota that use these habitats. However, how great an influence changes in habitat represent, and the mechanism by which communities are affected, is the subject of research and discussion. For example, some authors suggest that physical habitat may be the most important single factor controlling composition and abundance of fish (Schlosser 1985; 1987), and that there is a relationship between population and usable habitat, although this remains contentious (see Chapter 8). Whatever the primary determinant of community structure, which probably varies on a spatio-temporal scale in any event, fish community structure is strongly influenced by habitat composition and stability (Bain *et al.* 1988).

Few definitive studies are available regarding the effects of regulation on biotic interactions, such as on predator-prey, host-parasite and competitive interactions. Hence, conclusions on this particular effect are largely inferential. For example, research by Schlosser (1987) indicated that predation may have an increasingly pronounced effect as a consequence of diminishing flows, such as those associated with river regulation, as predators and prey are forced into close proximity. Recent work on the Sabie River during conditions of extreme drought, corroborates this. In this protracted period of low flow, an increase in predation both by certain fish species, and by birds, was documented as fish were trapped in shrinking pools (Pollard *et al.* 1996). Further, the increasingly unfavourable conditions in pools resulted in a decrease in the condition of fish and an increase in parasitic infestations.

Yet, even with the growing body of information chronicling man's alterations of river systems, it is clear that the literature is largely confined to documenting single components of the aquatic ecosystem, and that on an ecosystem scale, these effects remain largely speculative. This is not surprising due to the complex nature of the topic, but as pointed out by Cummins (1992), the hallmark of recent lotic research is its interdisciplinary approach. I would suggest that the recent holistic conceptual frameworks of Ward & Stanford (1987) and Stanford & Ward (1992), which underscore the importance of interlinkages, offer a conceptual model which can significantly advance our understanding of the various components vital to maintaining productive riverine systems. Despite this, the corollary is that holistic models are contingent on reliable information gathered at the component level, without which a holistic understanding is implausible.

River regulation in the South African context

The rapidity of dam development in South Africa has not been matched by a corresponding quantity of ecological documentation on their downstream consequences, with much of the research of the 1970s concentrating mainly on the functioning of reservoirs (see review of O'Keeffe 1990). The last decade has seen a reversal in this trend, with an increased focus on lotic systems and the effects of disturbance emanating from a number of research initiatives (see below). Nonetheless, in view of the fact that in excess of 500 dams (over 50 000 m^3 capacity) span the rivers of the country, this information represents only limited local improvements in our knowledge. Chutter (1973) reviewed the effects of exploitation on South African rivers and anticipated future trends as a result of increasing river regulation. These included downstream changes in the fauna, increased plankton production, impediments to fish migrations, modifications to the water chemistry and temperature, and changes in channel morphology.

Some 25 years on, these effects have not been mitigated, leading Davies *et al.* (1995) to conclude that the impacts of anthropogenic disturbance on South African rivers has been massive. There has been regulation on all major systems, including IBTs, and in many cases, the rivers have been converted from perennial to intermittent systems. Some of the most striking examples of this are seen in the previously perennial rivers flowing through the eastern region of the country towards Moçambique. Evidence indicates that the Luvuvhu River first stopped flowing in 1948, with flows now ceasing in most years, and likewise, the Letaba and Olifants Rivers now only flow for a few months a year (O'Keeffe & Davies 1991). Furthermore, many systems have deteriorated as a result of organic enrichment, salinisation and acid pollution, and the introduction of exotic and invasive plants and animals.

The first substantial reference to the ecological consequences of impoundments was that of Chutter (1963), who found that two dams on the Vaal River fundamentally affected the characteristics of the river. Their influence was to stabilise flows with consequent algal blooms and decreased current speeds below the dam, which affected changes in the downstream fauna. For example, high densities of oligochaetes, even in the absence of organic pollution, were ascribed to in the deposition of soft sediments, as a result of flow stabilisation (Harrison *et al.* 1963). High densities of benthic invertebrates, especially filter-feeding hydropsychid trichopterans, below the dams, were attributed to the release of waters rich in plankton which had built up in the transparent waters of the barrage, where mineral pollution had caused flocculation of suspended sediments. Chutter (1969) later described an 8 km recovery distance downstream of the dam for the benthic invertebrate community with the exception of the Simuliidae, which persisted for some 50 km downstream. Pitchford & Visser (1975) compared pre- and post-impoundment temperature conditions downstream of the Verwoerd Dam on the Orange River and documented a reduction in the pre-impoundment 19.6 °C temperature range, to one of 12.8 °C. This, and conditions of flow constancy, has also led to a massive proliferation of the pest blackfly *Simulium chutteri*, the female of which is a blood feeder of domestic livestock (Chutter 1967). Changes in fish abundances of the lower Orange River, possibly as a consequence of disrupted life cycles, have also been ascribed to the effects of these dams (Benade & van Vuuren 1993).

With the construction of the Pongolapoort Dam in the province of Kwazulu-Natal, the Pongolo floodplain now receives artificially released floods that flush the system in a period of weeks (Merron & Bruton 1993). Subsequent studies have focussed on predicting the frequency, seasonality and duration of releases from the dam that would be required to release nutrients into the floodplains, the mainstay of productivity in the system (Coke & Pott 1970; Rogers 1980; Heeg & Breen 1982).

Further research on impoundments in the 1980s included a comparative study of the Palmiet (southwestern Cape) and Buffalo (eastern Cape) Rivers which specifically documented the physical and chemical characteristics downstream of six impoundments of different sizes in different parts of the rivers (Byren & Davies 1989; Palmer & O'Keeffe 1990a,b; O'Keeffe *et al.* 1990). Findings indicated an increase in nutrients below all six dams investigated, a reduction in annual flow range below small impoundments in the upper reaches and, a decrease in the average temperature below medium-sized dams in the middle reaches.

A more recent step forward for research in South Africa has been the recognition that South African rivers have several marked differences which set them apart them from north temperate rivers on which most of the regulated river research has been carried out (O'Keeffe *et al.* 1989b; Davies *et al.* 1993, 1995). For example, many South African rivers are geologically young and consequently steep and fast-flowing and have less well-developed floodplains than the older, temperate systems. With the exception of those rivers flowing over Table Mountain Sandstone, most are characterised by highly turbid waters, at least seasonally. Further, the highly variable rainfall and runoff result in extreme flooding and drying events. Consequently, both the conceptual models that have been developed to explain lotic ecosystem-functioning, and the documented effects of impoundments, may differ markedly from those of northern, temperate systems. Much of the recent work in South Africa has thus concentrated on testing some of these conceptual paradigms (RCC, SDC) (King *et al.* 1987a,b; Davies *et al.* 1989; Stewart & Davies 1989; O'Keeffe *et al.* 1990; Palmer 1991; Prochazka *et al.* 1991; Ratcliffe 1991; Snaddon *et al.* 1992; Stewart 1992). The unpredictable climate and non-retentitive nature of the systems led O'Keeffe *et al.* (1989a) to suggest that these systems may conform more closely to the Winterbourn model of stochastic influences, than the predictable patterns expounded in the RCC. They point out that under conditions of such variability it is unlikely to find species that are adapted to regular seasonal changes. Moreover, if environmental events are major determinants of ecosystem-level functioning, then river regulation, which removes much of the hydrological variability, may have far more serious consequences in South Africa than those anticipated from Northern Hemisphere literature.

Much of the support for this thinking is based on work from Western Cape rivers, which documents allochthonous inputs and leaf-pack dynamics, retention and decomposition (King *et al.* 1987a,b; Davies *et al.* 1989; Stewart & Davies 1989; Prochazka *et al.* 1991; Ractliffe 1991; Snaddon *et al.*1992; Stewart

1992). It is clear that characteristics of these systems manifest in fluctuating periods of "stability" and "instability", the nature of which is dictated by winter spates (King *et al.* 1987a,b). Stable periods of low discharge corresponds to periods when leaf fall reaches an extended peak and consequently organic matter accumulates in the stream. Unstable periods on the other hand, correspond to high, flashy discharges when spates scour the stream bed and particulate food resources are scarce. Further, the nature of allochthonous input in headwaters differs from that of northern temperate climes on both sides of the Atlantic in two ways. Firstly, leaf fall tends to be protracted (with spring peaks) and hence are not as pronounced as the autumnal pulses evident in streams of north America (Davies *et al.* 1989). Secondly, many headwaters of the Western Cape are not forested, and therefore biota are reliant on autochthonous, rather than allochthonous production (Davies *et al.* 1993). As such, it has been suggested that these rivers are inhabited by hardy opportunists able to exploit stable conditions between stochastic events and that possess life history attributes that allow them to survive harsher episodes (see review by Davies *et al.* 1995), although Dr. King (Freshwater Research Unit, University of Cape Town, *pers. comm.*) points out that this "hardy" characteristic is generally only evident in some of the species in disturbed streams. Also, it should be noted that these western Cape Rivers of South Africa are atypical of the rest of the subcontinent as a whole, being acidic, low in sediments and in an area of winter rainfall that is relatively predictable.

In addition to the aforementioned characteristics that distinguish South African rivers in general, more recent research specifically in the warmer eastern region of South Africa (and site of the study area of this thesis) has pointed to differences that typify rivers in this region. Two major differences include (a) the semi-arid characteristics of the environment and hence highly unpredictable flow patterns, and (b) rivers underlain by bedrock (and hence described as "bedrock controlled") which do not conform to geomorphological models of alluvial systems (van Niekerk *et al.* 1995). Such information further cautions against applying models developed for temperate, alluvial rivers to those of this eastern area without rigorous testing.

More recently, Davies *et al.* (1993) have cautioned against the complete repudiation of the RCC in Southern Hemisphere rivers, calling for more robust documentation of anthropogenic effects prior to concluding that these systems deviate from current lotic paradigms. More recent work appears to support at least one component of the RCC, that of functional feeding groups or FFGs (Palmer 1991, reviewed in Davies *et al.* 1993), in that different invertebrate species were associated with different habitats and could meaningfully be classified into FFGs. The upstream reaches of the Buffalo River (a semi-arid system in the Easter Cape Province) were shown to be dominated by shredders, and the middle and lower reaches by scrapers, brushers and other collectors, reflecting the predictions of the RCC. Further, as described earlier, the comparative study on the Buffalo and Palmiet Rivers provides partial support for the predictions of the SDC, with the exception of nutrient availability and temperature (Byren & Davies 1989; O'Keeffe *et al.* 1990; Palmer & O'Keeffe 1990a). Contrary to the predictions of the SDC, which predicts that no changes in nutrients will occur below dams on sixth order or smaller rivers, O'Keeffe *et al.* (1990) documented an increase in nutrients below all six dams investigated.

In view of the results discussed above, a more plausible analysis of whether or not South African systems lend support for current conceptual paradigms, subscribes to the view that South African systems probably lie somewhere on the trajectory between the RCC-Winterbourn models (Allanson *et al.* 1990).

1.4 ASSESSMENT OF INSTREAM FLOW REQUIREMENTS OF RIVERS

The preceding overview described the deleterious conditions associated with river regulation that have precipitated the need to mitigate these effects. This need has become embodied in the concept of *instream flow requirements (IFR)* (e.g. Gore 1978; Gore & Judy 1981) for rivers. In this regard, a number of approaches have evolved which reside on the assumption that there is a point below which discharge is reduced that results in a progressive or immediate loss of habitat, disruption of ecological processes and loss of species, and hence threatens the functioning of the entire system. These approaches, extensively reviewed elsewhere (see for example Stalnaker & Arnette 1976; Loar *et al.* 1985; Estes & Osborn 1986; Mordhart 1986; Karim *et al.* 1995; Stalnaker 1994; Jowett 1997) are summarised below.

Formal methodologies for prescribing IFRs began in the USA as early as the 1950s (Stalnaker 1982; Trihey & Stalnaker 1985), whilst such assessments only began in Britain, Australia and New Zealand in the 1980s. The evolution of IFR methodologies is manifest in three fairly distinctive approaches (Loar *et al.* 1985): the hydrological approach, hydraulic-rating methodologies, and habitat-rating methodologies.

The original methods, known as ***hydrological***, or threshold-setting methodologies, subscribed to a "flow-statistic logic" based on an analysis of historical flow records (Trihey & Stalnaker 1985). The Montana or Tennant Method (Tennant 1976), 7Q10 (seven-day, 1-in-10 year flows) and Average Base Flow are examples of such an approach. A fixed percentage of flow, normally termed the minimum flow, was apportioned to the IFR (Stalnaker 1979). This value, which is set irrespective of the peculiarities of individual situations, inherently contained the concept that "minimum flows" were synonymous with IFRs (Cavendish & Duncan 1986; see also Stalnaker 1990), and resulted in a simplistic and incomplete picture (Mr. R. T. Milhous, US Fish & Wildlife Service, Colorado, US, *pers. comm.*). An additional criticism centred on the lack of additional information, which precluded an understanding of the relationship between flow and a particular river resource, such as habitat.

Consequently, the development of more sophisticated methods was evident in the growth of incremental and predictive approaches in the late 1970s and 80s. Although the ultimate objective was, and is, to understand the consequences of flow modifications on the stream biota, most techniques have focussed mainly on the relationship between flow and habitat, as a proxy (Figure 1.4). This relationship is generally researched via *habitat-modelling or assessment* approaches, which describe the relationship between incremental changes in discharge and habitat. The relationship between habitat and fish, on the other hand, is usually conducted via a regression-based approach (Bozek & Rahel 1991; see also Scarneccia & Bergersen 1987; Wesche *et al.* 1987). Regression - based models identify general habitat features, such as stream size or gradient, that are correlated with fish abundance or size-structure

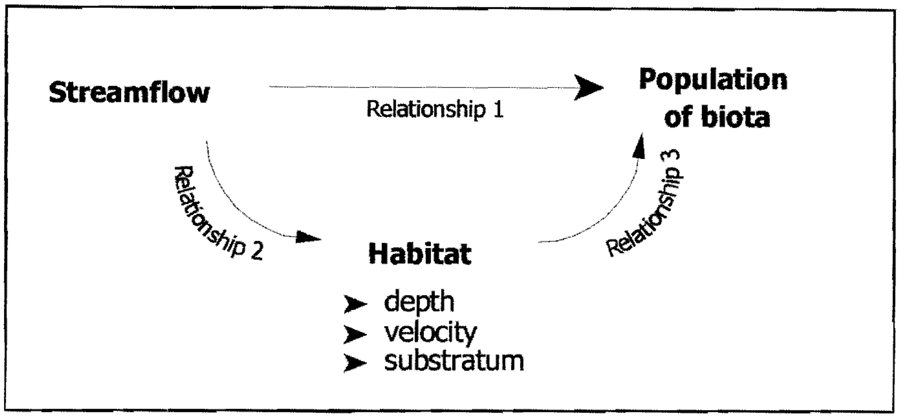


Figure 1.4 Conceptual approach of habitat-assessment models (modified from Shirvell 1986).

(McClendon & Rabeni 1987; Scarnecchia & Bergersen 1987). That is, they identify stream reaches where fish will be most abundant but they do not identify specific, physical habitat use, which can be provided via a complimentary microhabitat analysis. Nonetheless, it is important to note that there is a growing body of evidence to support that concept that a wider number of landscape and biological factors influence the use of habitat than microhabitat variables alone (e.g. Grossman *et al.* 1995; Pusey *et al.* 2000; see Chapter 8 for further discussions of this).

The first of these so-called *habitat-assessment* (or *habitat-discharge* approaches; Trihey & Stalnaker 1985), was the ***hydraulic-rating method*** (Loar *et al.* 1986), which uses changes in certain hydraulic variables with discharge to determine an IFR. Hydraulic variables, such as wetted perimeter, are measured usually using single cross-sections. These detail habitat features such as substratum, depth and velocity which are considered to be the most limiting to target organisms (Stalnaker 1979).

Another group of habitat-assessment approaches known as the ***habitat-rating*** methodologies, provide detailed analyses of the quality and quantity of habitat available to the target organism under question, as a function of discharge. In this case, habitat is described using multiple transects at a reach (Stalnaker 1979). Early applications of these methods were fairly specific, such as to provide flows for fish passage and in some cases, combinations of methodologies were used. One of the best known of such habitat-based approaches, the Instream Flow Incremental Methodology (IFIM) which is described in detail in Chapter 2, was designed to deal with IFRs for a target fishery resource, but has subsequently broadened to include flows for invertebrates and ecosystem needs.

For the purposes of this summary, a fourth approach which could be termed the ***holistic approach*** is receiving greater attention, in that all components of the ecosystem and their interrelationships are addressed. Examples include the Expert Panel Assessment Method and Holistic Approach of Arthington and others (e.g. Arthington *et al.* 1992) both from Australia, and a South African approach known as the Building Block Methodology (BBM; King & Louw 1995; King *et al.* in press, see Section 1.5).

1.5 RESEARCH IN SOUTH AFRICA TO DETERMINE IFRs

As early as 1969, the construction of the Pongolapoort dam prompted warnings from ecologists of the potential deleterious effects on the Pongola floodplain (Coke & Pott 1970), some of which have been described in the preceding discussions. Thereafter a set of investigations, designed to detail and to ameliorate the downstream effects, followed (e.g. Heeg & Breen 1982). However, the first formal recognition of water for instream flow needs for South African rivers was introduced by Roberts (1983) when, in projecting future water demands in the country, he calculated an allocation to "conservation" of 11% of the country's MAR (this figure was later modified to 8% of the exploitable water resources; Jezewski & Roberts 1986). Roberts acknowledged that this figure was simplistic in that it was based on coarse, countrywide estimates of water for estuaries, lakes and nature reserves. As such, it could not be used for individual rivers (see also Breen *et al.* 1984), but nonetheless provided the catalyst for future work in the region.

In 1987, as a result of workshops designed to assess the flow requirements of ecosystems, two approaches were developed to derive preliminary estimates for IFRs (King & O'Keeffe 1989):

- The "Skukuza" approach required a cumulative assessment of the consumptive and non-consumptive water requirement for each ecosystem component, and allocated amounts of water to each. Flooding and flushing flows were then superimposed on the derived base flows.
- The "Flow Simulation" approach utilized statistical treatment of hydrological records (virgin daily flow), as well as relevant ecological knowledge, to arrive at an ecosystem requirement. This relied on identifying monthly limits between which base flows should remain. Flooding and flushing requirements were then superimposed on the resultant base flows.

At the same time, a major initiative to assess the applicability of a detailed empirical American methodology, the Instream Flow Incremental Methodology (IFIM), was undertaken and is reported in King & Tharme (1994). Their research focussed on temperate systems in the western region of South Africa. Additionally, considerations regarding the suitability of this methodology for the warmer, sub-tropical systems, of the east of the country provided the impetus for my research (Chapters 2 - 9). In general, tropical systems are especially poorly understood (see for example Pringle 2000).

The last decade has seen a growth in research efforts into IFR evaluations. These concentrated largely on the rivers of the Western Cape, and those of the Kruger National Park (KNP), through the KNP Rivers Research Programme. Several approaches and components of IFRs are being tested, mainly in the least perturbed of these rivers, the Sabie River. They include the determination of the habitat requirements of the aquatic biota; sediment transport; geomorphological attributes of the system and responses to changes in the flow regime and; the relationships between groundwater and the riparian communities. Results of this research are reported in Heritage & van Niekerk (1994; 1995); Heritage *et al.* (1995a,b; 1996; 1997); van Coller *et al.* (1995); van Niekerk *et al.* (1995); Birkhead *et al.* (1996a,b); Broadhurst *et al.* (1996); Cheshire (1996); O'Keeffe *et al.* (1996); Pollard *et al.* (1996); Weeks *et al.* (1996), details of which are referred to in appropriate sections throughout this thesis. Additionally, O'Keeffe & Davies (1991) used simulated monthly hydrological data for the Sabie River under natural and afforested conditions, to develop a range of possible flow regimes.

Lastly, the urgent need for instream flow determinations that are legally required to accompany current and planned water developments, as well as to mitigate past perturbations, precipitated the development and evolution of the aforementioned, local approach, the BBM (King *et al.* in press). This multidisciplinary and iterative method uses the best available hydrological, geomorphological and ecological data pertaining to the river system under question, to create a modified flow regime designed to maintain the river in some predetermined state. Identification of this state - the "desired future state"- forms a key concept in the BBM approach. The result of the BBM application is the provision of an IFR recommendation for the river in question. This approach has been used on a number of systems, including the Lephalala River; Berg River; Tugela River and the Sabie River (King & Louw 1995). It should be noted that this method remains to be tested since (a) this is a recently-applied approach and sufficient time must be allowed for the rivers in question to respond to the modified flow regimes, and (b) this approach has been applied to development projects which have not yet been constructed (Dr. J. King, Freshwater Research Unit, University of Cape Town, *pers. comm.*). Details of the BBM approach are given in King & Tharme (1994) and in a forthcoming manual (King *et al.* in press). Finally, a further approach known as DRIFT (Downstream Response to Imposed Flow Transformations), is currently being developed (Brown & King in prep.).

1.6 MOTIVATION FOR RESEARCH AND THE APPROACH CHOSEN

It was against this background of diminishing water resources, and the declining ecological integrity of South African rivers, that this research was motivated. It was evident that decisions regarding IFRs were hampered by a dearth of ecological information and by the lack of tested, and hence appropriate approaches to defining instream flow needs. These issues were even more pressing in the face of continued and rapid development. Such was the case in the Sabie River Catchment (Chapter 3), which was under increasing pressure from proposed impoundments. In response, a research initiative was established to provide pre-impoundment data and, ultimately, a more comprehensive understanding of the catchment as a whole (see Figure 3.2). However, none of this work focussed specifically on a tributary of the Sabie River, the Marite, which was the site of the proposed Injaka Dam (Chunnett, Fourie & Partners 1990). Since this was the most likely of all the proposed dam sites, this tributary was chosen for the research reported in this thesis.

In selecting an appropriate approach for the determination of an IFR, consideration was given to a number of factors. To date, with the notable exception of work by King and Tharme (1994), few of the IFR models developed to assess the effects of flow modifications on aquatic biota have been tested for their applicability in southern Africa. Furthermore, the transferability of such models to warmwater systems requires careful consideration (Nestler 1990) since these systems differ, as described above, from the temperate or cold Northern Hemisphere areas for which the models were developed. Additionally, the high species richness of warmwater rivers generally prevents quantifying the habitat requirements of all species and necessitates a rigorous approach to the selection of fewer, representative species (Orth 1987; Leonard & Orth 1988; Bain & Boltz 1989).

Clearly, a comprehensive approach to determining instream flow needs would involve an assessment of the compound effects of impoundments on the structural and functional attributes of biota in the receiving reaches. The complexities governing cause and effect, coupled with pressures to provide answers in the face of increasing development, renders such an approach intractable, even for the most well-equipped and funded agencies. These realities directed interest towards the development of both predictive IFR models (Armitage 1994), as well as to the potential use of certain biota that can act as proxies for ecosystem responses to impoundments. In line with this rationale, a set of IFR methods which focus specifically on the loss, or gain, of habitat with flow alterations has received considerable attention. These habitat-assessment approaches (see Section 1.4) should be regarded as a step towards understanding the relationship between streamflow and organisms (Shirvell 1986; Figure 1.4).

Traditional stream ecology had attempted to explain the distribution and abundance of stream animals in terms of their physico-chemical and/or bioenergetic requirements, nutrient limitations, or the availability of organic matter. However, research in the 1980s (reviewed by Statzner *et al.* 1988), suggested that the distribution of stream organisms is much more closely correlated with their hydraulic requirements, such as sheer stress, current speed, depth, substratum and cover. These variables in effect define *habitat*, or more precisely, *physical microhabitat* (King & Tharme 1994). Potentially one of the major effects of impoundments is to alter the hydrological character of the receiving reaches, and hence to change the distribution and abundance of habitats. Instream-habitat modelling has become an increasingly standard means of assessing the habitat of aquatic biota in the face of escalating water-resource development, with IFIM constituting the most universally-applied instream flow model (Nestler *et al.* 1989; Chapter 2). Therefore IFIM was selected as the approach for this work. As a complimentary project, its applicability was also being tested in Western Cape rivers at the same time that my research was being developed (reported in King & Tharme 1994).

Consequently, the research represented in this thesis was initiated to explore the local applicability of this internationally used model by investigating the microhabitat requirements of some life-history stages of a target species, modelling the effects of flow modifications on their habitat, and critically assessing the results. This assessment provided the basis for reconsidering approaches to protecting instream habitats.

Definition of terms describing physical habitat

The literature reflects the wide array of terms that have emerged to describe the area in which a species is found (see Rowntree & Wadeson 1999), including as *habitat*, *hydraulic habitat*, *physical (micro)habitat* and *biotope*. All of these terms refer specifically to variables that comprise physical habitat, most frequently water depth, bed substratum, velocity and cover.

In IFIM, *habitat* is understood as macrohabitat and microhabitat. Theoretically, the term *macrohabitat* refers to within-channel conditions of water quality and temperature, the hydrological regime, sediment dynamics and channel morphology (Bovee 1982), but this definition is not always applied consistently(4).

---

(4) See for example, Bozek & Rahel (1991) who incorporate a broader suite of variables than those specified within IFIM, such as spawning gravel and vegetation.

Microhabitat, on the other hand most describes the local, small-scale physical or hydraulic variables of depth, velocity, substratum and cover. The more comprehensive view of habitat which includes a suite of variables reflecting food, water chemistry, temperature and biotic parameters such as predation, is not implied.

More recently, there has been a trend towards the use of the term *biotope*, particularly in the South African and British literature. In its broadest definition, *biotope* refers to homogeneous environment which satisfies the habitat requirements of a biotic community and includes biological, chemical and physical features (King & Tharme 1994). However, in an attempt to standardise terminologies, the term *hydraulic biotope* which has been adopted in habitat-related research in South Africa, excludes the biotic components of habitat as well as water quality and temperature. Thus Wadeson (1994) defined *hydraulic biotope* as "a spatially distinct in-stream flow environment characterised by specific hydraulic and substrate attributes". In contrast, the term *physical biotope*, defined on the basis of flow characteristics alone (Prof. M. Newson, Department of Geography, University of Newcastle upon Tyne, *pers. comm.*) is used by British researchers (e.g. Padmore 1997).

For the purposes of this study, the use of terms will reflect the evolution of their use in habitat studies. Since Chapters 2 to 9 deal specifically with IFIM, the term *habitat*, which abbreviates *physical microhabitat*, will be used to reflect IFIM nomenclature. This term is superceded by the use of *biotope* in Chapter 10 to 13, in keeping with current trends in habitat studies in South Africa.

1.7 STATEMENT OF AIMS AND OBJECTIVES OF THIS WORK

Aim:

The aim of this work is to assess the potential downstream effects of the proposed Injaka Dam on the physical habitat of a flow-sensitive fish species of the Marite River, a sub-tropical southern African system, with particular emphasis on the hydraulic modifications associated with low-flow conditions.

Objectives:

1. To test the applicability of a quantitative, habitat-assessment approach, namely the Instream Flow Incremental Methodology (Bovee & Milhous 1978), with a view to exploring its potential use as a contribution to recommending IFRs in the context of a sub-tropical river system. The sub-objectives are:
    a. to quantify the hydraulic microhabitat requirements of the adult, and possibly other life-history stages, of a target species, as required by the IFIM;
    b. to describe microhabitat changes of the target species as a function of discharge and;
    c. to evaluate the possibility of setting IFRs based on this approach.
2. To explore alternative habitat-assessment approaches to determine IFRs.

1.8 OVERVIEW OF THE STRUCTURE OF THIS THESIS

This research is broadly divided into four parts, as follows.

In Part I, this chapter has provided the background and motivation for the research, and Chapter 2 provides an overview of the concepts and application of the IFIM methodology. Part II sets the scene with a description of the study area in Chapter 3.

This is followed by Part III which details the results of the IFIM initiative to the study area, in Chapters 4 through to 9. These include an assessment of catchment equilibrium and macrohabitat conditions and the establishment of study sites (Chapter 4); the monitoring of macrohabitat conditions and collection of calibration data (Chapter 5); the selection of a target species (Chapter 6), the reproductive ecology (Chapter 7), and hydraulic microhabitat use of that species (Chapter 8); and finally, the habitat availability for that species as calculated by the PHABSIM model (Chapter 9).

Part IV involves an assessment of the IFIM approach and the development of an alternative approach, formulated as the Geomorphological-Biotope Assessment or GBA, which is introduced and described in Chapter 10. Chapter 11 uses the GBA to quantify the availability of hydraulic biotopes in the study river as a function of flow, whilst Chapter 12 provides a framework for linking data on habitat-availability with that of habitat-use. Ultimately, the results of these two approaches, IFIM and the GBA, are assessed in Chapter 13, which closes with recommendations for future research directions.

2

Overview of The Instream Flow Incremental Methodology (IFIM) and PHABSIM

2.1. INTRODUCTION

A range of approaches has evolved for assessing the instream flow requirements, or IFRs, of rivers (see Chapter 1). From an ecological perspective, the overarching goal of these is to quantify the relationship between organisms and streamflow. To this end, a subset of IFR approaches, known as *habitat-assessment approaches*, has evolved to explore changes in habitat in relation to streamflow (Shirvell 1986, see Figure 1.4). They are based on the assumption that physical habitat becomes limiting with changes in flow, and that this is reflected in changes in the distribution and abundance of the biota. A major advance in these approaches has been the increased focus on their predictive potential. One of the most widely used and complex of these methodologies, and chosen for the purposes of this research, is the Instream Flow Incremental Methodology (IFIM) and associated computer packages (Gore & Nestler 1988), developed by the Instream Flow Group in Colorado (Bovee 1982). The most important of these is PHABSIM (PHysical HAbitat SImulation Model), now PHABSIM version II.

The purpose of this chapter is to provide a broad overview of this methodology and outputs, which will be more fully illustrated through its application (reported in Chapters 4 to 9). The following outline is by no means comprehensive; there is an extensive literature which details various aspects of IFIM and PHABSIM, with each account providing some valuable information. For example, the theory, techniques and application of IFIM are discussed by, amongst others, Bovee & Milhous (1978), Bovee (1982, 1986), Leonard *et al.* (1986), Orth (1987), Gore & King (1989a,b); Bullock *et al.* (1991); King & Tharme (1994) and Stalnaker (1994). A number of authors provide useful evaluations of IFIM, including Bain *et al.* (1982), Orth & Maughan (1982), Armour *et al.* (1984), Orth & Leonard (1990) and King & Tharme (1994). The specific application of IFIM to coolwater species is provided by Bovee (1978), and to warmwater species by Orth & Leonard (1990) and Nestler (1990).

As stated by King & Tharme (1994), there is no brief but clear description of the methodology, nor a comprehensive account of concepts and techniques that have become redundant. Their work probably represents the most thorough account to date and readers are referred to this for further detail. The objective of this synopsis therefore is simply to rationalise the extensive documentation into a broad overview of the methodology. Nonetheless, coming to terms with the exhaustive information on IFIM can be daunting, and the key steps have therefore been abstracted, and summarised, in Figure 2.1.

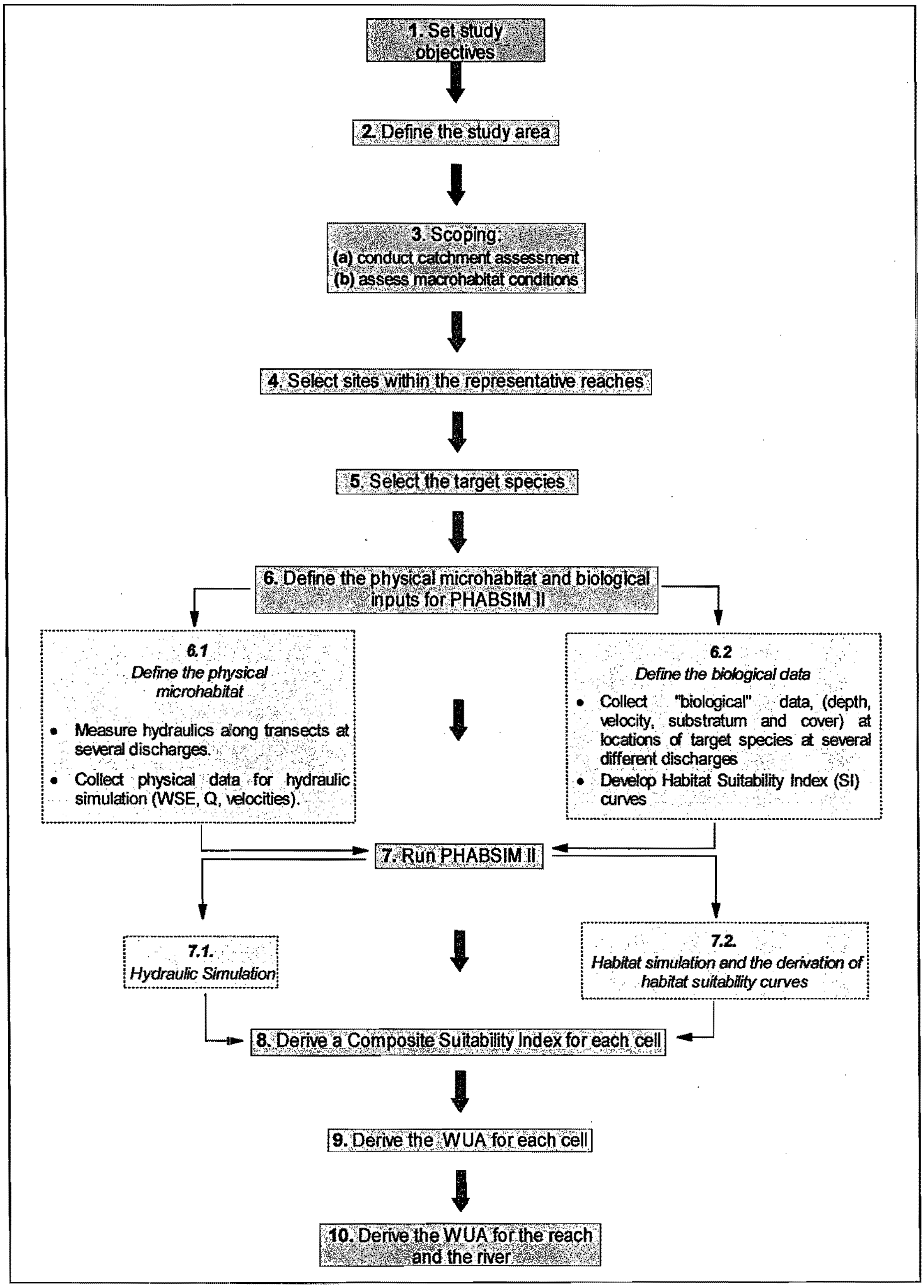


Figure 2.1 Summary of the sequential steps involved in the application of IFIM and PHABSIM II. Note that although the term "biological data" is used in IFIM studies, these data comprise physical habitat variables and therefore the term "environmental" would be more appropriate. Abbreviations as follows: SI = Suitability Index; WSE = Water Surface Elevation; Q = discharge; WUA = Weighted Usable Area (see text for details).

2.2 OVERVIEW OF THE RATIONALE OF IFIM AND PHABSIM

In its entirety, the IFIM process is said to evaluate the effects of incremental changes in streamflow on channel structure and water quality, both embraced in the concept of macrohabitat, and physical microhabitat, described as follows (Bovee 1982):

- The primary constituents of **macrohabitat** are water quality and temperature and secondarily, geology, slope, elevation, water yields and sediment and chemical yields (Chapter 4).
- The physical variables of depth, velocity, substratum and cover at the location that an organism was sighted, or captured, comprise **microhabitat** or microhabitat criteria (Chapter 8).

In reality, the physical habitat routine (PHABSIM) is the most frequently used, often to the exclusion of the other components (Scott & Shirvell 1985; Orth 1987).

The objective of IFIM, together with PHABSIM, is to develop a habitat versus flow relationship that is quantitatively defensible. To this end, IFIM is simply a multidisciplinary tool, or set of analytical procedures that, through PHABSIM II, allows one to model and evaluate the effects of incremental changes in flow on the habitat of a selected species. The final output of IFIM is quantitative information on the availability of physical microhabitat for selected, target species over a range of discharges.

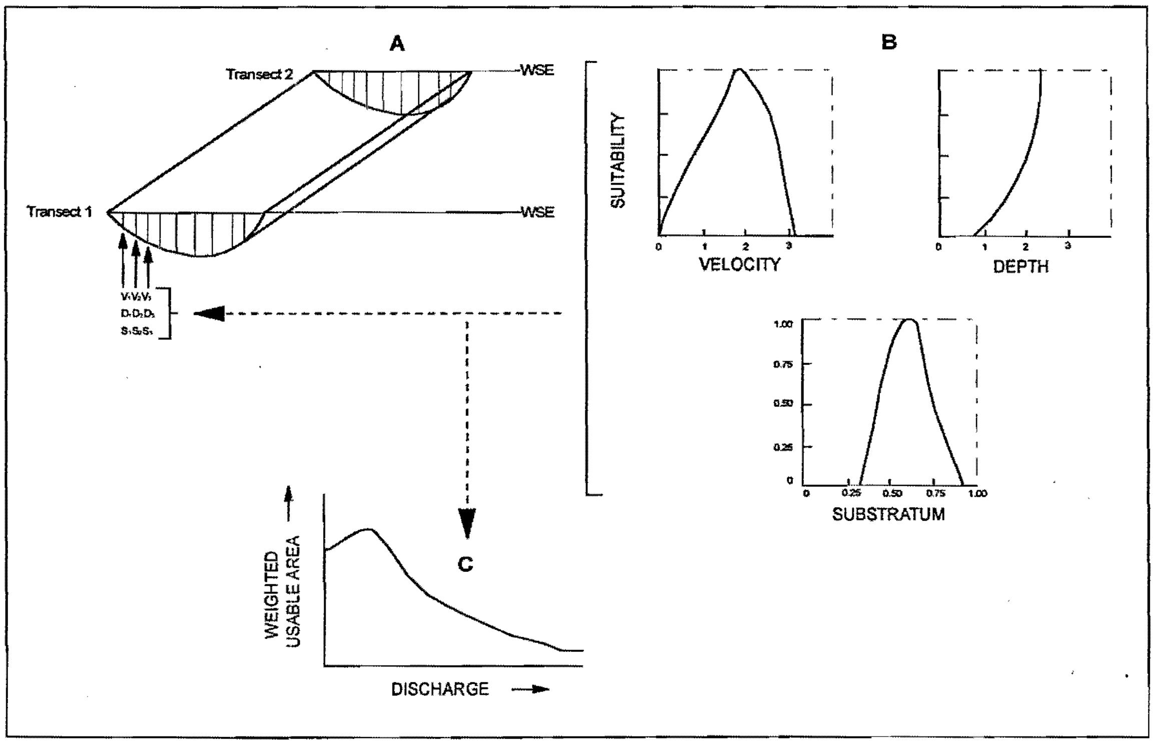


Figure 2.2 Overview of PHABSIM rationale. Hydraulic data from the transects (A) are linked to the water height or water surface elevation (WSE) and discharge measurements to provide calibration data for the hydraulic programmes of PHABSIM II. The SI curves, which represent the suitability of the habitat (B) are linked with simulated hydraulic data to predict changes in total habitat area, known as weighted usable area (WUA) with incremental changes in discharge (C) (after Gore and Nestler 1988).

An overview of the conceptualisation of the model is illustrated in Figure 2.2. and is explained in steps 1 to 10, below. The translation from flow to habitat is broadly achieved as follows. Once sites and target species have been selected on the basis of the objectives and outcomes of scoping (steps 1 to 5), the IFIM protocol involves a hydraulic description of the study site, which serves as the calibration data for PHABSIM, and a quantification of the habitat used by the target species at various flows (step 6). PHABSIM then uses this information to compute the amount of "suitable" habitat, known as the weighted usable area (WUA), over a range of measured, and unmeasured, flows (steps 7 to 10).

Theoretically, prior to simulation of the physical habitat variables directly related to flow, consideration is given to a number of parameters, namely: thermal regime, chemical water quality and allochthonous input. If these factors do not appear to be limiting, physical habitat is considered to be the major factor affecting fish production (Stalnaker 1979; Bovee 1982; Orth 1987).

2.3 STEPS INVOLVED IN THE USE OF IFIM AND PHABSIM

An overview of the IFIM/ PHABSIM protocol follows, accompanied by Figure 2.1. The details are elaborated in the appropriate chapters.

STEP 1. Set the study objectives

Bovee (1982) states that an explicit statement of the objectives is important since this governs the study approach, design and analysis. For example, the outcomes of the project may be intended for planning, management, impact assessment or mitigation purposes. In practice, the objectives of research programmes in the United States and South Africa differ markedly. In South Africa, research objectives tend to focus on ecosystem maintenance, whilst those in the United States frequently focus on the maintenance of a species of interest (King & Tharme 1994).

STEP 2. Define the study area

The study area (Chapter 3) provides a sample of the variation in hydraulic conditions and habitat types, as well as the proportional composition of each habitat type, at representative sites. Depending on the objectives, the study area may be at one of three scales: river basin (see Kershner & Snider 1992, for example); site-specific instream-flow allocation; or project-impact related, which may include several study sites (Bovee 1982).

STEP 3. Scoping

Step 3a. Conduct an assessment of the catchment equilibrium

Essentially, if a catchment is in equilibrium, the dynamic physical components of a catchment such as sediment and water yield, interact to produce characteristics that alter seasonally about some average condition in a predictable fashion (i.e. *equilibrium).* These components are controlled by catchment processes and land-use patterns which ultimately affect channel structure (Bovee 1982).

The objective of this step is to establish if the catchment is currently in a state of equilibrium and likely to remain so with the development in place. The assessment is based on historical and current data on water, chemical and sediment yields, both to establish baseline conditions for the river, as well as to highlight any apparent trends of change in these. This constitutes a critical step in that it provides the endorsement for continuing with the IFIM initiative, and yet it is seldom reported on in the literature. Clearly, setting flow recommendations based on conditions of disequilibrium is unfounded and future conditions need to be ascertained.

Step 3b Assess the macrohabitat conditions of the study area

The IFIM incorporates measurements of both macrohabitat and microhabitat (Bovee 1982). *Macrohabitat* includes water quality, temperature and channel morphology, with similar conditions comprising a macrohabitat zone. The rationale for this differentiation within IFIM is that *macrohabitat* is defined as the aggregate of average conditions of variables that do not change at the *microhabitat* level (Armour *et al.* 1984). The primary characteristics of temperature and water quality define the limits of suitability for each species, and hence dictate the *longitudinal succession of species.* The link with microhabitat is made through the secondary constituents of geology, slope, elevation, water yields and sediment and chemical yields, which are considered to be determinants of geomorphic characteristics of the river, such as channel structure. Hence, they govern the types and spatial distributions of microhabitats - characteristics to which fish and invertebrates respond directly (Bovee 1982).

The objective of the macrohabitat assessment is to evaluate if, and where, macrohabitat variables alter significantly with progressive distance downstream in order to (a) define limits of suitability for the target species, (b) zone the river, which constitutes the first step in site selection, and (c) define which macrohabitat variables will be monitored throughout the study period.

A number of criticisms have been levelled at the concept and definitions of "macrohabitat" (discussed in Chapter 4). Moreover, macrohabitat analyses are conspicuously absent in the literature on IFIM applications suggesting that they are seldom undertaken or, at least, are not documented. Consequently, this step has remained largely theoretical and untested, with some exceptions such as that of King & Tharme (1994).

STEP 4. Selection of microhabitat sites

Theoretically, one of the objectives of the macrohabitat analysis is to provide the necessary information for site selection (Chapter 4) at which microhabitat availability, and use, are quantified. Site selection involves a hierarchical approach, in which the river is zoned by way of macrohabitat variables, at increasing scales of resolution. These include *zones,* followed by *segments, representative or critical reaches* and finally, *sites.* Distinguishing features of these components are summarised in Table 2.1 and described and assessed in Chapter 4.

Representative, and critical, stream reaches are the focus of IFIM studies, and are defined by Bain *et al.* (1982) as follows:

- **Representative reaches** contain a distribution of gross habitat features (for example, a riffle-run sequence) similar to that observed over large areas of the stream.
- **Critical reaches** are areas of unique or rare habitat that are essential to the well-being of the species of interest.

Table 2.1

Explanation of terms used in IFIM to describe the various hierarchical components that are identified within rivers, at increasing levels of resolution, and that ultimately guide site selection (after Bovee 1982).

TERM	DESCRIPTION
Zone	• Collection of similar segments. All segments have the same channel morphology and flow.
Segment	• Differentiated on the basis of changes in flow and/or channel morphology. Changes in base flow of 10-15% warrant the demarcation of a new segment. • Factors affecting channel morphology include slope, sediment supply, bank materials, vegetation and flow regime, indicated by points at which channel sinuosity, and the width to depth ratio, change by more than 25%. • Segments may or may not have different water quality, temperature and species composition.
Representative reach	• Contains a distribution of gross habitat features similar to that observed over large areas of the stream. • Length of 10 to 14 times the stream width (see assessment in Chapter 4). • At least 10% of the river must be included (see assessment in Chapter 4). • May comprise part of or the whole segment. • May contain critical reaches.
Site	• Location in a stream where some characteristic of habitat is measured • May comprise macro- or micro-habitat sites

STEP 5. Target species selection

The use of a target species as a proxy is rationalised, in IFIM, on the basis that an analysis of the habitat requirements for all species in the study area is beyond the capacity of most research projects. The inherent assumption is that the provision of conditions for the maintenance of the target species will satisfy the requirements of the remainder of the organisms present in the study area. It is imperative therefore that the selection of a target (or indicator species) reflects the research objective (Chapter 6). For example, some species may be good indicators of conditions of reduced, but not increased, velocity (Bovee 1982) and inappropriate use could be to the detriment of the remainder of the biota.

Although the timing of target species selection is unclear from Bovee (1982), I would suggest that this step should follow scoping to facilitate an objective choice of target species.

STEP 6. Define the physical microhabitat and biological inputs for PHABSIM II

Step 6.1 Defining the physical microhabitat at a site: calibration data for microhabitat availability

Conceptually within IFIM, the study reach comprises a complex mosaic of four variables which include depth, velocity, substratum and cover. PHABSIM II describes their distribution on the basis of strategically placed transects at each site (Figure 2.3; and see Chapter 5). These transects are used to (a) describe the longitudinal distribution of different habitat types, on the basis of "cells" within the stream (Figure 2.3), and to (b) describe how these cells alter in terms of the four hydraulic variables over a range of discharges. Once quantified, this physical description of a site provides the calibration data for the PHABSIM routine which simulates changes in habitat as a function of discharge (Bovee & Milhous 1978; Milhous *et al.* 1984).

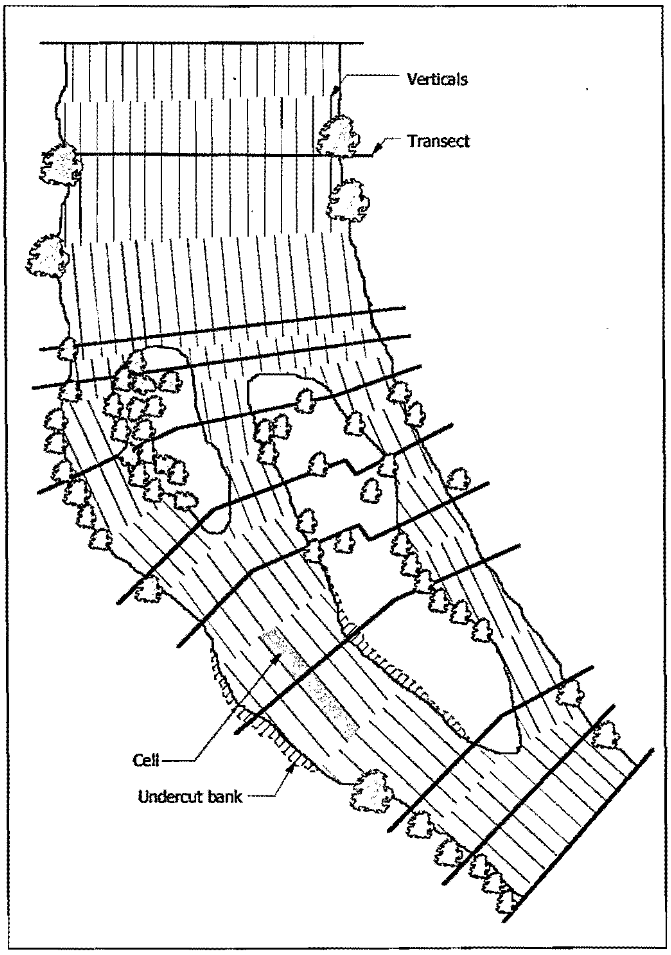


Figure 2.3 Conceptualisation of habitat availability within IFIM. The available physical habitat is described on the basis of transects placed across the study area at all hydraulic controls (see Chapter 5) and major habitat types. Measurements of hydraulic variables are made across the transects and the point at which these are taken, called "verticals", delimit the boundaries of so-called cells. Each cell extends part way upstream and downstream to the next transect. These measurements are used to define the distribution of different microhabitats in a stream reach and are considered constant within each cell (after Bovee 1982).

The physical data that are required for the calibration of all hydraulic simulation routines are summarised below (Bovee & Milhous 1978):

1. The cross-sectional profile of each transect is described by measurements of ground height along a transect.
2. Water surface elevations (WSE), describing the height of the water, or stage, at each transect are measured over a range of discharges.
3. The distance between transects (stationing) on both the left and right river banks, is taken.
4. The heights of transect headstakes (the endpoints of the transects) are surveyed.
5. Discharge at each transect (normally measured during the initial macrohabitat visit), and thereafter, a mean discharge for the site (measured at each visit) taken at a consistent transect, are required.
6. At each surveyed point along the transect (i.e. those described in (1)), descriptions are required of substratum particle size and proportions, cover (instream, offstream and overhead), and any additional features deemed to be important for microhabitat (King & Tharme 1994).

Most hydraulic programmes also require the following (King & Tharme 1994):

7. Sequential velocity measurements across each transect. Depths can be recorded at the same time if the transect is to be used for discharge calculations, but are not required for input to PHABSIM II as the model calculates depths from WSEs.

Step 6.2 Defining the biological data[1]*: Microhabitat use and the development of suitability index curves*

Two types of biological data are required by IFIM, but usually only one type is collected (King & Tharme 1994). These are:

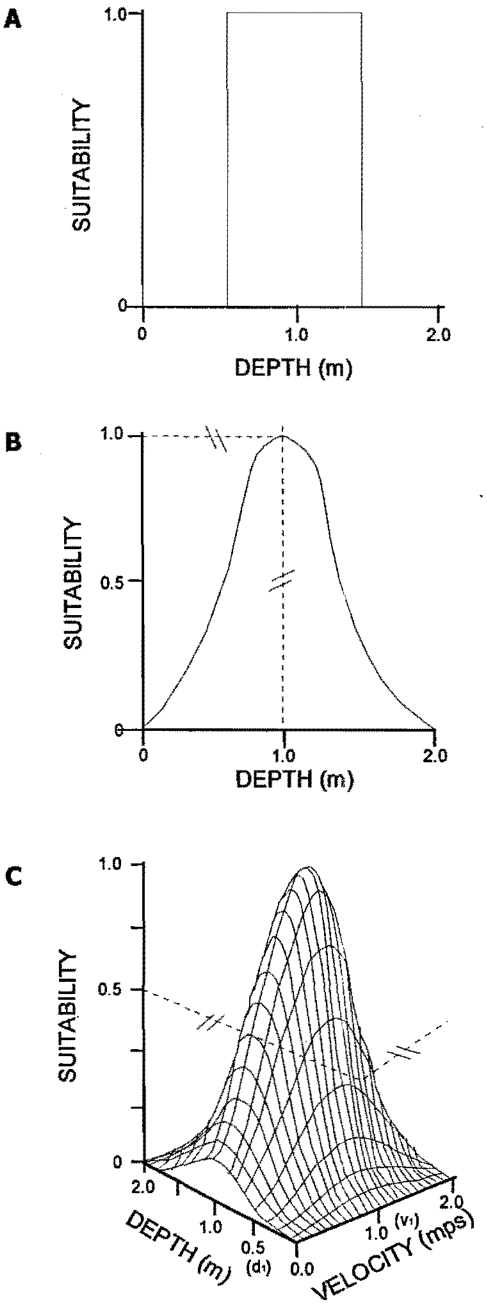
1. The tolerance ranges of the target species to macrohabitat variables such as water quality and temperature are required to define the distribution limits of suitable macrohabitat. These data are infrequently reported upon in any IFIM study and seldom available in South Africa.
2. Data describing the microhabitat preferred by the target species in terms of depth, velocity and channel index or CI, which represents a combination of substratum and cover. These data are used to derive **microhabitat suitability criteria** or **suitability curves**(2), which describe the (assumed) range and optimal conditions used, or preferred, by a target species.

The latter data, also known as **SI curves** (see Chapter 8), comprise the "biological" input to PHABSIM, and may be derived as use, or preference, data. These curves are graphical representations of the behavioural response of a species (or lifestage) to a particular variable and are expressed in one of three formats (Figure 2.4). Independent of other variables, suitability criteria render a suitability index between 0.0 (unsuitable) and 1.0 (suitable), for any variable. The implicit assumptions in the derivation of SI curves are that (a) all levels of variables are equally sampled and are equally available for use and, (b) habitat use remains constant throughout all seasons, if seasonally-specific curves are not constructed.

---

[1] See comment in Figure 2.1 on the use of this term by IFIM.

[2] An array of synonymous terminology is used in IFIM; the term *suitability curve* is synonymous with *suitability index curve*, *SI criteria* and *habitat suitability criteria*, *function* or *model*.



Binary format rates the suitable range of a single variable (depth, velocity or CI) as suitable (1.0) or unsuitable (0.0) with no gradation and no consideration for values outside of the range, regardless of the quality of other variables in that cell.

Univariate curves reflect the argument that within a range of suitable conditions, there is a narrower range that the target species selects, as preferred or optimal, for that variable. Again, suitability is defined between 0.0 and 1.0, with the gradations representing increasing or decreasing preference conditions.

Multivariate response curves (or "joint suitability functions") represent the interaction or correlation between two or more variables. Development of these curves is still problematic and they are rarely developed.

Figure 2.4 Format presentations for habitat criteria: (A) binary, (B) univariate curves, and (C) multivariate response surfaces (after Bullock *et al.* 1991).

The source of data from which SI curves are derived, is described by *categories* (Bovee 1986). Category I criteria are developed solely from the literature or professional judgement. Normally however, SI criteria are based on field measurements of the density, or abundance, of the target species over ranges of velocity, depth and CI (Bain *et al.* 1982). Conditions at the point where an organism was captured constitute a description of *microhabitat use*, and all samples, irrespective of the presence of the target organism, constitute the *microhabitat availability*. Category II criteria only describe microhabitat use in that the biota may use sub-optimal conditions because the preferred conditions are limited, or unavailable. Category III criteria, on the other hand, embrace the concept of preference by taking into account microhabitat use as a function of that available (Chapter 8). Additionally, *conditional criteria* (Bovee 1986) stratify seasonal or lifestage differences in microhabitat use or preference.

Three basic approaches to the creation of SI curves, detailed by Bovee (1986 p.118-150), have been developed; namely histogram analysis, non-parametric tolerance limits and function-fitting. Once described, the co-ordinates of the SI curves form the basic information on the physical microhabitat requirements of the target species and are the input data for PHABSIM II.

STEP 7 *Running PHABSIM II*

The major objective in using PHABSIM II is to determine the relationship between discharge and habitat over a range of measured and simulated discharges (Chapter 9). The output is given as an *index of available habitat* denoted as **Weighted Usable Area (WUA)**. The following principles underlie this objective (Bovee 1982):

- Each species exhibits preferences within a range of habitat conditions that it can tolerate,
- these ranges can be defined for each species and,
- the area of stream that provides these conditions can be quantified as a function of discharge and channel structure.

PHABSIM involves a two-step approach to derive a habitat-discharge curve: hydraulic simulation and habitat simulation (Bain *et al.* 1982).

Step 7.1. *Hydraulic simulation*

Hydraulic simulation is defined as a description of changes in distribution of velocity, depth, substratum and cover, all as a function of discharge. The information required to calibrate the hydraulic programs was described in Step 6.1. The measured flows are called calibration flows (Bullock *et al.* 1991).

The aim of hydraulic simulation is twofold:

1. to determine a stage-discharge relationship for each transect and,
2. to determine the velocity-distribution discharge relationship.

The concept of a stage-discharge relationship is poorly dealt within the IFIM manuals, but is simply a description of the relationship between water height (stage) in the channel and the discharge. Once established, discharge can then be ascertained simply by monitoring the water level. One method of depicting this relationship, known as the rating-curve method, illustrates this relationship (Figure 2.5).

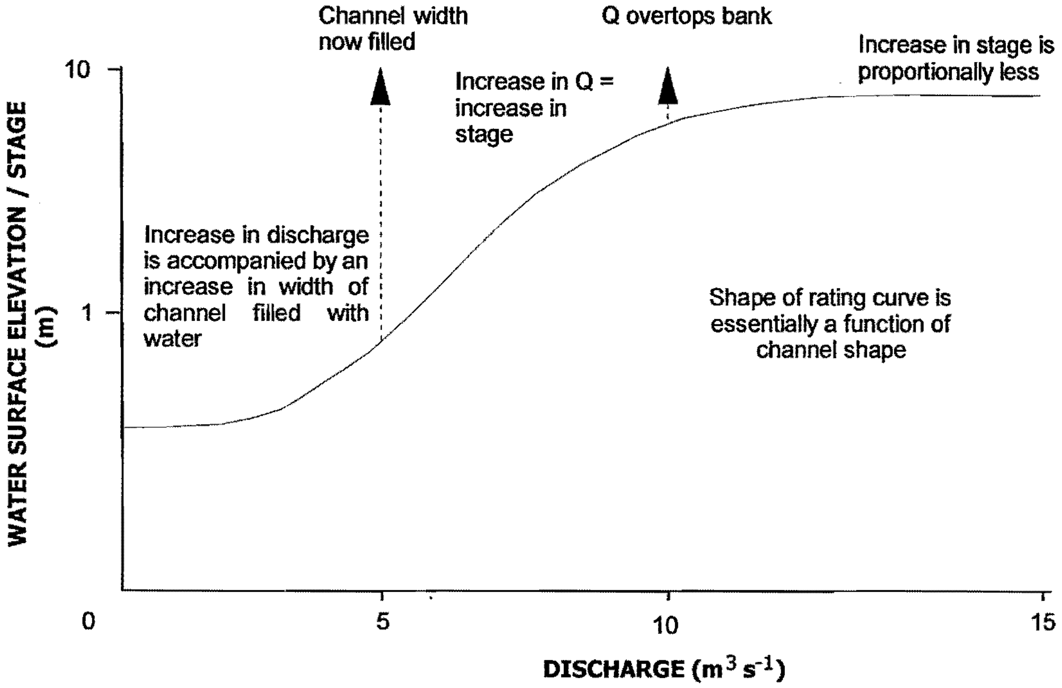


Figure 2.5 Diagrammatic representation illustrating key features of an S-shaped rating curve, derived from plotting stage versus discharge over a wide range of measured flows (Q = discharge). This curve allows one to determine discharge by measuring the stage, and describes points at which the channel is filled and overtopped (after Bovee & Milhous 1978).

There are three basic hydraulic simulation routines available within PHABSIM, referred to as WSP (Water Surface Profile simulation routine, IFG2), MANSQ (Mannings Stage Discharge hydraulic simulation routine) and IFG4 (Instream Flow Group 4 hydraulic simulation routine). A choice of one (or more) of these can be used to predict the distribution of velocity and depth over a river reach (Bullock *et al.* 1991). Use of each model is determined by the quantity of data collected (Bain *et al.* 1982). For simulation discharges:

1. IFG4 predicts the water surface elevation using a simple stage-discharge relationship (Figure 2.5), and predicts velocities on a cell-by-cell basis using *Mannings n.* This is a roughness coefficient and can be thought of as a "calibration" factor, which integrates the effects of flow resistance caused by bed roughness, presence of vegetation and the amount of sediment and debris carried by flow (Trieste & Jarrett 1987, *cited in* Gordon *et al.* 1992). IFG4 treats each transect independently.
2. Where IFG4 fails to adequately predict WSE due to poor model calibration, MANSQ can predict WSEs using the solution of Mannings Equation. MANSQ models each transect independently.
3. WSP is a standard step model for the prediction of WSE, with transects treated dependently. Computations are carried step-by-step from one transect to the next, covering the entire reach. Since neither MANSQ nor WSP can predict cell velocities, IFG4 is used to do so, but delivers average velocities for the transect.

Step 7.2. Habitat simulation and habitat suitability indices

The translation from flow to habitat occurs when each cell in the stream (Figure 2.3) is evaluated against the SI criteria of the organism in question (see Step 6.2), to determine the overall "quality" or suitability of the cell, which is provided as a composite value. These quality values range between 1.0 (entirely suitable as a microhabitat) and 0.0 (unsuitable habitat).

The combination of biological data and hydraulic simulation outputs is performed by one of four IFG-developed computer programmes (see Chapter 9): HABTAT, HABTAE, HABTAV and HABTAM (Milhous *et al.* 1989). The basic simulation programme is HABTAT, with others being a variation on this. Using the SI curves for the relevant species life-stage, outputs from the hydraulic simulation for each cell are translated by HABTAT into cell-specific **habitat suitability indices (HSI)** for individual variables.

STEP 8 Derive a composite suitability index for each cell

A **Composite Suitability Index (CSI)** for each cell (i) is derived as a summation of the HSI for the individual variables (Chapter 9), as follows (Orth & Maughan 1982):

$$CSI_i = fv\ (V_i) \times fd\ (D_i) \times fs\ (S_i) \qquad \text{Equation 2.1}$$

where $fv\ (V_i)$ is the suitability factor for the velocity in cell i
$fd\ (D_i)$ is the suitability factor for the depth in cell i
$fv\ (S_i)$ is the suitability factor for the substratum in cell i

STEP 9 Derive the WUA for each cell

The "usability" of a microhabitat cell for the biota in question is described by the index, known as WUA, or **weighted usable area,** which is the final output of PHABSIM. The WUA for each cell is derived from the product of the CSI and the *surface area* of each cell (Milhous 1982):

$$WUA = C_{i,s} \times A_i \qquad \text{Equation 2.2}$$

where $C_{i,s}$ is the suitability index for the combined hydraulic characteristics of the cell (i), for a target species (s); A_i = the surface area of the cell.

STEP 10 a Derive the WUA for the reach

The total physical microhabitat, or optimum habitat, for a species or lifestage in the reach at a certain discharge, is calculated by PHABSIM as the sum of WUA for each cell. This is given by the equation (Bovee 1982; Milhous *et al.* 1984):

$$WUA\ (Q)_s = \sum_{i=1}^{n} f(v_i \times d_i \times CI_i) \times A_i \qquad \text{Equation 2.3}$$

where WUA is the useable habitat area (ft^2) in the stream at the flow Q_1 for a species (s); v = velocity, d = depth and CI = channel index (normally substratum x cover), all at point 1. The CI is assumed to remain constant over all simulated discharges. The function "f" is the criterion that relates the physical parameters (v, d, CI) to the habitat suitability of the target species

STEP 10 b Derive the total WUA for the river

Finally the habitat, expressed as WUA is extrapolated to the entire river, as follows (Bovee 1982):

$$TWUA = WUA \times L \qquad \text{Equation 2.4}$$

where TWUA is the total weighted usable area for a target species in ft^2; WUA is the reach weighted usable area in ft^2 per 1000 ft; L = length of stream having suitable water quality and temperature (macrohabitat zone), in miles or kilometres

Although the output of WUA implies an *area*, the interpretation is ambiguous and could, alternatively, infer *quality* or *suitability* (King & Tharme 1994). This issue is elaborated in Chapter 9.

A habitat-discharge curve of the WUA indices against streamflow depicts the availability of suitable habitat for a species, or lifestage, as a function of incremental changes in streamflow. Theoretically, the outputs of WUA for each site are extrapolated to the entire study area on the basis of the *macrohabitat zones* (Step 3b). This information can then be used to negotiate a modified flow regime that is considered acceptable in light of the study objectives.

2.4 POTENTIAL APPLICATION OF IFIM

The IFIM was developed and used primarily in moderate to high-gradient, temperate rivers of the western United States, with a focus primarily on fisheries, although this was later extended to macro-invertebrates (Mr. R.T. Milhous, US Fish & Wildlife Service, Fort Collins, *pers comm.*). Both their motivation and development in the USA have been governed by rather limited fisheries concerns. In contrast, in South Africa, Australia and more recently, the UK, research into IFRs has been directed primarily by a broad ecosystem focus (King & Tharme 1994). The potential uses of IFIM and PHABSIM have included addressing (a) minimum flow requirements (called compensation flows in the UK), such as from dams or abstractions, (b) hydro-peaking problems such as bypass and dual flows, (c) the protection of endangered species and, (d) the control of exotic species (R.T. Milhous, *pers comm.*).

Nonetheless, IFIM is now being tested for a number of different scenarios such as low gradient systems, vegetational choking of rivers, geomorphologically complex systems, sub-tropical ecosystems, migratory bird habitat and aspects of river conservation. The research objectives that have been directing IFIM initiatives in various countries include (i) fisheries maintenance in Canada (e.g. Shirvell & Morantz 1983), Australia (Richardson 1986), New Zealand (Irvine *et al.* 1987) and Norway (Heggenes & Saltveit 1990; Heggenes *et al.* 1990); (ii) invertebrate maintenance in New Zealand (Jowett 1982; Jowett & Richardson 1990; Jowett *et al.* 1991) and; (iii) river conservation in South Africa (Gore *et al.* 1992; King & Tharme 1994), Australia (reviewed in Richardson 1986; Karim *et al.* 1995) and Britain (e.g Armitage & Ladle 1989; Bullock *et al.* 1991). In France, IFIM has been used largely as a retroactive tool to justify past water allocations and fisheries management (R.T. Milhous, *pers comm.*).

2.5 CONCLUDING REMARKS

Understanding the concepts and methodologies that comprise IFIM and PHABSIM II is a frustrating task, primarily due to the lack of any cohesive documentation. Further, the use of PHABSIM is not without controversy and the assumptions, logic and mathematics of the method have been challenged (see Orth & Maughan 1982; Mathur *et al.* 1985a,b; Mosley & Jowett 1985; Scott & Shirvell 1985; Orth & Maughan 1986; Richardson 1986; Shirvell 1986; Orth 1987; King & Tharme 1994). These criticisms, and others identified in this study, are elaborated in the following chapters and are summarised in Chapter 10.

A number of problems which were encountered specifically in mastering of the methodology are worth mentioning. Firstly, the interchange of a plethora of synonymous terms makes any initial understanding of IFIM exceptionally difficult. This was particularly evident in the scoping (which may partly account for the fact that scoping is rarely reported on in IFIM studies), and in the development of suitability curves. Moreover, a rationalisation of the range of terms, which include criteria, functions, indices, and models, that are applied to habitat suitability curves, is needed.

Secondly, the sequence of steps is unclear but is an important consideration because decisions made at each step are often predicated on the outcome of the last step. For example, according to Bovee (1982, p.31), target species selection is undertaken after the assessment of catchment conditions. However, elsewhere, Bovee (1982 p.5) suggests that this step is undertaken prior to any other step, in that one is required "determine the length of stream having suitable conditions"- the inference being *suitable for the target organism that has been selected.* Possibly this reflects the American focus on the protection of a specific species, where selection is a *fait accompli* at the onset, in contrast to species selection based on broader ecosystem protection objectives.

Having noted these concerns, it is important to emphasize the objectives for which IFIM was developed. It was designed in the US as a water management model (and *not* an ecological model), specifically for negotiating flow regimes and is restricted to evaluating the changes in the variables most closely affected by flows on fish and invertebrates (Armour *et al.* 1984; Leonard *et al.* 1986). Milhous (*pers. comm.*) cautions against "all-answer" expectations from PHABSIM and recommends using those components of the model that are applicable to the objectives and logistic opportunities of the project.

Even in the light of these precautionary comments, it is suggested that a prudent reevaluation of both the steps and terms included in this approach by IFIM proponents would greatly advance the implementation of PHABSIM, particularly for those steps that provide the validation for the study.

PART II

Setting the scene

3

The Marite River Catchment and Study Area

3.1 INTRODUCTION

Theoretically, IFIM requires a thorough understanding of catchment conditions of the study area so as to evaluate the impacts of current, and future, land-use and water resource developments on the channel morphology and macrohabitat conditions (see Chapter 2). This chapter provides an overview of the biophysical parameters, available water resources and land-use patterns of the Marite River catchment, in which the study is located. Reference is also made to major hydrological changes that have typified the region, as well as current and potential water shortages and planned water-resource developments. Unless stated otherwise, most of the information regarding the water resources is taken from two extensive reports on the Sabie Sand Catchment (Development Bank of South Africa 1989; Chunnett, Fourie & Partners 1990). Much of the available information pertains to the Sabie River Catchment (henceforth referred to as the SRC) as a whole, but where possible, data have been adjusted to reflect conditions for the Marite sub-catchment.

3.2 THE MARITE RIVER STUDY AREA

Together with the Sand River, the Marite River is the most significant tributary of the Sabie River. The Sabie is one of six major river systems flowing eastwards through the Kruger National Park (KNP) to Moçambique (Figure 3.1), and has gained prominence as the only perennial system of this conservation area that has remained so throughout the last decade. The Sabie River Catchment (Figure 3.2) falls within the Incomati River basin, an international drainage basin shared by South Africa, Swaziland and Moçambique (Figure 3.1).

With a drainage of 480 km^2, the Marite sub-catchment constitutes 7% of the Sabie Catchment. Some 62 km in length to its confluence with the Sabie River, the Marite rises in the Drakensberg mountain range at an altitude of 1400 m (ASL), and flows eastwards to the Maritsane River confluence and thereafter, in a southerly direction to its confluence with the Sabie River at Hazyview at 450 m. The study area focusses on a 35 km stretch of river downstream of the Injaka Dam site (24°53'; 31°07') at the Maritsane confluence (Figure 3.2, see also Figure 4.6). The general characteristics of the Marite River Catchment are summarised, together with comparative figures for the Sabie River, in Table 3.1.

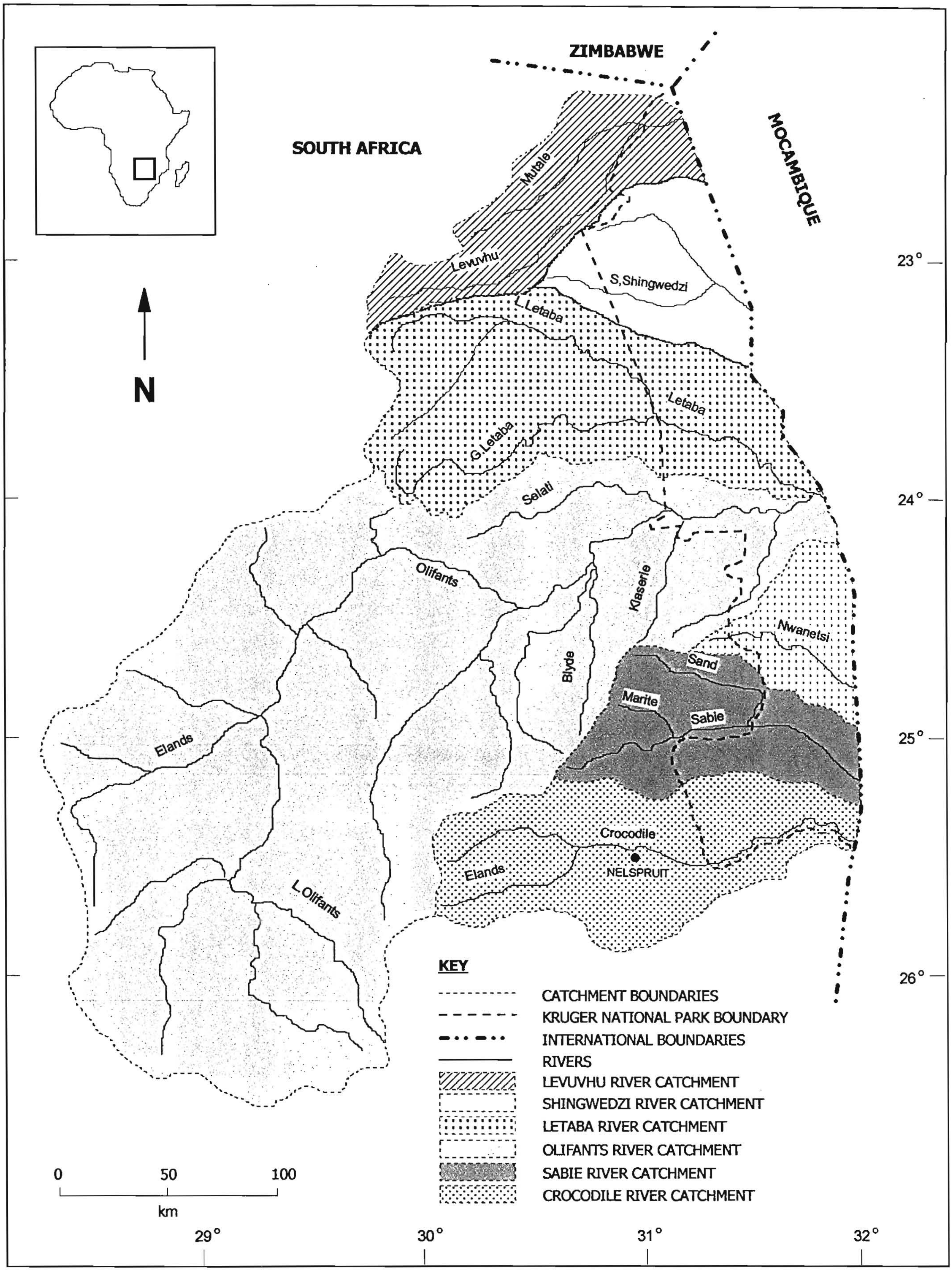


Figure 3.1 Major river systems and associated catchments of the eastern escarpment lowveld and Kruger National Park (South Africa). Note the position of the Sabie River Catchment.

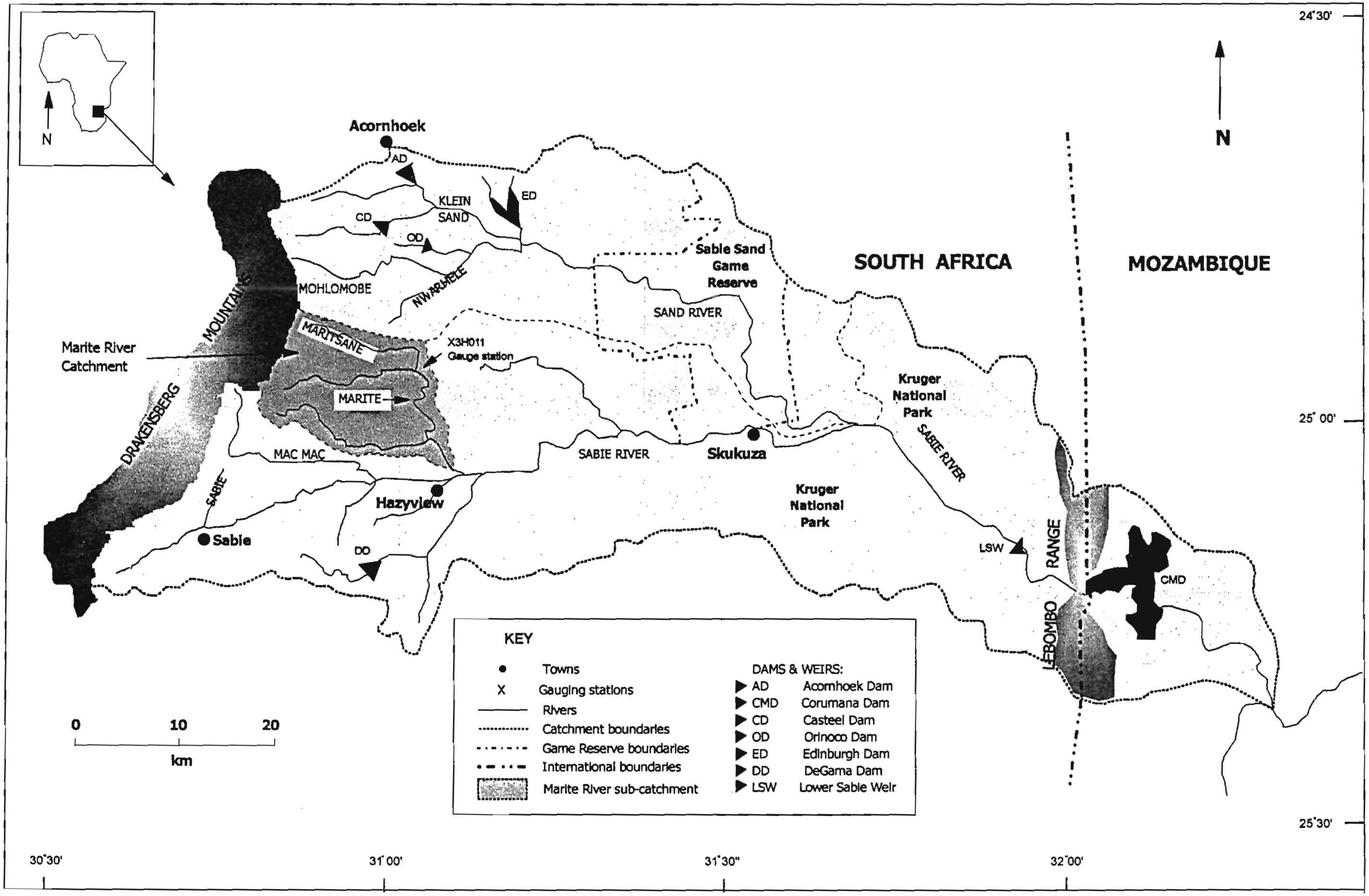


Figure 3.2 Map of the Sabie River Catchment and tributaries, indicating the Marite River sub-catchment study area.

Table 3.1

Summary of the main characteristics of the Sabie and Marite sub-catchments (after Chunnett, Fourie & Partners 1990). Values for the Marite (calculated from statistics on minor sub-catchments) comprise part of the statistics for the Sabie Catchment.

CHARACTERISTIC	SUB-CATCHMENT	
	MARITE	SABIE
GENERAL		
Total Catchment Area (km^2)	480	4472
River Length	62	230
Altitude (m. ASL)	450 - 1400	120 - 2000
Sediment Yields ($mg\ l^{-1}$)		< 1.8
Mean Annual Temperature (°C)	9 - 28	6 -34
MAP ($mm\ a^{-1}$)	1900 - 800	2000- 600
Evaporation ($mm\ a^{-1}$)	1400 - 1500	2200- 1850
WATER RESOURCES		
MAR ($Mm^3\ a^{-1}$)	153(1) / 139(2)	488
Groundwater (utilisable) ($Mm^3\ a^{-1}$)	n/a	34
RIVER ZONATION		
Mountain Source & Cliff	*	*
Waterfall Zone	*	*
Mountain Stream Zone	*	*
Foothill Sandbed Zone		
Lowveld Zone	*	*
NATURAL VEGETATION		
N.E. Mountain Sourveld	*	*
Lowveld Sour Bushveld	**	*
Lowveld		**
Arid Lowveld		*
AFFORESTATION (HA)	224	66 621
TOTAL FISH SPECIES	~20	~42

BIOPHYSICAL DESCRIPTION AT A MACRO-LEVEL

Geology and soils

The geology of the SRC comprises the Basement Complex, the Transvaal Sequence and the Karoo Sequence (Figure 3.3). The major lithostratigraphic unit underlying the study area is the Basement Complex. This consists mainly of potassic granites, granodiorite and minor intrusions of diabase and gabbro, as well as a major central intrusion of diorite (tonalite).

The most extensive soil types are shallow, sandy, nutrient-poor lithosols, except towards the base of the

---

[1] 1985 (Chunnett, Fourie & Partners 1990).

[2] 1996 (DWAF 1996).

catena(3) where deep duplex soils are common. There is little quantitative information regarding the extent of soil erosion for the region but, in comparison to other densely populated areas in South Africa it does not appear to be widespread, and is mostly localised around roads and settlements and along drainage lines (Pollard *et al.* 1998). Although sediment yields are regarded as relatively low, sedimentation of dams in the SRC has been documented (Chunnett, Fourie & Partners 1990).

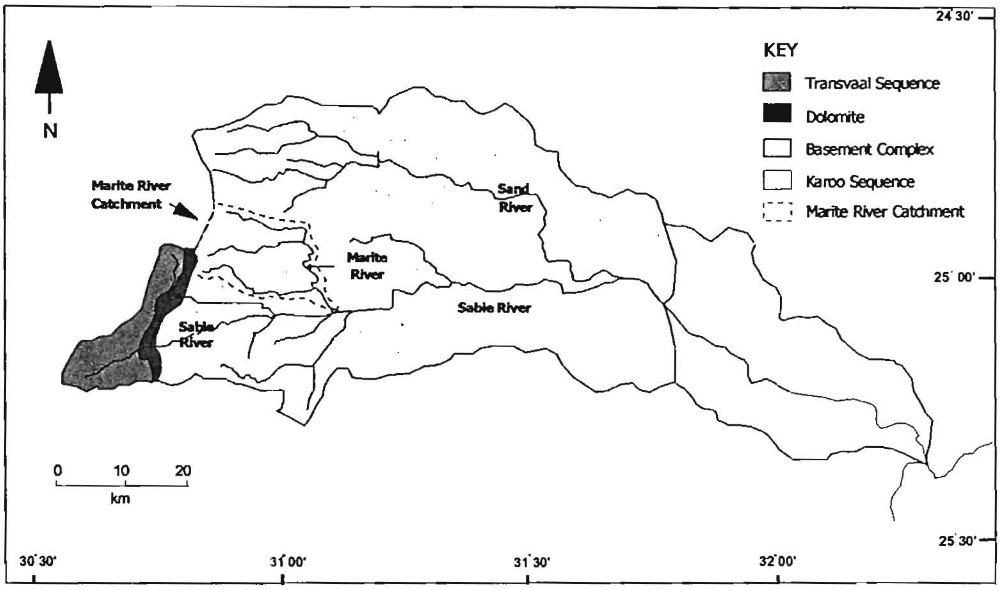


Figure 3.3 Geology of the Sabie and Marite River catchments

Climate

The Marite straddles Middleveld and Lowveld topographical and climatic regions (Chunnett, Fourie & Partners 1990), with the study area comprised primarily of the former. The climate is sub-tropical with hot, humid summers (18 °C - 28 °C in January) and mild winters (9 °C - 22 °C in July). Absolute maxima in excess of 40°C have been recorded. High summer temperatures result in high evaporation rates which are considerably in excess of rainfall (Infraplan 1989), varying from 2200 mm in the east to 1850 mm in the west (Figure 3.4).

Topography has a major influence on rainfall, and a rainfall gradient from west to east exists across the SRC. The mean annual precipitation (MAP) of the Marite Catchment varies from 1900 mm a^{-1} in the west, to 800 mm a^{-1} at its confluence with the Sabie River (Figure 3.4). The study area lies between the 800 mm and 1000 mm rainfall isohyets. Rainfall is markedly seasonal with 90% falling between October and

---

[3] A catena refers to the soil profile that typifies the lowveld where the downslope movement of clay particles and bases has resulted in shallow, sandy, nutrient poor soils on the ridgetops, whilst bottomland soils are relatively deeper, clayey and nutrient rich.

March (summer), usually in the form of thunderstorms. Rainfall is very variable from year to year and major droughts occur every 8 to 9 years (Tyson 1986). Intra-seasonal drought(4) is common. The last and the most severe drought in recorded history in the region was in 1991/1992.

Periods of higher than average rainfall were: 1934-42, 1952-60, and 1971-78, whereas 1943-51 and 1961-1970 were drier. From 1979 onwards, a dry period has prevailed, with a 38% decrease in expected annual rainfall for the Lowveld (Mason 1994). Superimposed on this shorter cycle is a longer 100 year cycle, with the last dry period extending from 1860-1970 (Pienaar 1985).

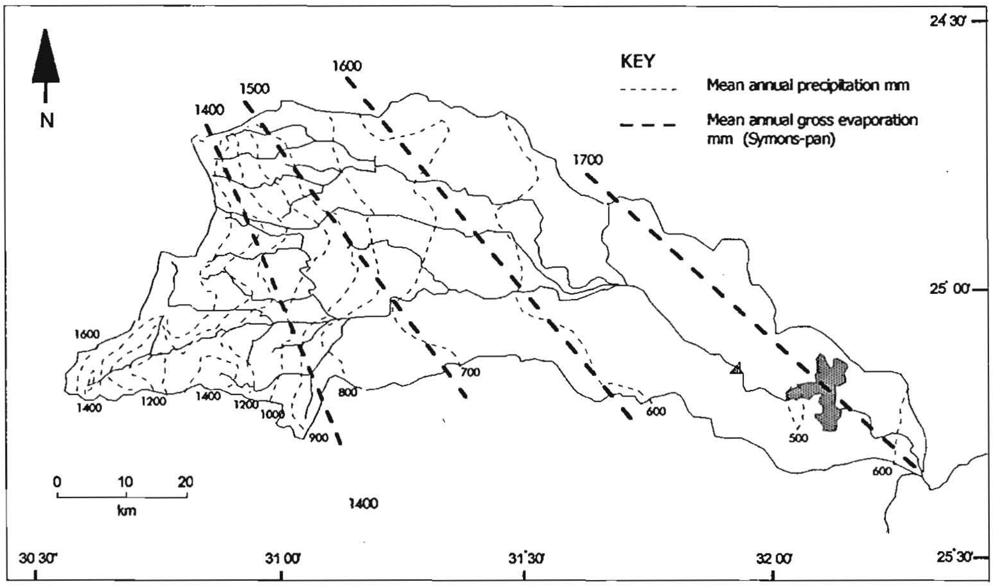


Figure 3.4 Mean annual precipitation and mean annual gross evaporation of the Sabie River Catchment

Vegetation

The study area is broadly classified as a moist forest biome, characterised by a mixture of trees, shrubs and grasses (Rutherford & Westfall 1986; Shackleton 1993). In terms of vegetational classification (Figure 3.5), the study area falls predominantly within the Lowveld Sour Bushveld (Veldtype 9), with the exception of a small portion of Northeastern Mountain Sourveld near the source (Acocks 1988).

The riparian zone of the Marite River is degraded and invaded by exotic stands of *Lantana,* pine and eucalyptus, with the exception of the headwaters and a small stretch prior to the Sabie River confluence. Little empirical data exists regarding vegetational changes in the Middleveld portion of the catchment, but certainly a reduction in woody biomass around rural communities is evident, as well as a whole scale reduction in indigenous vegetation (grassland and moist forest) due to afforestation.

---

[4] Drought is defined as a situation in which monthly or annual rainfall is less than 75 % of average rainfall (Infraplan 1989).

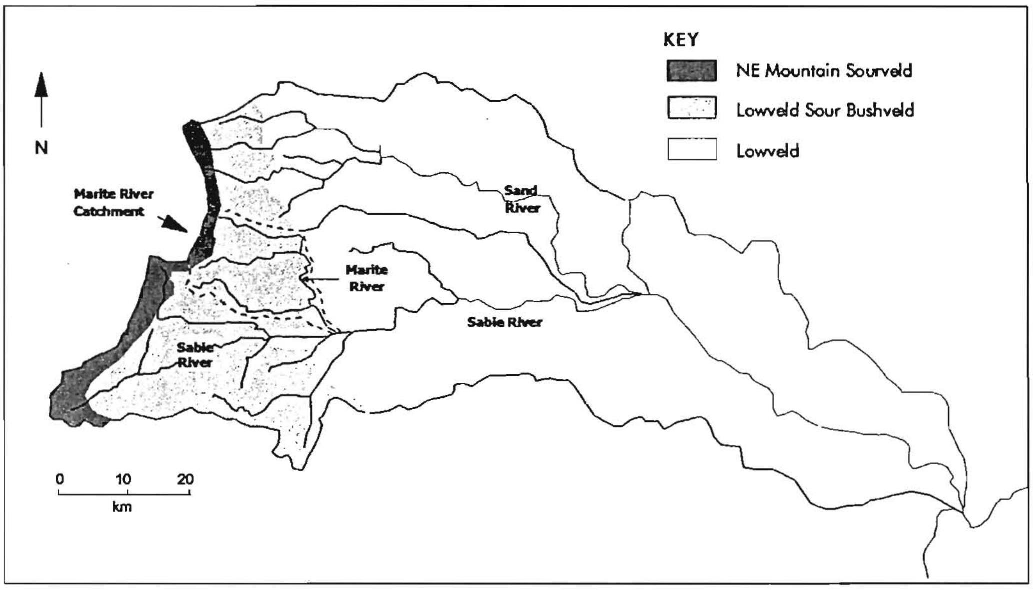


Figure 3.5 Vegetational zones of the Sabie River Catchment (after Acocks 1988). Note that most of the Marite River Catchment is under exotic afforestation.

Water Resources

With limited groundwater, surface waters comprise the greatest portion of the water resources. The Sabie and Marite rivers, and tributaries, are shown in Figure 3.2. The headwaters are situated in a humid, mountainous region of high precipitation where most of the runoff is generated, but thereafter they descend rapidly into a semi-arid region of low rainfall that generates little runoff. In the SRC, about 90% of the runoff is generated in just 28% of the catchment; consequently, the entire catchment relies heavily on the headwaters to furnish water supplies. Approximately 37% of the mid-Sabie runoff is contributed by the Marite River (Table 3.2).

The estimated virgin mean annual runoff (MAR) of 192 $Mm^3\ a^{-1}$ for the Marite sub-catchment has been reduced by afforestation, by an estimated 20%, to 153 $Mm^3\ a^{-1}$. Cyclical periods of drought and wet years are evident from the hydrograph (Figure 3.6; see discussion on climate). The hydrology, discussed in Chapter 4, reflects the rainfall seasonality that is typical of sub-tropical systems, with the highest flows occurring in summer (October to March) and low-flows in winter.

Table 3.2
Estimates of the MAR (1985), and sub-catchment contributions, of the Sabie-Sand Catchment (Chunnett, Fourie & Partners 1990). Figures for the Sabie include those of the Marite River study area.

DEVELOPMENT CONDITION	**MAR (M $m^3 a^{-1}$) per sub-catchment**			
	Marite River	**Sabie River**	**Sand River**	**Total**
Virgin	192	606	156	762
Under afforestation	153	488	145	633*
Contribution to SRC	31-37%	77%	23%	
% decrease from virgin	↓ 20%	↓ 20%	↓ 10%	↓ 17%

* Revised figures estimate the MAR after afforestation as 570 $Mm^3\ a^{-1}$ (Connigarth Consultants 1994).

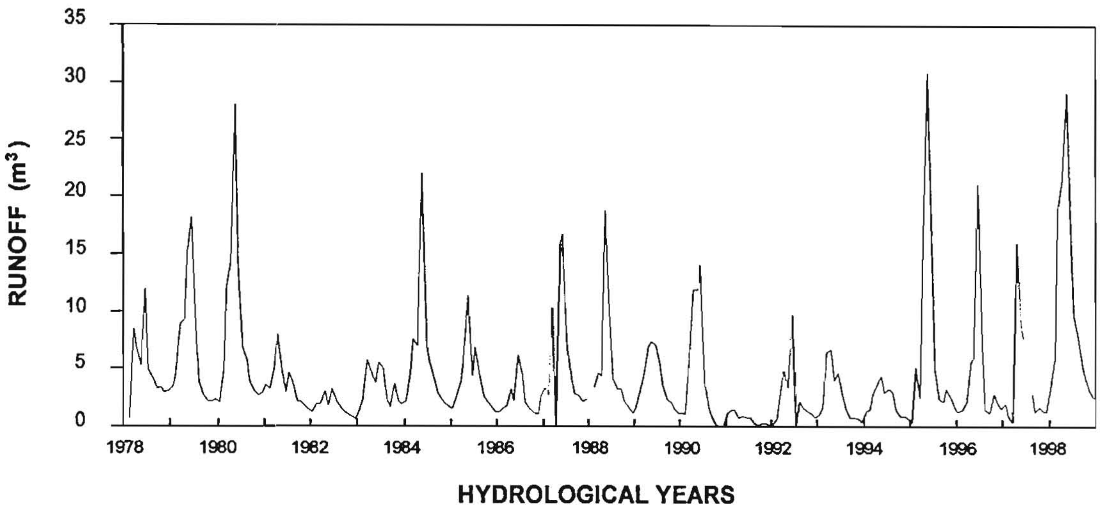


Figure 3.6 Hydrograph for the Marite River (hydrological years), based on historical flow data from November 1978 to October 1998. Gaps indicate missing data.

Aquatic biota and their conservation status

In terms of diversity, fish communities of the SRC rivers are among the most diverse in southern Africa, with 45 fish species recorded within the KNP boundaries (Pienaar 1978). The ecological value of the SRC is rated as high due to the presence of rare endemic, and non-endemic, species of flora in the upper reaches, and the presence of three fish species that are either endemic, or of uncertain status, in the lower reaches. Two fish species, *Chiloglanis anoterus* and *Varicorhinus nelspruitensis* are endemic to the escarpment regions of the Pongola and Incomati river basins. Further, *Opsaridium zambezensis* is listed as a red data species.

No specific data regarding the aquatic biota of the Marite were available at the start of this study. Data from this study and that of Weeks *et al.* (1996) documented 20 fish species (see Table 6.1). The spotted bass, *Micropterus punctatus,* is an alien species and possibly represents the first record from the eastern region of the country (Dr. P. Skelton, JLB Smith Institute, Grahamstown, *pers. comm.*). The diversity of the invertebrate community is considered to be high and some indication of community structure is given by Weeks *et al.* (1996).

O'Keeffe *et al.* (1996) proposed that the mid-Sabie and Marite rivers comprise what they have termed the Foothill Zone Assemblage of fish which are, however, distinctive for the two rivers. The assemblage of the Marite is classified as aseasonal, and dominated by the catlet *C. anoterus,* whilst that of the Sabie is seasonal, and dominated by cyclids in the early summer, and by cyprinids until the end of winter low-flows.

POPULATION AND LAND-USE

Population estimates

The population estimate in 1998 for the SRC stands at between 500 000 and 600 000 people, with a further 167 000 people outside the catchment dependent on water from the SRC (Pollard *et al.* 1998). There are an estimated 28 000 people (1998) in the Marite Catchment (Local Government Report 1998). The study area lies in the Bushbuckridge district of the SRC which, defined primarily on a historical apartheid basis, comprises the former "homeland" areas of Gazankulu and Lebowa. As a consequence of these former policies which forcibly relocated people into the area, population densities between 146 and 303 persons per km^2 are some of the highest in rural South Africa (Pollard *et al.* 1998).

Present land-use

Exotic afforestation (mainly pine and gum), together with a small amount of commercial farming, account for the highest percentage of all land-use within the Marite sub-catchment. From its source, the Marite descends through well preserved natural forest and then into extensive exotic afforestation and a small area of commercial, irrigated agriculture (tobacco and coffee) in the middle reaches. Densely populated rural areas, with some cash crop cultivation and commercial agricultural lands dominate the lower reaches.

3.3 SITUATION ANALYSIS OF THE REGIONAL WATER RESOURCES

Hydrological changes in all of the major rivers of the eastern region of South Africa have created concern for their integrity and functioning, as well as for their associated catchments. It is instructive to contextualise hydrological modifications in the Marite Catchment within the changes that have typified the region as a whole (Figure 3.1).

Of these systems, five were perennial and one, the Shingwedzi, was naturally seasonal (O'Keeffe & Davies 1991). The first deterioration was evident some 45 years ago when the perennial Letaba ceased flowing and subsequent cessations have transformed this river into an annual system. A similar situation occurred in the Levuvhu River in the 1960s and later, in the Olifants River. The Crocodile River now exhibits flow constancy as a result of regulation and both the Crocodile and Olifants have suffered heavy pollution and invasion by alien plant species (O'Keeffe & Davies 1991). The Sabie River is the least perturbed of the major rivers of the KNP and this is reflected in the small distributional changes in fish species that have occurred over the past 30 years (Russell & Rogers 1989). In comparison, a net loss of species has characterised the other KNP rivers: the Letaba, Olifants and Crocodile Rivers have lost between four and six fish species, and the Luvuvhu River has lost nine species.

Agricultural abstraction is regarded as the primary cause for the increasing demands on the water resources (O'Keeffe & Davies 1991) and, together with afforestation, has been implicated in the hydrological modifications evident today (Chunnett, Fourie & Partners 1990). This situation has been exacerbated by the past allocation inequities between the various user sectors, and has been accompanied by escalating conflict. For example, the SRC boasts the highest percentage of afforestation of any catchment in South Africa, and the reduction in stream flow caused by afforestation (Smith & Scott 1992), has led to disputes between timber growers and other downstream users during past dry cycles (Pollard *et al.* 1998). Whilst specific figures are not available for the Marite Catchment, the total demand for the SRC was estimated at 324.6 $Mm^3 a^{-1}$ in 1985, and is projected to increase to about 518.6 $Mm^3 a^{-1}$ in 2020. The highest demands are from afforestation and agriculture, which together account for 65% of the total.

As the precarious status of the regional water resources became apparent, the ecological profile of the Sabie River has increased. It is the only perennial system of the Kruger National Park that has continued to flow, albeit at diminished levels, and thus the pressure to ensure the long-term ecological integrity and sustainability of the main river, and its tributaries, is high. Furthermore, the aridity of the SRC and the frequency of drought, coupled with current and projected population densities and water demands, means that there is insufficient water to meet current needs at the required assurance levels. This situation provided a drive for further water resource developments, mainly in the form of dams, although the enthusiasm for impoundments has waned somewhat since 1994, and has been replaced by a more cohesive water-conservation approach to water resource management (see Chapter 1).

3.4 WATER RESOURCE DEVELOPMENT PLANS FOR MARITE RIVER

The flow of the Sabie, Marite and Sand Rivers have remained relatively unobstructed, with a small weir on the Sabie River and a number of small dams in the upper reaches of the Sand system (Figure 3.2). Existing storage facilities are small, totalling an estimated gross storage capacity of 29 Mm^3, of which the bulk (14 Mm^3) is provided by Da Gama Dam. The largest dam on the system is that of the Corumana Dam in Moçambique which has a gross storage capacity of 1200 Mm^3.

In view of the current and expected water shortages within the SRC, Injaka Dam was selected from eight water storage options considered by the Department of Water Affairs & Forestry (DWAF). This development also includes the construction of the Bushbuckridge Interbasin Transfer (BTP) completed in 1996, which will transfer 12 $Mm^3 a^{-1}$ from the Marite River to the Sand sub-catchment (Connigarth Consultants 1994). With a surface area of some 795ha, and storage capacity of 123 Mm^3, the Injaka Dam and the BTP will supply water to consumers in the Marite, Sand and Sabie sub-catchments (DWAF 1991). It is estimated that water will be allocated as follows: domestic and industry, 58%; irrigated agriculture, 27%; and game reserves, 15%. Construction began in late 1995 and completion is due in time to store water during the 2001 wet season.

In order to mitigate the potential flow problems associated with water resource development that are evident in the other rivers of the region, the KNP Rivers Research Programme was established in 1990 to determine ecological flow requirements for this system (see Section 1.4). With the Marite River as the site of the proposed dam, the work reported in this thesis was initiated to provide a detailed focus on this major tributary.

3.5 CONCLUDING REMARKS

The overarching characteristic of the rivers of the Sabie system is the dependence of the entire catchment on the limited, upper mountainous reaches and tributaries to furnish most of the water resources. The rivers descend rapidly into a semi-arid region with low precipitation and high evaporation rates. Consequently, a fragile balance exists between sufficient water production (quality and quantity) in the upper portion of the catchment, and the high water demands of the water-deficient remainder. Potentially, the impacts of uncontrolled development will be to undermine this balance and hence the sustainability of the system. Already, the consequences of a substantial reduction in the MAR of the Sabie and Marite are evident in the inability of the system to generate sufficient water during times of stress, such as drought. Additionally, increasing and accelerating water demands in the drier middle and lower reaches will further stress the system. It is estimated that demand will have outstripped supply in some 15 years.

Already hydrological changes are transforming the Sabie River from a relatively predictable system, to progressively less predictable one (Prof. B. Davies, Freshwater Research Unit, University of Cape Town, *pers. comm.*). Knowing this, mitigatory measures need to be addressed for the proposed Injaka Dam on the Marite River. The impoundment of rivers, whilst ameliorating water shortages, can act to exacerbate these hydrological modifications, with serious ecological implications. At the same time, ecologically-determined flow releases from the dam can contribute, partly, to safeguarding the ecological integrity of the system. The relatively pristine nature of the Sabie system, particularly when viewed against the transformations of other easterly-flowing rivers, place a particular onus on researchers to provide such information for future management.

PART III

Application of IFIM and PHABSIM

4

The Assessment of Catchment Equilibrium and Macrohabitat Conditions, and the Selection of PHABSIM II Study Sites

4.1 INTRODUCTION

One of the assumptions underlying IFIM studies is that prevailing stream conditions will be representative of those in the future. This is verified through scoping which, theoretically, is a prerequisite of any IFIM study and includes an assessment of the current and future catchment equilibrium, and macrohabitat conditions (Bovee 1982, see Figure 2.1). This step has two principal objectives: to assess the validity of continuing with an IFIM study, as well as to delimit macrohabitat zones of the river (see Chapter 2).

This chapter seeks to elaborate, and assess, the concepts of catchment equilibrium, macrohabitat and site selection through their application to the Marite River. The IFIM requires establishing both macrohabitat and microhabitat sites which may coincide (Bovee 1982). These sites are used to (a) monitor macrohabitat variables (see below) to ensure that they remain stable (Chapter 5), and (b) to determine microhabitat(1) availability, and use, by selected biota (Chapters 8 & 9).

4.2 THE CONCEPTS OF CATCHMENT EQUILIBRIUM AND MACROHABITAT CONDITIONS

Prior to a discussion of the concepts of *equilibrium* and *macrohabitat*, it should be noted that the relationship between these terms is unclear from Bovee (1982) and hence subject to different interpretations. For example, King & Tharme (1994) inferred a temporal distinction, so that channel equilibrium encompassed an appraisal of past and present conditions, whilst the macrohabitat assessment predicted the post-development conditions. In contrast, I interpreted a hierarchical relationship between them so that the condition of the catchment is expressed in the macrohabitat conditions of the river (Figure 4.1). For example, Bovee (1982, p.4) states "If a land use change has recently changed the characteristics of the watershed, these changes are reflected in the stream macrohabitat". Figure 4.1, based on my interpretation of IFIM documentation, attempts specifically to both describe these terms and their relationship to one another.

---

[1] *Microhabitat* refers to the distribution of small-scale habitats *across* the channel described by the hydraulic variables of depth, velocity, substratum and cover (see Chapter 8).

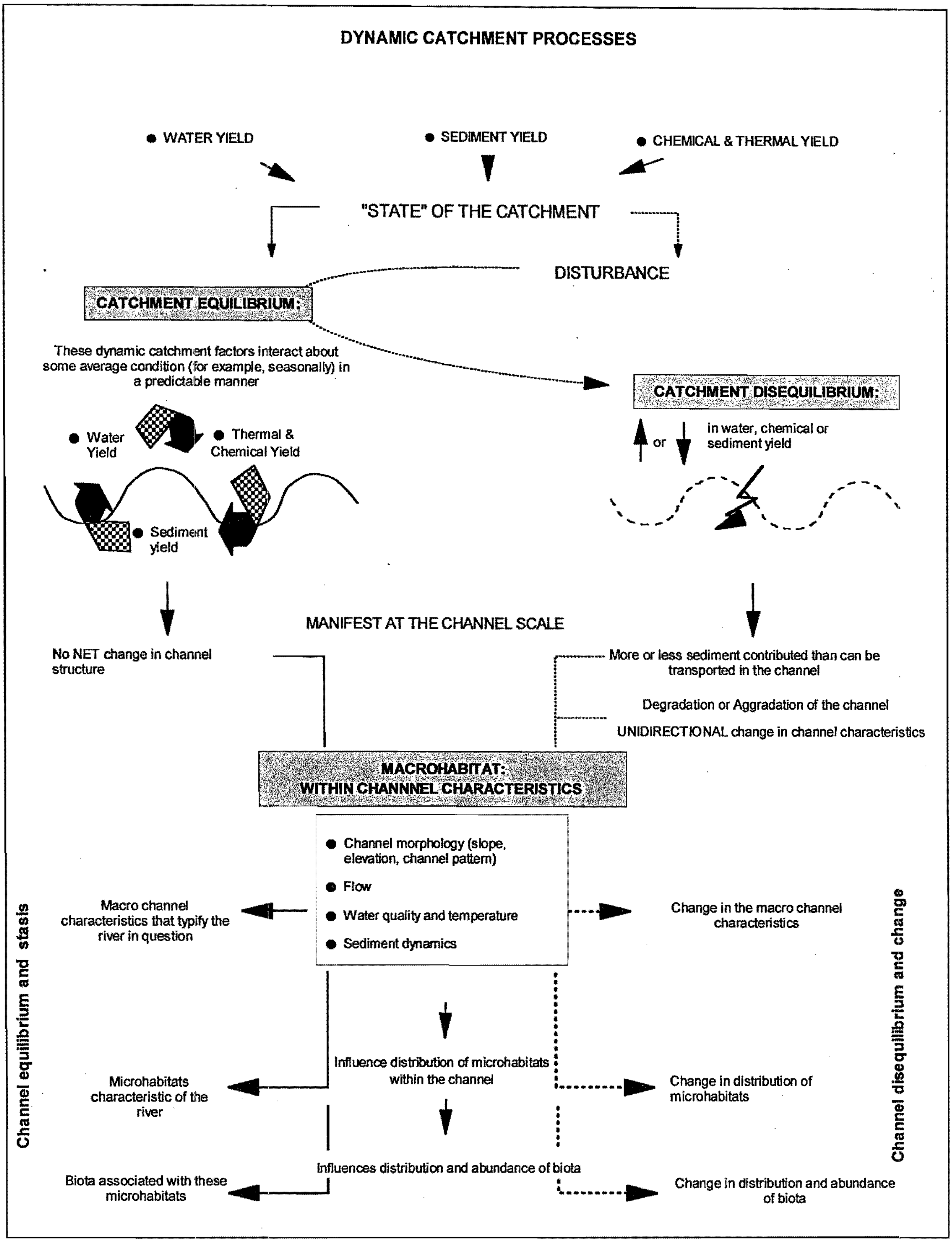


Figure 4.1 Schematic representation of catchment equilibrium and disequilibrium, and channel macrohabitat, indicating the hierarchical relationship between them (see text for details). An assessment of these parameters comprises the scoping exercise in IFIM, a critical prerequisite for continuing with the IFIM study, and for the selection of sites.

According to Bovee (1982), the overall "state" of a catchment can be described as one of *equilibrium* or *disequlibrium*. These "states" are determined by the interaction of three dynamic catchment factors: water, sediment, and chemical and thermal yields which, in turn, determine the channel morphology of a river (Figure 4.1). These factors vary as a function of rainfall and runoff, resulting in erosional and depositional patterns that typify the river. Although channel structure may change at a localised level, for example seasonally, no *net* changes over time occur. However, a new development within the catchment may precipitate conditions that contribute either more (aggradation) or less sediment (degradation or erosion) than can be transported, with unidirectional and permanent changes in channel structure. In this case, the catchment is said to be in *disequilibrium*. The term "equilibrium" appears to be synonymous with that used by Petts (1984), who coined the term "quasi-equilibrium" to describe a catchment condition in which the overall geomorphological processes are maintained.

In theory, an IFIM study should only proceed if the catchment is currently in equilibrium and the project will not permanently affect the flow/ sediment load relationship. In the case of disequilibrium, Bovee (1982) outlines three options: (1) predicting "new" equilibrium conditions and recommending remedial measures; (2) postponing the study until equilibrium is reestablished; or (3) discontinuing the study and monitoring changes.

Macrohabitat, a term coined by IFIM proponents, is used to describe *longitudinal, within-channel conditions*, defined in terms of four variables: water quality and temperature, hydrological regime, sediment dynamics and channel morphology (Bovee 1982). With the exception of the last, these variables are the same as those that define catchment equilibrium but in this case, appear to pertain to channel considerations and not to catchment- wide processes. Similar conditions of channel morphology and flow over a longitudinal section of the river, delimit a *macrohabitat zone.* Theoretically, certain macrohabitat parameters, principally temperature and water quality, govern the longitudinal distribution of species at a macro scale - the "limits of suitability" referred to by Bovee (1982 p.58). The underlying assumption is that a consistent pattern of species distribution reflects constant macrohabitat conditions.

In summary, the primary objectives of this component are:

- to evaluate whether or not the catchment is currently in equilibrium, and will remain so with the development in place.
- to evaluate macrohabitat variables, so as to (a) highlight any major longitudinal variations in macrohabitat, and hence define macrohabitat zones for site selection and which represent the limits of suitability for biota, (b) highlight which macrohabitat variables would warrant monitoring throughout the study, and (c) distinguish specific areas of the river that may be susceptible to change.

4.3 ASSESSMENT OF CATCHMENT EQUILIBRIUM AND MACROHABITAT CONDITIONS OF THE MARITE RIVER

The assessment of channel equilibrium precedes that of macrohabitat conditions, since the latter assumes a persistence in channel structure and dimension (Bovee 1982, p.22).

ASSESSMENT OF CATCHMENT EQUILIBRIUM

In order to assess catchment equilibrium, historical and current data on water, chemical and sediment yields are inspected, both to establish baseline conditions for the river, as well as to highlight any apparent trends of change. Past and present land-use patterns are likely to impact on these yields, most notably on those of sediment. Additionally, Bovee (1982) outlines certain diagnostic features at the scale of channel morphology that may indicate changes in channel structure and hence disequilibrium. The role of each macrohabitat variable in the assessment is summarised in Table 4.1

Table 4.1

Summary from Bovee (1982) of the role of each macrohabitat variable in the assessment of catchment equilibrium and macrohabitat conditions, and the broad consequences of changes in each variable.

ROLE OF VARIABLE IN THE ASSESSMENT	INSTREAM IMPACTS OF CHANGES IN MACROHABITAT VARIABLE
1. Hydrology or stream flow This acts as the integrator of the other macrohabitat variables and influences sediment loads, channel morphology, water quality and temperature. The assessment determines if: (a) changes in the flow regime will cause major changes in these and, (b) how changes would affect both the macro- and microhabitat of the species in question (Bovee 1982).	Large-scale catchment disturbance may alter the water yield by reducing resistance to overland flow and compacting the soil. Changes in the hydrology will influence both the macrohabitat variables and microhabitat distribution and abundance. Comments: Flow alterations are normally indicated by an increase in surface runoff during precipitation, and a reduction in base flow (2) during dry periods.
2. Sediment yield The shape of the channel is determined by (a) the amount of sediment reaching a stream and, (b) the ability of a stream to transport sediment.	If channel aggradation or degradation occurs, the hydraulic characteristics of a stream, and hence, the characteristics of microhabitat, will change.
3. Water chemistry The water chemistry of a stream in an undisturbed catchment generally reflects homeostasis between stream flow and non-point chemical loads, which are governed by catchment geology and land-use. Temperature is intrinsically linked to streamflow as a function of water volume, velocity and the width-depth ratio.	Theoretically, changes in these variables alter the amount of available macrohabitat, and hence the suitability for biota down the longitudinal profile of the river. Comments: Bovee (1982) refers to "developing a profile" as a means of verifying changes in the chemical or thermal loading rates, but gives no further detail. Thereafter, he suggests superimposing the tolerance of the target species to each water quality parameter, on this profile, to determine a "suitable stream length". This assumes that such tolerance data are available.

---

[2] Base flow refers to discharge that is sourced from groundwater reserves during periods of little or no precipitation.

However, the guidelines provided by Bovee (1982) are inadequate. Notably, the limits of catchment processes that would constitute a unidirectional change in catchment equilibrium are poorly defined and thus decisions regarding long-term change were made with some caution (see discussions below).

- ***Hydrology of the Marite River***

An analysis of the key characteristics of the hydrology of the Marite River included a description of wet and dry years, annual, monthly and daily flow regimes, and monthly flow exceedence values. Theoretically, it is against this information that potential future hydrological changes are assessed.

Continuous gauged data are monitored at only one point (gauge X3H011) in the upper reaches of the Marite River (24^{0}53.25' S and 31^{0}05.5' E), directly downstream of the Injaka Dam site (see Figure 3.2). This gauge provides limited historical daily flow records from 1978 to present [(3)] (see Figure 3.6) and, unless stated otherwise, these data were used for this analysis. Point measurements of discharge during the study were taken as part of the macrohabitat monitoring and are reported in Chapter 5.

Estimates of the surface water resources vary between 153 Mm^3 a^{-1} in 1985 (Chunnett, Fourie & Partners 1990) and 139 Mm^3 (DWAF 1996). Typical of a sub-tropical system, the annual flow regime of the Marite River is markedly seasonal, with summer high-flows between October and March, and winter low-flows between April and September (Figure 4.2). Approximately 20% of the total flow volume was recorded in February and 3% in both August and September (Figure 4.2a). The variation in monthly flow volumes is high in the wet months (Figure 4.2b), and most pronounced in February, varying between 1 Mm^3 (1992) to 31 Mm^3 (1996). Similarly, variations in the daily flows (Figure 4.3) are highest in February (0.2 - 16 m^3 s^{-1}) and lowest in August (0.04 - 0.9m^{3}s^{-1}). The monthly flow duration curves (Figure 4.4), indicated that 50% of the flows in February exceed 2 m^3 s^{-1} and in August, they exceed 0.07 m^3 s^{-1} .

Theoretically, IFIM requires the prediction of the altered flow regime with the water resource development in place. At the start of this thesis, discussions on the dam design, timing of the project and release schedules were still underway [(4)] and hence there was little certainty regarding the anticipated modifications to the flow regime. Moreover, there were indications that new policies governing release schedules from dams were emerging. Thus, whilst the hydrological analysis proved useful in both describing the key characteristics of the hydrology of the Marite River and later interpretations of work on habitat requirements (Chapters 8, 10 -12), it could not meet the objectives of assessing channel change satisfactorily.

---

[3] Patched and extended records for virgin and developed conditions have been derived for 1921 to 1991 by Chunnett, Fourie & Partners (1990), and from 1948 to present by the Institute for Water Research (Dr. D. Hughes, IWR, Rhodes University, *pers. comm.*). Simulation was conducted using the deterministic Pitman Hydrologic Monthly Runoff Model, both under natural (virgin) conditions and maximum expected afforestation.

[4] Instream flow requirements (IFR) for the Marite, which included data from this thesis, were derived at a workshop in August 1996 (DWAF 1998). Quantification of the "Reserve" (see Chapter 1) is still being finalised.

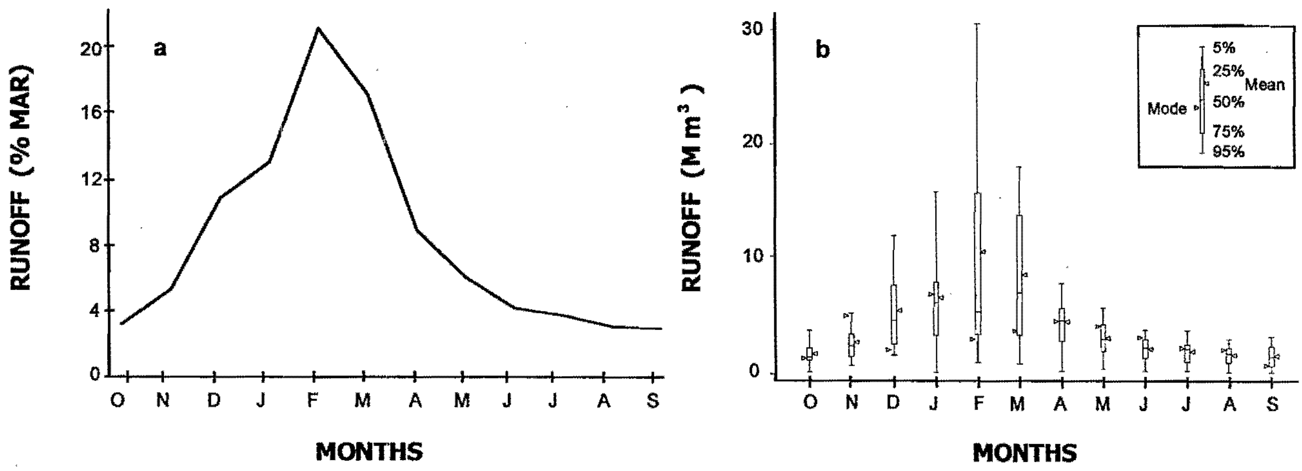


Figure 4.2 Hydrological characteristics of the Marite River, based on monthly flow volumes from 1978 to 1998, showing the seasonal nature of the system: (a) Seasonal distribution of discharge as a percentage of the MAR; (b) Comparative monthly flow volumes for all months indicating the median, mode and exceedence percentiles.

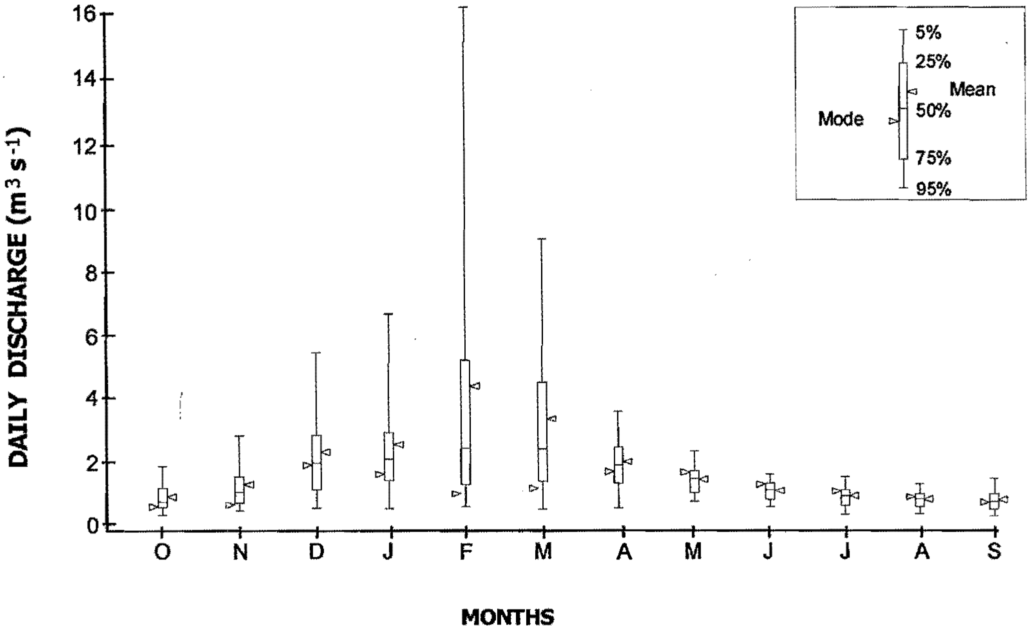


Figure 4.3 Average daily discharge data for the Marite River, indicating variations around the mean for each month. Calculated from historical flow data from 1978 to 1998. Note the high degree of variability in the wet season (November to March).

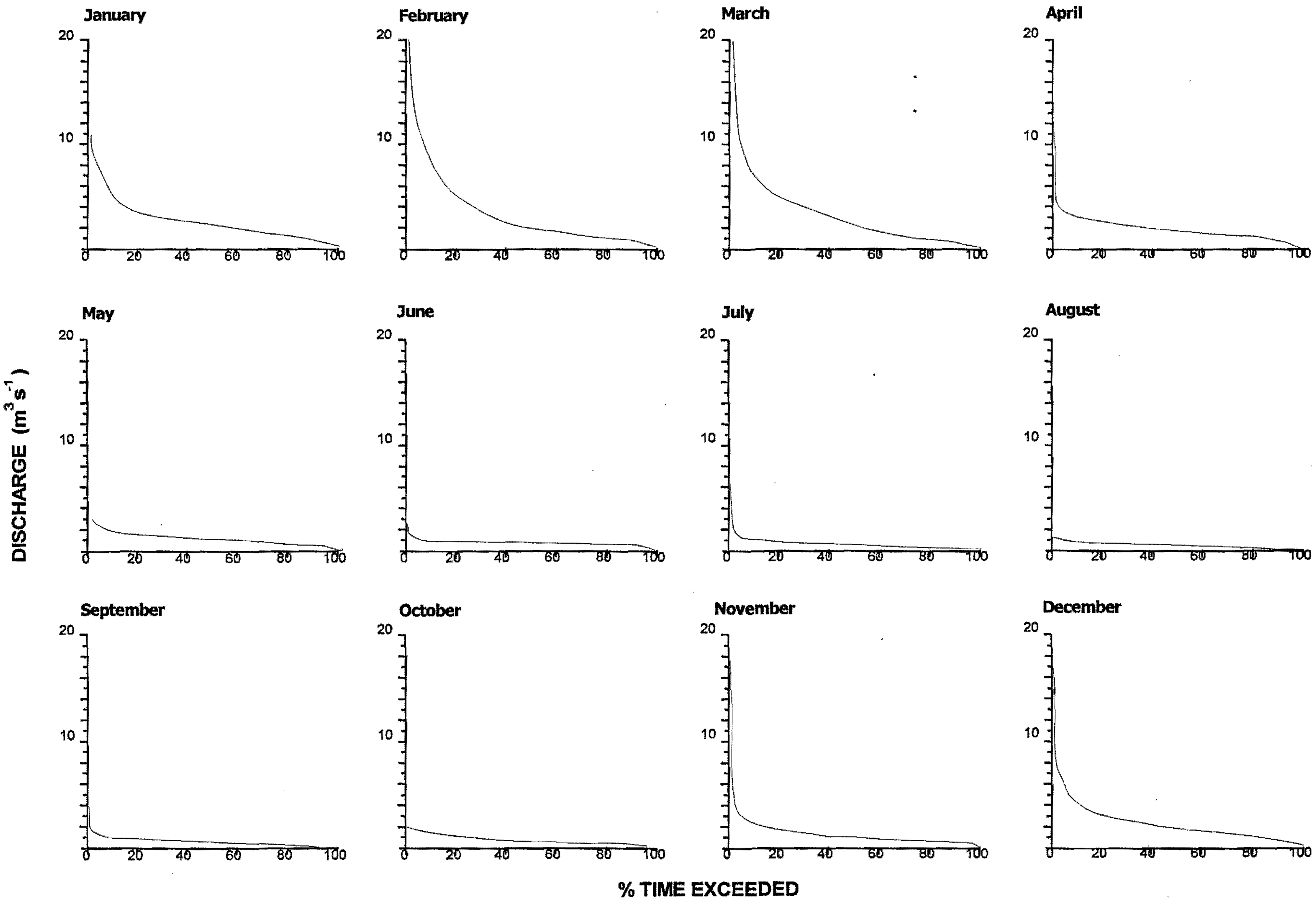


Figure 4.4 Monthly flow duration curves for the Marite River, indicating discharge versus percentage of time exceeded. Calculated from historical daily discharge data from 1978 to 1998. Note the stable base flows from April to October.

- ***Sediment yields and channel geomorphology***

A number of approaches to assessing current and future channel geomorphology are documented in King & Tharme (1994). These include bankfull discharge; hydraulic geometry equations; channel cross-section geomorphology; or an assessment of aerial photographs. The limited historical data and expertise eliminated the use of the first three approaches. Attempts to use aerial photographs and orthophotos were unsatisfactory due to the poor resolution and incomplete orthophoto coverage of the catchment. Thus, the assessment of sediment yields and geomorphology relied almost entirely on professional assistance from a hydraulics engineer, Dr. A. van Niekerk (Centre for Water in the Environment, University of the Witwatersrand, *pers. comm.*) and a fluvial geomorphologist (Prof. K. Rowntree, Department of Geography, Rhodes University, *pers. comm.*).

From the limited data on sediment yields, which is also a broad indicator of erosion potential, Chunnett, Fourie & Partners (1990) concluded that the sediment loads for the Marite sub-catchment (400t km^2 a^{-1}) are low. Neither aerial photographs nor video footage of the river suggested any recent, major changes in land-use activities. This information was coupled with an assessment of the processes that govern channel morphology. With few exceptions, the Marite River downstream of the dam site is underlain by bedrock (Dr. van Niekerk, *pers. comm.*). Such rivers are resistant to degradation but can display considerable aggradation (Bovee 1982).

Against this relatively coarse level of information, the final conclusion was that large-scale modifications of the channel structure of the Marite would be unlikely because:

- land-use activities were likely to remain the same;
- aggradation would be unlikely in view of the low sediment loads; and
- degradation would be unlikely as the bedrock-controlled systems are resistant to degradation.

It was recognised, however, that particular sections may be locally susceptible to erosion or deposition.

- ***Water Quality and temperature***

Monthly water quality readings, commencing in 1979 were recorded by DWAF at gauging station X3H011 (see Figure 3.2). The record is relatively complete with the exception of missing data between 1984 and 1986. The overall assessment is that the water quality of the Marite River is good, with no detectable pollution. However rural settlements, to which services are nonexistent, and irrigation (both limited to the final 4 km stretch of the Marite River) may act as potential sources of point and diffuse pollution. Results of a preliminary survey of the macro-invertebrate fauna of the Marite River, as recommended by Bovee (1982), corroborated the evidence of good water quality (J. Wells, *pers. comm.*).

Predictions of future water quality would require modelling approaches which were beyond the scope of this project. Again, without knowing the operational rules of the dam, little could be deduced regarding flow releases and associated impacts on the sediment loads, water quality and temperature.

However, inputs from the catchment seemed unlikely to change since no changes in land-use patterns were anticipated. Thus, it was concluded that the water quality parameters suggested that the catchment was in equilibrium and that it would remain so if suitable release schedules could be negotiated.

ASSESSMENT OF THE MACROHABITAT CONDITIONS AND ZONES WITHIN THE MARITE RIVER

Since no comparative data of macrohabitat variables between different reaches of the Marite River were available, two steps were undertaken to provide a broad description of the Marite:

1. A profile of the river (Figure 4.5) was plotted from topographical maps (1:50 000). This, together with a limited number of orthophotos (1:10 000), was used to identify significant changes in relief. The profile was used to determine the downstream distance of major tributaries from the Injaka Dam site and to calculate changes in gradient .
2. A reconnaissance survey to eight sites (Figure 4.6) of the Marite River assessed the relative (a) water quality and temperature, (b) discharge, (c) channel form and width, (d) bed particle size, (e) status of the riparian vegetation, (f) major in-channel habitat types and, (g) the fish and invertebrates, to examine major distributional differences that could be linked to macrohabitat changes. This survey was conducted during constant, low-flow conditions of winter so as to limit the effect of floods on the macrohabitat variables. Methods for collecting discharge and water quality data are reported in Chapter 5.

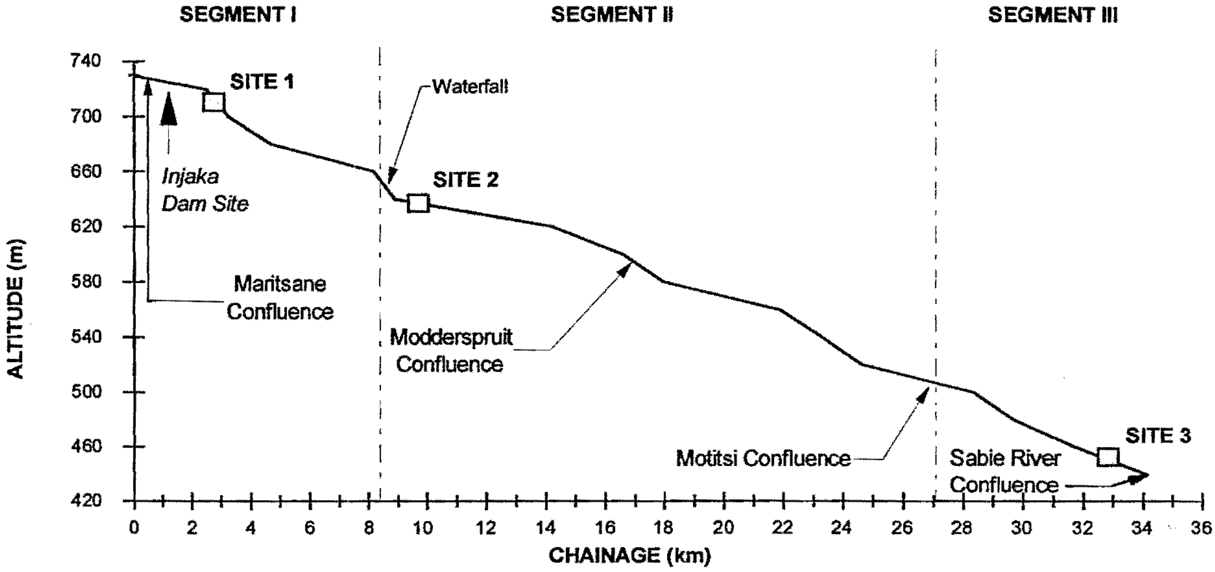


Figure 4.5 Longitudinal profile of the Marite River study area indicating segment boundaries and the locality of the IFIM macrohabitat and microhabitat study sites.

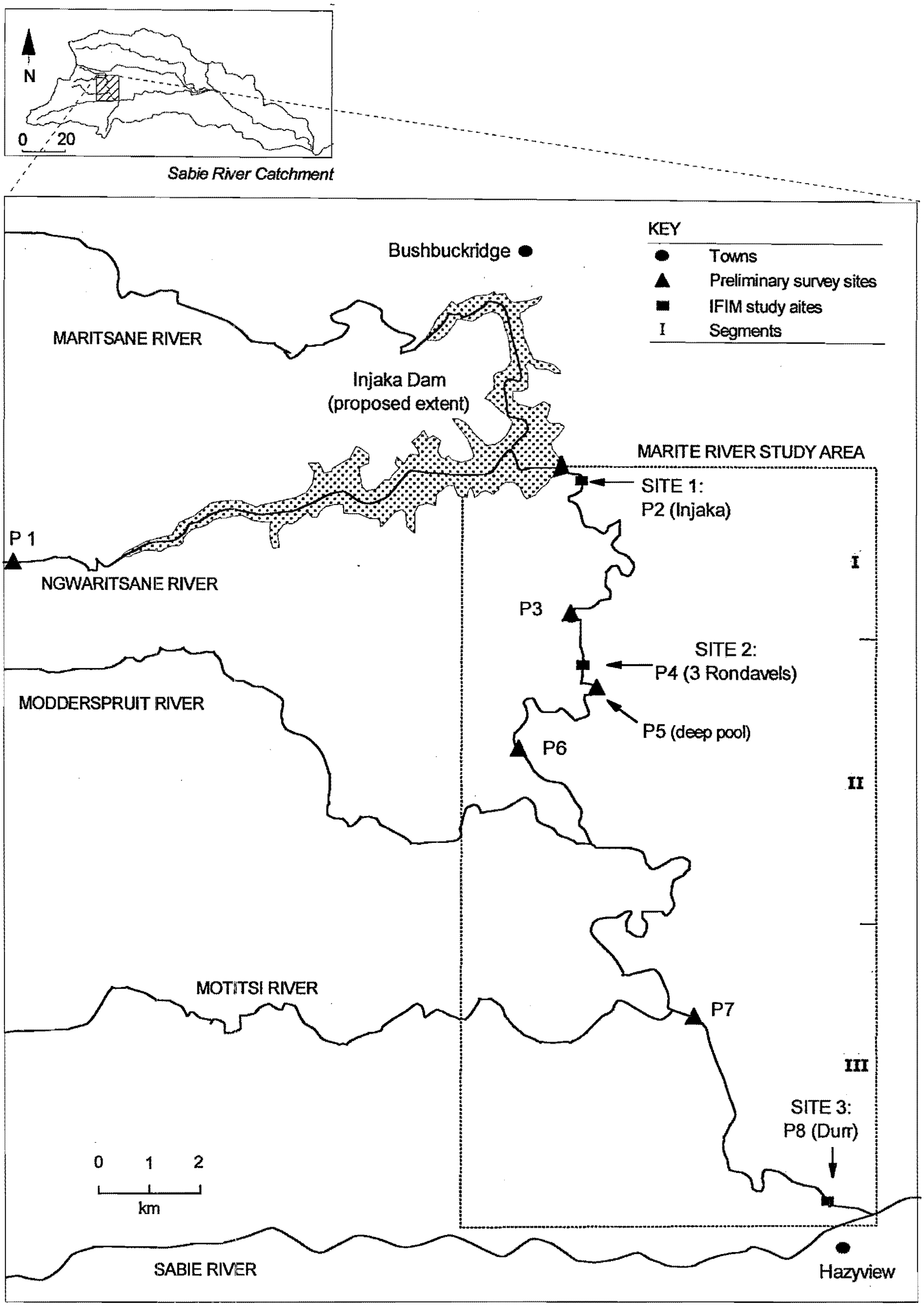


Figure 4.6 Marite River study area, indicating preliminary study sites (P1- P8), IFIM study sites, and position and extent of the proposed Injaka Dam. Segment boundaries (indicated by Roman numerals I - III) that were used in site selection, are also shown (see text for details).

Results of the preliminary survey (Table 4.2) indicated little longitudinal differences in almost all of the chemical parameters. The total suspended solids (TSS) were consistently low and likewise, temperature remained relatively stable with a small increase at the downstream site. Discharge remained stable with the exception of a 17% increase after the Motitsi River confluence (see Figure 4.6, sites P7 & P8). The three upstream sites had approximately 40% fewer fish species than the lower sites, and were characterised exclusively by coldwater species. The downstream increase in species was accounted for by the addition of warmwater species. In defining macrohabitat zones, Bovee (1982) suggests demarcating critical habitats for species (see Chapter 2, Step 4) but this was not possible due to a paucity of such information.

The flow and water quality data suggested that the study area comprised a single macrohabitat zone although the moderate increase in discharge and temperature at the downstream sites suggested the possibility of a second zone, extending into the Sabie River. This was taken into consideration in the final selection of macrohabitat sites.

Table 4.2

Summary of site specific macrohabitat variables and other data collected during the preliminary survey of the study area (see Figure 4.6). The corresponding IFIM sites are also indicated.

	PRELIMINARY SURVEY SITE							
CHARACTERISTIC	**P1**	**P2**	**P3**	**P4**	**P5**	**P6**	**P7**	**P8**
IFIM site		Site 1		Site 2				Site 3
Channel Type	Single	Multiple	Single	Single	Single	Single	Single	Multiple
Average Wetted Channel Width (m)	5	12	10	10	8	7	20	18
Gradient (m km^{-1})	4.8	26	4	4	4	4.5	5.5	8
Major Habitat Types	Shallow runs & pools	Boulder rapids, runs, pools	Pools, runs & riffles	Riffle-run	Deep pools, runs	Pools & runs	Vegetated runs	Boulder rapids, runs, pools
Dominant Bed Particle	Sand	Bedrock, boulder	Sand, bedrock	Sand, cobble	Sand	Sand, cobble	Bedrock, boulders	Bedrock, boulders
Discharge (m^3 s^{-1})	0.35	0.69	0.53	0.55	0.55	0.67	0.8	0.8
Temperature °C	12.8	13.3	14.4	15.2	15	15.3	15	15.1
TSS (g l^{-1})	0.09	0.09	0.09	0.09	0.09	0.09	0.09	0.09
PH	7.8	7.6	7.7	8	8	8.1	7.9	8
Warmwater fish species	N	N	N	?	?	Y	Y	Y
Coldwater fish species	Y	Y	Y	Y	Y	Y	?	N

Conclusions with regard to channel equilibrium and macrohabitat conditions in the Marite River

In conclusion, a decision had to be made on the basis of relatively little data and inadequate guidelines as to the validity of proceeding with IFIM, and ultimately, professional judgement provided the main guidance. The Marite sub-catchment is a relatively small area that has undergone a limited amount of land-use development. This was considered unlikely to change in a post-development scenario and hence, the chemical and sediment yields were unlikely to change. The bedrock-influenced character of the Marite suggested that at a broad scale, severe degradation would be unlikely, and low sediment loads limited the likelihood of aggradation. Therefore the catchment was considered to be in equilibrium and no major changes were anticipated in the future. Little was known about the operational rules for the dam and therefore categorical conclusions regarding flow releases, sediment loads, water quality and temperature were not possible. On the basis of the protocol for defining macrohabitat conditions, the Marite River appeared to comprise one macrohabitat zone, with a potential transitional area to a second zone evident in the lower reaches.

4.4 STUDY SITE SELECTION

THEORY AND METHODOLOGY OF STUDY SITE SELECTION

After the assessment of channel equilibrium, site selection is one of the most important steps in IFIM since data from these sites are extrapolated to the entire length of the river (see Maddock & Bird 1996). To this end, sites must be representative of certain predetermined conditions which are described by a (theoretically) rigorous approach within IFIM. All steps are taken from Bovee (1982), unless otherwise indicated. The IFIM protocol and terminology for site selection were described in Chapter 2 (Table 2.1). In summary this involves defining macrohabitat zones, segments, representative and/or critical reaches and finally, sites.

Bovee details three different strategies for study site selection (Figure 4.7), as follows:

1. Segments are delimited based on changes in both channel morphology and flow regime, and sites are chosen to represent each of these segments.
2. Segments are delimited based only on changes in flow regime, resulting in fewer segments than the first approach. Two sites are selected within the first segment to represent different reach types within one segment. Only one site is selected in the second segment and no site in the third segment, on the basis that "the channel is the same" for both segments.
3. The third strategy is essentially a simpler version of the second one, but only one site, straddling the two reaches, is used to represent the first segment.

Bovee (1982) recommends the second approach which balances the high financial costs of the first against the imprecise results of the last.

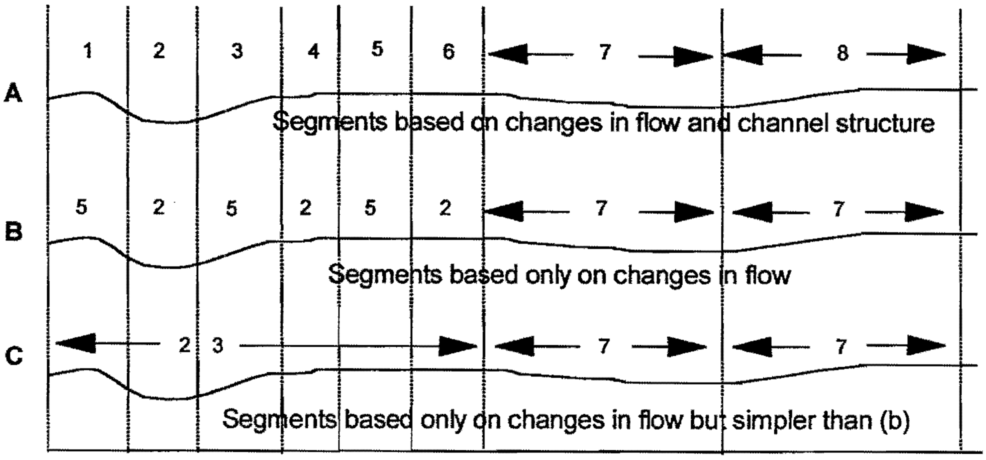


Figure 4.7 Figure provided by Bovee (1982) to illustrate three strategies (A-C) for designating river segments and selecting sites. Although unspecified, numbers presumably designate different segment types, and similar segments are denoted by the same number.

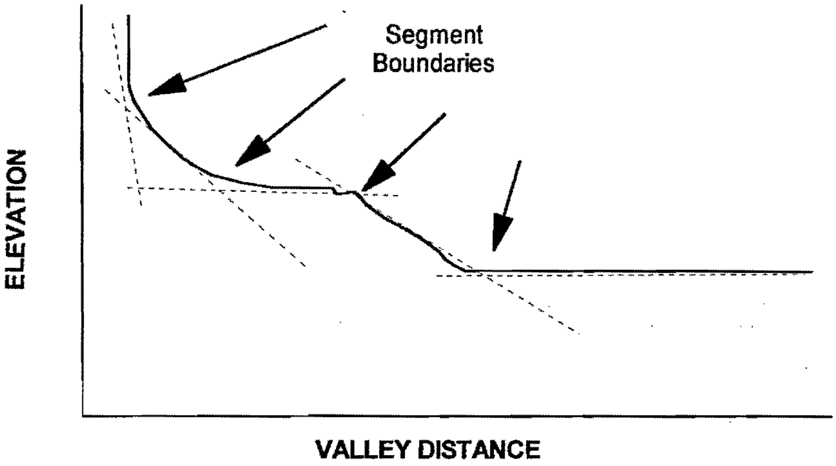


Figure 4.8 Figure provided by Bovee (1982) to illustrate how tangents are placed on the longitudinal profile of the study stream in order to demarcate segment boundaries.

Thus, demarcating segment boundaries requires data on both longitudinal flow and channel morphology. To calculate the flow regime for ungauged streams, Bovee recommends using a technique known as *the drainage area-precipitation product* to obtain an estimate of changes in the volume runoff. Since this method relies on precipitation records, which were not available for the Marite River, it could not be used. Changes in channel morphology are identified on the basis of changes in slope, calculated as the fall per unit distance (Gordon *et al.* 1992), or channel pattern (Bovee 1982). Figure 4.8 illustrates the method Bovee advances to identify changes in slope. Channel pattern refers to the planimetric form of a river (Gordon *et al.* 1992) and can be classified as straight, meandering, braided or anastomosing. These patterns are distinguished primarily on the basis of sinuosity and channel multiplicity. A sinuosity index, derived by dividing the channel thalweg distance by the down-valley distance, can be used to classify channel patterns (1 = straight river; 4 = high degree of meandering).

SITE SELECTION IN THE MARITE RIVER STUDY AREA

The study area constituted that section of river below the proposed Injaka Dam to the confluence with the Sabie River, a distance of 35 km (Figure 4.5). Many of the options provided by Bovee for demarcating segments were constrained by limited data. Determining changes in the flow based on precipitation records was a case in point. The assessment of changes in channel morphology relied mainly on identifying changes in slope so that initial segment boundaries were demarcated according to the procedure described in Figure 4.8. These were later refined using information from the preliminary survey. The alternative, which appraises changes in channel pattern, was also attempted. Although calculating thalweg distances for deriving sinuosity indices was not possible, coarse changes in sinuosity were assessed from topographical maps. The average channel width was estimated from ten width measurements, taken 200 m apart at each site, during the preliminary survey (Table 4.2).

The river was broadly divided into three segments (Figure 4.5). The boundary between segments I and II reflected a marked change in slope, with a waterfall delimiting the boundary. The gradient of Segments I, II and III was 16.2 m km^{-1}; 8.8 m km^{-1} and 9.7 m km^{-1}, respectively. The boundary between Segments II and III reflected an increase in discharge at the confluence of the Motitsi River, and an increase in channel width (i.e. channel pattern). A potential segment boundary existed at the confluence with the Modderspruit tributary but was disregarded due to its inaccessibility. The three segment boundaries were broadly confirmed by the fish distributions recorded in the preliminary survey.

Attempts to then demarcate representative reaches within segments, based on the habitat requirements of species (Bovee 1982), met with limited success due to a paucity of information. Further, the random selection of potential sites was constrained by the inaccessibility of many of the sites. Finally, it was decided that each segment would be represented by a site, and that each site should include a distribution of macro-habitat features in the proportions prescribed by Bovee (1982). Three sites (Plates 4.1 - 4.3) one from each segment, were selected from eight potential sites (three sites in both Segments I and II and two in Segment III). Their locations are shown in Figures 4.5 & 4.6, and their co-ordinates are as follows: Site 1: 24^{0}54' S, 31^{0}05' E; Site 2: 24^{0}55', S 31^{0}05' E; Site 3: 25^{0}01', S 31^{0}08' E. A description of each site, together with those used for the preliminary survey, is given in Table 4.2.

Since only one macrohabitat zone was identified (see Section 4.3), macrohabitat and microhabitat conditions were monitored at the same sites. The possibility of a second zone in the lower reaches was accounted for by locating a study site in this zone.

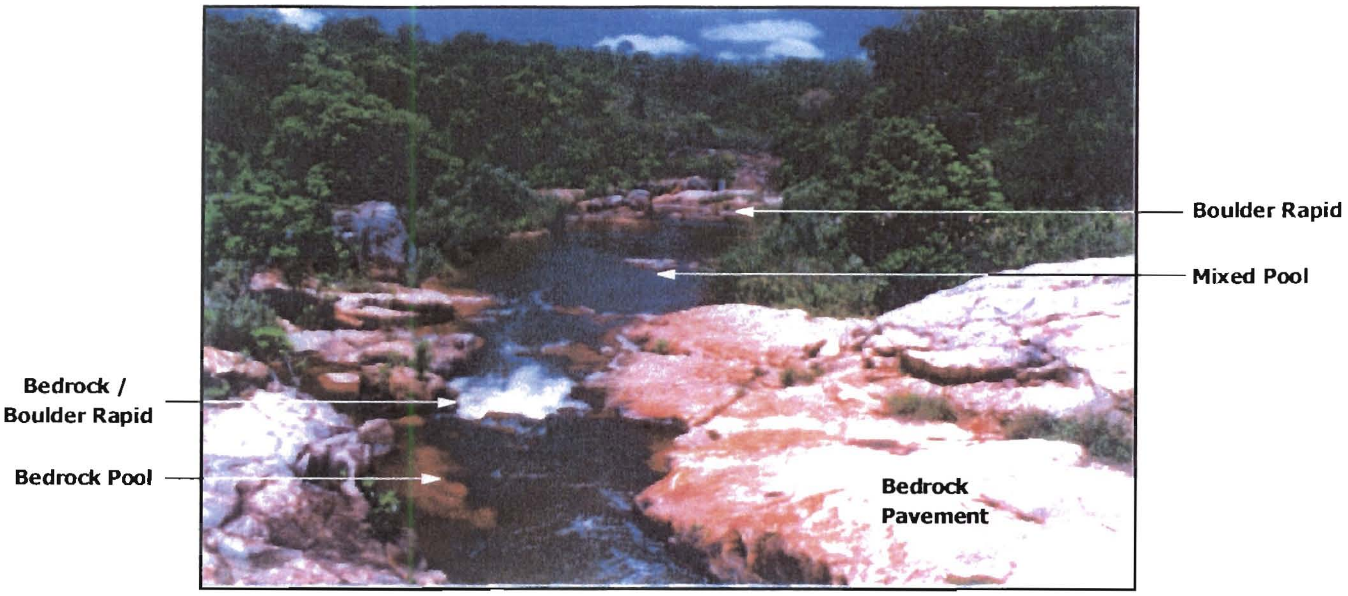


Plate 4.1 Downstream section of Site 1 on the Marite River. This corresponds to a Mixed Pool Rapid (MPR) channel type, described in Chapter 10. The bedrock-dominated river channel is evident, and the key geomorphic features are indicated (see Table 10.2).

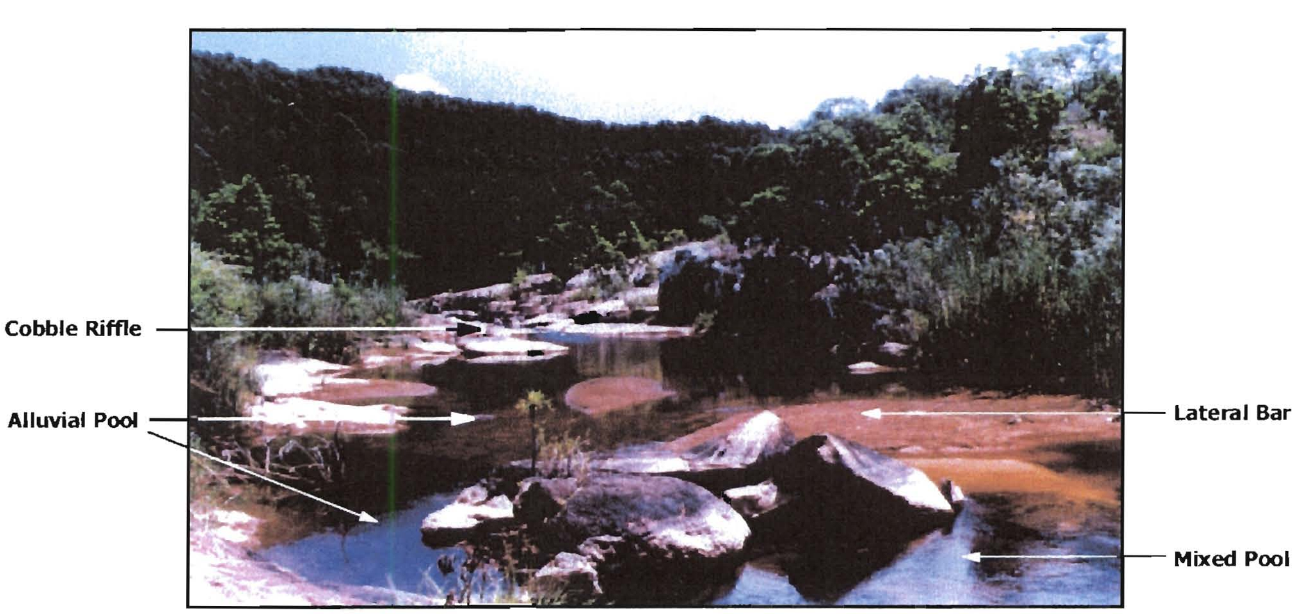


Plate 4.2. Upstream section at Site 2 on the Marite River. This view corresponds to a Mixed Single Thread (MST) channel, described in Chapter 10. The key geomorphic features are also indicated (see Table 10.2).

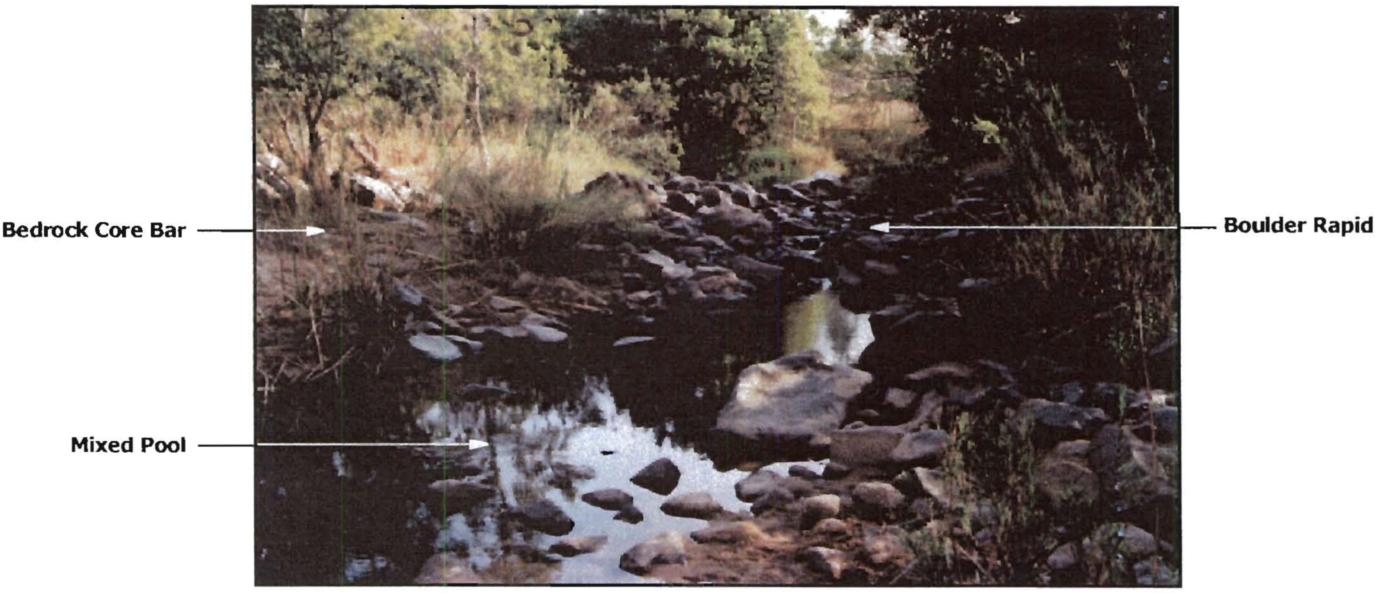


Plate 4.3 a. Downstream section at Site 3 on the Marite River. This view corresponds to a Mixed Pool Rapid (MPR) channel, described in Chapter 10. The key geomorphic features are also indicated. This photograph was taken at the height of the drought at a discharge of 0.04 $m^3 s^{-1}$.

Plate 4.3 b. Upstream section at Site 3 on the Marite River. This view corresponds to a Mixed Anastomosing (MAN) channel, described in Chapter 10. The key geomorphic features are also indicated.

4.5 DISCUSSION

Scoping

As suggested by King & Tharme (1994), the scoping exercise probably represents the single most disjunct procedure within IFIM. In general, it appears to be disregarded by most researchers, or is not reported, and hence has remained largely untested. Consequently, it has not benefited from the iterative refinements that some of the other aspects of the IFIM methodology have undergone.

Two of the most serious drawbacks are the guidelines and definitions, which are unclear and difficult to synthesise. Despite their importance in the exercise, the terms *catchment equilibrium* and *macrohabitat*, and their relationship, are confusing. Further, although one is required to evaluate if catchment conditions will change permanently, the limits that constitute unidirectional change are too vague. Consequently, judgements in this thesis had to be made largely on subjectively designated bounds. This issue warrants particular attention since the effects of impoundments and changes in channel morphology are well documented (see Section 1.3). The construction of a dam is likely to have effects on the flow/sediment load relationships and thus to affect channel morphology (at least for some distance downstream and depending on the channel types and position of tributaries) which would render the IFR inaccurate. Moreover, many instream flow assessments are likely to be made in rivers undergoing catchment change due to land-use change or longer term climatic events (Prof. A. Arthrington, University of Brisbane, *pers. comm.*). The advice in the case of disequilibrium (see p. 57) is less than useful given the realities of time, and the informational dearth that is common to many IFR studies. In the case of the Marite River, potential changes associated with a modified flow regime may be relatively subtle, but whether or not these changes would constitute a state of disequilibrium, was difficult to evaluate.

Further, the logistical and financial costs of including this component can be high and little consideration is given to situations in which data are limited. For example, documenting the flow regime at a number of sites is generally beyond the bounds of all but the best-equipped studies. Moreover, this relies on adequate rainfall or gauge records, which are frequently unavailable. One is also required to "determine the flow regime with the project" (Bovee 1982, p.10), but since the aim of IFIM is to achieve this very step, this seems somewhat circuitous and premature. Likewise, using macrohabitat to define the "limits of suitability" for a species presupposes that these limits are known, although this is often not the case.

With so few studies undertaking this step, it appears that the validity of continuing with IFIM has not even been considered in most cases. A number of reasons for this may exist. Possibly, the fact that IFIM is currently the only legally defensible method that is recognised in the USA for assessing instream flow allocations, seems to provide the ultimate ratification. Technically, IFIM can proceed without scoping and, potentially, this legal endorsement has resulted in the "expendable" (and costly) aspects of IFIM being disregarded. With almost no peer review it appears that there is little onus on the researcher to undertake, or test, a step that is largely overlooked in any event. Lastly, if a catchment is deemed to be in disequilibrium, the alternatives suggested by Bovee (1982) may reflect little practical applicability. Consequently, unlike other aspects of IFIM, the assessment of channel equilibrium and macrohabitat has remained as an unchallenged, theoretical addendum to the overall process. Only recently has the issue site representivity and extrapolation of site-specific results to the study area been confronted (Maddock & Bird 1996; Maddock 1999).

Assessment of the IFIM approach to site selection

Site selection proved to be almost equally as onerous as the assessment of channel equilibrium and macrohabitat. The rationale behind some of the guidelines appear circuitous and requires explanation, as do some of the definitions used and issues of scale.

As a point of departure, the guidelines given in Bovee (1982) for identifying segment boundaries are ambiguous (see Table 2.1 and Figures 4.7; 4.8). It is argued that the logic, or at least the presentation, is flawed in that the diagrams contradict one another, and the text. Since an inordinate amount of time was spent in trying to define segment boundaries, the problems encountered are described below.

Consider Bovee's description of techniques for designating river segments in Figures 4.7 and 4.8. Theoretically, a segment comprises a series of similar reaches (i.e. similar microhabitat characteristics). Figure 4.7 suggests that these segments consist of a series of *non-contiguous* reach types (say type 2) located at different points down the river. Figure 4.8, on the other hand, appears to contradict this since segments are presented as single, *continuous* sections of the river. This suggests that each segment is made up of a single reach-type that is never repeated downstream. Sites would be chosen differently depending on which approach one adopted. Ultimately, since neither approach appears to reflect the patterns in channel morphology that exist in reality, these guidelines are regarded as unsatisfactory (see Chapter 10).

Ambiguities in scale were also encountered in site selection. For example, Bovee (1982) states that reach lengths should be 10-14 times the channel width in order to include a full cycle of the geomorphic features, but later states that a reach should include 10% of the length of the river. In the Marite River this would constitute distances of between 120 and 220 m in the former case, and 3500 m in the latter case; differences that are clearly difficult to resolve. This also implies that there can only be a maximum of ten reaches in any river. Resolving the relationship between macrohabitat zones and segments was equally problematic. The literature suggested a hierarchical link between them, with segments making up a macrohabitat zone, and yet this was inconsistent. Bovee states that macrohabitat zones have similar water quality and temperature conditions (see Table 2.1), whilst elsewhere he states that segments comprise different flow and channel morphologies but "not necessarily different water quality and channel morphology". Quite what this represents in reality, and at what scale, is obscure since a segment might then straddle two macrohabitat zones.

Many of the concepts in the manuals are poorly defined and loosely applied. Bovee groups reaches on the basis that they exhibit "similar microhabitat characteristics", and also refers to reaches with "poor microhabitat", but fails to detail what these are. Furthermore, the use of terms such as "poor microhabitat" implies that this is a ubiquitous condition that can be objectively defined.

In the selection of sites, Bovee (1982) assumes a detailed knowledge of the microhabitat requirements of the target species and recommends selecting sites that include the entire range of conditions that a species might occupy. However, this counters any attempt to select sites objectively (i.e. irrespective of whether or not they represent the habitat used by a specific species). Like many of the procedures in IFIM, this probably reflects the inherent bias towards the management of a single fishery, or sport, species that often motivates IFIM studies.

Notwithstanding these problems, the rationale behind the hierarchical approach to site selection is to provide a basis for including the full range of habitats (or geomorphic features), that characterise northwestern US streams. Retrospectively, it was recognised that these geomorphic features differ from those found in rivers in southern Africa (see Chapter 10). In fact, much of the preceding discussion highlights the importance of a classification system for rivers that explicitly defines the spatial relationship between various features at different scales. This is an area, in my opinion, that is inadequately treated in the IFIM methodology and hence forms much of the basis of the proposed alternative approach (the Geomorphological-Biotope Assessment) described in Chapters 10 to 12.

In summary, the only criteria used for site selection with any degree of success was that of coarse data on changes in slope, discharge, water quality and temperature down the river course, a broad understanding of land-use, and geological and erosion data. A preliminary survey was needed to collect most of these data.

4.6 CONCLUSION

The compound effect of these difficulties has resulted in a scoping exercise that is confusing and time consuming to reconcile and implement, and seldom reported. Certainly, in this study, it was addressed with limited success. Probably one of the most indicting judgments of this component was made by one of the authors of PHABSIM II who concluded that the assessment of catchment equilibrium and macrohabitat has been rudimentary or non-existent to date, and consequently many studies do not provide a defensible base from which to continue with the IFIM initiative (R.T Milhous, US Fish & Wildlife Service, *pers. comm.*).

Equally, site selection represents a critical step in an IFIM application in that conditions at a site are considered representative of a predetermined section of the river and hence results are extrapolated to the entire study area. However, the many problems associated with this step render it difficult to implement, and hence the representivity of sites is questionable. Within IFIM, both the assessment of catchment equilibrium and macrohabitat conditions, as a precursor to site selection, require considerable overhauling and refinement.

5

Monitoring Macrohabitat Conditions and the Collection of Hydraulic Calibration Data

5.1 INTRODUCTION

The concept of macrohabitat, described primarily by the variables of water quality and temperature, was detailed in Chapter 4 (see Section 4.2). These variables are used both for the macrohabitat assessment which describes the prevailing conditions at the start of the study, as well as to delimit macrohabitat zones within which the macrohabitat conditions are monitored. The availability of physical microhabitat available at a site is described by the hydraulic variables of depth, velocity, substratum and cover, and their quantification at known discharges comprises the *hydraulic calibration data* for input to PHABSIM II (see Figure 2.1). The hydraulic calibration data, together with that of microhabitat use (Chapter 8), are then used by PHABSIM II to compute total available habitat, as a function of discharge for a particular species (Bovee 1982; see Chapters 2; 9).

This chapter describes the macrohabitat conditions of the Marite River over the period that the IFIM research was conducted and describes the collection of hydraulic calibration data. The use of the latter information, and outputs of the calibration routine, are given in Chapter 9. This chapter concludes with an assessment of these steps of IFIM.

The later part of the macrohabitat monitoring covered a protracted drought which was considered to be the most severe in recorded history in the region (Pollard *et al.* 1996). Although beyond the scope of a standard IFIM study, this provided the opportunity to document the physical and chemical characteristics of extremely low-flows, which are conditions that may be associated with impoundments (see Chapter 1). This in turn allowed for an assessment of the potential effects of protracted periods of extremely low-flows on the habitat of the indicator species.

5.2 MONITORING MACROHABITAT CONDITIONS OF THE MARITE RIVER

SAMPLING REGIME

Both the macrohabitat and microhabitat data were collected at the three selected study sites described in Chapter 4 (see Figure 4.6), namely Injaka (Site 1), 3 Rondavels (Site 2) and Durr (Site 3). The data were collected on a tri-monthly basis, with the exception of two additional field trips in July 1991, and September 1992, which were focussed, respectively, on the juvenile lifestage of the indicator species, *Chiloglanis anoterus* (see Chapter 6), and on drought conditions (Table 5.1). Note that only two sites were visited in March 1992 due to theft of equipment at the third site.

Table 5.1

Sampling regime, sites sampled (see Figure 4.6), and the purpose of each field trip. MH= collection of macrohabitat data; MAU= collection of microhabitat availability and use data. WSE = Water Surface Elevation (see text for details). This does not include additional monthly trips to collect information on reproductive condition (see Chapter 7).

DATE	FIELD TRIP TYPE	OBJECTIVE	SITES SAMPLED
Aug. 1990	Preliminary survey	• MH • General survey of fish & invertebrates	8
Nov. 1990	Standard	• Establishment of transects • MH & MAU	1,2,3
Feb. 1991	Standard	• MH & MAU	1,2,3
April 1991	Calibration data	• WSE & velocity calibration	1,2,3
June 1991	Standard	• MH & MAU	1,2,3
July 1991	Target early juvenile microhabitat use	• MH & MAU	1,2,3
Aug. 1991	Calibration data	• Hydraulic calibration data	1,2,3
Sep. 1991	Standard	• MH & MAU	1,2,3
Nov. 1991	Calibration data	• WSE & velocity calibration	1,2,3
Dec. 1991	Standard	• MH & MAU	1,2,3
Feb. 1992	Standard	• MH & MAU	1,2
Sep. 1992	Calibration data Drought Survey	• WSE & velocity calibration • MH & MAU	1,2,3

COLLECTION AND ANALYSIS OF DISCHARGE, TEMPERATURE AND WATER QUALITY DATA

Discharge data were derived from a continuous gauge at Injaka dam site (Site 1), and from spot flows measured at the "discharge" transects at each site, on each sampling occasion (see Section 5.3). Discharge (Q) is determined by the summation of measured flows in each "cell" (see Figure 5.5) along a transect. Flow in each cell is the product of cell width (w), cell depth (d) and mean cell velocity (v), expressed by the following formula (Bovee & Milhous 1978):

$$Q= (w) \times (d) \times (v) \qquad \text{Equation 5.1}$$

Cell-width(w) is the sum of half the lateral distance along the transect from each vertical point to the adjacent cell. Cell-depth(d) is the depth at each transect interval, measured to the nearest cm. Mean cell-velocity (v) was determined at six-tenths of the distance from the water surface to the bottom (theoretically the depth of mean velocity), for depths less than 75 cm. For depths greater than 75 cm, the mean of three velocity measurements taken, at "two-tenths, sixth-tenths and eight-tenths" depth was used (Bovee 1982). In the case of edge cells, the mean depth of three verticals (0 depth, depth of reading and adjacent cell depth) is derived, as is mean velocity. For edge cells, cell-width is taken as the width of the edge cell, plus half the distance of the adjacent cell.

Temperature and water quality were measured at each site on eight occasions. Water quality variables included dissolved oxygen, conductivity, pH, turbidity, total suspended solids (TSS), total dissolved solids (TDS), and nutrients. All readings were taken close to the water surface unless stated otherwise.

Water temperature was measured using an Aqua-lytic Oxi 921 oxygen meter, calibrated against atmospheric pressure. Minimum-maximum temperatures were recorded using submerged thermometers at each site over 24 hours. Dissolved oxygen readings (expressed as percent saturation and mg l^{-1}) were taken at dawn in order to measure oxygen at its lowest level, as recommended by Dallas & Day (1993). Conductivity (at 25°C) was measured using a DiST 3 ATC dissolved solids tester with a range of 100 to 19900 µS, and pH using a pHep pH meter. Turbidity was determined using the Analite 150 Mk 2 nephelometer with a range of 10 - 20 000 NTU, pre-zeroed in distilled water. Total suspended solids were determined by the weight difference after passing a known volume of water through a pre-combusted (450°C, 5h), tared Whatman GF/F filter and drying at 60°C for a minimum of three hours. The organic fraction was determined after further combustion (450°C). Total dissolved solids (TDS) were calculated using conductivity values x 6.6 (Dallas & Day 1993).

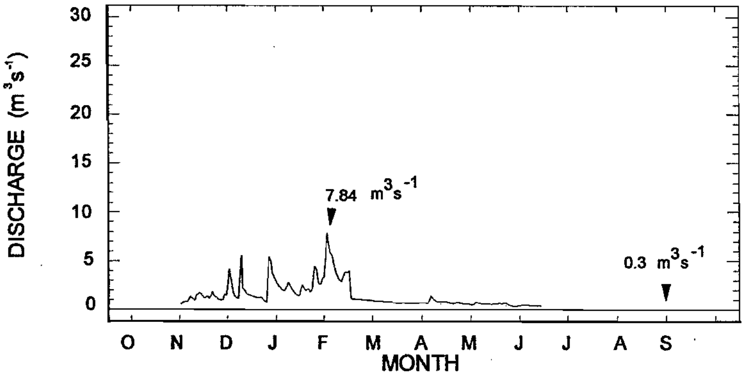
Water for chemical analysis of nutrients was collected, filtered through Whatman GF/F filters (450 µm) and preserved, on site, using a 1% solution of mercuric chloride. These samples were analysed for nitrite, nitrate, soluble reactive phosphate (SRP) and ammonia using standard auto-analytical techniques by the Hydrological Research Institute, Pretoria. Unfortunately, although samples were collected at every trip, only samples from two trips were analysed.

GENERAL MACROHABITAT CONDITIONS OF THE MARITE RIVER THROUGHOUT THE STUDY

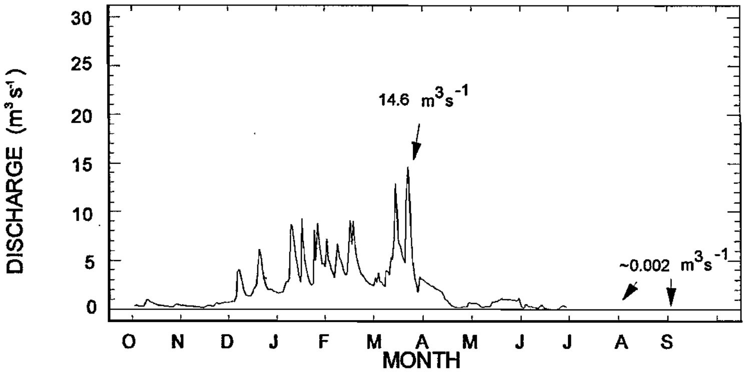
The seasonal nature of the system is evident in the relatively constant, base-flows during the dry season (April to September), and in the progressive increase in discharge with the onset of the rainy season in October, continuing through to March (summer), and peaking in February (Figure 5.1, see also Section 4.3). Summer flows are pulsed and delivered in the form of freshes and floods. The lowest flows were evident between October 1991 and September 1992 at the height of the drought. No discharge records were available for the periods November 1991 to March 1992, and May 1992 to August 1992, as the gauging weir was inoperative. However flow in the Marite River never ceased (Figure 5.1), although flows in the Sabie-Sand rivers dropped to previously undocumented levels. That of the Marite decreased to 0.02 m^3s^{-1} in October 1992, compared to a previous all-time low of 0.16 $m^3 s^{-1}$ (October 1983 and November 1990).

Site-specific discharge measurements indicated a progressive increase in discharge downstream (Figure 5.2), due to increasing runoff and additional input from the Motitsi tributary. The increase in flow between sites 1 and 2, and sites 2 and 3, were approximately 12% and 38% respectively, with a higher variation noted in the wet season. Agricultural abstractions probably account for instances when discharges at Site 3 were lower than those of Site 2.

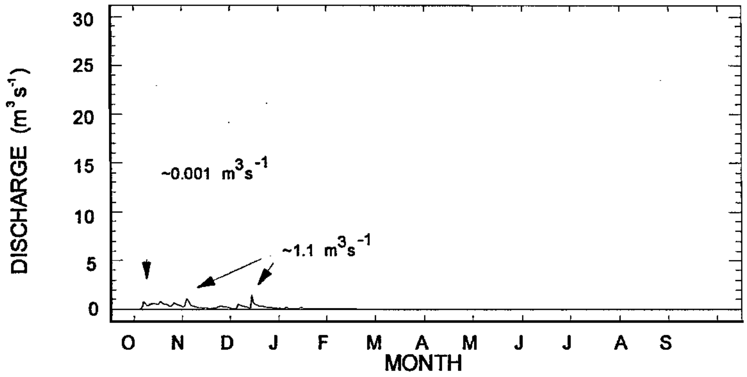
A. OCTOBER 1989- SEPTEMBER 1990



B. OCTOBER 1990- SEPTEMBER 1991



C. OCTOBER 1991- SEPTEMBER 1992



D. OCTOBER 1992 - APRIL 1993

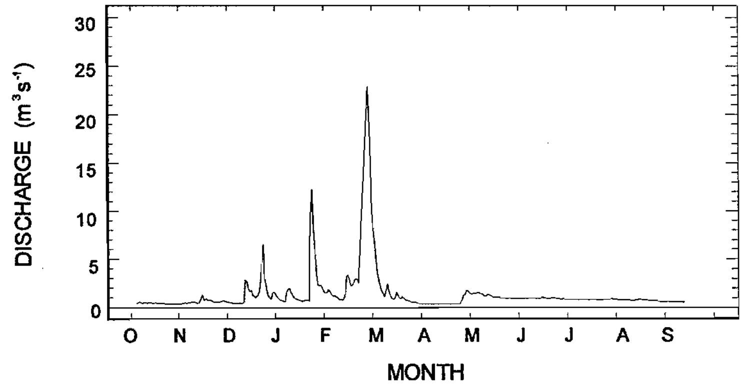


Figure 5.1. Hydrographs for the Marite River covering the IFIM study. Figures are based on daily discharge figures from gauge station X3h011, (see Figure 3.2) for the study period (data for 1989 and 1993 are included for comparison). Missing data points reflect periods during which the gauging station was inoperative and not points of zero flow. Figures indicate spot discharge readings.

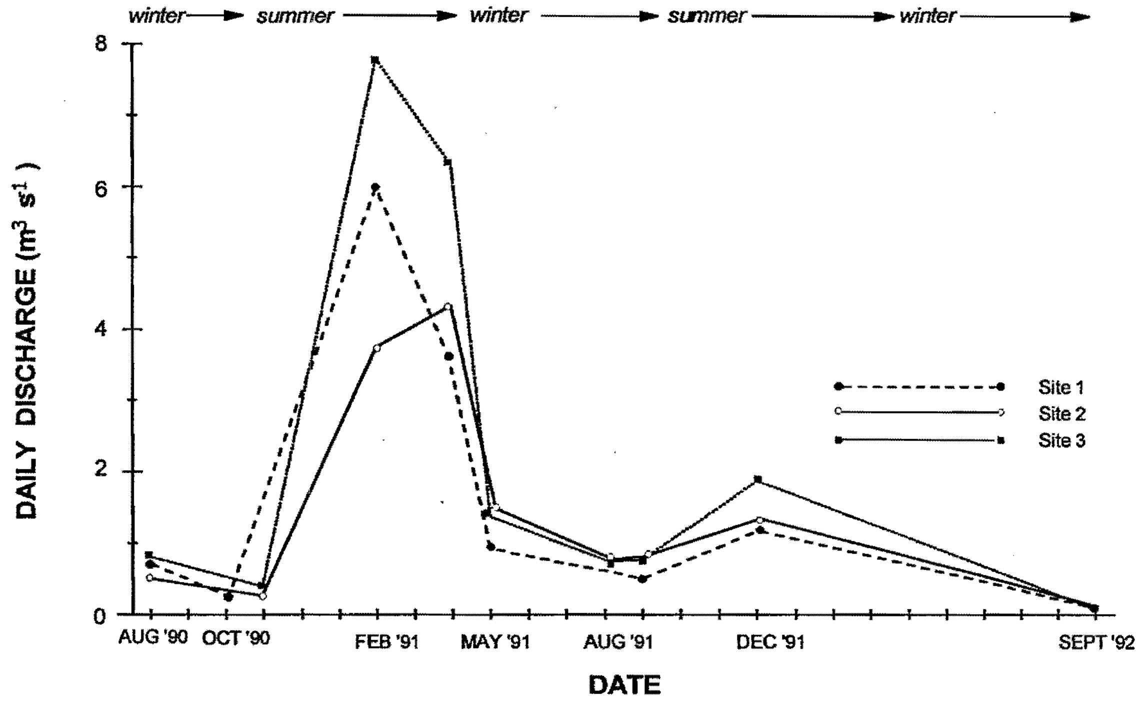


Figure 5.2 Spot discharge measurements at all sites on the Marite River over the IFIM study period.

Detailed results of water quality variables are provided in Figures 5.3 and 5.4, and Table 5.2. Relative median temperatures were consistently highest at Site 3 (Figure 5.3 a, b). The widest temperature range was recorded at Site 1 (10°C - 30.5°C) and the narrowest at Site 3 (15°C - 30°C). Temperatures during the drought were elevated in comparison to those of the preceding year.

The river was generally well oxygenated (Figure 5.3 c, d), but concentrations decreased during the drought (Figure 5.3.c), particularly at Site 1 where levels declined to 78%. This reflects the compound effects of extremely low flows, which were most pronounced at this site, and high ambient temperatures, which decrease oxygen solubility (Dallas & Day 1993).

In general pH readings indicated a neutral or slightly alkaline environment, varying between 6.8 and 8.1 (Figure 5.3 e, f). The pH and increased slightly with downstream distance (Figure 5.3 f). Conductivity values were low, ranging from 3 to 7 m Sm^{-1}, but consistently highest at Site 3 (Figure 5.3 g,h). Values increased with the progression of the drought (Figure 5.3 g).

Turbidity was low, varying between 2 NTU cm^{-1} in dry months, and 35 NTU cm^{-1} in wet months (Figure

5.4 a, b). The highest value was recorded at Site 2 (Figure 5.4 b), probably due to the alluvial nature of this site. The decrease in discharge during the drought was accompanied by a reduction in turbidity. The total suspended solids (TSS) were low, varying between 0.002 and 0.076 g l^{-1} (Figure 5.4 c,d). The highest values occurred at Site 2, again reflecting the alluvial nature of this site. Concentrations were highest during the wet season but were lower during the drought. Unfortunately results of the composition of inorganics are incomplete but these were low during periods of low TSS values (~1%).

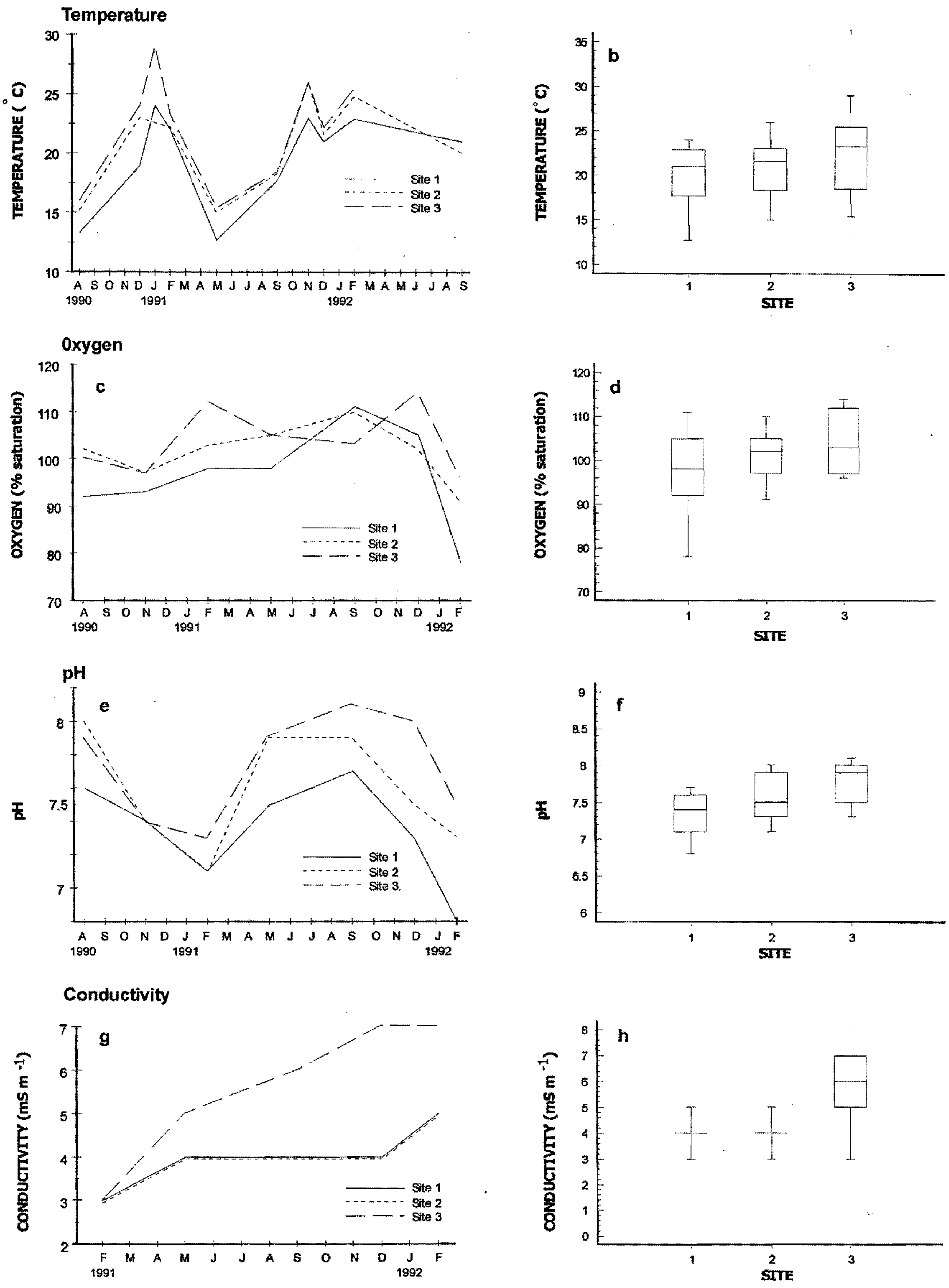
Total dissolved solids (TDS) were low, ranging between 20 and 46 mg l^{-1} (Figure 5.4 e, f), but consistently higher at Site 3, probably due to increased human activity (Dallas & Day 1993). The TDS increased as the drought progressed (Figure 5.4 a), although values still fell well below the global figure of 100 mg l^{-1} for most rivers and lakes (Dallas & Day 1993).

Limited data for nutrient concentrations (winter and summer) indicated little longitudinal variation (Table 5.2). Low concentrations of ammonium, nitrate and nitrite characterised all sites in both September and December. Likewise, levels of soluble reactive phosphorus, PO_4^{3-} were low and decreased after the rains.

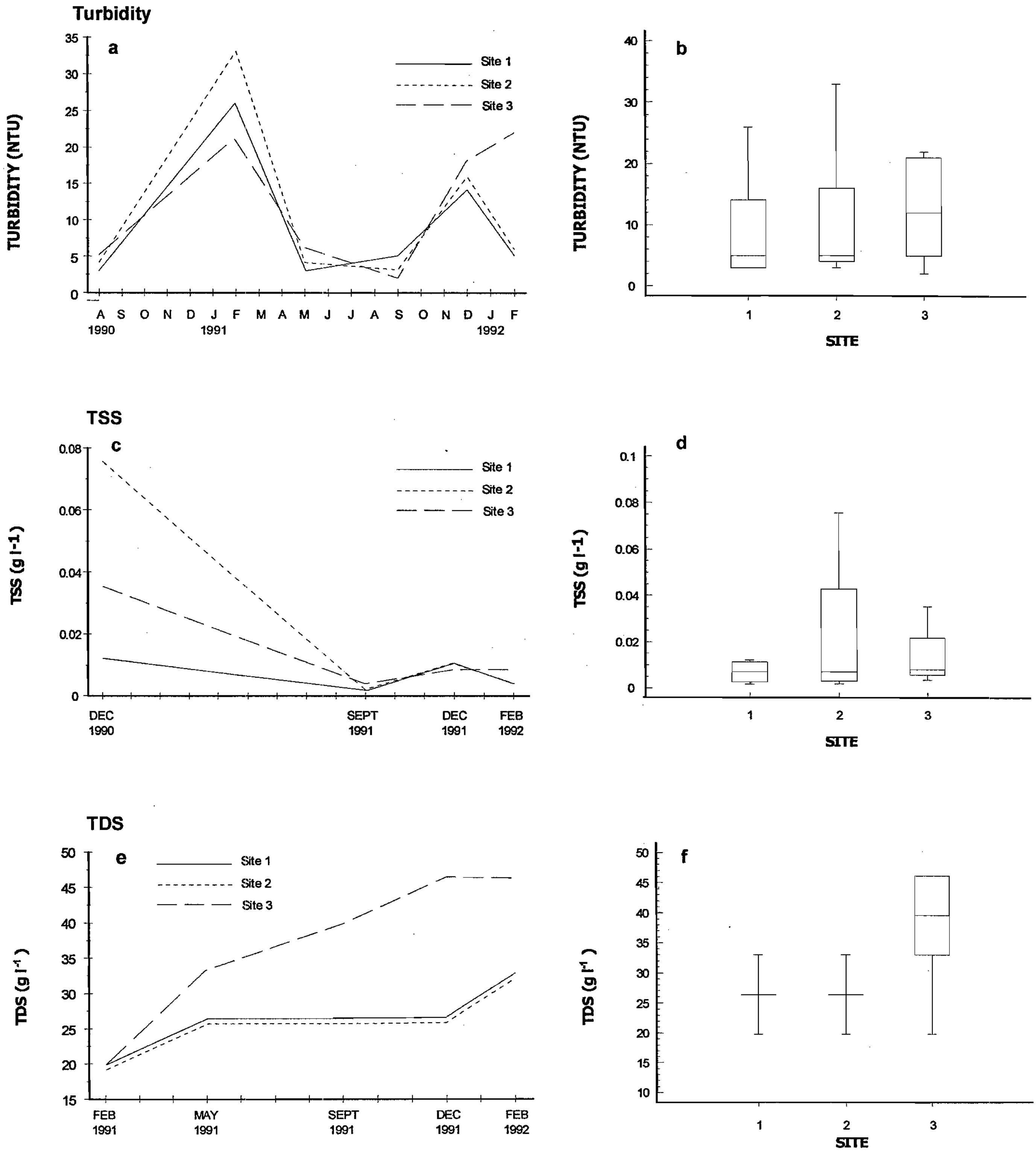
The water quality data were compared to those provided by DWAF for the Sabie-Sand Catchment (van Veelen & Swart 1992). Two management objective limits, the NOEL (No Observed Effect Level) and the MLA (Maximum Level of Acceptability), described by the authors, were used to see if any of the above values might be considered extreme. In most cases these limits were never exceeded, with the exception of temperature and turbidity. Summer values for both temperatures and turbidity almost continuously approached, or exceeded, the MLA of 25°C, and the NOEL of 16 NTU respectively. A number of factors could explain this. One possibility may be the reduction in flow by afforestation, leading to increased water temperatures. Alternatively, as noted by Van Veelen and Swart, the limited database may not reflect the full range of water quality conditions normally found in the river and may need to be re-evaluated.

Table 5.2
Nutrient concentrations at all sites for two months.

		NUTRIENTS (mg l^{-1})			
DATE	**SITE**	NH_4^-	NO_2^-	NO_3^-	PO_4^{3-}
Sep. 1991	1	0.04	0.04	0.04	0.023
	2	0.04	0.04	0.04	0.021
	3	0.04	0.04	0.04	0.012
Dec. 1991	1	0.06	0.04	0.04	0.006
	2	0.04	0.04	0.04	0.006
	3	0.04	0.04	0.04	0.008



Figures 5.3 Seasonal trends of four water quality variables at each site over the study period (left-hand column), and median values of each variable over all sampling trips (right-hand column). Box denotes inter-quartile range, horizontal line in box denotes median value and whiskers denote the range.



Figures 5.4 Seasonal trends of three water quality variables at each site over the study period (left-hand column), and median values of each variable over all sampling trips (right-hand column). Box denotes inter-quartile range, horizontal line in box denotes median value and whiskers denote the range.

5.3 THE MEASUREMENT OF HYDRAULIC CHARACTERISTICS: DEFINING MICROHABITAT AVAILABILITY

The PHABSIM approach to describing microhabitat availability was described in Chapter 2 (Step 6). In essence, deriving the hydraulic calibration data that are required by PHABSIM, is conceived on the basis of transects, which are used to describe the site. The hydraulic conditions that are measured at points along each transect are assigned to cells that extend between transects. Conceptually then, the river is viewed as a mosaic of cells between transects (Figure 5.5).

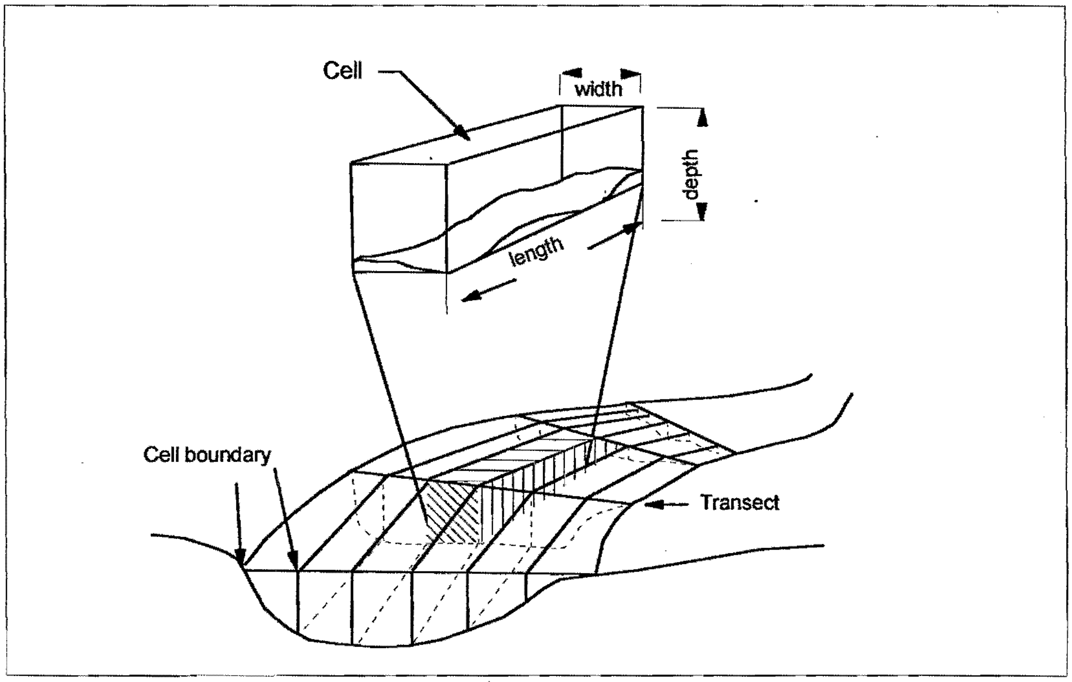


Figure 5.5 PHABSIM II conceptualisation of a stream reach described by transects. The hydraulic parameters of water depth, water velocity and substratum are measured at each transect subdivision and values of these variables are assigned to the area of each cell (after Shirvell 1986).

Transect placement serves two purposes:

- *Hydraulic simulation transects* are placed at, and parallel to, all of the *hydraulic controls* within the study sites. A *hydraulic control* is some physical feature of the bank, or streambed, that determines the stage-discharge relationship upstream (see Figure 2.5), such as the head of a riffle which causes water to back up behind it. The downstream transect must be placed at a hydraulic control in order for most hydraulic models to be run.
- *Habitat characterisation transects* are placed through the centre of a discrete habitat type, such as a pool or a riffle, so as to characterise that feature.

Transects provide a suite of information for use by PHABSIM II, including (1) distances between transects, (2) headstake elevations, (3) water surface elevation, (4) river profile, (5) discharge, and (6) hydraulic information (microhabitat) for each cell (Bovee & Milhous 1978 and see Chapter 2, Step 6).

Microhabitat variables are measured at intervals, or verticals, along each transect which delimit the lateral boundaries of so-called "cells" (Figure 5.5). Each cell is considered to have a unique combination of depth, velocity, substratum and cover which are assumed to remain unchanged for a specified distance up and downstream to the next transect. This distance, determined by the researcher is known as the "reach weighting". Jointly referred to as channel index (CI), substratum and cover characteristics are assumed fixed for each cell and are generally described at the initial field trip only.

COLLECTION AND ANALYSIS OF HYDRAULIC DATA FOR THE MARITE RIVER

The collection of hydraulic data involved two main activities (Table 5.1), namely: (1) site preparation and hydraulic characterisation, and (2) calibration trips to collect additional data on water surface elevations (WSE) and velocity distributions.

Site preparation involved establishing hydraulic and habitat transects in early 1991 at all three sites. These were later verified by a hydraulics engineer (Dr. A. van Niekerk, Centre for Water in the Environment, University of Witwatersrand, *pers. comm.*), and a number of transects were modified or added. Each transect was photographed and fixed-point photographs were taken of the "discharge transect" (see below) on each sampling occasion. Transect ends were identified either by numbered permanent metal headpins (headstakes) driven into each stream bank or were marked with paint. A scale map of each study reach was prepared and compass bearings, or pin-to-pin distances, were recorded so that headstakes could be relocated.

Ten transects were surveyed at Site 1 (Figure 5.6 A), seven at Site 2 (Figure 5.6 B) and eight at Site 3 (Figure 5.6 C). The lengths of the study sites were as follows: Site 1, 302.8 m; Site 2, 396.5 m and Site 3, 309.12 m. Transect identifiers, types and locations of transects, distances between transects and reach weighting are provided in Figure 5.6. The characteristics of each site are detailed in Table 5.3 (note subsequent geomorphological description of sites reported in Chapter 11).

Differential levelling was used to determine the cross-sectional channel (streambed) profile along each transect. Levelling was carried out at Site 1 in June 1991, and at Sites 2 & 3 in August 1991. Measuring tapes were set up along each transect and zeroed over the headstake. Distances were determined from the tape and confirmed by stadia readings. The intervals along each transect were governed by the occurrence of obvious discontinuities in substratum composition or channel shape, or alternatively taken at between 0.5 - 1.5 m intervals. Where possible, the points were equally spaced so that cells were approximately the same size (Bovee 1982). These points were used for the collection of hydraulic data.

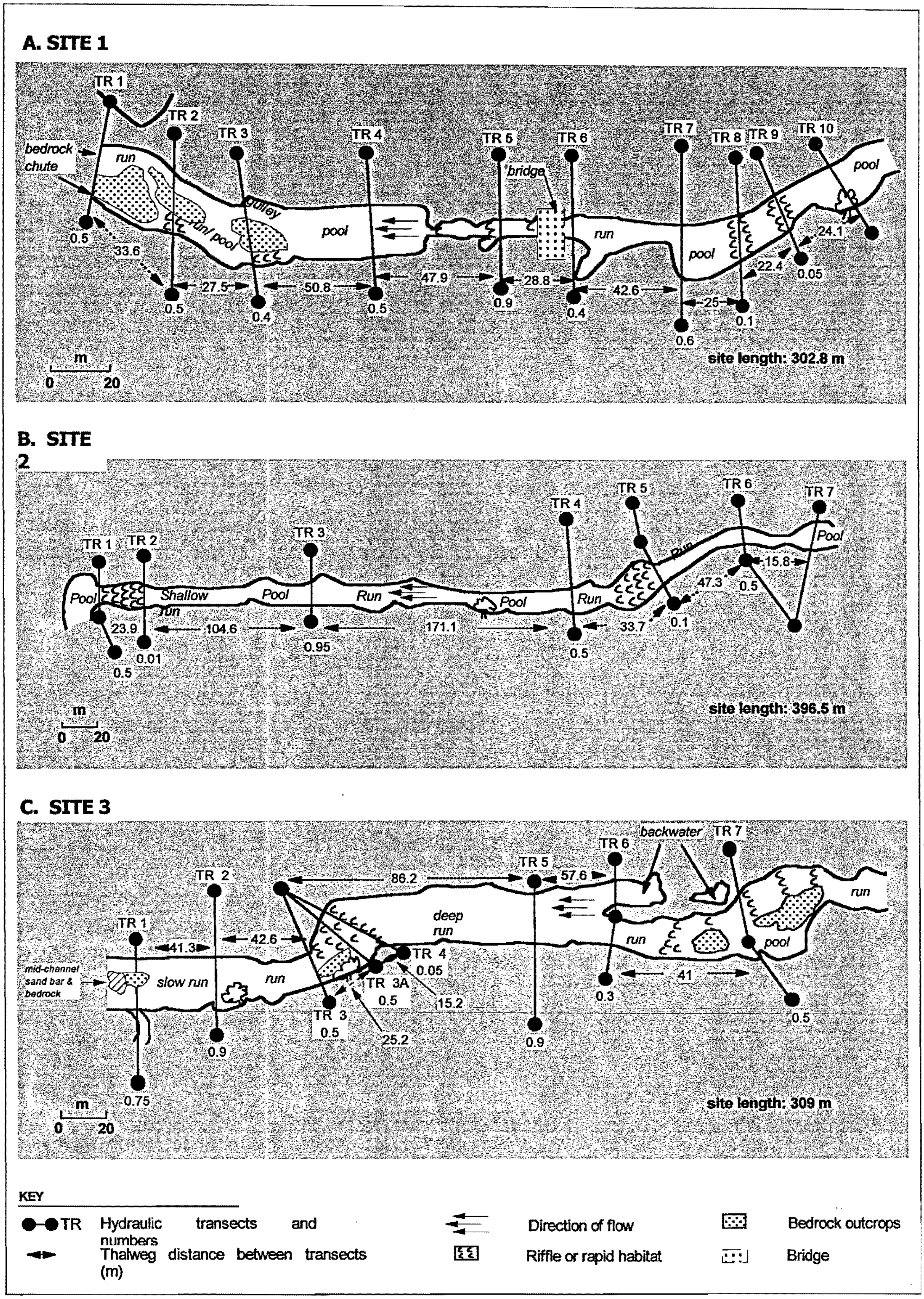


Figure 5.6 Schematic representation of IFIM Sites: (A) Site 1, (B) Site 2 and, (C) Site 3 on the Marite River. Transect numbers, distances between transects (m) and the broad habitat types are shown. Reach weightings are indicated below each transect (see text for details).

Table 5.3
General description and summary of distinguishing characteristics of study sites selected for IFIM microhabitat and microhabitat monitoring.

	SITE 1 (INJAKA)	SITE 2 (3 RONDAVELS)	SITE 3 (DURR)
General description	Massive outcrops of granitic bedrock and fairly rapid drops in profile. Boulder rapids present.	Extensive stretches of slow, sand runs with relatively short stretches of cobble and bedrock riffle. Deep pools present.	Massive granitic outcrops, and anastomosing channels. Fairly extensive runs and bedrock and cobble riffles.
Altitude (m ASL)	710	635	450
Average Wetted Channel Width (m)	12	10	18
Gradient m km^{-1}	~ 26	~ 4	~ 8
Primary River Bank Material	bedrock, soil	sand, boulder	bedrock, sand
Land use & potential sediment source	Afforestation and undeveloped communal land. Clear-felling may increase sediment loading	Afforestation and abandoned agricultural concerns.	Agriculture Contribution of Motitsi River
Riparian Vegetation	Highly modified, extensive invasion of *Lantana.* Gum plantations extend to the rivers edge on western bank.	Highly modified and invaded by exotic vegetation. Indication of citrus orchard extending into riparian zone.	Largely unmodified and intact although there are sparse stands of *Lantana.*
Water quality/ temperature	Good	Good	Good. Potential for modification due to agricultural inputs
No. of fish species			
Indigenous	11	14	17
Alien			1

All hydraulic data were collected in August 1991 which represented a low-flow period (Table 5.1). Measurements of cover, substratum, depth and velocity were made along each transect. Two separate codes were used to record substratum and cover (Table 5.4), at each interval along the transect. For substratum, an expanded Brusven index described by Bovee (1986) was used. The four-digit integer reflected the dominant and sub-dominant substratum type, whilst the decimal reflected the proportion of the sub-dominant substratum. Thus, a code of "1903.4" represented bedrock overlain by 40% algae. These codes were later combined and recoded into a simpler coding system for use with PHABSIM (see Section 8.6). Concurrently depth, using a wading rod, and velocity, using a Price AA current meter were recorded along each transect.

Velocity readings were taken to fulfill two objectives.

1. The transect with the most homogeneous profile was used to determine the discharge at a site (i.e the "discharge transect"). A calculation of discharge was made from between 20 and 25 readings of average velocities along a transect (see Equation 5.1).
2. Velocity readings at the remaining transects were taken in order to establish velocity distributions for the calibration data set required for PHABSIM II. This required slightly fewer readings at between 15 and 20 points.

Table 5.4
Field codes used for descriptors of (A) cover and, (B) substratum (after Bovee 1986).

A. COVER

CODE	DESCRIPTION	FUNCTION	COMPOSITION
1	No cover		
2	Instream Object	Velocity shelter	large rocks, partially submerged logs, bedrock ledge
3	Instream Overhead	Visual isolation	undercut banks, riffles, floating vegetation,deep pools, surface turbulence
4	Offstream overhead	Visual isolation (indirect)	canopy, shadows
5	Combination 2+3; 2+4	Velocity shelter & visual isolation	emergent veg., log jams, any superimposed object with overhead cover

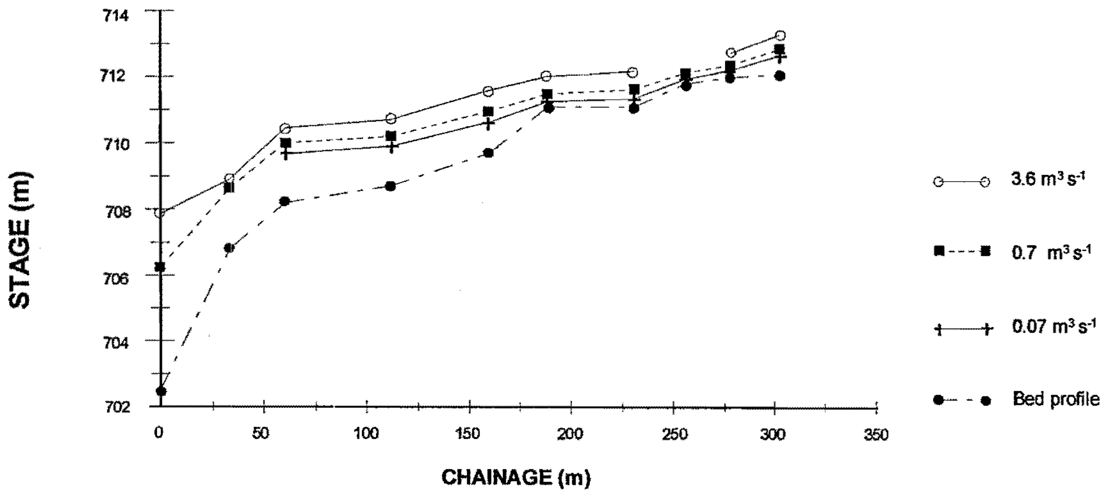
B Substratum (abbreviations: ‖ = parallel; ⊥ = parallel)

CODE	Substratum type	Size (mm)	CODE	Substratum type	Size (mm)
01	organic detritus	/	13	large cobble	130-250
02	vascular plants	/	14	small boulder	250-500
03	attached algae	/	15	med. boulder	500-1000
04	clay/ silt	/	16	large boulder	1000-2000
05	sand	/	17	v.large boulder	2000-4000
06	coarse sand	1-2	18	bedrock	plain, unfractured
07	v.fine gravel	2-4	19	bedrock	plain, jointed
08	fine gravel	4-8	20	bedrock	tilted, ‖, unfractured
09	m. gravel	8-16	21	bedrock	tilted, ⊥, unfractured
10	c. gravel	16-32	22	bedrock	tilted, ‖, jointed
11	v.c. gravel	32-64	23	bedrock	tilted, ⊥, jointed
12	small cobble	64-130			

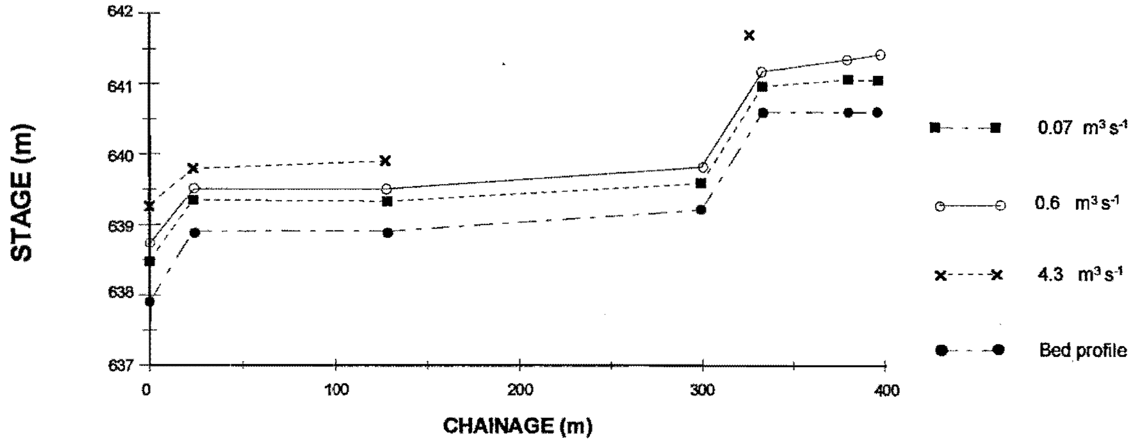
The water surface elevation (WSE) for each transect was measured by means of differential levelling. The WSE were determined for all transects on three occasions (Table 5.1) which corresponded to summer high flow, receding flow through autumn, and winter low-flow conditions. A coinciding discharge measurement was taken at the discharge transect. Subsequent changes to the locations of some of the transects meant that WSE were taken on different dates for those transects.

The stage-discharge relationships for each transect are shown in Figure 5.7. In general, the WSE increased in an upstream direction or remained the same as the previous transect. Further hydraulic outputs derived from PHABSIM II, such as the simulated stage-discharge relationships, follow in Chapter 9. Detailed transect profiles, as well as the channel form described by each transect, and the WSE, taken at the time of transect surveying, are provided in Appendix A. The nature of the channel bed is reflected in the water surface profile so that homogeneous beds have smooth water profiles, whilst the turbulent flow is evident in the irregular water surfaces of uneven channel beds. Additionally, the WSE frequently varied between channels of transects that spanned multiple channels.

a. SITE 1



b. SITE 2



c. SITE 3

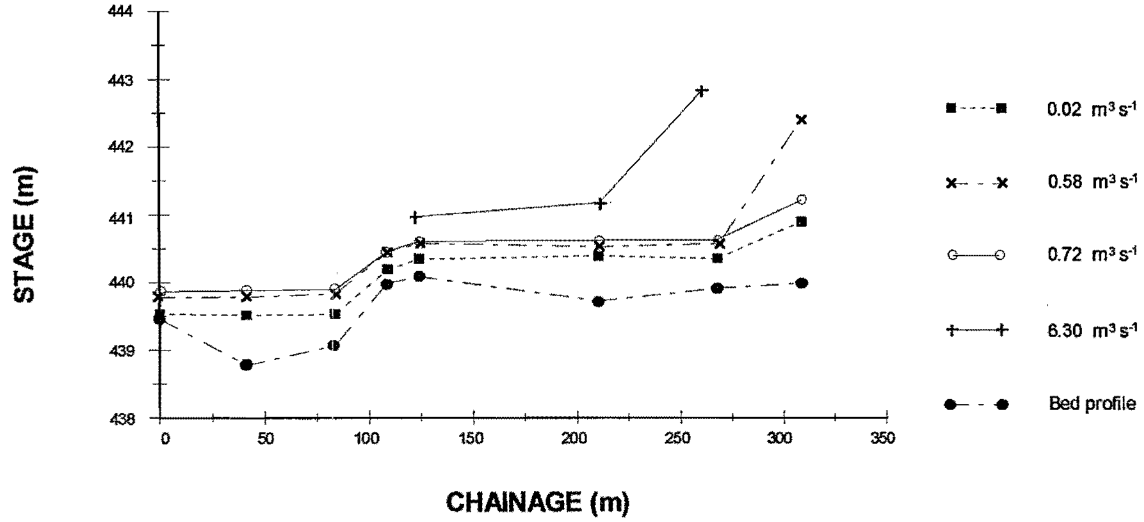


Figure 5.7 Stage-discharge relationship for each transect at (a) Site 1, (b) Site 2 and, (c) Site 3, over a range of discharges. Discontinuous data represent spot readings, data that have been omitted due to erroneous readings or instances in which readings could not be taken. "Stage" refers to the water surface elevation (m. ASL) at each transect (see Chapter 2, Step 7 for an explanation of stage-discharge curves).

5.4 DISCUSSION

Assessment of macrohabitat variables

In general, the water quality data collected during the study were consistent with those of historical data, and confirmed good conditions in the Marite River. No marked longitudinal differences existed in most of the variables, supporting the preliminary assessment that the study area comprises one macrohabitat zone. The increased temperature and discharge at Site 3 indicated that this may be the transition into a warmer, lowveld macrohabitat zone. This is corroborated by the fish species distributions, discussed in Chapter 6. Although speculative, the seasonal variations in water quality variables described above suggest that macrohabitat zones may shift seasonally and, in turn, cause a shift in the macro-distribution patterns of the biota. IFIM, in contrast, regards macrohabitat zones as spatially fixed entities.

Most of the water quality variables measured during the drought differed from those of the preceding seasons. Oxygen concentrations, turbidity and TSS were lower than the previous seasons, whilst temperature conductivity and TDS were higher. Thus, although the values fell within the ranges reported by van Veelen & Swart (1992), with the exception of oxygen and turbidity, the seasonal values were atypical. This suggests that although the macrohabitat conditions remained suitable through the early part of the study, this was no longer the case at the height of the drought. This conclusion was supported by the poor condition of many of the fish species, evident from heavy parasitic infections and disease, which are often associated with increased physiological stress. Similar results were reported from a parallel study of the effects of the drought in the lower Sand River, which ceased flowing during the drought. The extreme water quality conditions were implicated in the massive changes in species composition and abundance of the biota (Pollard *et al.* 1996). Whilst none of the water quality variables monitored in the research reported here altered to the same degree as those in the Sand River, uncharacteristic variations in some variables, such as oxygen, indicated a shift in the system.

Assessment of the collection of hydraulic calibration data

The guidelines presented by Bovee & Milhous (1978) for the collection of hydraulic variables are relatively straightforward. A subsequent assessment of the sites and transects by Mr. R.T. Milhous (US Fish & Wildlife Service, Fort Collins, *pers. comm.*) concluded that these had been appropriately chosen to encompass reach and habitat components of the Marite River. The principal problem encountered in the placement of transects was attaining a reasonable balance between a sufficient number of transects so as to adequately describe habitat and too many transects. The proclivity was toward the latter and in fact, three transects were deleted at Site 3 on the recommendation of Mr. Milhous. At Site 2, in contrast, he suggested that an additional transect should have been included to describe riffle habitat at very low flows.

At both Sites 1 and 3, characterised by multiple channels, transect placement was problematic, particularly in instances where a number of habitat types occurred along one transect. These sites presented several problems with regard to modelling by PHABSIM due to the complex channel systems and different WSE in multiple channels (see Chapter 9). Milhous advised establishing empirical stage-discharge relationships in rocky channels to avoid choosing inappropriate hydraulic controls. This, however, requires substantially more measurements of WSE than the suggested three measurements taken. Additional hydraulic modelling difficulties are discussed in detail in Chapter 9, but it is worth noting that this can be a frustrating component if implemented without the support of appropriate professionals within the field of fluvial hydraulics.

5.5 CONCLUSIONS

Monitoring of macrohabitat variables of water quality and temperature is a fairly standard accompaniment to most aquatic research and in IFIM studies, provides the assurance that these conditions remain stable and hence do not influence species distribution throughout the study. In general, stable conditions characterised this study until the final nine months at the height of the drought. The progression of the drought allowed for a quantitative assessment of the effects of low-flow conditions on the physical and chemical properties of the river.

Procedures for the collection of calibration data at microhabitat sites are relatively well documented by Bovee & Milhous (1978). The major problems encountered involved the placement of transects, particularly across multiple channels.

6 Fish of The Marite River and the Selection of an Indicator Species

6.1 INTRODUCTION

Both the paucity of basic ecological data, as well as logistical limitations, mean that quantifying the instream flow requirements (IFR) of the entire community is beyond the scope of most studies. Warmwater streams, with high species and habitat diversity, pose particular challenges (Winger 1981; Orth 1987). Thus *target,* or *indicator,* species have been used, essentially as a surrogate measure (Landres *et al.* 1988) of the flow requirements of the community (Bovee 1982; Mosley 1985; Bain & Boltz 1989).

Although some research has focussed on invertebrates as indicator species (e.g. Gore 1978; 1987a,b; Gore & Judy 1981; Orth & Maughan 1983; King & Tharme 1994), the literature reflects a general bias towards the use of fish for IFRs (e.g. Bovee 1978; Orth & Maughan 1981;1982; Tsai *et al.* 1983; Hamilton & Nelson 1984; Twomey *et al.* 1984; Moyle & Baltz 1985; Stier & Crance 1985; Raleigh & Zuckerman 1986; Irvine *et al.* 1987; Leonard & Orth 1988; Schlosser 1990a; Waite & Barnhart 1992). This focus is usually governed by the amount of available information, or by their profile as sport or fisheries species.

As a point of departure for species selection, Leonard & Orth (1988) recommend predicting the habitat-discharge relationship for the species of interest. In the case of invertebrates, ecological data of this kind are nonexistent for the Marite River but are comparatively better, albeit at a qualitative level, for fish which were therefore selected as the "target component" (*sensu* King & Tharme 1994). More recent work on the invertebrate communities of the Sabie River system (O'Keeffe *et al.* 1996) has at least provided the basis for their future consideration in instream flow assessments.

Given the importance of a target species approach, I suggest that this is a critical, but frequently neglected step in IFR assessments such as IFIM. Accordingly, the terms *target* and *indicator* species are discussed and I argue for a clear distinction between them. Guidelines for the selection indicator species are then developed and applied to the fish species of Marite River, which are also described. This is followed by a discussion of the effects of flow modifications on different habitats, and the species that inhabit them.

6.2 THE CONCEPTS OF TARGET AND INDICATOR SPECIES

The terms "target species" and "indicator species" are frequently interchanged, although the former is more common (e.g. Mosley 1985; Bovee 1986; Orth 1987; Leonard & Orth 1988; Bain & Boltz 1989; King & Tharme 1994). Nonetheless, I suggest that these terms are not synonymous because they imply different project objectives. Despite this, the conceptual basis, and assumptions and guidelines of this step have not been adequately examined within IFIM. Although Bovee (1986) provides two classification systems for target species selection based either on fisheries or broad ecosystem interests, he fails to develop these concepts further and assigns the term "indicator" specifically to guilds (see below).

I suggest that a target species is chosen for predetermined reasons, such as in the case of endangered species or fisheries management. Choice is usually subjective and importantly, flows for the maintenance of target populations do **not** necessarily ensure suitable conditions for other, flow-sensitive species (Landres *et al.* 1988). In the US, instream flow assessments are based commonly on the target species approach.

An indicator species on the other hand, is one whose characteristics are used as an index of attributes that are too difficult, inconvenient or expensive to measure, for other species or environmental considerations of interest (Landres *et al.* 1988). The definition proffered by Bovee (1974) is *the species which demonstrates the narrowest range of tolerance or requirements for any particular biological function.* Importantly, different lifestages can be treated as indicator "species" since they frequently have different flow requirements (Polis 1984; Landres *et al.* 1988). Moreover, the structure of adult fish assemblages can be governed by the habitat requirements of their progeny (Polis 1984; Mérigoux & Ponton 1999).

By implication, in providing flows to meet the requirements of an indicator species, the needs of the remaining, less sensitive biota, will be met (Bovee 1974). This assumption can be narrowed if the anticipated flow modifications are used to guide the selection (see Section 6.3). For example, protracted low flows, a decreased variability in discharge, increased incidences of floods or hydro peaking, would require representation by different indicator species. Hence, in contrast to the target species approach, the choice of an indicator species is, theoretically, based on objective criteria that arise from the project objectives and impacts. Mr. R.T. Milhous (US Fish & Wildlife Services, Fort Collins, *pers. comm.*) regards the use of indicator species as a viable, but little used, option in the US.

Both the target and indicator species approach are not without criticism. Landres *et al.* (1988) reviewed the conceptual framework, assumptions and guidelines and concluded that the use of indicator species is often inappropriate due to poor definitions and a discordance within the ecological literature. Despite their concerns, they conceded that the continued use of indicator species is likely, and offered a framework founded on ecological criteria (see later discussions).

The option of guilds

Due to the constraints of using a single species to represent complex community structure, a number of authors proposed using guilds to provide a broader community perspective (e.g. Bain & Boltz 1989; Lobb & Orth 1991). Guilds are defined as aggregations of species *"exploiting the same class of environmental resource in a similar way"* (Root 1967). Accordingly, indicator species are chosen to represent different guilds, on the premise that species exploiting similar resources should be similarly affected by changes in those resources (Landres *et al.* 1988). The aggregation of species into functional, or structural, groups is common practice in ecology (e.g. Balon 1975; Horowitz 1978; Gorman 1987, 1988; Bain *et al.* 1988; Vannote *et al.* 1980). Stream fishes have been grouped according to their morphologies (Gatz 1979; Mahon 1984), life history characteristics (Mahon 1984) and trophic status (Schlosser 1982a,b; Angermeier & Karr 1983; Leonard & Orth 1988; Bain & Boltz 1989; Orth & Leonard 1990). *Habitat-use guilds* have also been employed by a number of researchers (e.g. Gorman 1987, 1988; Bain *et al.* 1988; Syms 1995), and have been specifically applied to fish in instream-flow studies (e.g. Bovee 1982, 1986; Gorman 1987, 1988; Leonard & Orth 1988; Lobb & Orth 1991).

A number of authors advocated (e.g. Severinghaus 1981), and applied (e.g. Balon 1975; Johnson 1981) the guild approach for impact assessments, but were criticised by Landres (1983) and others (e.g. Verner 1984; Szaro 1986;Landres *et al.* 1988). Essentially, the major concern was that the use of guilds departed from the original definition proposed by Root (1967). Simply grouping species by any functional characteristics, such as trophic status, does not afford affiliation to a guild if it does not refer to the sharing of resources (Bain & Boltz 1989). For example, within IFIM Bovee (1982) defines a guild as "... a group of species having similar habitat requirements and *exhibiting similar responses to changes in streamflow*". Bain & Boltz (1989) point out the last part of the definition is inconsistent with that of Root (1967), since it focuses on a *response*, and not on resource use. They also argue that the guild membership does not necessarily mean that all members will respond similarly. Landres (1983) also raised concerns at the implication that guilds function as single ecological entities since, although species may overlap on some resource gradient such as habitat-use, this cannot be extrapolated to represent another resource use, such as food. Further, different guilds have been shown to influence markedly the IFR recommendations. In the James River basin, Leonard & Orth (1988) elegantly illustrated how the exclusion of riffle species, for example, resulted in flow recommendations that were almost three times lower than when they were included.

Not only is within-guild variability species a problem (Leonard & Orth 1988), but so is within-species variability, as a function of age, locality or activity (Bain & Boltz 1989). Theoretically, different lifestages would be accounted for in Root's definition, in that different ages might be assigned to different guilds. However, the implications for data requirements of including indicators of guilds and lifestages are enormous (Bain & Boltz 1989) and this level of resolution is rare in South Africa, particularly for invertebrates.

In view of these comments, the approach used in this study was that of a single indicator species, with the caveat that all lifestages would be considered. The underlying assumption was that a single species and its lifestages, if judiciously chosen, could provide sound data from which to recommend IFRs for the system.

6.3 ECOLOGICAL CONSIDERATIONS AND THE DEVELOPMENT OF CRITERIA FOR THE SELECTION OF INDICATOR SPECIES

Some guidelines for the selection of target species do exist, but these vary considerably. Within IFIM, Bovee (1986) lists the following criteria, more appropriate for target species, to facilitate selection:

- Intended audience.
- Importance to fisheries management (threatened or endangered species, sport or commercial species, support or competitor/ predator species).
- River adaptation (obligate riverine, facultative riverine, facultative lacustrine).
- The status of existing information.

An alternative framework, based on project-specific criteria, is offered by Landres *et al.* (1988). Their approach is more closely aligned to the ecosystem concerns apparent in South Africa, and this work was directed largely by their recommendations. Broadly, my approach (Figure 6.1) considered the study objectives, the habitats most likely to be impacted by the anticipated flow modifications, and species that use these habitats for some, or all, of their life cycle.

To address the research question, species selection is contingent on the *objectives* of the study (Landres *et al.* 1988). From these, the hydrological impacts of the development can be anticipated and, in turn, point to vulnerable *habitat types*. Research findings, mainly from the USA or UK, indicate that hydraulic habitats respond differently to changes in the flow regime and that certain habitats are more "sensitive" to flow modifications. The importance of this is seen in the associated biotic changes. For example, research in warmwater streams reveals that species diversity is strongly correlated with habitat diversity (Schlosser 1982a; 1987). By implication, a loss of habitat will result in a concomitant change in species abundance and distribution, although as pointed out by Orth (1987), this influence does not operate continuously.

Generally, the literature suggests that a loss of riffle-habitat is associated with conditions of low flows, and of pool habitat with higher flows. For instance, Bovee (1986) classified deep pools, backwaters and slough channels, as "robust habitat-types" on the basis that they are "not very sensitive to flow changes". Since their maximum habitat occurs at very low (often zero) flows, this may be true for conditions of low flow, but not necessarily for high flows (Orth & Leonard 1990). Leonard & Orth (1988) classified different habitats according to their habitat-discharge relationships. They demonstrated that

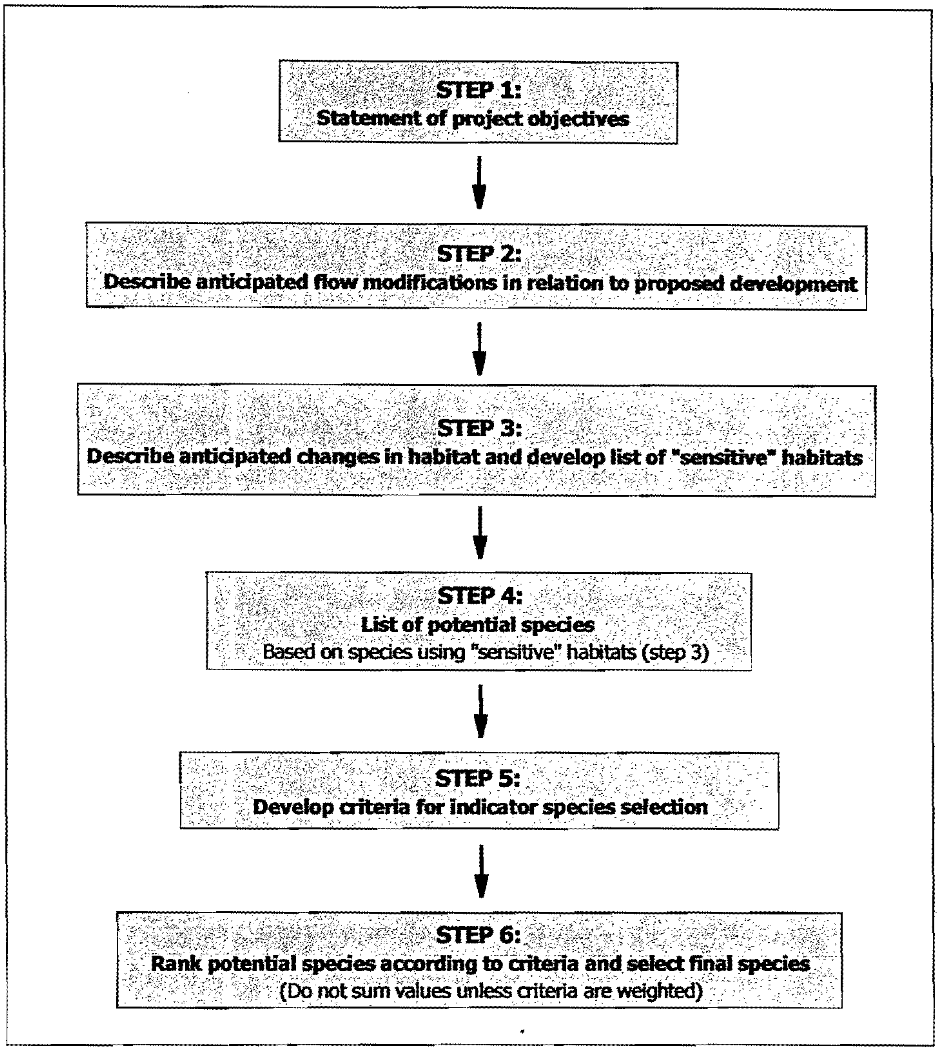


Figure 6.1 Proposed framework for the selection of an indicator species

in habitat categories dominated by riffles, microhabitat availability was zero at low flows, and peaked at intermediate discharges. Indeed, Orth & Leonard (1990) suggested that the microhabitat availability of riffle-dependent species was most limited under conditions of low flows although, based on the work of Bain *et al.* (1988), Leonard & Orth (1988) also suggested that shallow, slow-water margin habitats may be equally vulnerable. At low flows, riffles are characterised by fast, shallow water, and pools, by deep, slow-moving water. At high flows this pattern is reversed, with water velocity being highest in pools, and lowest in riffles (Winger 1981).

Having identified potentially sensitive habitats, attention can be given to species that utilise these and to the criteria by which to evaluate their suitability as indicator species. Bain & Boltz (1989) recommend focussing only on obligate riverine species on the basis that they tend to have more specific stream-habitat requirements and therefore tend to be the most sensitive to flow modifications. Although species or lifestages with the narrowest range of habitat needs will generally be the most sensitive to flow modifications (Orth 1987), Leonard & Orth (1988) point out that this requires testing because vulnerability to flow modifications depends on factors other than microhabitat availability. Under conditions of reduced flow, Orth (1987) indicates that those species restricted to shallow, fast-flowing habitats, and those dependent on the slower waters, are the most likely to suffer. Furthermore, the sensitivity of a lifestage may vary, particularly during reproduction or the early weeks of life (Bain & Boltz 1989).

This discussion points to the importance of selecting species based on study-specific criteria (Landres *et al.* 1988). The following section illustrates the development of criteria associated with anticipated reductions in flow.

6.4 THE SELECTION OF INDICATOR SPECIES OF THE MARITE RIVER

The selection of an appropriate indicator species was based on a literature review coupled with a preliminary field survey.

AVAILABLE BACKGROUND INFORMATION

Information regarding the macro-distribution of fish species of the Northern Province and Mpumalanga regions of South Africa (formerly Transvaal), into which the study area falls, was provided principally by Le Roux & Steyn (1968) and Pienaar (1978), as well as Crass (1964), Jubb (1967), Bruton *et al.* (1982) and Bell-Cross & Minshull (1988). Additionally, Lowe-McConnell (1987b) deals with the distribution of African fish fauna, principally at family level. Some additional information for the Limpopo and Incomati was available from Gaigher (1969). More recently, extensive surveys by Russell and Rogers (1989) have documented changes in species distribution and composition but only for that portion of the Sabie River within the boundary of the Kruger National Park (KNP). An analysis of the distribution and status of certain species of the Transvaal rivers beyond the KNP boundaries was provided by Kleynhans (1984). Studies of the fish fauna within the Marite River itself were nonexistent.

Aspects of the biology and ecology of certain species found in neighbouring river systems were gleaned from Gaigher (1973), Bruton & Kok (1980), Kleynhans (1984), Kleynhans & Engelbrecht (1988) and Dr. I. Russell (Cape Nature Conservation, *pers. comm.*). These provided some indication of "sensitive" species based on changes in their abundance and distribution.

PRELIMINARY FIELD SURVEY

The reconnaissance survey, described in Chapter 4 (see Figure 4.6) provided an initial species list for the Marite, which was upgraded on subsequent field trips (Table 6.1). Collection methods for fish are described in Chapter 8.

Table 6.1

Longitudinal distribution of fish species of the Marite River (species list arranged to reflect longitudinal zonation). Shading highlights Foothill Zone. A = alien species. ■ = population present; □ = few individuals; ○ = one individual. Temperature tolerance (TT) of each species is indicated as follows (Weeks *et al.* 1996): C= cold, stenothermal; CWT= cold, warm tolerant; E= eurythermal; WCT= warm, cold tolerant.

SPECIES	**COMMON NAME**	**TT**	**SITE**		
			1	2	3
Amphilius natalensis	Natal mountain catfish	C	■	■	□
Amphilius uranoscopus	common mountain catfish	C	■	■	■
Barbus argenteus	rosefin barb	C	■	■	□
Barbus brevipinnis	shortfin barb	C	■	■	□
Barbus marequensis	largescale yellowfish	E	■	■	■
Varicorhinus nelspruitensis	Incomati chiselmouth	C	■	■	■
Chiloglanis anoterus	pennant-tailed rock catlet	CWT	■	■	■
Chiloglanis swierstrai	Lowveld catlet	WCT	□		
Barbus polylepis	smallscale yellowfish	C	○		
Anguilla bengalensis	mottled eel	E	○		
Anguilla mossambicus	long-fin eel	E		■	■
Marcusenius macrolepidotus	bulldog	WCT		■	■
Labeo molybdinus	leaden labeo	WCT		■	■
Barbus eutaenia	orangefin barb	E		■	■
Barbus unitaeniatus	longbeard barb	WCT		○	○
Tilapia sparmanii	banded tilapia	E		■	■
Pseudocrenilabrus philander	southern mouthbrooder	E			■
Opsaridium peringueyi	barred minnow	WCT			■
Clarias gariepinus	sharptooth catfish	WCT			■
Micropterus puntatus	spotted bass				○**A**
No. of species			10	13	18
TOTAL					**20**

INDICATOR SPECIES SELECTION

The primary aim of the Marite River project (see Section 1.7) was *"To assess the downstream effects of a proposed dam on the habitat of a flow-sensitive fish species ...emphasising hydraulic modifications, associated with low-flow conditions".* Based on evidence from the literature (see preceding discussion), which recommends that riffle species are the focus for low-flow studies(Bain & Boltz 1989), the use of riffle-habitats for all, or part of, the life cycle, constituted the primary criterion for the selection process (Table 6.2). Further criteria included flow-dependency, evidence of distributional changes, abundance, distribution in study area and available information. Since some species require flowing waters, but do not necessarily inhabit riffle habitats, the first two criteria are not necessarily synonymous. Ecological information on all species found in the Marite, particularly in relation to the developed criteria, was summarised and used to derive a list of potential candidates. The final ratings for each criterion are shown in Table 6.2. Values were not summed since criteria were not weighted. Evidence of a sensitivity to flow reductions was inferred from work by Russell & Rogers (1989) who documented changes in the distribution and abundance of fish communities in the KNP, since the records of Pienaar (1978) and Gaigher (1969) in the 1960s.

Table 6.2

Criteria developed for indicator-species selection. Each criterion is rated relative to other species; ratings between criteria are not comparable. Abbreviations: *B.arg = B. argenteus; B.bre = B. brevipinnis; B.mar = B. marequensis; C.ano = C. anoterus; L.mol = L. molybdinus; M. mac = M. macrolepidotus; O.per = O. peringueyi; V. nel = V. nelspruitensis*

RANKING CRITERION	**SPECIES**							
	B.arg	***B.bre***	***B.mar***	***C.ano***	***L.mol***	***M.mac***	***O.per***	***V.nel***
Riffle dwelling for some, or all, of life history 1=low; 2= possibly; 3= for part of life-cycle or a biological activity; 4= strictly.	2	?	3	4	3	2	4	3
Flow-dependency 1=low; 2= possibly; 3= for part of life-cycle or a biological activity; 4= strictly.	2	?	3	4	2	2	4	3
Record of regional distributional changes/ disappearance 1= none; 2= increased or decreased; 3= disappeared	3	?	2	3	1	2	3	?
Abundance 1= rare; 2= present, but in relatively low numbers; 3= abundant.	1	?	3	3+	1	1	1	3+
Widespread distribution 1= within study area; 2= limited distribution; 3 = marginal or absent	1	2	1	1	2	2	1	2
Availability of information, particularly seasonal habitat requirements	General paucity of information characterised all species							

Two potential species, *Chiloglanis paratus* and *Labeo cylindricus*, were not found during the preliminary survey and hence were discounted. Further, *Amphilius uranoscopus*, thought to be present in the Marite River, was also discounted after difficulties in distinguishing it from the closely related species *A. natalensis*. It was later confirmed that both species occur in the Marite River. Although listed as a red data species (Skelton 1987), the low numbers of *O. peringueyi* disqualified them. The species finally chosen was *Chiloglanis anoterus*, the pennant-tailed catlet (Family: Mochokidae; shown in Plate 6.1 and Figure 6.2), since it was judged to best meet the criteria (Table 6.3).

With 34 species, Mochokidae is a family of small to moderately sized (< 72 cm) catfish inhabiting the fresh waters of Africa (Burgess 1990). A distinctive feature of the genus is the modified lips to form a disc for attachment to rocky substrata in fast flowing waters. Most species of the genus are bottom dwelling, and are nocturnal or crepuscular. They prefer shallow, fast flowing riffles and rapids with loose rocks. Their diet consists of invertebrates or algae, which they scrape from rocks. They are unable to adapt to other modes of feeding and can starve in the face of food shortages. However, although they appear to ingest diatoms, invertebrates appear to be the only digested component. They are serial spawners, breeding during the rainy season. The breeding, nursery and juvenile habitats are unknown.

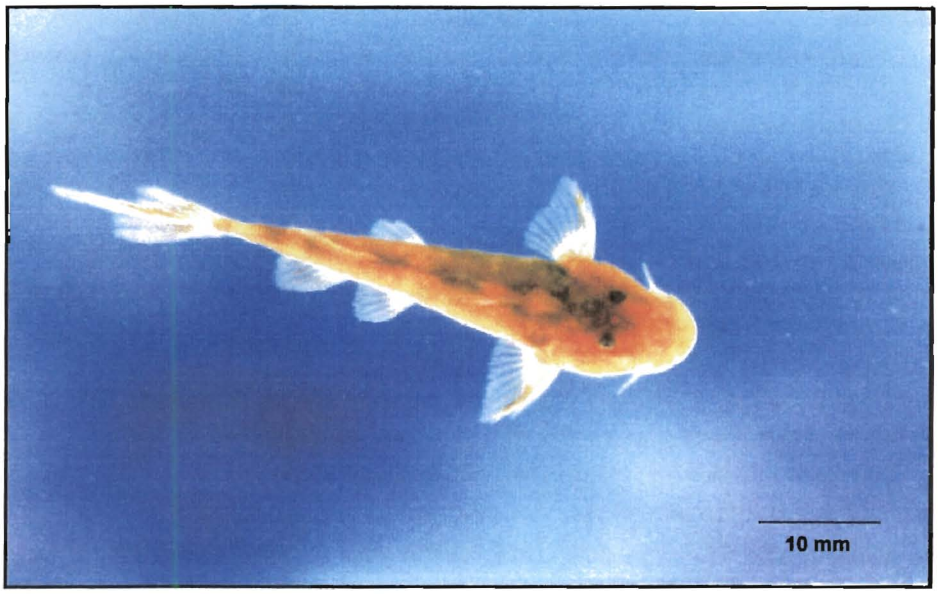


Plate 6.1 Dorsal view of an adult male *C. anoterus*. Note the extended median caudal ray which differentiates males from females in this species.

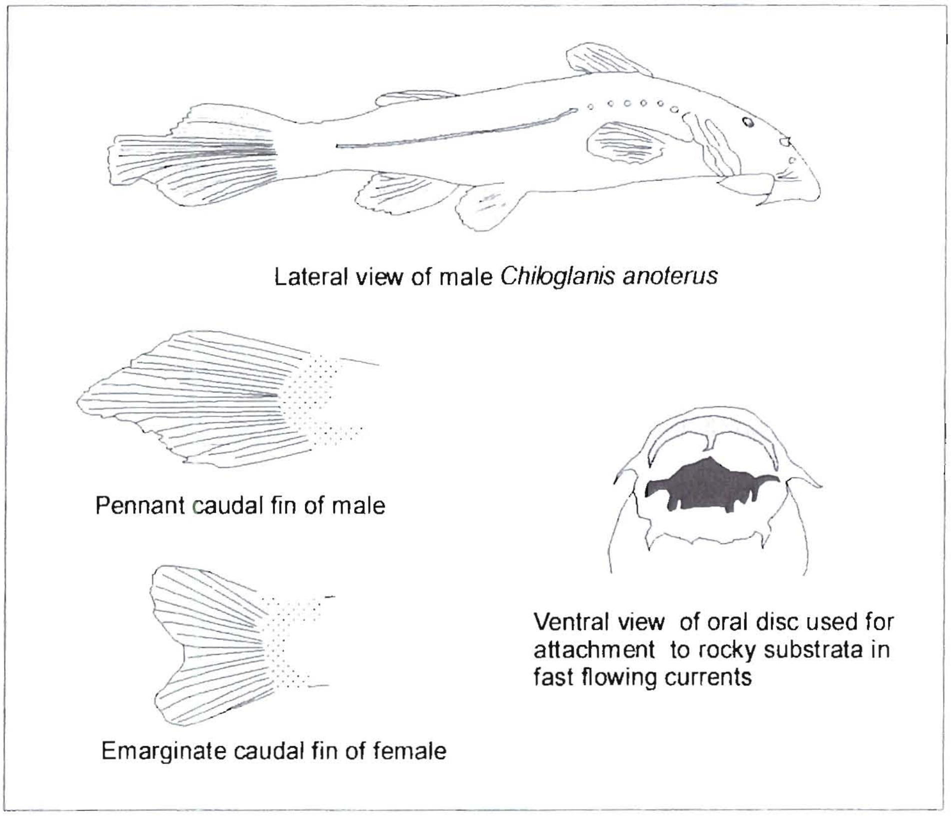


Figure 6.2 Key morphological features of *C. anoterus*.

Table 6.3
Applicability of selection criteria to *C. anoterus*, the chosen indicator species

1. Habitat use

Chiloglanis anoterus is always captured in riffle habitats and thought to be restricted to riffle areas (Pienaar 1978; Kleynhans 1984; but see Chapter 8)

2. Flow-dependency and sensitivity to changes of flow at some stage in their life history:

Chiloglanis anoterus does not survive in stagnant water (Pienaar 1978). Furthermore, a reduction in range and numbers following flow modification has been reported (Russell & Rogers 1989).

3. Changes in the distribution

No longer found in the Crocodile River - attributed to low or cessation of flow (Russell & Rogers 1989).

4. Abundance

Within its habitat, *C. anoterus* is the most abundant species (Kleynhans 1984; 1986).

5. Restricted catchment or geographic distribution

Endemic to Incomati and Pongolo systems (Gaigher 1969)

6. Amount of information available

Characteristics and known biology and ecology of *C. anoterus* as available at the start of the study, are described above.

6.5 DISCUSSION

Indicator species selection, (either single or multiple species) is a critical step at the outset of a habitat-based assessment for IFR, because of the assumptions of representivity. However, both the limited guidelines and ecological data presented challenges to making an objective choice. Nonetheless, a framework was developed for indicator-species selection based on the objectives of the study and the anticipated downstream effects.

Habitat-flow relationships: Limitations of transferring currently available information

Research into habitat-flow relationships is by no means complete, and current work in southern Africa is principally based on findings from the Northern Hemisphere, the rivers of which exhibit different geomorphological and hydrological characteristics to those in South Africa (Dr. A. Van Niekerk, Centre for Water in the Environment, University of the Witwatersrand, *pers. comm.*; see Chapter 10). As discussed, evidence from North American streams indicates the riffle habitat of the selected species, *C. anoterus,* tends to be the most severely effected by protracted low flows (Winger 1981; Bovee 1986; Leonard & Orth 1988; Bain & Boltz 1989; Orth & Leonard 1990). However, whilst the term "riffle" is used somewhat generically to describe areas of high velocity with turbulent flow, recent work in South Africa has differentiated this habitat type into riffles and rapids (van Niekerk *et al.* 1995). Rapids comprise bedrock substrata whereas riffles, which are rare in the Sabie system, consist of transported materials. Questions arise therefore as to whether or not the habitat-flow relationships derived elsewhere, apply to both habitat types here, and indeed, if the transferability of models is valid at all (see Chapter 8).

Furthermore, the hypothesis that riffle habitats are the *most* susceptible to change as a result of low-flow conditions requires further scrutiny, particularly in warmwater systems with a more complex array of habitat types. Based on a review of research in warmwater streams, Bain *et al.* (1988) proposed that species in shallow, slow-water stream margins are more susceptible to daily flow fluctuations than those in deeper areas of the stream reach. Evidence in support of this was provided from work that showed the importance of vegetated, and edge-channel habitat as nursery areas for young fish in a large, warm-water stream in West Virginia (Lobb & Orth 1991). These comments also underscore the fact that in general, terms describing habitat types are too broad and loosely applied and is an issue that is further addressed in Chapter 10.

Flow-sensitive species and the development of criteria for indicator species selection

Current paradigms of "flow-sensitive species" require testing. In this research, the term "sensitive" has been applied both to habitats and to species. In terms of habitat, sensitivity directly relates to a reduction in quantity and quality of specific sets of hydraulic conditions due to changes in stream discharge. Sensitivity, as applied to species, is used in a generic sense, in that it encompasses a suite of behavioural and physiological factors and interactions. In describing a species as such, the implication is that this is a *ubiquitous condition conferred on a species that manifests in response to any flow modification.* However, as discussed earlier, species can only be described as "sensitive" to a particular set of conditions, and often only at a particular time. This underpins the importance of clearly specifying anticipated project impacts in order to avoid misrepresenting the entire communities' needs on the basis of a single, erroneously chosen species.

Additionally, there is a need to develop selection criteria that are based on project objectives and that do not encompass the inherent bias towards sport or commercial species sometimes evident in the American system. Although considerable effort was invested in developing criteria appropriate for this work, even these were based on different interpretations of sensitivity.

In South Africa, the classification of species sensitivity is principally limited to responses to pollutants. In terms of responses to alterations in the flow regime, some attempts have been made to classify species on a relative scale of sensitivity, but the criteria on which this was based are not explicit. For example, Kleynhans & Engelbrecht (1988) do not provide the criteria on which they based their sensitivity rating of Transvaal fish species, so that it is difficult to discern if a rating of "high sensitivity" reflects one, or multiple factors. Later work by Kleynhans (1991, and not available at the start of this project) detailed some of the criteria that he considered important indicators of sensitivity. These included temperature, stagnant water, fast-flowing water, low abundance and distribution. However, abundance and distribution in themselves do not necessarily indicate the sensitivity of a species, unless comparative data are available. Furthermore, Kleynhans summed ratings to give a total sensitivity rating; it is argued that these factors should be weighted according to priority if a total rating is to be of value.

Notwithstanding these comments, professional judgement in classifying sensitive species is invaluable, particularly in view of the dearth of data. Nevertheless, depending on what questions are asked, or how broad or ambiguous these are, professional assessment may vary considerably. For instance, Kleynhans (1991) rates species on a scale of 1 (not sensitive) to 5 (very sensitive). Under his system, *Barbus marequensis* is rated as insensitive, specifically to the *factors that he lists* (given above). In contrast, other scientists rated this species as sensitive, because of its apparent intolerance to low-flow conditions during the breeding period (Dr I. Russell, Cape Nature Conservation; Dr. P. Skelton, JLB Smith Institute, Grahamstown, *pers. comm.*). Thus, the onus is on the researcher to design questions according to the project objectives and anticipated flow changes.

Further, the complex biotic responses to changes in flow can only be partly explained as a result of changes in habitat (Bain *et al.* 1988; Leonard & Orth 1988) and a number of reasons for changes in species composition or abundance, ascribed to flow manipulations, are cited in the literature. For example, peak flows can result in the displacement of small, shallow-water fishes (Harvey 1987). Protracted periods of low flow on the other hand, can increase vulnerability to predation (Schlosser 1982a; 1987). Under conditions of low flow, fish may also be susceptible to stranding (Bain *et al.* 1988), or to variable food availability (e.g. Moyle & Baltz 1985). However, little of the work sheds any substantial light on *why* a specific species may be more or less "sensitive" to changes in flow and hydraulic habitat (i.e. cause and affect). For instance, some evidence indicates that velocity is a critical component of hydraulic habitat (Leonard & Orth 1988). Possible reasons that emerged from this study in relation to changes in velocity included a decline in the food resources, as well as physiological responses(see Chapter 5). In general, little mention is made of the physiological responses associated with changes in habitat, such as the reduction in oxygen concentrations associated with reduced velocities and increased temperatures (see Chapter 5). During the drought, *C. anoterus* experienced physiological stress, probably due to lowered oxygen concentrations in riffles and, consequently, were susceptible to parasitic infestations (see Chapter 8). Likewise, a survey of the 1992 drought in the Sabie and Sand Rivers indicated that certain motile species associated with depth and volume showed signs of physiological stress under conditions of shrinking habitats, which manifested in disease (Pollard *et al.* 1996). Research that highlights the causal factors of a species' inability to tolerate flow modifications will greatly further our understanding of biotic responses to flow modifications and their ratings as tolerant or intolerant to these.

6.6 CONCLUSION

The focus on a single species can be risky if chosen for the wrong reasons, and in general, indicator species selection receives insufficient attention in an IFIM process. The selection of a single, target species in the US reflects the historical development of IFIM in that country where, despite pleas for an ecosystem approach (e.g. Stanford 1989), fisheries maintenance is often the governing objective. Consequently, the accompanying guidelines are inappropriate for use in South Africa which subscribes to an ecosystem-approach to IFRs. These differences lend support to the argument for a clear distinction in applying the terms "target" and "indicator" species. The approach developed here for indicator species attempts to address the ambiguities of a target species approach, and is contingent on the objectives of the study. The use of guilds was considered but this approach carries its own liabilities. Thus, the approach was to focus on all lifestages of the selected indicator species, *C. anoterus,* since the habitat requirements of juveniles differ from those of the adults and can be considered as a separate ecological "species" (*sensu* Polis 1984). The microhabitat requirements of *C. anoterus* are detailed in Chapter 8.

The limitations of a single-species approach must be taken into consideration since the conclusions of a habitat assessment reside primarily on an appropriate selection. Unless microhabitat data are available for all the species in a system, most researchers target a particular species, or a group of species, albeit inadvertently. Species responses to flow modifications, as well as habitat complexity and habitat-flow relationships are poorly understood in southern African rivers, and warrant further research.

7

The Reproductive Biology of *Chiloglanis anoterus*

7.1. INTRODUCTION

Since river regulation has been implicated in influencing the reproductive success of stream biota, knowledge of the reproductive attributes of the target species provides critical information on which to refine IFR recommendations (see Chapter 2). The effects of river regulation on reproduction are fairly well documented (e.g. Anderson & Nehring 1985; Saltveit & Brabrand 1985; Coon 1987; Casado *et al.* 1989; Copp 1990; Rulifson & Manooch 1990; Cambray 1991; and see Chapter 1). These effects are commonly ascribed to hydrological modifications and associated variables, such as temperature, discharge, chemistry (e.g. Crisp 1985; Graham & Orth 1986; Cassidy 1989), and to the alteration of environmental cues that are necessary for reproduction (Saltveit & Barbrand 1985; Jackson 1989). Other factors provoking changes in reproductive success are increased silt loads that smother eggs (Muncy *et al.* 1979; Scullion 1983; Carling & McCahon 1987, Platts *et al.* 1989), loss of fish larval habitat and inhibitory effects on development (e.g. House & Boehne 1985; Rimmer 1985; Grande & Anderson 1990). The effects are seldom the result of a single factor but are rather the outcome of multiple factors. For example, Schlosser (1982b) presents evidence to indicate that the dynamics between channel morphology, the energy base and seasonal fluctuations in discharge interact to determine, amongst other things, the reproductive success of fishes.

Although not a conventional step within the IFIM, aspects of the reproductive biology of the target species, *Chiloglanis anoterus* were examined for two reasons. A primary concern was the need to address a major criticism of PHABSIM; namely, the lack of biological data collected to complement the input of physical data (e.g. Cada *et al.* 1983; Shirvell 1986; Orth 1987; Scott & Shirvell 1987). Information on the biological and ecological aspects of a riverine biota increases ones ability to accurately assess and validate the predictions generated by PHABSIM. In fact, very little is known about the reproductive biology of many of the lowveld riverine species, and this paucity of information consistently hinders more expansive research objectives.

Secondly, the egg and juvenile stages of fish development are considered to be the most vulnerable and often have different ecological and physical requirements to those of the adult stage (Bagenal & Braum 1971; Snyder 1990). Hence, within IFIM, the different lifestages of the target species are treated as ecologically distinctive entities with their own set of microhabitat, or SI curves (see Chapter 2). Clearly, deriving separate SI curves for each lifestage depends on defining the size at which they differentiate.

Although Kleynhans (1984) found no evidence of sexual maturity in *C. anoterus* below a standard length of 48 mm, preliminary findings from this study indicated that sexual maturity was reached in smaller individuals in the Marite River. Thus, part of the objective of my work was to determine lifestage sizes in order to develop SI curves for both adult and juvenile lifestages. Furthermore, the microhabitat requirements for both eggs and fry of *C. anoterus* were undescribed. An additional objective therefore, was to attempt to locate eggs and fry of this species in order to describe their habitat requirements.

The aim of this chapter is to describe the major reproductive attributes of *C. anoterus*, and to describe the size delimitation between various lifestages, particularly that of juveniles and adults. These findings are then discussed in relation to the flow-related variables that may be important in the reproductive cycle of this species.

7.2 DETERMINING THE REPRODUCTIVE ATTRIBUTES OF FISH

A number of reproductive styles exist in fish. In the semelparous or so-called "big-bang" spawners, all eggs mature synchronously and are shed in a single batch (Bagenal 1967). In contrast, in the repeated reproduction (iteroparity) of "serial spawners" (1), the ova mature in multiple batches that are shed successively within one reproductive season. The literature regarding the reproductive biology of *C. anoterus* points to this species being a serial spawner (Crass 1964; Kleynhans 1984) and hence is the focus of the following discussion. Iteoparity is generally determined from the egg-size classes present in the ovary, and is characteristically multimodal (Hempel 1979), consisting of recruitment, maturing and ripe eggs (Bagenal & Braum 1971).

A *reproductive strategy*(2) is defined by Wootton (1984) as "That complex of reproductive traits that fish will attempt to manifest so as to leave some offspring. Such traits include age at first reproduction, size and age-specific fecundity, size and nature of gametes, degree of parity, timing of reproductive season, (and) organisation of reproductive behaviour...". A number of terms, summarised in Table 7.1, are used to describe these reproductive attributes.

Fecundity, defined as "the number of ripening eggs in a female prior to the next spawning period" (Bagenal & Braum 1971), is the currency used to determine the reproductive attributes of a species. Accurate estimates of fecundity are important in describing the dynamics of fish populations (Conover 1985), as they indicate the number of eggs spawned, and hence the potential recruitment. Little is known about patterns of fecundity in serial spawners even though it is a relatively common mode in tropical fish (Conover 1985). Determination of annual egg production (annual fecundity) in serial

---

[1] Serial spawners may be referred to by alternative terms such as *multiple spawners, batch spawners* or *fractional spawners* (e.g. Bagenal & Braum 1971; DeMartini & Fountain 1981; Snyder 1990).

[2] Whilst the term "strategy" is commonly applied in the literature on reproduction, the term "mode" is preferred, since strategy implies that animals strategise rather than adapt

spawners is difficult (Bagenal & Braum 1971), primarily because of the difficulty in determining how many eggs are spawned per batch (batch fecundity), and how many batches are spawned annually (Bagenal & Braum 1971).

Table 7.1
Description of terms used in this study to describe the reproductive attributes of *C. anoterus*

TERM	DESCRIPTION
Serial or multiple spawner	Species in which the ova mature in multiple batches that are spawned successively in a season (Bagenal 1967).
GSI or Gonadosomatic Index	This index is used to indicate the breeding season. The index provides a partial picture of the temporal investment in ovarian tissue by females in the population. It is normally calculated as the weight of the ovaries divided by the total fish weight (or total weight minus ovarian weight), x 100. The amplitude of the GSI is high (25% or greater) in species that spawn over a short period and low in species that spawn several times in a season (<5%) (Wootton 1979).
GI or Gonadal Index	Index system developed in this study specifically for the *external* (field) assessment of breeding condition. Represents an abbreviated version of stages of gonadal development (see Table 7.2).
Fecundity	Number of ripening eggs in a female prior to the next spawning (Bagenal & Braum 1971).
Recruitment fecundity	Previtellogenic eggs from which a batch of eggs, that accumulate yolk, sequentially arise (Bagenal & Braum 1971).
Batch Fecundity	Number of eggs in most advanced age class per gram of ovary-free body weight (Conover 1985). Used primarily in reference to serial spawners.
Relative fecundity	Numbers of eggs per gram of body weight (Bagenal 1978)
Total or Annual fecundity	Annual egg production. In serial spawners, annual fecundity has been calculated as the product of the number of spawns and mean number of eggs per spawn (Wootton 1979). However, Conover (1985) used the total number of eggs (recruitment plus mature) per female just prior to the beginning of spawning, minus the recruitment egg retention per female at the end of the spawning season.
Spawning frequency	Number of times a serial spawner releases a batch of eggs in a season.

Fecundity determinations require an examination of egg numbers early in the breeding season prior to the shedding of eggs (Bagenal & Braum 1971). The conventional approach has been to count only the largest eggs above a "certain arbitrary size" under the assumption that the smallest eggs would be reabsorbed or spawned in later spawning episodes (Conover 1985). The size of eggs that a researcher may choose to count is not fixed. For example, Hunter & Goldberg (1980) only counted the number of eggs in the most advanced mode. If the assumption that small eggs are reabsorbed is invalid, fecundity may be grossly underestimated, however (DeMartini & Fountain 1981; Conover 1985). In contrast, Conover (1985) proposed an alternative approach, that of enumerating the total number of eggs (recruitment plus maturing) in females just prior to the breeding season, and subtracting the recruitment eggs retained at the end of the breeding season. An implicit assumption in this calculation is that the reservoir of recruitment eggs is formed largely prior to the breeding season, and not carried over from the previous season (Conover 1985). In fact Conover cautions that whilst this may hold true for the species on which he was working, *Menidia menidia* (Atlantic silverside), this pattern has yet to be established for other serial spawners. Thereafter, Conover estimated spawning frequency by dividing the estimated total number of eggs shed per female by the mean batch fecundity. Annual fecundity has also been estimated by multiplying the batch fecundity by spawning frequency (Hunter & Macewicz 1980; DeMartini & Fountain 1981).

Approaches to determining spawning-frequency are varied, and include (i) the use of ova-diameter frequency plots (Lauth 1988); (ii) dividing the total fecundity by the batch fecundity; (iii) enumeration of the numbers of recently-spawned females by noting the presence of post-ovulatory follicles (Hunter & Macewicz 1980) or; (iv) ready-to-spawn females with hydrated eggs (DeMartini & Fountain 1981; Middaugh & Hemmer 1992).

7.3 MATERIALS AND METHODS

A combination of field-based and histological assessments, elaborated below, was used to elucidate the reproductive attributes of *C. anoterus*. The key attributes included the (i) size-at-maturity; (ii) breeding season; (iii) reproductive mode and spawning frequency; (iv) fecundity estimates and; (v) egg development.

Individuals of the indicator species, *C. anoterus,* sampled between November 1990 and March 1992, were used in this analysis (see Table 5.1). A total of 2246 fish were examined, of which 1801 could be sexed (1012 females and 789 males). Field assessments, which are described in the appropriate sections below, were used to examine the size-at-maturity, sexual dimorphism, the breeding season and batch fecundity. These results were also analysed and further refined through the histological assessment which was used to determine the gonadal development and GSI values, egg-size classes and fecundity estimates. A description of the histological examination follows.

PROCESSING AND HISTOLOGICAL EXAMINATION OF GONADS

Between 8 and 20 individuals were collected on a tri-monthly basis (see Table 5.1) and examined in the laboratory for breeding condition, indicated by gonadal recrudescence. Once breeding condition was evident, collections were increased to a monthly basis during the breeding season so that gonadal development could be followed. On collection, standard measurements (standard length, weight; see Chapter 8) were taken and animals were placed in iced water for about ten minutes in order to anaesthetise them, and then preserved in 10% formalin. The gonads of both males and females were excised and weighed to the nearest mg. Gonadal specimens were transferred to 70% ethyl alcohol after 14 days, as advised by Dr. J. Cambray (Albany Museum, Rhodes University, Grahamstown, *pers. comm.*). The GSI values and eggs-size classes were calculated from these specimens (see below).

DETERMINING THE REPRODUCTIVE ATTRIBUTES OF *C. anoterus*

Sexual dimorphism, size-at-maturity and structure of the breeding population

Sexual dimorphism is pronounced in adult *C. anoterus,* with males displaying extended median caudal rays (see Plate 6.1). Consequently, the relationship between the onset of sexual dimorphism (external assessment) and gonadal development (histological assessment) was examined in order to establish their links.

The size-at-maturity (L50), or dimorphism, is defined as the length at which 50% of the fish are mature (Ni & Sandeman 1984), and is most commonly used to delimit the onset of maturity (e.g. Welcomme 1969; Tommasson *et al.* 1984). This was estimated from external observations in two ways. The first approach used the following equation (after Ni & Sandeman 1984):

$$P = \frac{1}{1 + e^{-(\alpha+\beta L)}} \qquad \text{Equation 7.1}$$

where, P = proportion of fish sexed; $\alpha+\beta$ = coefficients; L = standard length; logit $P = \ln(P/1-P) = \alpha+\beta L$; and $L50 = -\alpha/\beta$

The second approach plotted the cumulative frequency of females with eggs. These results were later corroborated by the histological examination. From this, a code of the gonadal stage, modified from Bruton (1979) was developed for *C. anoterus* (Table 7.2) and assigned to each individual.

Once the juvenile and adult lifestages were differentiated, the sex ratio of the population was estimated.

Table 7.2
Codes and characteristics of gonadal stages, identified histologically, of *C. anoterus* from the Marite River (modified from Bruton 1979). Being multiple spawners, each stage potentially includes all preceding stages. The field assessment of breeding condition was only able to assign values to stages IV and V in females, and stage V in males.

STAGE		CHARACTERISTICS
I	Immature Virgin	Minute sacs close under vertebral column, apparently empty.
II	Developing Virgin	Sexual products have not yet begun to develop. Testes and ovaries transluscent grey. ♀- Transparent oocytes just visible to naked eye, clearly at x1 magnification. Generally <1mm in size.
III	Developing	Rapid increase in weight of gonads in progress. Testes= pinkish, finger-like filaments visible. ♀- eggs distinguishable to naked eye as defined eggs. Largest egg class ~<1.5mm but some may be slightly larger.
IV	Maturity	Sexual products mature but not extruded when light pressure applied. ♂- Testes cream or slightly pinkish, swollen. ♀- generally 3-20 eggs present, between 1.6 - 2mm in size. Eggs opaque to slightly orange.
V	Ripe	Sexual products of ♂ & ♀ exuded in response to light pressure on abdomen. ♂- testes extremely swollen. ♀- Largest egg class round and between 2.1 - 2.7mm in size, numbering on average between 10-30.

Breeding Season

The breeding season was determined in the field from external observations of the breeding condition of males and females and confirmed later through GSI values and fecundity estimates (see below). Gravid females, which display a lateral distension of the abdominal cavity when viewed from above, are relatively easy to identify. These females were assigned a gonadal index (GI; see Table 7.1) defining their reproductive state, which was determined by the presence of mature or maturing ova, visible through the abdominal wall. The GI was an abbreviated version of the indices of the gonadal stages given in Table 7.2. Males were assigned a GI of "5" (i.e. ripe) if milt was extruded under slight pressure. Since the field assessment could not ascertain early reproductive development (stages I and II), it was complemented with results from the histological assessment which provided detailed values of gonadal development, or GSI.

The Gonadosomatic Index (GSI), an index of gonadal maturity and hence breeding season, was estimated by expressing gonad weight as a percentage of body weight (Snyder 1983).

$$GSI = \frac{\text{gonad weight} \times 100}{\text{total body weight}} \qquad \text{Equation 7.2}$$

Reproductive mode and frequency of spawning

Eggs from the laboratory specimens of females (see above) were separated manually, enumerated and their diameter measured. The median diameter (a random axis) of all eggs was measured using an ocular micrometer. Ova-diameter frequency plots for non-ripe and ripe females were used, together with the GSI values (see above), to determine the reproductive mode of *C. anoterus*. Multimodal frequencies and low GSI values are usually indicative of multiple spawning. The number of spawns was estimated from these modal configurations and from comparisons to the total and batch fecundity.

Fecundity

Both the total and batch fecundity were estimated from the total number of eggs counted from females caught in each month. Recruitment fecundity was determined by counting all eggs that were stage III and smaller (see Table 7.2). The total fecundity was derived from the total egg count for each animal. Least squares regression was used to predict the potential total fecundity, using lengths and weights of females as independent variables. Only adult specimens from the breeding season were used for the this analysis (December to March), and eggs from the smallest size class (1-5 mm) were excluded, because of difficulties in counting total egg numbers.

Egg development

Fertilised eggs were incubated in the laboratory in order to examine their development. By applying gentle pressure along the belly of the fish towards the genital aperture, eggs were stripped from the female in the field. Eggs and milt were expelled into a dish and mixed carefully after the addition of water. In the laboratory, fertilised eggs were placed in gauze-covered plastic containers and aerated from below. An antifungal agent, Protozin was added to tank water after preliminary attempts to incubate eggs failed due to excessive fungal growth. Approximately two eggs were collected every 24 hours until all eggs had hatched and were preserved in 4% formalin (Dr. J. Cambray, *pers. comm.*). Standard water chemistry measurements were taken concomitantly. Eggs were later examined for development.

7.4 RESULTS

Sexual dimorphism, size-at-maturity and structure of the breeding population

Equation 7.1 predicted that a length of 33 mm (SL) delimits 50% sexual differentiation in *C. anoterus* (n=422). Externally, this was also the size at which the development of the third caudal lobe in males started developing. Field observations of females with developed eggs indicated that 50% maturity was achieved in larger females than those predicted from this calculation. The smallest individual captured with developed eggs was 34 mm and, for the population, 50% maturity (cumulative; n=427) occurred at a length of 39 mm (3) (Figure 7.1). Externally, all individuals were sexually differentiated at a length of 41mm (Figure 7.1).

Histologically, the first evidence of gonadal development was observed at a length of 34 mm, and at 39 mm all females displayed at least stage II gonadal development (i.e. onset of development; see Table 7.2; n= 89). All males showed evidence of gonadal development at a corresponding length. Based on the L50, together with histological evidence of gonadal development, a length of 39 mm was adopted to delimit the onset of sexual maturity.

In agreement with the value quoted by Kleynhans (1984), the average sex ratio for *C. anoterus* males to females was 1: 1.28 (n= 1801). Southwood (1988) confirmed that sex ratios may depart from the 50:50 ratio.

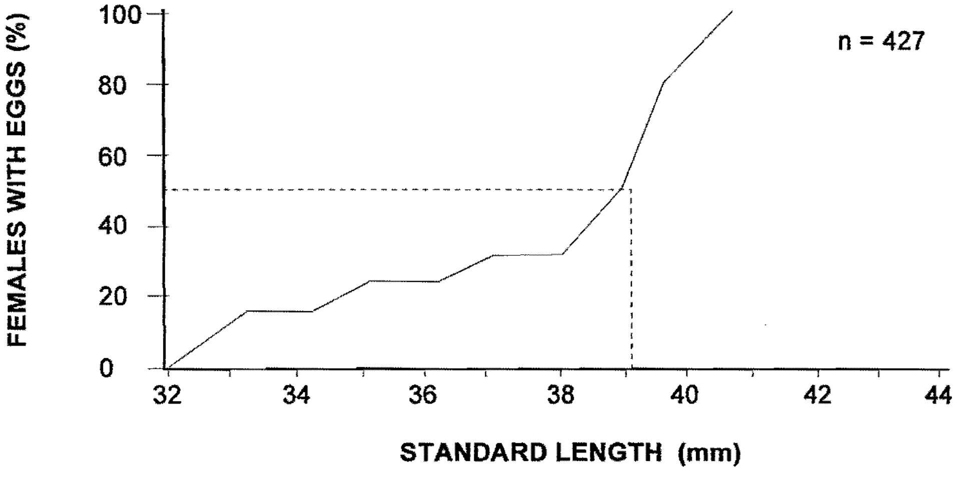


Figure 7.1 The length at sexual maturity (cumulative frequency) of *C. anoterus* in the Marite River, determined from field observations of females with eggs.

---

[3] A further size differentiation of juveniles was also made based on their habitat use (see Chapter 8). Up to a length of 31mm, "early-juveniles" were found on sandy substrata in runs. Above this size they occurred in rapids, when they were referred to as "late-juveniles".

Breeding season

The GSI values revealed an extended breeding season from October to March (Figure 7.2; n=78), which coincides with the wet season. This is followed by gonadal quiescence between May and September (winter). The onset of gonadal development, verified by the presence of recruitment eggs, was already apparent in September (see Figure 7.4). This suggests that gametogensis started in August. The bulk of the population was sexually mature from December through to February, after which the GSI declined (Figure 7.2). This was corroborated by external observations of breeding condition in females (Table 7.3). The limited numbers of individuals precluded the development of GSI values for males. However, it was interesting to note that the macroscopic inspection of males revealed that 4% of all adult males were producing milt in June, during the "resting phase".

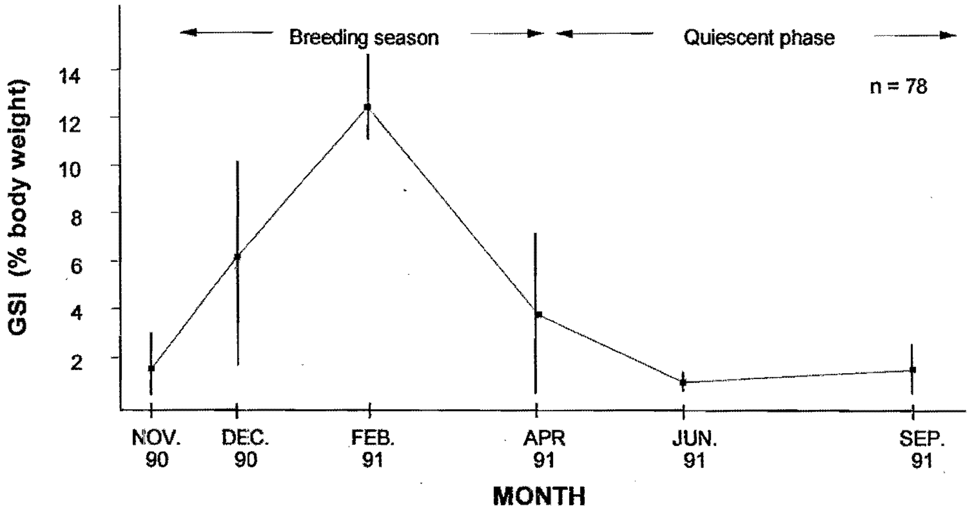


Figure 7.2 Mean Gonadosomatic Index (GSI) values for *C. anoterus*, determined histologically, illustrating the breeding season. Vertical bars indicate standard deviation.

Table 7.3
Percentage of females in breeding condition for each month, as determined by external observation.

Jun. 1990	Sept. 1990	Nov. 1990	Dec. 1990	Feb. 1991	Mar. 1991	n
0 %	2 %	59 %	59 %	51 %	6 %	524

Reproductive mode and frequency of spawning

Evidence of gonadal maturation indicated a multimodal egg-size frequency distribution for both (a) non-ripe (n=48) and, (b) ripe (n= 30) individuals (Figure 7.3), signifying that *C. anoterus* is a serial spawner. In ripe females, the frequency distributions suggested three egg-size classes (Figure 7.3b) of increasing stages of maturity. The most advanced size class was clearly distinguishable from immature ova. Due to the marked increase in counts, the eggs between 4 and 5 mm did not appear to be contiguous and rather suggested two sequential classes.

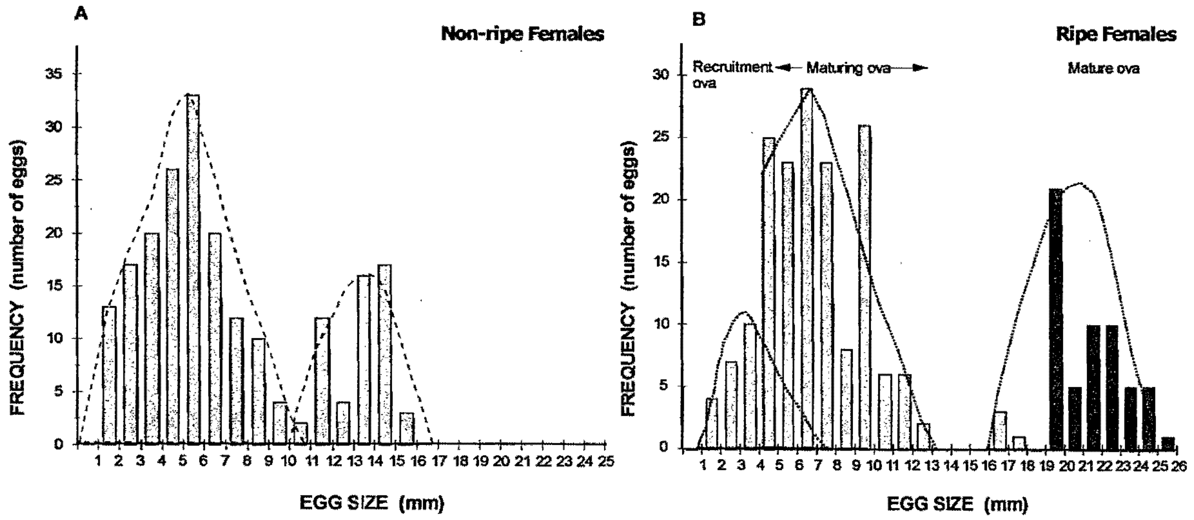


Figure 7. 3 Frequency distribution of egg-size classes from female *C. anoterus* captured in the Marite River. The distribution of egg classes in (A) non-ripe females, indicates two, or potentially three modes of egg sizes, and in(B) ripe females indicates at least three modes of egg sizes.

Fecundity

The recruitment and total fecundities are shown in Figure 7.4. The mean total fecundity varied between 85 eggs at the start of the breeding seasons and increased to between 108 and 162 eggs at the height of the breeding season. Total and recruitment fecundity declined with the progression of the breeding season (Figure 7.4).

The fecundity of *C. anoterus* in the Marite River, is related linearly to the standard length (Figure 7.5; n=27). The line of best fit is described by the following equation:

$$y = -120.229 + 4.02367 \text{ SL} \qquad \text{Equation 7.3}$$

where y = absolute fecundity, $r^2 = 0.73$, $p < 0.001$

A regression of fecundity against length, predicted that at 48mm SL (the modal length of the breeding population), *C. anoterus* would produce 73 eggs. An average of 67 eggs was produced by females of this size, which is slightly less than the projected number. Log transformation of the data (Bagenal 1978) produced a slightly weaker correlation (r^2 = 0.70). No significant relationship was found between fecundity and weight, suggesting that weight could not be used as an estimate of fecundity.

In the field it was found that a female of 50 mm (SL), produced an average of 22 eggs per batch. This represents approximately 25% of the projected absolute fecundity of 81 eggs at this age, suggesting a total of three or four spawning events in a season.

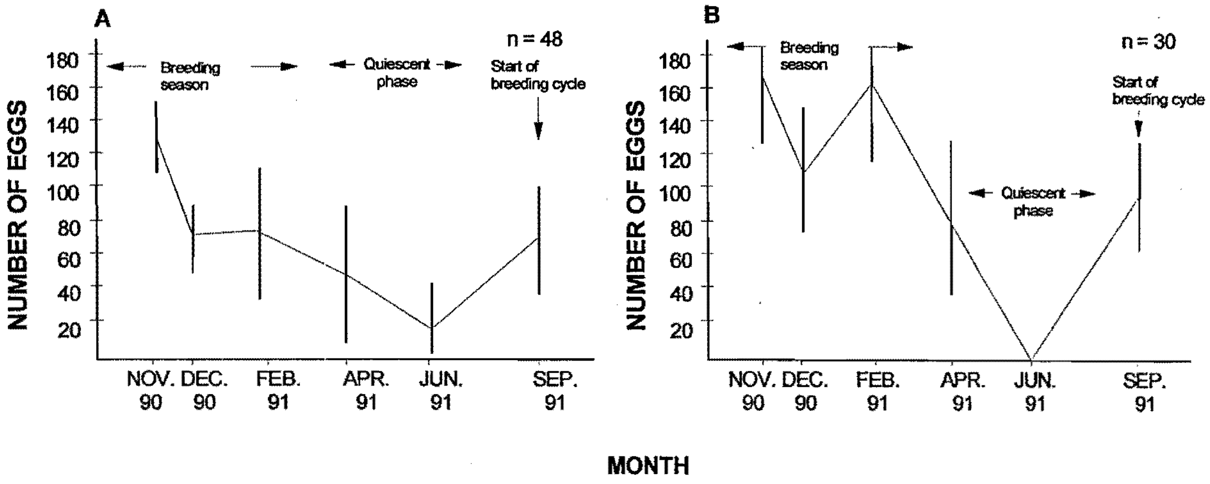


Figure 7.4 Progression of (A) recruitment fecundity (n =48) and, (B) total fecundity (n =30) of *C. anoterus*. Vertical lines represent standard deviation.

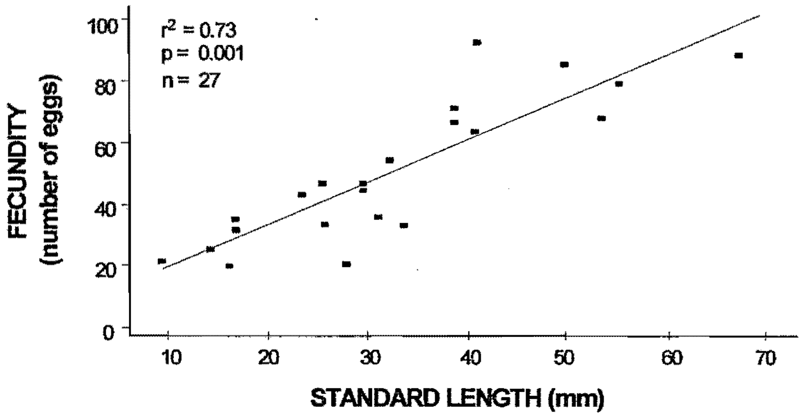


Figure 7.5 The relationship between total fecundity and standard length in *C. anoterus* in the Marite River.

Egg development

Most fertilised eggs exhibited fungal growth and decomposed within a few days following introduction to the tanks. Since only three batches of eggs were incubated to hatching, no conclusive statements of their development and conditions required, can be drawn. However, it is interesting to note that under conditions of 71 - 90% oxygen saturation, and temperatures between 20 - 29°C, the eggs hatched in approximately four days. Furthermore, the large eggs (approximately 2.6 mm in diameter) are slightly adhesive, a characteristic associated with a number of behavioural traits (see later discussion).

7.5 DISCUSSION

Size at maturity

The differentiation between juveniles and adults is important in microhabitat studies since it allows for the development of separate habitat-suitability curves for each lifestage (see Chapters 2 and 8). In *C. anoterus* caudal development slightly precedes but is closely followed by gonadal recrudescence. All *C.*

anoterus of 39 mm SL exhibited developing (stage II) gonads, and this length was selected to delimit the adult and juvenile lifestages. At a size of 39 mm, animals are in their first spring or second summer, and average about 13 months old.

My data show that sexual maturity (4) is achieved in *C. anoterus* in the Marite River at a shorter standard length than described by Crass (1964) or Kleynhans (1984). Kleynhans found no evidence of sexual maturity in females below 48 mm (SL), and Crass delimited sexual maturity at 45 mm (SL). Variability in the onset of egg production is a common feature of serial spawners (Nikolsky 1963). According to Stearns & Crandall (1984), size at maturity is not fixed, but responds along a trajectory of age and size. It is quite possible therefore that factors such as discharge, temperature and/ or food abundance may influence the size at sexual maturity in *C. anoterus*. Typical of fish (Bagenal 1978; Conover 1985; Lauth 1988; de Villiers 1991), the potential fecundity of *C. anoterus* increases as a function of the length. The implication of this relationship is that a female that invests more energy in growth than egg production, will ultimately achieve greater fecundity (Wootton 1979).

Reproductive attributes of C. anoterus

The production of few, large eggs is a recognised characteristic of the reproductive ecology of *Chiloglanis* (Kleynhans 1984; de Villiers 1991). This is indicative of a number of features such as territoriality and parental care of eggs (Balon 1985).

The low standing-crop of ovary-weights (1.5% - 12% of body weight) of *C. anoterus* is characteristic of multiple-spawning fishes (Bagenal 1978). Typical values include 2-14% in *Cyprinodon nevadensis* (Shrode & Gerking 1977), and 4% in the Queenfish (DeMartini & Fountain 1981). In annual spawners, the GSI can be between 20 and 30% or greater, since all eggs are produced and develop synchronously (Wootton 1979). Further evidence for multiple spawning is presented in the multimodal distribution of egg-size classes. Kleynhans (1984) only distinguished two classes of egg size: large and small. My analysis suggested that at least three, and possibly four egg size classes exist, similar to that reported for other serial spawners (Conover 1985; Lauth 1988).

Multiple spawning confers a number of advantages, primarily that of increased fecundity, especially in small fish (Nikolsky 1963; Gale & Gale 1977). It also diminishes competition for a number of resources (Wootton 1984), such as food and breeding sites (Gale & Gale 1977; Kramer 1978; Gale & Buynak 1982), and compensates for unpredictable fluctuations in the environment. By allowing fish to "hedge their bets", it decreases the chances of an entire generation being eliminated due to stochastic environmental disturbance or sub-optimal conditions (Kramer 1978; DeMartini & Fountain 1981). There is also a

---

[4] Certain authors have failed to discriminate between terms defining *individual* and *gonadal* maturity, resulting in unclear interpretations. Length-at-maturity is that length at which maturation of first gametes is observed (Balon 1985) and applies to the *individual*. Some authors (e.g. de Villiers 1991) have interchanged the terms *immature* and *Stage I* (Table 7.2) but the latter refers only to gonadal development. Clearly, a sexually mature 60 mm female can have Stage I (immature) gonads. This is not synonymous with an immature individual.

tendency for smaller species to have longer breeding seasons in order to offset the disadvantages of decreased fecundity associated with their smaller sizes (e.g. Welcomme & Merona 1989).

The total fecundity reported by Kleynhans (1984), working in the Inkomati and Pongola systems, was higher than those found in this study. For example, Kleynhans estimated 258 eggs for a 65mm (SL) female compared to 131 eggs for the same size female from the Marite River. Interestingly, population studies have shown that a great deal of plasticity exists, both in egg size and numbers (Stearns & Crandall 1984; DeMartini 1991). For example, female dace (*Leuciscus leuciscus*) responded to stress by producing fewer, bigger eggs (Stearns & Crandall 1984). Heins (1991) showed a direct correlation between runoff and the oocyte diameter of longnose shiner, *Notropis longirostris*. Overall, food availability has been implicated as the most important environmental factor determining fecundity (Wootton 1979). It is likely that fecundity in *C. anoterus* is governed by the interaction between a suite of these factors and lower egg numbers, relative to those reported elsewhere, could reflect stress associated with the worsening drought conditions.

Likewise, spawning frequency varies in response to similar biotic and abiotic factors. For example, experimental studies by Townshend & Wootton (1984) suggested that not only does improved food availability increase the spawning frequency, but it also reduces the interval between them. Since relative fecundity is a function of increasing body size, Demartini & Fountain (1981) showed that larger females of the queenfish began spawning earlier in the season and further, spawned for longer than smaller females. This factor alone would result in variable spawning frequency. Estimates of batch fecundity point to *C. anoterus* spawning between three and four times a season. This would classify this species as a partial spawner, in which approximately a third of the ova are released at one time (Lowe-McConnell 1987 a). If this is true, inferences can be made with regard to possible spawning cues (see below).

Timing of reproduction

The general paradigm for the timing of spawning holds that it has evolved to ensure that the young hatch and commence feeding during the season most favourable for their survival (Bye 1984). Thus, the annual cycle of gametogenesis must precede the spawning season so as to ensure that gonadal development commences before the environmental changes that initiate increased productivity. However, it is not yet clear whether gametogenesis is under endogenous or exogenous control. This topic is reviewed by Bye (1984) who supports the postulate that annual sexual maturation is under endogenous control and the timing of spawning is under exogenous control. Nonetheless, this is undoubtedly oversimplified since the relationship between endogenous and exogenous rhythms is certainly a compromise (Bye 1984; Milton & Blaber 1991).

With regard to exogenous control, evidence from the literature points to the various environmental determinants for reproduction. One example of this was evident in smallmouth bass, *Micropterus dolomieu* when spawning was triggered by a sudden environmental shift, produced by the interaction of discharge and temperature (Graham & Orth 1986). Although many experimental investigations have seemingly elucidated these cues, Bye (1984) points out that, by implicating only one determinant, the complex synergistic effects between endogenous and exogenous control can be overlooked.

In temperate regions, day length, temperature and food availability predominate as the primary determinants of gametogenesis and spawning. In tropical environments on the other hand, reproductive timing is thought to be influenced by flow, nutrient deficiencies, climatic effects on larvae (e.g. turbulence), or biotic pressures, such as competition for food or living space (Schlosser 1990 a). The importance of biotic interactions was advanced by Kramer (1978) who showed that related species in the same Panamanian stream spawned in the wet and dry season respectively. He suggested therefore that factors such as food availability and competition for spawning sites may be important in the control of reproductive seasonality in the tropics.

Much of the evidence from the tropics suggests that reproduction in many fish species is linked to the start of the rainy season (Kramer 1978; Lowe-McConnell 1979). Schlosser (1982 a, b) found that the abundance of small fish underwent large annual fluctuations due to the effect of variation in discharge on reproductive success. Similarly, Coon (1987) concluded that the yearly variation in recruitment success depended on the timing and severity of summer flooding. Flow variations have been suggested to indirectly influence timing of spawning in striped bass by affecting changes in water temperature (Rulifson & Manooch 1990). Preliminary evidence from the Sabie River in South Africa suggests that most species breed during high water levels, possibly cueing their reproduction to the onset of the rains and increased flow (Weeks *et al.* 1996). However, the proximate cues are still unclear and could include temperature, flow rate, water quality, or an interaction of these.

Nestler *et al.* (1988) suggest that flow spikes (more commonly called "freshes" in South Africa), and to a lesser extent temperature, function as spawning cues for the Colorado squawfish (*Ptychocheilus lucius*). Such pulses of increased discharge, and increased temperatures, characterise the flow patterns of the Marite River during the rainy season (see Figure 5.1). It would seem plausible that these flow-pulses (and some or all of the flow-related variables) may act as the proximal cue for spawning in *C. anoterus.* As serial spawners, a number of females, of different size, would be ready to spawn at different times throughout the season, thus taking advantage of these recurrent flow events.

I suggest that, based on indirect evidence, increased breeding condition is linked with a gradual, seasonal increase in discharge and temperature, but verification is required. The onset of the breeding season and subsequent spawns may be closely timed with diatomaceous algal blooms and a subsequent increase in associated riffle invertebrates (particularly chironomid larvae), which comprise the major component of the diet of these fish (personal observation). A possible scenario for *C. anoterus* is as follows. In winter, water levels and temperatures are low, during which gametogenesis may be initiated under exogenous control. In September (Spring) there is an increase in water temperature which indirectly stimulates egg production. This may be in one of two ways. Either the increase in water temperature results in an increase in algal growth and hence nutrients to the fish, which stimulates egg production, or increased water temperature results in increased metabolism which stimulates egg production (Dr. P. Skelton, JLB

Smith Institute, Rhodes University, *pers. comm*). Pulses in discharge may be the cue that initiates individual spawning events. Additionally, flood pulses may be important in flushing the spawning beds of sedimentary material, which can smother eggs (see review by Muncy *et al.* 1979). It may be, as suggested by Dr. Skelton (*pers. comm.*), that such flow pulses may provide better water quality conditions for egg development since embryogenesis requires high oxygen levels to avoid bacterial infection. Spawning activity in *C. anoterus* then normally ceases with a drop in water temperatures (and discharge), characteristic of subtropical latitudes (Lowe-McConnell 1987a). Thereafter, juvenile development is favoured by dispersal to slow-flow, and shallow runs at the onset of the dry season.

Spawning sites

Attempts to locate eggs *in situ* were unsuccessful. This was particularly difficult due to high discharges, turbidity and the nature of the substratum which made it impossible to use standard gear (e.g. Bagenal & Nellen 1980). Most of the cobbles and boulders of the rapids were embedded in the parent substrata and could not be lifted for inspection. However, it was clear from the work on artificially fertilised eggs that *C. anoterus* have slightly adhesive eggs that are probably attached to rock substrata. Moreover, since ripe adults were also found in rapids, it is possible that this species is a crevice-spawner. Here, eggs are attached to the rock and hence afforded protection from high velocities normally associated with riffles, but where there is sufficient oxygenation to meet development requirements.

7.6 CONCLUSIONS

The objectives of exploring the reproductive ecology of the target species, *C. anoterus* were governed largely by the broader IFIM and microhabitat objectives of the overall thesis. This necessitated determining the size delimitation between adults and juveniles was required in order to develop separate habitat use functions, as well as to refine PHABSIM II outputs on the basis of ecologically sound criteria. For example, with regard to potential anthropogenic effects, a lack of information regarding the cues for the maturation of eggs and the onset of spawning, as well as the conditions needed to support propagules, could result in management options that inadvertently alter or suppress such cues.

In the Marite River, juvenile and adult size differentiation of *C. anoterus* occurs at 38 mm (SL). They are multiple spawners, exhibiting a protracted spawning season from October to March. Flow (including flow pulses) and temperature are implicated as key determinants in the spawning of this species, the timing of which coincides with an increase in the primary food source. It is likely therefore, that any broad-scale modifications to the flow regime of the Marite River could adversely affect the reproduction and recruitment of *C. anoterus* by dampening or eroding environmental cues, as well as the conditions necessary for their growth and survival. Inappropriate flood releases during the dry season could flush juvenile fish from unprotected habitats. The mode of reproduction in this species is consistent with Bruton's (1989) theory on precocial forms that are specialists and best able to survive in stable, crowded environments. Anthropogenic destabilisation could be most damaging for such species.

8

The Use of Hydraulic Microhabitat by *Chiloglanis anoterus*

8.1 INTRODUCTION AND OBJECTIVES

The loss of habitat is now of global concern (e.g. Ehrlich & Ehrlich 1981; Lovejoy *et al.* 1984; Wilson 1988; Tilman *et al.* 1994) and understanding the habitat requirements of a species, or population, is a key management consideration. Typically, the habitat requirements of a species are described in terms of the habitat availability, the utilization of, and preference for, certain habitat types by the population. Consideration is also given to which of these habitats is critical to survival of the population (White 1987). In aquatic systems, and specifically in the IFIM approach, this detail is provided by microhabitat suitability, or SI curves (see Chapter 2), where microhabitat refers specifically to physical or hydraulic habitat, described by the variables of depth, velocity, substratum and cover.

As detailed in Chapter 6, information on the habitat use of *Chiloglanis anoterus*, the indicator species, was limited. In brief, they are reported to be restricted to riffle habitats and do not survive in stagnant conditions. However, little is known as to whether or not this restriction is true across all seasons, or for all lifestages. This chapter therefore aims to describe the utilised and preferred hydraulic microhabitat of juveniles and adults of *C. anoterus*, in the Marite River in order to meet two objectives.

The first objective is to produce a description of microhabitat use in the format required by PHABSIM. The results of the microhabitat analysis comprise the "biological input" (see Section 2.3) which, when linked with the hydraulic output of PHABSIM, are used to simulate the available habitat for *C. anoterus* over a range of discharges.

Nonetheless, as they stand, no inferences regarding habitat availability or use can be made from the SI curves. The second objective, therefore, is to test the following hypotheses:

1 The indicator species, *C. anoterus* does not select particular microhabitat conditions and therefore microhabitat use tracks microhabitat availability.

2 Microhabitat availability does not differ significantly between sites, at a specific time (flow).

3 Microhabitat use by *C. anoterus* does not differ between sites, at a specific time (flow).

4 Microhabitat use does not differ significantly between juvenile and adult *C. anoterus* at a specific site and time.

5 Microhabitat use by *C. anoterus* does not exhibit a seasonal variation.

This chapter provides a brief overview of the conceptual basis of SI curves, as well as an outline of how data are collected and manipulated in order to produce such curves. This provides the basis for both the development, and assessment, of SI curves for *C. anoterus* for three lifestages (early- and late-juveniles, and adults). Further, although somewhat beyond the ambit of a standard IFIM initiative, data on habitat use through the 1992 drought offers interesting insights into the effects of extreme physical conditions on the target species, as well as the mathematical behaviour of SI curves under such conditions.

8.2 CONCEPTUAL FRAMEWORK OF SUITABILITY INDEX (SI) CURVES

The SI curves(1) are graphic representations of a species', or lifestages', behavioural response to a particular hydraulic variable (see Chapter 2). Ultimately, the co-ordinates of the SI curves form the basic information on the physical microhabitat requirements of the target species and are used as the "biological" input data for PHABSIM II (Bovee 1986; see Section 2.3). Irrespective of their intended input to PHABSIM II, many researchers now describe microhabitat use by way of SI curves.

The most frequently used hydraulic variables include depth, velocity, substratum and cover. The last two are combined within PHABSIM and called Channel Index, or CI (Slauson 1988). The SI curves are constructed from field measurements of the density, or abundance, of the targeted species over ranges of each of the hydraulic variables. They describe the response (the range and optimal conditions utilised, or preferred) of the species to any one of these variables (Bain *et al.* 1982). The response values (normalised) can describe number of organsims per sample, population density, biomass or productivity (Slauson 1988). Independent of other variables, these data render a suitability index, between 0.0 and 1.0, for any single variable. The implication is that a value of "0" represents totally unsuitable habitat, whilst a value of "1", which has the highest frequency, represents optimal habitat. Depending on the methods of data collection, these curves may describe microhabitat *utilisation* alone (Category II criteria) or *preference* (Category III criteria- a combination of microhabitat utilisation and microhabitat availability) of the species for particular physical conditions (see Section 2.3).

8.3 THEORY OF DATA MANIPULATION AND THE CONSTRUCTION OF SI CURVES

Considerations in terms of data treatment for SI curves include sample size requirements, sampling bias and strategies, methods of curve construction and the treatment of end points and data pooling.

---

[1] Within IFIM, terms pertaining to habitat descriptions are frequently interchanged and SI curves may also be called *habitat suitability curves, models or indices,* or *species criteria* (Slauson 1988). The hydraulic variables are also referred to as *habitat suitability criteria.* These criteria might reflect a particular life history stage and/or season, in which case they are referred to as *conditional criteria* (Bovee 1986; see Chapter 2).

SAMPLE SIZE REQUIREMENTS FOR SI CURVE CONSTRUCTION

Due to the logistical and analytical implications, as well as possible damage to the resource, issues of sample size need consideration (Jackle & Barrett 1988). Various authors (e.g. Bovee 1982; US FWS 1985; Bovee 1986; Jackle & Barrett 1988) recommend that a minimum of 150 samples per lifestage is necessary to develop habitat preference curves. Jackle & Barrett (1988) caution against fixed sample size and suggest that the variance of the population, and the accuracy required, should govern this decision. They recommend a modified formula of that proposed by Eason (*cited in* Jackle & Barrett 1988):

Equation 8.1

$$n = tc\,[p-1]^2 \frac{(s^2)}{(a^2)}$$

where n = recommended sample size; tc [p-1] = critical value derived from Student's t-distribution; p = presample size; s = sample standard deviation; a = accuracy (units ± the true mean)

Alternative formulae are given in Armour *et al.* (1984) and Bovee (1986). The variability of habitat availability data is much greater than utilisation data and typically requires sample sizes twice as large (see Bovee & Zuboy 1988).

SAMPLING BIAS AND SAMPLING STRATEGIES

Sampling bias refers to both "fright" bias, in which an organism's behaviour changes due to the investigator and, "investigator" bias in which sampling design is inadequate (Bovee 1986; Bain 1988). Whilst fright bias is commonly taken into account (working upstream and avoiding times when fish are likely to be in transit), sampling design is frequently neglected (Bovee 1986; Bain 1988) and hence merits consideration.

Johnson & Nielsen (1983) detail four sampling strategies: (i) simple random, (ii) stratified random, (iii) clustered, and (iv) systematic, to which Bain *et al.* (1982) adds a fifth: (v) proportional sampling. Choice depends on the organism under investigation, the preparation time versus the resources available, the efficiency of the sample design and its compatibility with the observation technique. Given the concerns raised by Bovee (1986) and Bain (1988), descriptions of these methods, their advantages and disadvantages, and criteria for choice are provided in Table 8.1 (included at end of chapter).

METHODS FOR THE CONSTRUCTION OF SI CURVES AND THE TREATMENT OF END POINTS

Three basic approaches, elaborated by Bovee (1986), have evolved for SI curve construction, namely (1) histogram analysis, (2) nonparametric tolerance limits and, (3) nonlinear regression. Additionally, Slauson (1988) describes a fourth curve-fitting technique, that of running filters, which can also be used to smooth curves created with other techniques. Selecting an appropriate option is dependent on the advantages and limitations of each approach, and these are summarised in Table 8.2 (included at end of chapter). Due to their relative flexibility, simplicity and accuracy, *histogram analysis* is the most frequently used technique for SI curve construction (Cheslak & Garcia 1988).

Frequency-analysis data typically exhibit an irregular distribution due to the occurrence of fish in schools, an insufficient number of samples, and measurement error. Generally, these irregular points do not have a biological basis (Bovee 1986). Defining the curve is difficult with these uneven data distributions, and hence the frequency polygon is smoothed. This can, however, be at the expense of accuracy since continued clustering of data can distort the original information. Although two more accurate techniques exist, namely: minimising the residual sum of the squares (Bovee 1986) and least squares regression analysis (Bovee 1986; Slauson 1988), they are seldom used. An additional method, discussed by Slauson (1988), is that of *running filters* (Table 8.2). Cheslak & Garcia (1988) point out that the treatment of data for channel index, which may represent both discrete and continuous variables, has been largely neglected.

In curves that do not require smoothing, the tails of the curves are represented by raw data points (King & Tharme 1994). However when curves have been smoothed, a number of options for defining end points exist (Slauson 1988). They may be represented by the original points, or sketched by eye as a continuation of the curve, or estimated as the median Y-value of three points. Further discussion regarding the treatment of endpoints is given in King & Tharme (1994).

DATA POOLING

One of the most critical considerations in the derivation of SI curves is pooling data collected from different reaches, rivers or times into a common database (Bovee 1986; Locke 1988). As pointed out by Locke (1988), data pooling is an inevitable step in most studies since data are rarely collected only from one site, on one day or using one technique. Data pooling also overcomes the problems of deriving large numbers of curves that are specific to a site, season or life-stage and which then become unwieldy and difficult to interpret (but see comments below). Considerations for pooling data include sample size requirements; multi-technique approaches; numbers of study sites; weighting site-specific data to reflect the size of the area and the time spent at the site; characteristics of different rivers; unequal sampling effort; and sampling in different seasons and discharges.

For Category III curves, data are pooled to produce an overall description of microhabitat use and preference, either by combining raw data (*combined curves*), or by developing individual preference curves for each site and pooling these (*composite curves*). Locke (1988) recommends the latter procedure composite curves account for differences in microhabitat availability between sites.

CODING SUBSTRATUM AND COVER

Whilst depth and velocity are represented by values directly measured in the field, both substratum and cover have to be coded in such a way as to represent proportions of either of these variables. Codes describing channel indices (CI) consist of one or more numeric digits, with each digit describing a specific aspect of the substratum or cover. Although four digits can be accepted by PHABSIM II, King & Tharme (1994) advise restricting codes to three or fewer digits, with restricted options within each digit. This is because higher numbers of digits result in a large number of permutations that describe a complex mosaic of cells within the channel, with few matches to the coded requirements of the indicator species. Despite the inclusion of a biotic component such as algae in the codes proposed by Bovee (1986), its presence cannot be computed in the habitat routines of PHABSIM (King & Tharme 1994).

8.4 METHODOLOGY

FIELD SAMPLING TECHNIQUES

Chapter 5 provided a description of the three study sites (see Figure 5.6), and the sampling regime (see Table 5.1).

Sampling strategy and mapping

The sampling strategy most compatible with the objectives and logistical constraints of this study was modified cluster sampling (Bovee 1986; see Table 8.1). This strategy involved producing a detailed site map which delineated the location and size of each major habitat type. The area of each habitat type, which included riffles, runs, backwaters and pools, was calculated from the area occupied by each grid on the base map. On subsequent visits, a semi-quantitative on-site analysis was made of the relative habitat proportions against the base map. This field appraisal was used to determine the number of samples needed for each habitat type at each flow. Each habitat type was then stratified into 1 m^2 grids and numbered on a sketch map.

For the initial data collection in November 1990, habitats were sampled in proportion to the percentage in which they occurred. This trip, together with the results of the preliminary survey (see Chapter 4) confirmed that *C. anoterus* are found almost exclusively in riffles. Since riffles occurred in lower proportions than most other habitat types (15% at Sites 1 and 3, and 25% at Site 2), it was necessary to increase representation of samples in order to maximise microhabitat determination for *C. anoterus.* Therefore, for the remaining field trips, samples in riffles were taken in inverse proportion to the frequency of occurrence of that habitat type (i.e. if riffles represent 15% of the habitat, 85% of the samples were collected in riffle areas). The additional samples were allocated to remaining habitats in proportion to their occurrence. Collections in other habitat types were maintained in order to confirm habitat restriction and to include samples that contain conditions outside of the normal, or preferred, range of the target species. This is important because the SI curve intersects zero when fish are no longer found over an interval of a variable (Bovee 1986).

A total of 785 samples was taken over the sampling period. The number of samples taken⁽²⁾ was governed by sampling conditions and varied between 25 and 40 samples per site on each occasion. The $1m^2$ sample entity was selected using a random number table. Sampling locations were marked on the sketch map and located via lateral and longitudinal distances. Samples with depths of greater than 1m were discounted because of decreased capture efficiency due to poor visibility, danger of crocodiles and hippopotamus, and reduced electroshocker efficiency.

Collection of biological data

Observational techniques are not suitable for *Chiloglanis* as these fish are often found under rocks. A benthic sampler was tested but was difficult to position in such a way as to preclude fish escaping. Therefore, electrofishing which is compatible with modified cluster sampling (Bovee 1986), was used. One of the major criticisms of electroshocking is that it tends to disrupt fish positions. However, in the case of *C. anoterus*, which is a benthic, rheophilic species, electrofishing would appear to be the most effective method of capture, since disturbance more frequently elicits a hide, rather than flight, response (Dr. I. Russell, Cape Nature Conservation, *pers. comm.*). Electrofishing was conducted by means of a portable 550 watt Robin generator with coiled copper electrodes 20cm long and 50cm apart. Two hand nets with a mesh size of 1 cm were used.

The sampling run was started at the lower end of the stream reach and conducted in a direction counter to flow. The probe was held out of the water whilst the nets were set on the substratum, on the downstream side of the sample area. A single thrust with the probes was then used in a 1 m^2 area. Thereafter, a numbered marker, consisting of a sinker and float, was placed in each sample locality. When fish were netted, they were placed in buckets or plastic bags with numbers that corresponded to the marker, and sampling was continued. Fish were later identified and lengths (standard lengths) recorded. In addition, adults were sexed, weighed (using a 10g Pesola scale), and the reproductive condition of each was recorded (see Chapter 6). Fish were then returned to the water. A total of 3868 fish was caught over the study period. This included 2383 *C. anoterus*, comprising 254 early juveniles, 416 late juveniles and 1713 adults (Table 8.3). Hydraulic microhabitat measurements were then taken at the markers (see below).

---

[2] For this study, the guideline recommending a minimum of 150 data points per life stage (see Section 8.3) was followed. On the basis of the number of sites and field trips, 20 samples per site, per field trip, was set as the minimum.

Table 8.3
Sampling date, discharge and numbers of *C. anoterus* caught on each sampling occasion.

DATE	FIELD TRIP TYPE	DISCHARGE ($m^3 s^{-1}$)	NUMBERS		
			ADULTS	EARLY JUVENILES	LATE JUVENILES
Nov. 1990	Standard	0.31	87	18	22
Feb. 1991	Standard	5.84	193	6	42
June 1991	Standard	1.1	428	76	89
July 1991	Target early juveniles	0.25	56	37	57
Sep. 1991	Standard	0.65	339	58	50
Dec. 1991	Standard	1.45	209	28	82
Feb. 1992	Drought (2 sites)	1.14	215	24	33
Sep. 1992	Drought Survey	0.07	186	7	41
TOTALS			1713	254	416

Collection of Physical Microhabitat Data

At each site and at each sampling point, irrespective of the presence of fish, hydraulic microhabitat data were collected; namely velocity, depth, substratum and cover.

Depth measurements were recorded using the wading rod of the current meter; if the depth varied over the sampling area, an average of three measurements was recorded. Velocities were measured at a midpoint in the sample with a Price AA or mini current meter. In accordance with IFIM protocol (see Chapter 5), velocities were taken at 0.66 depth (from the surface) for depths less than 0.75m. If the depths were greater, additional velocities were also taken at 0.2 and 0.8 depths so as to calculate the mean water velocity. A number of authors advocate for the use of "focal" or "nose" velocity (Bovee 1986; Statzner *et al.* 1988) and therefore, if fish were captured behind or under hydraulic cover, an additional reading was taken as close to the point of capture as possible.

The same four-digit integer code that was described in Chapter 5 (see Table 5.4) was used to describe the cover and substratum. These complex substratum codes were later combined into a simpler, single coding system for use with PHABSIM (see below).

DATA MANIPULATION

Certain procedures, described below, were undertaken in the manipulation of data. These included:

1. Recoding cover and substratum codes for the development of a joint code.
2. Re-weighting the microhabitat availability data so as to produce a true representation of microhabitat availability.
3. Ranking microhabitat data in order to (a) develop the SI curves and (b) to test the hypotheses (Section 8.1).
4. The development of microhabitat-preference SI curves for each site and field trip.

5. The development of composite utilisation and preference curves for each season (site-composite curves).
6. The development of composite curves for all data (total-composite curves).

1. Recoding cover and substratum for the development of a joint code

The original four digit code describing substratum and cover (Table 5.4), had to be simplified to make the necessary linkup to conditions simulated for cells in the PHABSIM II runs. Since *C. anoterus* always use cover, the revised code referred to substratum alone (i.e. cover was implicit). This new code comprised two digits, with the tens representing the dominant substratum, and units the sub-dominant substratum (Table 8.4). Thus, a code of "64" represented a dominant substratum of boulders, with some gravel.

Table 8.4

Modified substratum code, derived from original field codes given in Table 5.4, developed for use in Suitability Curves and PHABSIM II

ORIGINAL CODE	REVISED CODE	SUBSTRATUM TYPE	SIZE (mm)
1 - 3	1	organic detritus, vascular plants, attached algae	/
4	2	mud (mud, silt, clay, soil)	≤ 0.05
5 - 6	3	sand (very fine- very coarse)	0.05 - 2
7 - 10	4	gravel (small- medium)	2 - 32
12 - 13	5	cobble (large gravel, small- large cobble)	32 - 250
14 - 15	6	boulder (small- medium)	250 - 1000
16 - 17	7	large boulder	1000 - 4000
18 - 23	8	bedrock	< 4000

2. *Microhabitat availability- weighting the data*

As stated, the target riffle habitat was sampled in inverse proportion to occurrence whilst the remaining samples were allocated proportionally to the rest of the microhabitats to give a balanced representation of the non-target habitats. Thus, with the exception of the first field trip, data had to be weighted to reflect the true proportions of habitats available, as follows:

i. Data were sorted to reflect unique sample numbers, giving the total number of samples.

ii. These samples were assigned to habitat type (riffles; runs; pools and backwaters), and samples for each habitat type were counted.

iii. The area of each of the non-riffle habitats was calculated as a percentage of the total. This then provided the area of riffles as a percentage of the total. These percentages constituted the weighting factors.

v. Within each class of depth, velocity and CI (see 3, below), counts are worked out as a percentage of the total, and then multiplied by the above weighting factor:

$$\frac{\text{class count habitat type (a)}}{\text{total count of all classes of habitat type (a)}} \times \text{weighting factor for habitat type (a)}$$

3. *Development of microhabitat availability and utilisation models*

Due to its relative flexibility, frequency histogram analysis was used to construct curves (Table 8.2). Exploratory data analysis treated all sites and all field trips separately and data were further stratified into early-juvenile (< 31mm SL), late-juvenile (31 - 38mm SL), and adult lifestages (see Chapter Seven).

Preliminary class intervals for continuous variables of depth and velocity data from each field trip were calculated using Sturges equation (Equation 8.2 (see Table 8.2). These were then adjusted to derive a standard class interval for all curves, as recommended by King & Tharme (1994). To facilitate comparison, the same class intervals were used for both utilisation and preference curves. Intervals were set at 0.10 m for depth, and 0.25 $m^3 s^{-1}$ for velocity.

Microhabitat-use curves were constructed from field measurements of depth, velocity and CI in samples in which adult or juvenile *C. anoterus* occurred, whilst microhabitat availability was computed from all samples. Both availability and use models were developed in the following way:

1. Raw data were ranked
2. These data were allocated to chosen size classes.
3. The relative frequencies of these class values were calculated. Curve smoothing was undertaken only on curves that displayed a highly irregular distribution and was limited to a single pass. The final values were normalised (the relative frequency per class interval is divided by highest relative frequency) and used to plot the SI curves. Curves for depth and velocity were hand drawn by fitting a smooth curve through the normalised frequency distribution. Normalised bar histograms were used to show substratum use.

Specifics pertaining to the development of composite curves are described below.

DATA ANALYSES AND MODEL COMPARISON

Preference data, about which no statistical inferences are made, are considered to be of limited value because they only provide a ratio of utilisation versus availability (Allredge & Ratti 1986). To address this issue, the approach recommended by Neu *et al.* (1974) and Byers & Steinhorst (1984) was considered. The availability and use of water depths and current velocities by *C. anoterus* were compared using the chi-square test to test the validity of the null hypotheses. Early juveniles were not analysed due to insufficient numbers. To protect against the probability of a type-I error due to multiple testing, the Bonferroni correction factor was applied at each level of analysis (Sokal & Rohlf 1995), with the first level alpha set at 0.05. The comparison of substratum data was confounded by the large number of classes that could not be further grouped without an unsatisfactory loss of information.

4. *Development of microhabitat preference models*

Microhabitat preference curves, which reflect use as a function of microhabitat availability (Category III curves), were created as follows:

i. Data were combined so that the relative frequency values of each class of utilisation data was divided by the equivalent value for availability, using the following formula⁽³⁾ (Bovee 1986):

$$Pr = \frac{P(\frac{E}{F})}{P(E)} \qquad \text{Equation 8.3}$$

where Pr = the relative Preference Index of a target species (for a specific set of environmental conditions); P(E/F) = Utilisation index (i.e. the probability of occurrence of a specific set of environmental conditions, given the presence of one or more individuals); P(E) = Availability index (i.e. the probability of occurrence of that specific set of environmental conditions in the stream at the time the organism was sampled).

ii. Results were then normalised to produce a preference curve.

5. *Data pooling and the development of composite SI curves*

So as to explore seasonal characteristics, data were pooled to produce **site-composite curves**, once they had been tested. The wet season was represented by data from November, December and February, and the dry season by data from June and September. Sites were weighted to account for differences in their area, as follows: Site 1; Site 2; Site 3 were weighted in the ratios 1:1.7:1.3 respectively. Once weighted, utilisation values were normalised. Data representing the protracted drought (March and September 1992) were analysed separately.

6. *The development of composite curves for all data (total-composite curves)*

Finally, as input to PHABSIM II, **total-composite curves** were derived by combining curves for all seasons to produce overall SI curves for early- and late juveniles, and for adults.

The end points of the SI curves were treated differently for preference and utilisation curves, and for each microhabitat variable. The lower tail of the depth curve was anchored at zero suitability for zero depth for both the utilisation and preference curves, as recommended by Milhous *et al.* (1990). The lower end point for velocity was determined as the proportion of entries in the lowest velocity class that had zero, or near zero velocities (King & Tharme 1994). The highest end points were anchored at the highest values (Baldridge & Amos 1981).

---

[3] Although most researchers derive preference values by way of this formula, alternative formulae are available, such as that of Jacobs (1974, *cited in* Heggenes & Saltveit 1990):

$$D = r-p/(r+p)- 2rp$$

where r = proportion of resource used by the fish, p= proportion of resource available in the environment. Application of this formula to these data produced similar curves but had the effect of exaggerating the lower values of the curve.

8.5 RESULTS

In terms of the broad habitat types, adult *C. anoterus* are almost exclusively restricted to rapids (Plate 8.1). Early juveniles, on the other hand, are found in low-velocity, sand/ cobble substrata runs (Plate 8.2). Late juveniles occur in both of these habitat types, but principally in the former.

OVERALL MICROHABITAT AVAILABILITY, USE AND PREFERENCE

The following broad descriptions of habitat availability, use and preference were evident from the SI curves (Figures 8.1 - 8.3).

- Depths between 0.2 - 0.4 m were most commonly available and utilised (Figure 8.1). All lifestages used the full range of depths available (between 0 - 1 m) and displayed similar curves.
- Available velocities ranged from 0 to 1.5 m s^{-1}, with outliers at 2.5 m s^{-1} (Figure 8.2). Early juveniles occupied a restricted range of velocities (near-zero to 1 m s^{-1}), with optima between 0.25 (use) and 0.75 m s^{-1} (preference). As cohorts matured, they used a wider range of velocities (near-zero to 1.5 m s^{-1}) and were found mainly in swifter waters. Adults displayed a similar curve to that of late juveniles but preferred higher velocities of 1.5 m s^{-1}.
- All *C. anoterus* utilise cover (visual and/or hydraulic) and hence cover is implicit in substratum descriptors. A total of 32 substratum codes was recorded (Figure 8.3). All lifestages used bedrock and algae, (although early juveniles select areas of lower velocities), but early juveniles were distinctive in that they used, and preferred, sand and detrital substrata over all others. As individuals matured, they shifted to cobble and bedrock. Adults used a wide range of substrata, from bedrock to gravel but never smaller than gravel, and preferred boulder and bedrock substrata (Figure 8.3).

Plate 8.1 Typical boulder rapid habitat of late juvenile and adult *C. anoterus* in the Marite River.

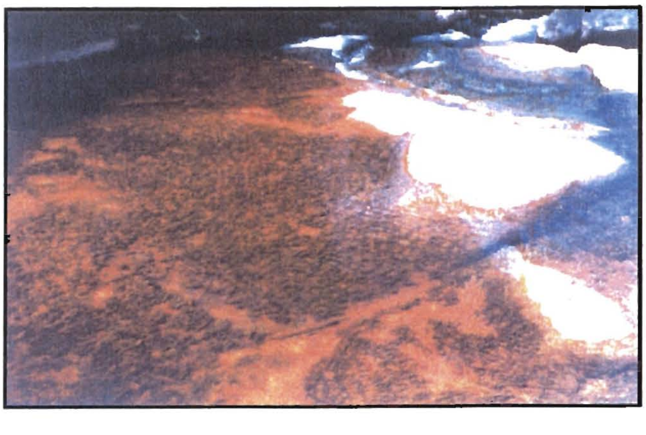


Plate 8.2 Typical shallow, slow-run habitat of early juvenile *C. anoterus* in the Marite River. Note the filamentous algae which offers hydraulic and overhead cover for the young fish.

SEASONAL MICROHABITAT AVAILABILITY, USE AND PREFERENCE

The range of available depths and velocities were similar in the wet- and dry-season, but their distributions varied seasonally (Figures 8.4 & 8.5). Peak depths increased from 0.2 m, to 0.4 m at discharges higher than 1.2 m^3 s^{-1}. In the case of velocity, a marked increased from 0.25 to 1 m s^{-1} only occurred at the highest discharge of 5.8 m^3 s^{-1}. Winter low-flows were characterised by a greater number of substratum types due to the addition of organic detritus, silt and gravel (Figures 8.6 & 8.7).

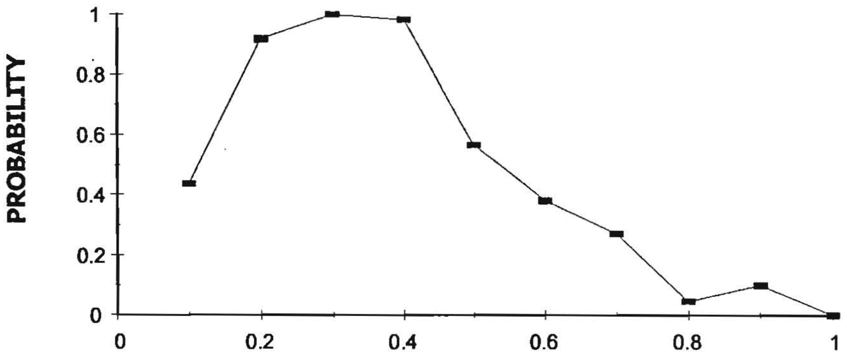
The range of utilisation and preference curves for depth, and velocity, was constant but the modes shifted seasonally, suggesting that *C. anoterus* will use deeper, fast-flowing habitats if available. The optimum velocities that were used and preferred fell between 0.5 and 1.25 m s^{-1}. No clear trends were evident, however, in that the optimum values did not seem to increase (or decrease) in any clear pattern as discharge increased. Similarly, preference appeared to decline and then increase (see later discussions). Generally, the patterns of substratum use remained seasonally constant, although adults were more common in boulders at the lowest discharge and thereafter on bedrock substrata. However, the preference functions varied considerably (Figure 8.7), and possible reasons for this are discussed in the following section. The seasonal shift towards the use of larger substrata by juveniles is probably accounted for by cohorts nearing maturity (December), when their substratum use is similar to that of adults (Figure 8.6).

MICROHABITAT AVAILABILITY AND USE DURING EXTREME LOW FLOWS

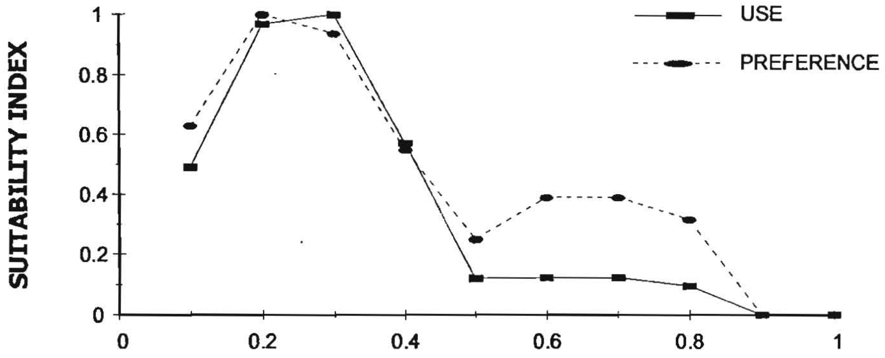
Both the range and distribution of available depths and velocities decreased with the drought (Figures 8.8 & 8.9). The optimum depths declined to 0.1 m, compared to 0.2 m of the previous year, and velocities declined from approximately 0.75 to 0.25 m s^{-1}. Substratum availability had changed considerably and was dominated by silt, clay and organic detritus (Figure 8.10).

Generally, the utilisation functions for depth, velocity for both adults and juveniles were narrower and the optima had decreased. Substratum use was similar to that of the preceding season. More important, preference curves had changed markedly, intimating that preference changes as a function of dewatering. For example, in the previous seasons, adults preferred habitats with depths of 0.4 m, and current speeds of 1 m s^{-1}, but now appeared to prefer depths of 0.2 m, with velocities of 0.75 m s^{-1}. This apparent shift in preference is dealt with in some length in Section 8.6.

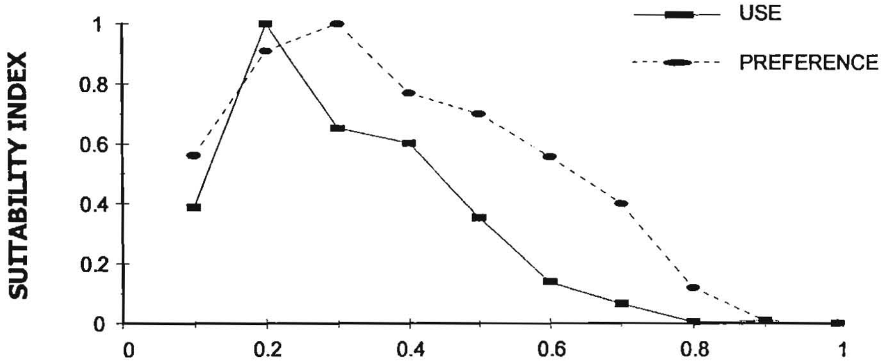
Depth availability



Early juvenile (<31 mm SL) depth use and preference



Late juvenile (31- 38 mm SL) depth use and preference



Adult depth use and preference

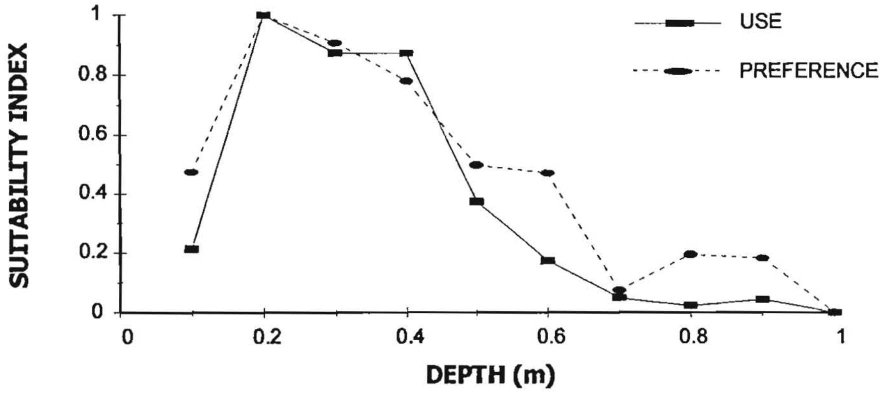
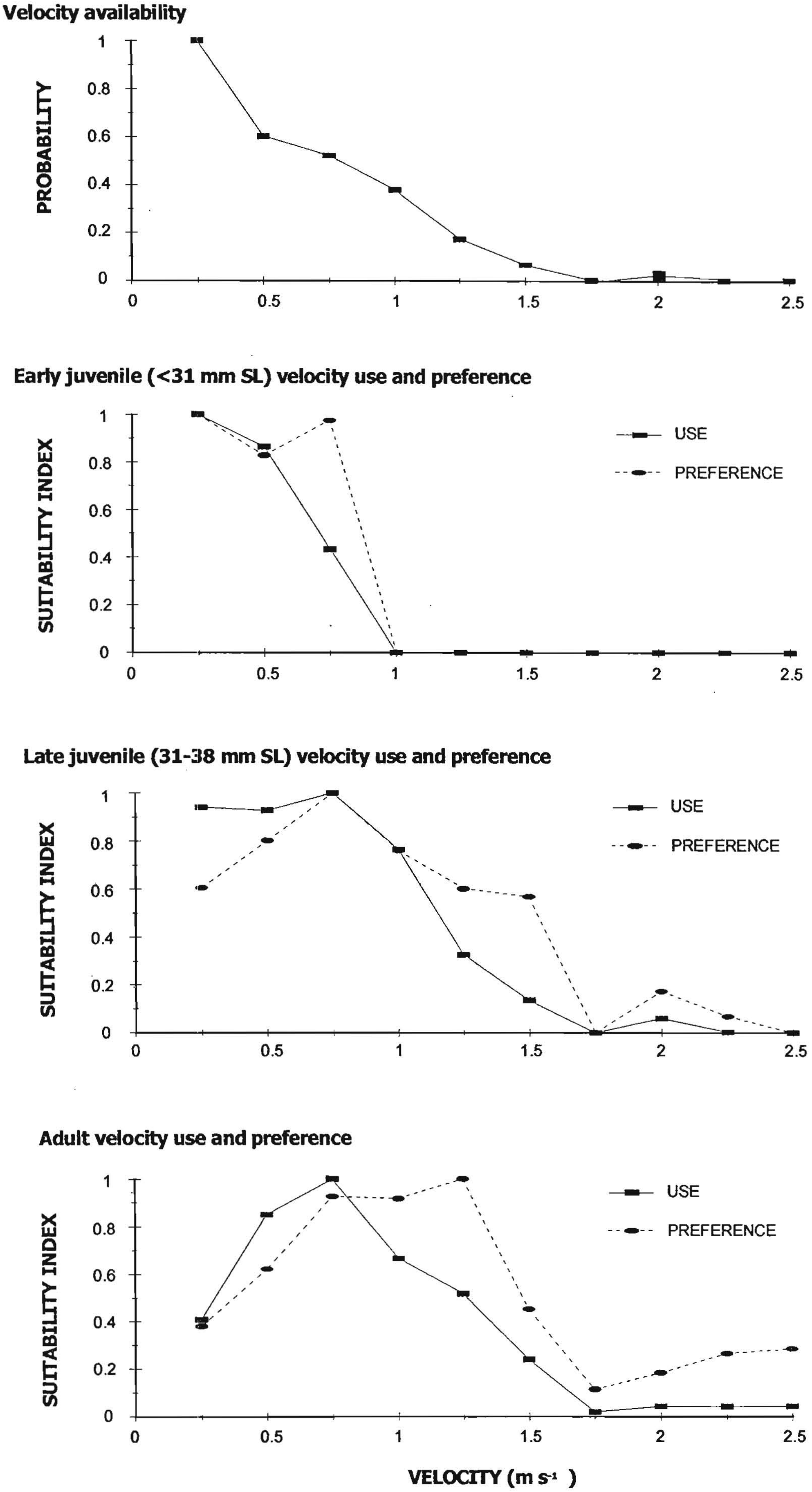


Figure 8.1 Total-composite SI curves (between discharges of 0.3 and 5.8 m^3s^{-1}) of depth availability, use and preference, for juvenile and adult *C. anoterus*. Note that all lifestages used a similar range of depths.


Velocity availability

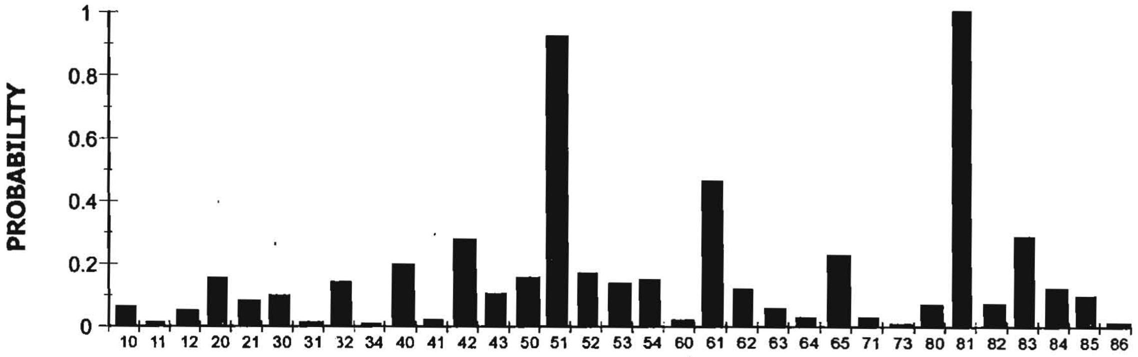
Early juvenile (<31 mm SL) velocity use and preference

Late juvenile (31-38 mm SL) velocity use and preference

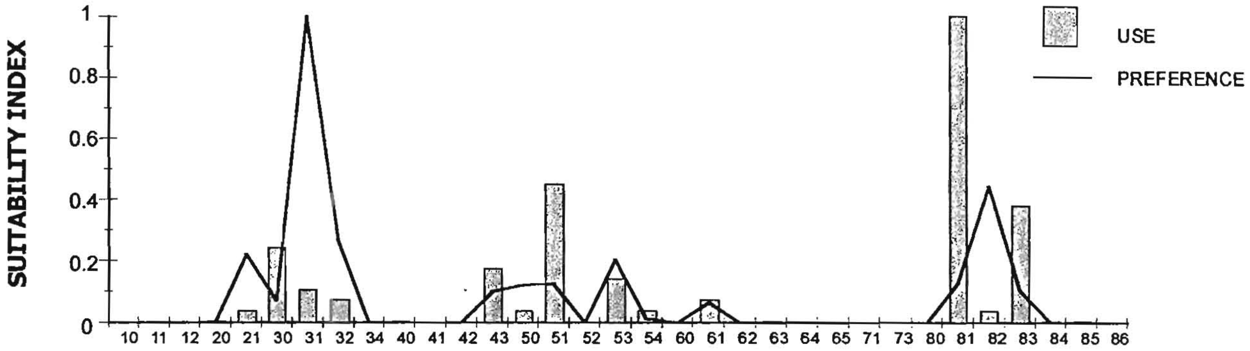
Adult velocity use and preference

Figure 8.2 Total-composite SI models (between discharges of 0.3 and 5.8 m^3s^{-1}) of velocity availability, use and preference, for juvenile and adult *C. anoterus*. Note the narrower range and low-velocity optimum evident for juveniles.

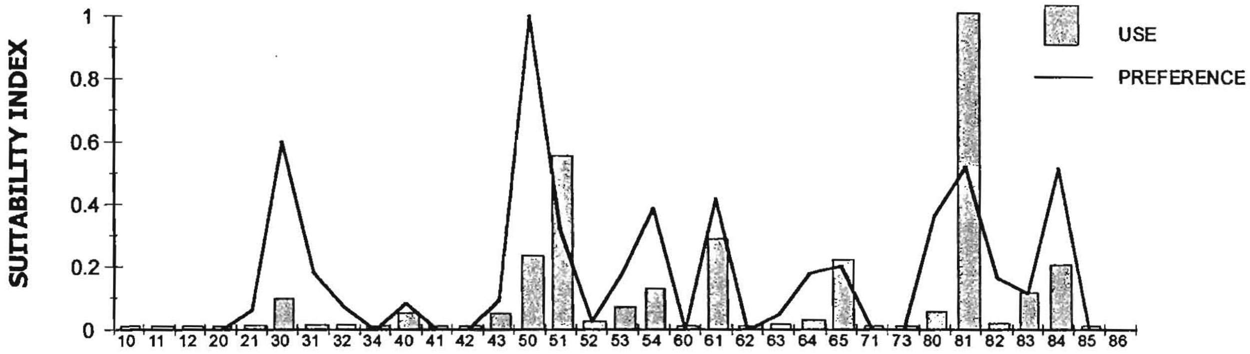
Substratum availability



Early juvenile (<31 mm SL) substratum use and preference



Late juvenile (31- 38 mm SL) substratum use and preference



Adult substratum use and preference

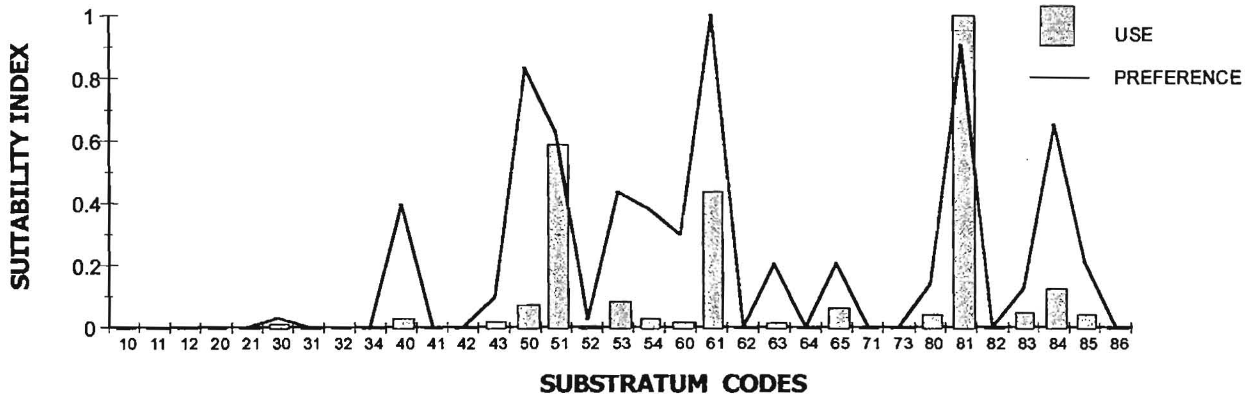


Figure 8.3 Composite substratum curves (between discharges of 0.3 and 5.8 m^{3}s^{-1}) of availability, use and preference for juvenile and adult *C. anoterus*. Substratum codes represent a combination of dominant and subdominant substratum types (see Table 8.4), as follows: 1= organic detritus, vascular plants & algae; 2= mud/ silt; 3= sand; 4= gravel; 5= cobble; 6= boulder; 7= large boulder; 8= bedrock. Note that all SI curves of use and availability implicitly include cover since *C. anoterus* is always uses hydraulic and/ or visual cover (see text for details).

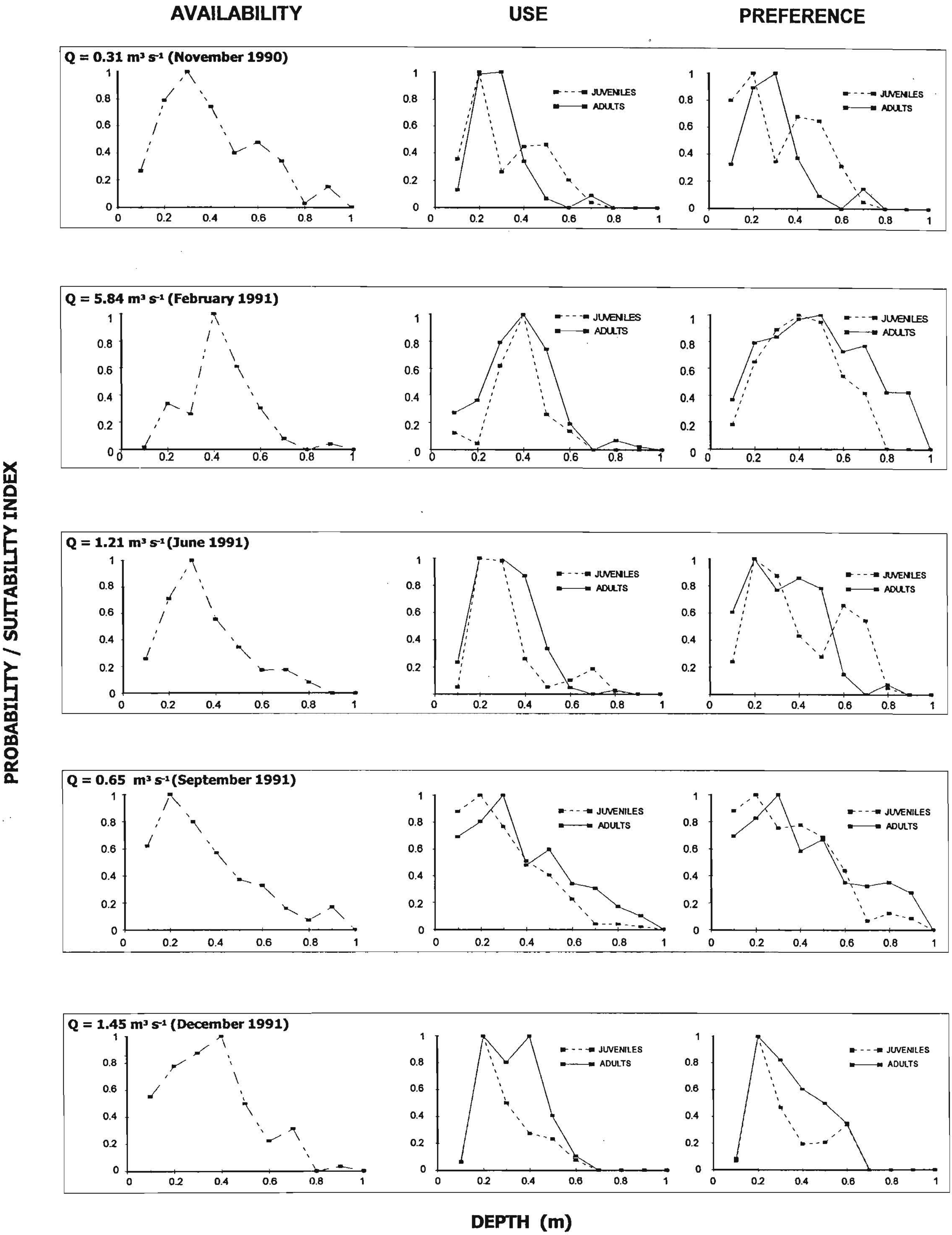


Figure 8.4 Site-composite SI models indicating the seasonal variations in available depths, utilisation and preference for late-juvenile and adult *C. anoterus*. Curve smoothing was limited to one pass (see text for details). Q = discharge.

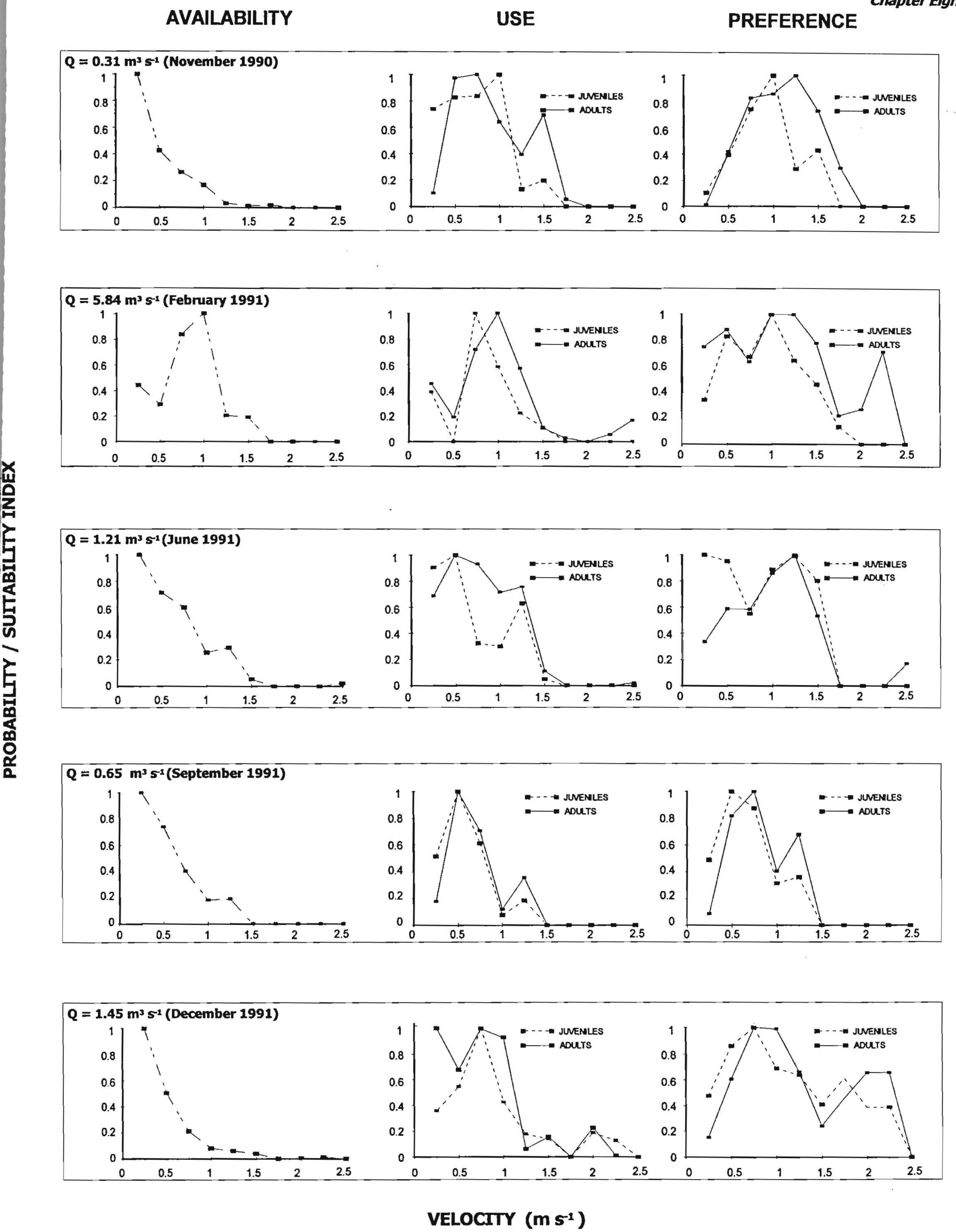


Figure 8.5 Site-composite SI models indicating seasonal variations in available velocity, utilisation and preference for late-juvenile and adult *C. anoterus*. Curve smoothing was limited to one pass (see text for details). Q = discharge.

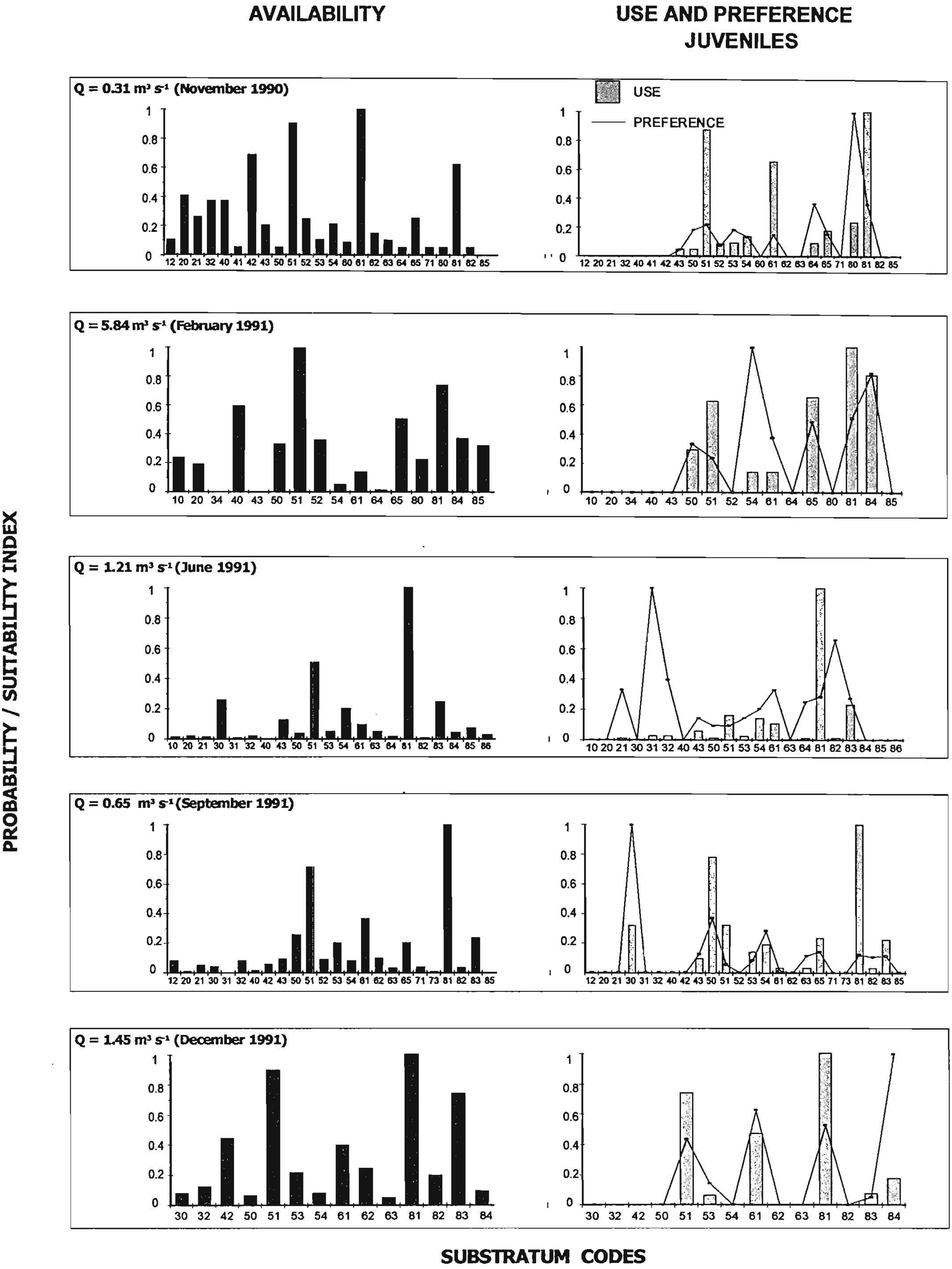


Figure 8.6 Site-composite substratum SI curves, indicating the seasonal variation in availability, use and preference for late-juvenile *C. anoterus*. Q = discharge. Substratum codes represent a combination of dominant and subdominant substratum types (see Table 8.4), as follows: 1= organic detritus, vascular plants, algae; 2= mud/ silt; 3= sand; 4= gravel; 5= cobble; 6= boulder; 7= large boulder; 8= bedrock. All codes used implicitly include cover.

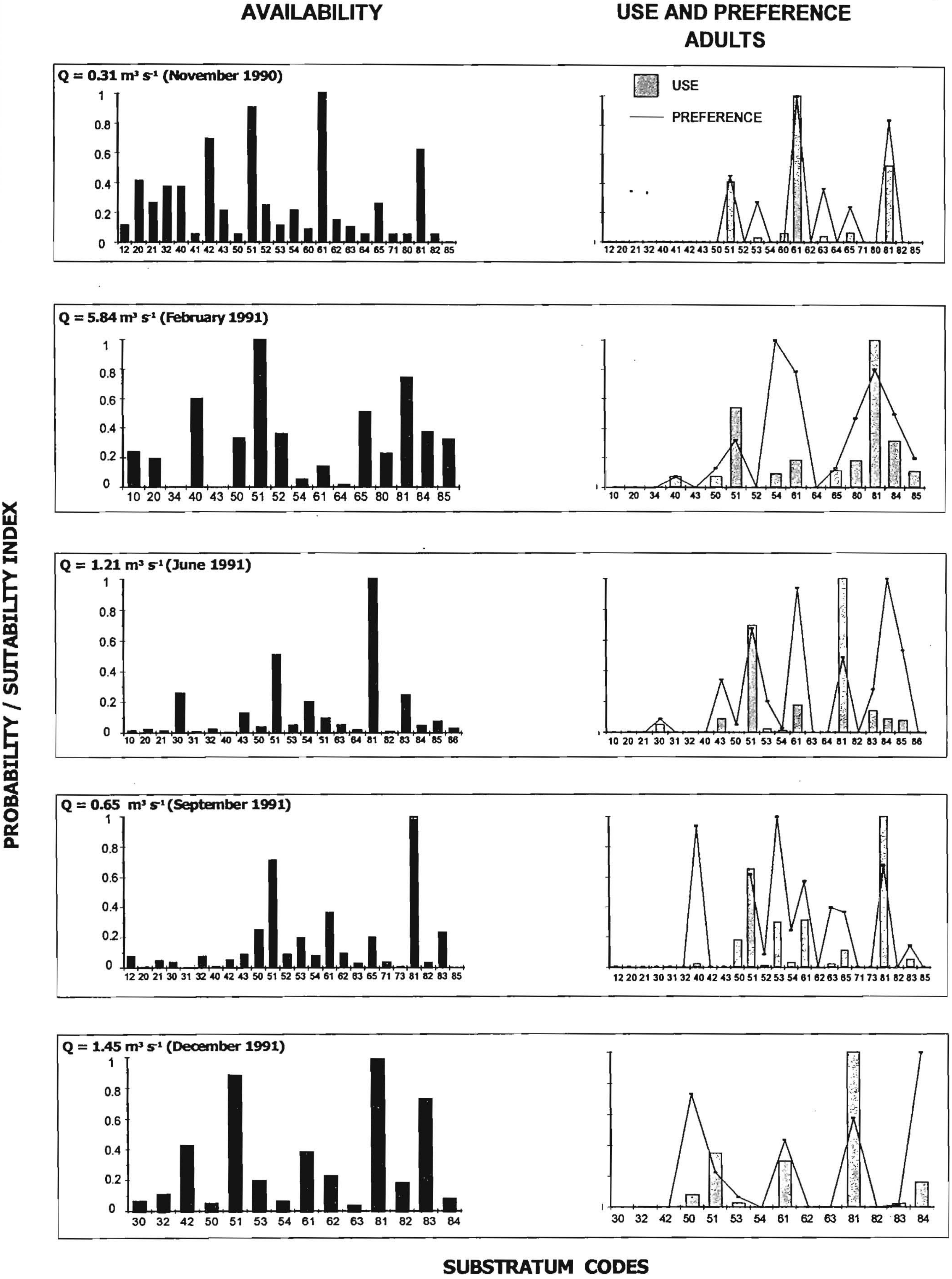


Figure 8.7 Site-composite substratum SI curves, indicating the seasonal variation in availability, use and preference for adult *C. anoterus*. Q = discharge. Substratum codes represent a combination of dominant and subdominant substratum types (see Table 8.4), as follows: 1= organic detritus, vascular plants, algae; 2= mud/ silt; 3= sand; 4= gravel; 5= cobble; 6= boulder; 7= large boulder; 8= bedrock. All codes used implicitly include cover.

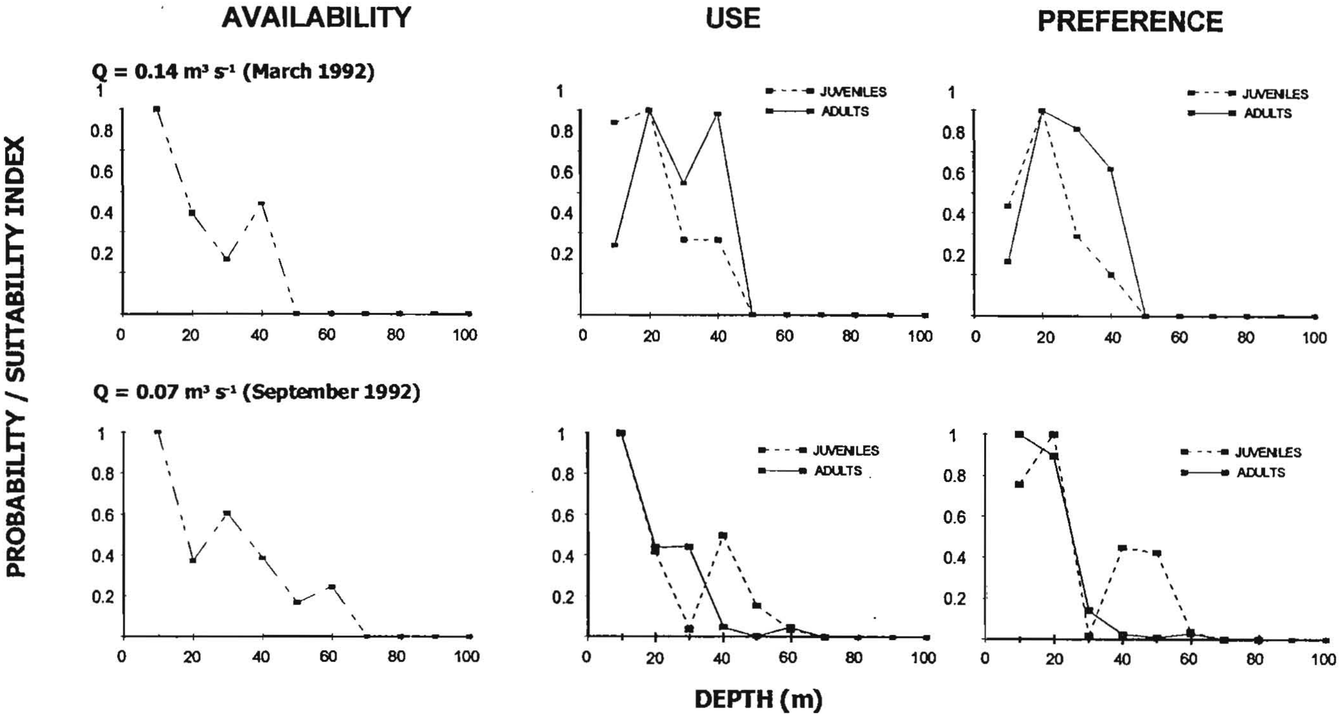


Figure 8.8 Site-composite SI models for depth over the drought indicating availability, use and preference for late-juvenile and adult *C. anoterus*. Comparing these SI curves to those in Figure 8.1, optimum utilisation values of SI curves at the lowest discharge are lower than those of the total-composite values, and the range of depths available and used are more limited (but see comments regarding preference in Figure 8.9). Note that March data were only collected at two sites.

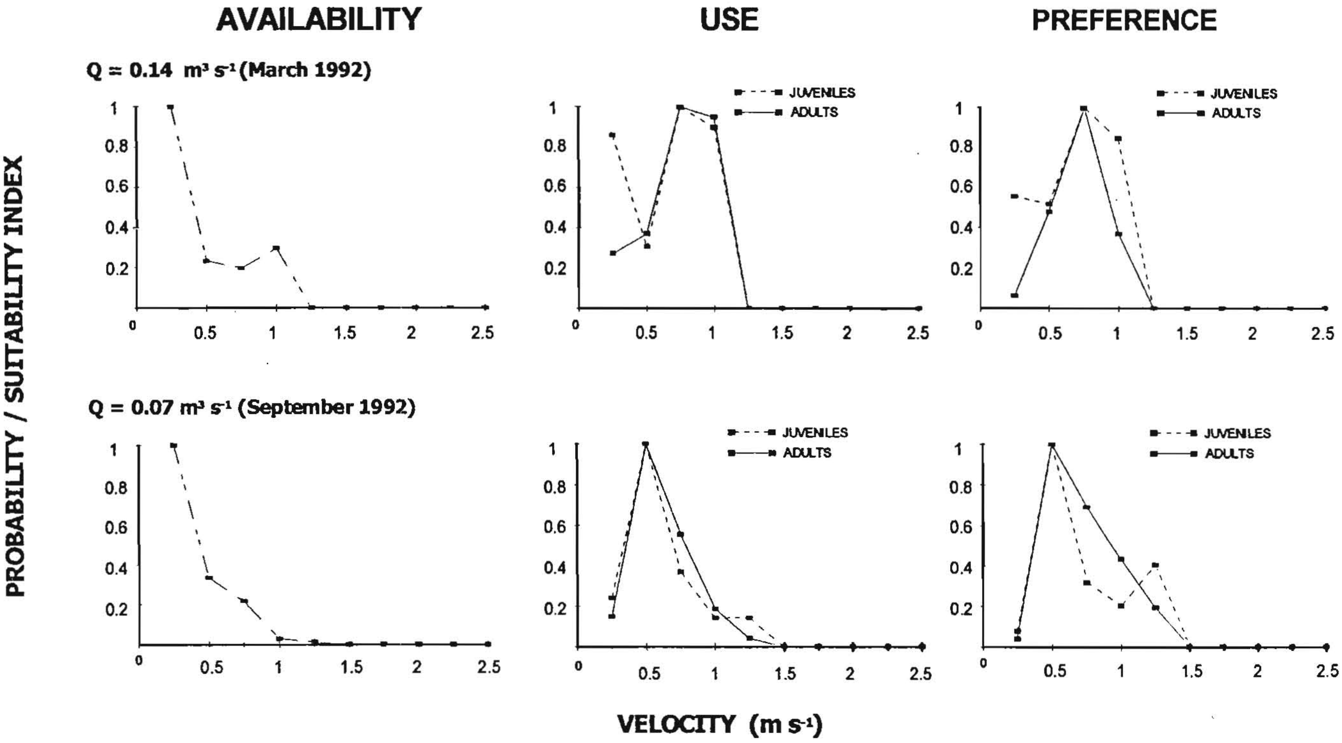


Figure 8.9 Site-composite SI models for velocity over the drought indicating availability, use and preference for late-juvenile and adult *C. anoterus*. Comparing these SI curves to those in Figure 8.2, optimum utilisation values of SI curves at the lowest discharge are lower than those of the total-composite values, and the range of velocities available and used are more limited. Note that preference appears to decrease with a progression of the drought (i.e. as the range of available velocities decreases). With little biological rationale, these results are believed to be anomalies of the determination of velocity availability (the same comments apply in the case of depth; see Section 8.6 for details). Note that March data were only collected at two sites.

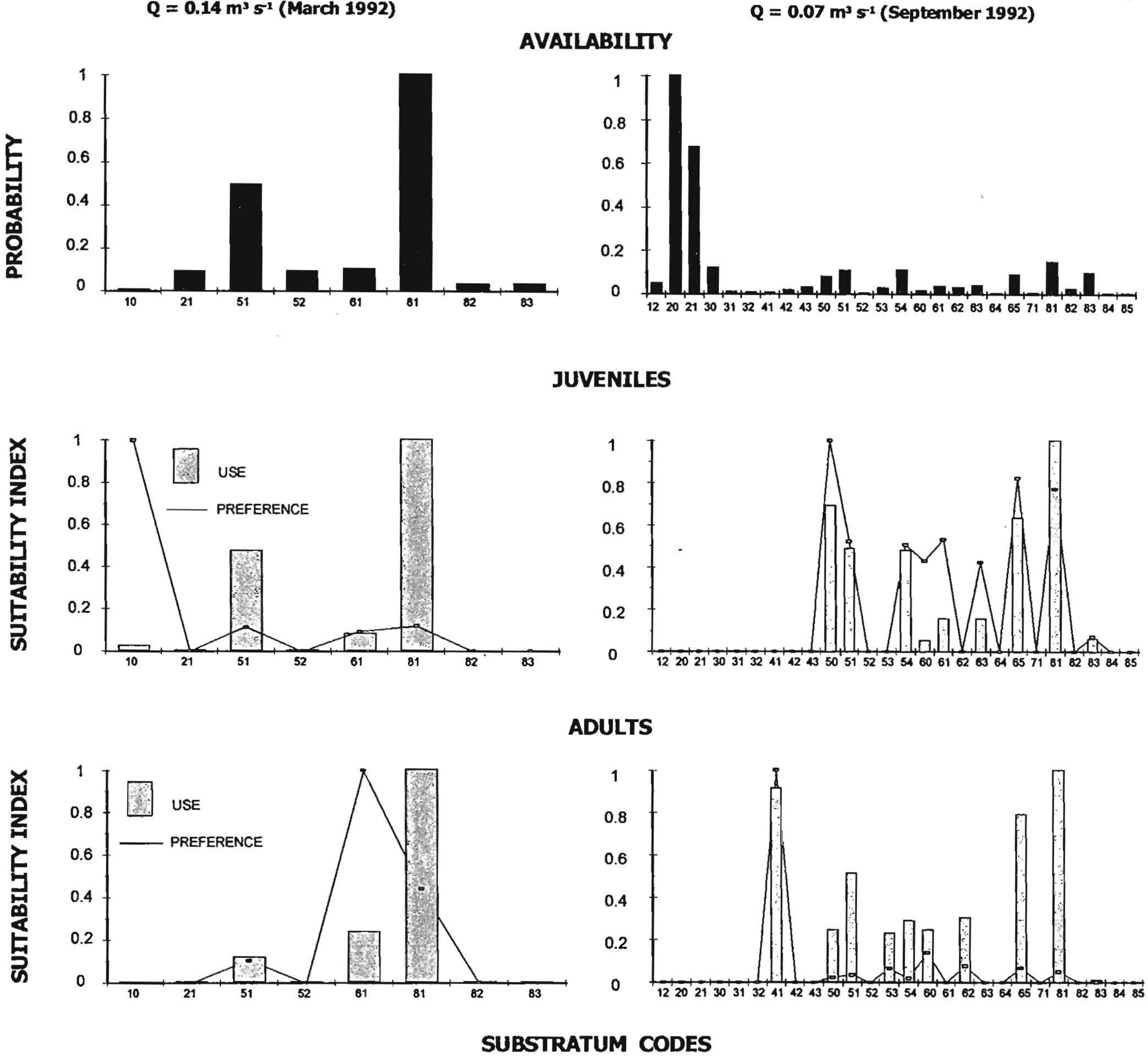


Figure 8.10 Site-composite substratum curves over the drought period indicating availability, use and preference for juvenile and adult *C. anoterus*. Note that March data were only collected at two sites. Q = discharge. Substratum codes represent a combination of dominant and subdominant substratum types (see Table 8.4), as follows: 1= organic detritus, vascular plants, algae; 2= mud/ silt; 3= sand; 4= gravel; 5= cobble; 6= boulder; 7= large boulder; 8= bedrock.

ASSESSING THE HYPOTHESES: MICROHABITAT AVAILABILITY AND USE BY JUVENILES AND ADULTS, AS A FUNCTION OF SPATIAL AND TEMPORAL FACTORS

1. *Chiloglanis anoterus does not select a particular microhabitat condition and therefore microhabitat use tracks microhabitat availability*

An analysis of data for the drought months was not possible due to clumped data distributions. The null hypothesis was rejected in the majority of months, and sites, for depth (21 out of 28 pairwise tests), and velocity (26 out of 28 pairwise tests; Table 8.5). Results therefore suggest that both juvenile and adult *C. anoterus* select for a specific range of depths and velocities.

Table 8.5

Relationship between availability and utilisation of depth and velocity, at all sites over the study period (excluding drought months). Significance, corrected for multiple testing, abbreviated as follows: df = degrees of freedom; NS = Not Significant at $p < 0.008$; * = Significant at $p < 0.008$; ** = Significant at $p < 0.001$; * = Significant at $p < 0.0001$. Empty cells= not tested due to limited data.**

		SITE					
		1		2		3	
FIELD TRIP		*p*	df	*p*	df	*p*	df
DEPTH							
NOV. 90	Juvenile	***	5	***	3	NS	5
	Adult	***	5	***	3	***	5
FEB. 91	Juvenile			**	3		
	Adult	NS	3	***	3	*	2
JUN. 91	Juvenile	***	4	NS	3	***	4
	Adult	NS	5	NS	5	***	6
SEP. 91	Juvenile	NS	4	*	2	***	4
	Adult	***	7	***	4	***	5
DEC. 91	Juvenile	NS	4	***	2	***	3
	Adult	***	6	***	4	***	5
VELOCITY							
NOV. 90	Juvenile	***	3	***	2	***	2
	Adult	***	3	***	2	***	2
FEB. 91	Juvenile			**	3		
	Adult	*	2	***	3	***	4
JUN. 91	Juvenile	***	3	***	2	***	4
	Adult	NS	3	***	4	***	5
SEP. 91	Juvenile	NS	3	***	2	***	2
	Adult	***	4	***	3	***	2
DEC. 91	Juvenile	***	2	***	2	***	2
	Adult	***	3	***	3	***	3

2. Microhabitat availability does not differ significantly between sites, at a specific time (flow)

Overall, results varied and the hypothesis was rejected in about 50% of the 19 pairwise tests (Table 8.6). The distribution of available water depths differed significantly between Sites 1 and 2 ($p< 0.008$), with the exception of December. Depths at site 2 were generally shallower than at Site 1. In almost all instances, there were no significant differences in available depths between Sites 2 and 3. No clear trends were evident in the case of velocity.

Table 8.6

Differences in microhabitat availability between sites within months ($p<0.008$). Significance, corrected for multiple testing, abbreviated as follows: df = degrees of freedom; NS = Not Significant at $p< 0.008$; * = Significant at $p< 0.008$; ** = Significant at $p< 0.001$; * = Significant at $p< 0.0001$**

MONTH	SITE	Depth		Velocity	
		p	df	*p*	df
NOV. 90	1-2	*	3	NS	3
	1-3	NS	4	NS	2
	2-3	NS	3	NS	2
FEB. 91	1-2	***	3	NS	3
	1-3	***	3	NS	3
	2-3	NS	2	***	3
JUN. 91	1-2	***	4	**	3
	1-3	***	5	NS	5
	2-3	***	5	***	5
SEP.91	1-2	***	5	*	4
	1-3	NS	5	***	3
	2-3	NS	5	NS	3
DEC. 91	1-2	NS	5	NS	3
	1-3	***	4	NS	3
	2-3	***	4	NS	2
MAR. 92	1-2	***	3	*	2
SEP. 92	1-2	***	5	*	3
	1-3	NS	5	***	3
	2-3	NS	5	NS	3

3. Microhabitat use patterns do not differ between sites, at a specific time (flow)

Data clumping precluded the analysis of data for the juveniles and for the drought. In terms of adults, significant differences were evident in the depths(12 out of 14 pairwise tests) and velocities (14 out of 15 pairwise tests) used at different sites (Table 8.7). In the case of juveniles, the null hypothesis was rejected for 5 out of 9, and 6 out of 9 pairwise tests for depth and velocity respectively. In both adults and juveniles, depth use was consistently different between Sites 1 and 2, but not between Sites 1 and 3. At Site 2, they used shallower depths and slightly slower current speeds. Thus, adults appear to use significantly different microhabitat use ($p<0.008$) at different sites, but this trend was less clear in juveniles.

Table 8.7

Differences in microhabitat use patterns between sites within months (p<0.008). Significance, corrected for multiple testing, abbreviated as follows: df = degrees of freedom; NS = Not Significant at *p* < 0.008; * = Significant at *p* < 0.008; ** = Significant at *p* < 0.001; * = Significant at *p* < 0.0001. Empty cells = no tests due to limited data**

		ADULTS				JUVENILES			
MONTH	**SITE**	**Depth**		**Velocity**		**Depth**		**Velocity**	
		p	df	*p*	df	*p*	df	*p*	df
NOV. 90	1-2	***	2	***	2				
	1-3	***	2	**	2	***	2		
	2-3	NS	2	***	2				
FEB. 91	1-2	***	3	***	3				
	1-3	***	3	***	3				
	2-3	***	4	**	3				
JUN. 91	1-2	*	4	***	4	*	3	**	2
	1-3	*	4	***	4	NS	2	**	2
	2-3	***	4	***	5	***	2	**	3
SEP.91	1-2	***	3	***	4	*	3	**	2
	1-3	***	2	NS	2	NS	2	**	2
	2-3	***	3	**	2	NS	2	NS	2
DEC. 91	1-2	***	4	NS	3	**	2	NS	2
	1-3	NS	4	***	4	NS	3	**	2
	2-3			**	3	***	2	NS	3

Table 8.8

Differences in microhabitat use between adults and juveniles at all sites over the study period. Significance, corrected for multiple testing, abbreviated as follows: df = degrees of freedom; NS = Not Significant at *p* < 0.008; * = Significant at *p* < 0.008; ** = Significant at *p* < 0.001; * = Significant at *p* < 0.0001. Empty cells = no tests due to limited data.**

MONTH	**SITE**	**DEPTH**		**VELOCITY**	
		p	df	*p*	df
JUN. 91	1	***	3	***	2
	2	NS	3	NS	4
	3	***	3	***	3
SEP. 91	1	***	3	***	2
	2			NS	2
	3	**	2	NS	1
DEC. 91	1	***	3	***	3
	2	NS	1	NS	3
	3	NS	3	NS	3
MAR. 92	1	***	2	***	3
	2			NS	2
SEP. 92	1	***	2		
	2	NS	1		
	3				

4. *Microhabitat use does not differ significantly between adults and juveniles at a specific site and time (flow)*

Data for November 1990 were not analysed due to insufficient categories. At Site 1, adults and juveniles exhibited highly significant differences in the distribution of depth and velocity used and this hypothesis was rejected (Table 8.8). At Site 1, adults used deeper, swifter velocity microhabitats than juveniles. The differences at Site 1 can probably be accounted for by the more complex array of habitat types than at Site 2 (see Chapter 11). In contrast, no significant differences were evident in their microhabitat use at Site 2 and results from Site 3 varied monthly.

5 *Microhabitat use at a site does not exhibit a seasonal variation*

Only data considered to be representative of a "normal" wet and dry season were used in this analysis (i.e. drought data were not included). The wet season was represented by February data and the dry season by June data. Juveniles were excluded due to insufficient data.

Highly significant differences were evident in microhabitat use by adults for depth and velocity (Table 8.9) between the wet and dry season ($p<0.008$) and therefore this hypothesis was rejected. These seasonal differences were due to a shift in to lower optimum values in the dry season, although the range of variables available remained consistent (see Figures 8.4 & 8.5 and the earlier discussion).

Table 8.9
Differences in seasonal microhabitat use, represented by February and June 1991. Significance, corrected for multiple testing, abbreviated as follows: df = degrees of freedom; * = Significant at $p < 0.0001$**

SITE	DEPTH		VELOCITY	
	p	df	*p*	df
1	***	2	***	3
2	***	4	***	4
3	***	4	***	5

In summary, the following conclusions can be drawn from the above analyses:

- Both juvenile and adult *C. anoterus* select for a specific range of depths and velocities.
- Microhabitat availability differed between sites in about half of the cases tested. Notably, depths were significantly shallower at Site 2. No clear trends were evident at Site 3. Likewise, no clear trends emerged in the case of velocity.
- Adults appear to use different microhabitats at different sites but trends were less clear in juveniles. This may reflect insufficient data for this lifestage.
- Differences in microhabitat use between juveniles and adults varied between sites.
- Highly significant seasonal differences in microhabitat use by adults was demonstrated.

8.6 DISCUSSION

Together with the work of Weeks *et al.* (1996), these results provide the first detailed descriptions of microhabitat use in juvenile and adult *C. anoterus*. They derived composite curves and, in general, there was concurrence between our findings. Additionally, I stratified the data to test for seasonal, site-specific and lifestage responses. My findings suggest seasonal differences in microhabitat use by adults, as well as between early and late juveniles. For example, as juveniles mature, they move from slow-velocity, sand runs into high-velocity-habitats with larger substrata. Similar substratum transitions with maturity have been shown in trout (Johnson & Kucera 1984) and Atlantic salmon (Rimmer *et al.* 1984).

Whilst providing some insight into microhabitat use, the lack of clear trends at some sites (and at certain times), and the apparent inconsistencies in results were perplexing. For example, although adult *C. anoterus* select particular microhabitat conditions (Hypothesis 1), these appear to differ between sites (Hypothesis 3). Secondly, adults and juveniles appear to share the same microhabitats at certain places and times, but not at others (Hypothesis 4). Both Angermeier (1987) and Heggenes & Saltveit (1990) caution against the interpretation of curves as absolutes and contend that in fact fish can adapt to a wide variety of habitat conditions, within ranges (see also Lanka *et al.* 1987; Kozel & Hubert 1989; Chapter 11). They suggest that a certain plasticity in use, dictated, in part, by the available conditions. It is likely that the simpler array of microhabitat types at Site 2 (see Chapter 11) simply forces adults and juveniles into similar conditions, causing convergence of the SI models. It is postulated that the available conditions are largely responsible for these seemingly disparate results and this issue is the focus of the following discussion. Alternatively, as suggested by Grossman *et al.* (1995), there is a logical flaw in approaches that do not include biological, and/or catchment determinants of habitat use (see discussion in Chapter 13).

Derivation and interpretation of preference models

Questions regarding the availability of a resource, such as habitat, and how it is exploited are critical to understanding the ecology and management of a system (Johnson 1980; White 1987). How investigators choose to explore these questions, and interpret results, differ. The use of *preference indices* (Ivlev 1961) attempts to capture the concept of habitat selection. Despite the fact that their use has been questioned, principally in terrestrial ecology (e.g. Strauss 1979; Johnson 1980; Allredge & Ratti 1986; Pienaar 1992), this has been largely ignored in microhabitat studies, with the exception of Slauson (1990) and Bartholow & Slauson (1990).

In this section, I hope to support contentions that preference indices are an unsatisfactory means to represent habitat selectivity. This is mainly due to their conditional nature in that they are influenced by the quantification of habitat availability, and the failure to consider the mathematical repercussions of this.

To assess whether or not SI preference models correctly, or even adequately, describe a species' selection of a resource, it must be recognised that the character of preference curves is fundamentally linked to availability estimates. Furthermore, since preference is, in reality, merely a measure of the relative density of an animal (proportion of habitat used divided by the habitat available), more needs to be known before assuming that high densities signify preference (Johnson 1980; van Horn 1983, Slauson 1990). Johnson (1980) defines preference as "the likelihood of that component being chosen if offered on an equal basis with others". Although *preference* is ordinarily claimed to be independent of availability, the "likelihood" of a resource being selected is described, within IFIM, by a ratio (see equation 8.3) that is derived as a function of the resource availability. The inference, therefore, of the unnormalised preference index, such as an index of 2.0, is that there are twice the number of animals in that habitat class as would be expected *if there were a uniform distribution of animals over all habitats in accordance with the distribution of habitat available.*

Nonetheless, values of habitat availability may not be absolute since estimates of habitat availability (and hence the resultant preference values) are influenced by a number of factors. Firstly, sampling constraints may exclude certain conditions and considerably change the description of available habitat. For instance, Peters (see discussion sessions *in* Bain 1988) suggests that maximum velocity beyond which electrofishing efficiencies declines is approximately 2.5 ft s^{-1} (0.762 m s^{-1}). Secondly, different curves can be produced by using different sampling techniques (Bain *et al.* 1988). Thirdly, preference calculations are governed by conditions that the investigator deems available (Johnson 1980), but which may differ considerably from what the animal considers available (White 1987; Shirvell 1989). For example, behavioural traits, such as territoriality, may preclude the use of a specific area even though the hydraulic data indicates that the area is suitable for use.

This discussion prefaces one of the most serious concerns regarding this component of IFIM, which relates to the quantification of habitat availability and the mathematical behaviour of the SI curves. According to the above definition, SI indices are derived on the basis that each resource component is offered on an *equal basis* and yet, this is rarely true in reality. The maximum possible preference rating then becomes a function of the availability. To demonstrate this, I have constructed various scenarios, presented in Table 8.10, which illustrate what happens to preference indices at different levels of availability. Consider a single depth class (say 0 - 0.10 m), available in increasing proportions (column 1). Scenario 1 assumes that this depth class has a 100% utilisation (column 2), whilst Scenario 2 assumes 40% utilisation (column 4). Preference values (P=U/A) are derived for each increased increment in availability for both scenarios (columns 3 and 5).

Table 8.10
Example of deriving preference indices as a function of increasing availability of a particular class component of habitat, at two different levels of utilisation (see text for details).

	SCENARIO 1		**SCENARIO 2**	
1	**2**	**3**	**4**	**5**
Availability of resource (%)	**Maximum Utilisation (%)**	**Maximum Preference**	**Maximum Utilisation (%)**	**Maximum Preference**
10	100	10	40	4
20	100	5	40	2
30	100	3.3	40	1.3
40	100	2.5	40	1
50	100	2	40	0.8
60	100	1.6	40	0.7
70	100	1.4	40	0.6
80	100	1.3	40	0.5
90	100	1.1	40	0.4
100	100	1	40	0.4

Two factors are evident from the resultant preference values. Firstly, as a particular depth class becomes increasingly available, the derived preference index decreases (columns 3 or 5). This implies that as a class of resource comprises a greater proportion of the total, the potential maximum preference is less. Secondly, the facility to directly compare preferred indices of components with varying availability renders similar ratings for very different situations. So, for example, an index of 1.3 can reflect two quite different availability and utilisation scenarios (columns 3 and 5). This illustrates the importance of an accurate determination of availability, since over or under representation of a particular class will greatly influence the derived preference value. Recognition of this problem has led some terrestrial ecologists in South Africa to use an index, informally termed "Barrat's or Viljoen's Index" (Dr. H. Biggs, Scientific Services, National Parks Board, Skukuza, *pers. comm.*), in which different values are generated in each case (see for example, Viljoen 1989).

These ambiguities raised concerns regarding some of the SI models derived in my work, which seemed to have little biological rationale. Hence a sensitivity analysis was carried out on a set of data that appeared to be inconsistent with other results. Data presented in Table 8.11 represent real data for depth availability, juvenile use and preference at one site in December 1991. In this instance, juveniles inexplicably appeared to prefer depths far in excess (0.5 - 0.6m) of those described at other sites, or even those for adults. The availability data were adjusted minimally in order to illustrate the effect on the derived preference indices. Adjustments amounted to a 4% adjustment (arbitrarily chosen) in both the 0.20 - 0.30 m, and 0 .50 - 0.60 m classes of available depths. As illustrated, minor adjustments to availability data caused a a marked decline in the optima from between 0.5- 0.6 m, to between 0.10 - 0.20 m. Thus, at the risk of repetition, it must be stressed that *any deviation in availability* data from that of reality, for whatever reason, can cause *a major shift in SI curves* produced and hence their interpretation.

Table 8.11

Example of the effect of minor adjustments of depth availability of two depth classes on the resultant suitability index of the preference curve.

Class	Availability (%)	Availability (normalised)	Utilisation (%)	Preference	Preference (normalised)
0-10	0.08	0.27	0.00	0.00	0.00
10-20	0.28	1.00	0.47	1.67	0.93
20-30	0.18	0.65	0.21	1.16	0.65
30-40	0.20	0.73	0.17	0.83	0.47
40-50	0.06	0.21	0.04	0.71	0.40
50-60	0.06	0.21	0.11	1.79	1.00
60-70	0.11	0.41	0.00	0.00	0.00
70-80	0.00	0.00	0.00	0.00	0.00
80-90	0.02	0.08	0.00	0.00	0.00
90-100	0.00	0.00	0.00	0.00	0.00
Minor adjustment to availability data					
0-10	0.08	0.27	0.00	0.00	0.00
10-20	0.28	1.00	0.47	1.67	1.00
20-30	0.14	0.50	0.21	1.52	0.91
30-40	0.20	0.73	0.17	0.83	0.50
40-50	0.06	0.21	0.04	0.71	0.43
50-60	0.10	0.36	0.11	1.06	0.64
60-70	0.11	0.41	0.00	0.00	0.00
70-80	0.00	0.00	0.00	0.00	0.00
80-90	0.02	0.08	0.00	0.00	0.00
90-100	0.00	0.00	0.00	0.00	0.00

Therefore, the inherent assumptions in the development of preference models, are that

1. The range of available habitats are sampled in the exact proportion to their occurrence.
2. All available habitats are described.

Investigators must be aware that these assumptions can be violated by sampling design and effort, as well as access to, and descriptions of, habitat. Thus, meeting these two assumptions is seldom possible. In my research, for example, constraints made it impossible to sample certain depths and velocities.

Additionally, the data from the drought offered some interesting insights into the interpretation of SI curves. This related to the apparent shift in preference, when fish appeared to "prefer" a narrower range of depths as depths decreased. Clearly, with little biological rationale, this outcome is merely a function of the declining microhabitat availability. This anomaly of SI curves was raised by Hanson at a workshop in 1988 (see Bovee & Zuboy 1988), but has received little attention since. Gore & Nestler (1988) caution that SI curves are only applicable during periods of median or base flows, presumably for a stable population (Morantz *et al.* 1987). Likewise, Heggenes & Saltveit (1990) stress that error is introduced when habitat changes are extrapolated to discharges substantially different from those for which the suitability models were developed. The implication for the interpretation of SI models is that the point in declining discharges at which preference models are invalid, must be explicit.

These limitations may explain some of the discrepancies in my data referred to earlier. For example, the seasonal differences in preference may simply be a function of varying availability and, as illustrated above, this bias will extend through both the utilisation and preference data. In view of the above discussion, it is suggested that *absolute interpretations* of SI values should be viewed with circumspection. This is particularly true of preference functions and their use requires further scrutiny. I would argue that a review of the literature reveals that so little emphasis is put on this aspect that SI curves of preference can only be viewed as coarse generalisations of microhabitat requirements.

Appropriateness of data pooling and the generality of models

Overall, microhabitat models developed at different sites and times appeared to be sufficiently different to caution against pooling data (although this may simply be due to estimates of availability- see preceding paragraph). Previous research has demonstrated the spatial and temporal variations in habitat use, and has led to many workers refuting the concept of representing microhabitat suitability as a single general model, and to a call for further testing (e.g. Sheppard & Johnson 1985; Shirvell 1989; Lobb & Orth 1991; Heggenes & Saltveit 1990; Bozek & Rahel 1992; Waite & Barnhart 1992; Stalnaker *et al.* 1996). Bozek & Rahel (1992) demonstrated that general models both over- and underestimate habitat abundance and advised that model generality was only appropriate in streams having similar habitats, although they failed to define "similar habitat".

Model variability has been ascribed to a number of factors. These include differences in microhabitat availability (see previous discussion and Moyle & Baltz 1985; DeGraaf & Bain 1986; Grossman & Freeman 1987); size-class differences (Moyle & Baltz 1985); diurnal and seasonal shifts (Campbell &

Neuner 1985; Sheppard & Johnson 1985; Grossman *et al.* 1987; Hearne *et al.* 1994); species interactions such as predation (Power 1984a; Moyle & Baltz 1985); food availability (Cerri & Fraser 1983; Power 1984b), activity (Shirvell & Dungey 1983) and sampling differences (Shirvell 1986). The interactions between some, or all, of these factors are potentially complex and interesting, particularly as flows approach extremes. Under such conditions, overlap in habitat use among fishes could result in increased predation or competition (Bain *et al.* 1988), which could manifest in different patterns of habitat use.

Additionally, weighting data in such a way as to avoid data bias due to differences in study site size and time spent at a site, is problematic in that weightings may in themselves carry an inherent bias. For example, Leonard (see discussion sessions *in* Locke 1988) points out that pooling the availability data may add conditions that some of the animals could never have selected since these conditions were not available. This would apply in the case of Site 2, with a simpler array of substrata types relative to the other sites.

Ultimately, I would argue that by presenting a single model for a species, researchers establish a myth of constancy. Whilst it is valid to assert that if all the ranges of habitats were sampled, then these curves should encompass all availability and use in the stream, the risk still exists that these curves are interpreted as absolutes for the sake of expediency. It is imperative to recognise the dynamic nature of habitat use (as a function of an array of factors, of which flow is only one), particularly when recommending flows for management purposes. Whilst most researchers recognise this, the desire to provide an overall single description may outweigh the unwieldy (but more meaningful) presentation of a number of curves and hence the myth of constancy is perpetuated.

Validity of describing microhabitat in terms of three variables and the assumption of independence

The importance of a variety of factors (and their interactions) in defining the suitability of habitat has long been recognised. For example, nearly three decades ago Connell (1975), in his work on community structure, implicated competition for food resources, physico-chemical stress and predator avoidance as the major pressures for selecting particular habitat configurations. Within PHABSIM, the use of SI curves and PHABSIM is predicated on two interrelated and fundamental assumptions. These are (a) depth, velocity and CI are the only variables determining the suitability of physical habitat, and (b) these variables act independently in their influence in habitat selection by fish or invertebrates (Scott & Shirvell 1985; Gore & Nestler 1988).

These assumptions have been strongly refuted by a number of authors (e.g. Orth & Maughan 1982; Cada *et al.* 1983; Shirvell & Dungey 1983; Mathur *et al.* 1985a; Scott & Shirvell 1985; Heggenes *et al.* 1996). They argue that not only are additional factors important in determining habitat use but also, they are interrelated. Such factors include additional hydraulic variables, such as nose velocity (Scott & Shirvell 1985; Gore & Nestler 1988) and shear stress (Layzer & Madison 1995); food availability (Cerri & Fraser 1988); chemical and physical conditions, which embrace factors such as gradient, (Cada *et al.*

1983; Heggenes & Saltveit 1990); and species interactions, such as competition and predation (e.g. Power 1987; Bain *et al.* 1988). In the case of *C. anoterus,* for example, the epilithic layer on substrata is considered critical to defining habitat since it is their major food source. Jowett & Richardson (1990) found that the best models for predicting the biomass of benthic invertebrates in a New Zealand stream, were those that included an index of periphyton, together with all three hydraulic variables. However, incorporating descriptions of periphyton is meaningless for use in PHABSIM II, since it cannot be modelled, although plant growth has been shown to influence PHABSIM outputs (Hearne *et al.* 1994). Recent work by Pusey *et al.* (2000) has pointed to the importance of catchment variables, and in particular discharge variability, in explaining variations in fish assemblage structure. In most cases, these variables accounted for almost as much of the assemblage structure as instream habitat features.

Additionally, the assumption of independence has been questioned (e.g. Orth & Maughan 1982; Scott & Shirvell 1985; Jowett & Richardson 1990; see also Bourgeois *et al.* 1996), and the topic has been extensively reviewed by Orth & Maughan (1982). They found that the interaction of the three variables explained considerably more of the variation in the density of certain fish species than each of the variables separately, and demonstrated that this assumption was most frequently violated in the case of depth-velocity interactions. A number of proposals have been put forward to counteract this concern. These include developing an exponential polynomial model, which incorporates a depth and velocity interactive factor (Gore & Judy 1981; Morin *et al.* 1986; Gore 1989), or the use of a laminar- sublayer thickness model which incorporates depth, velocity and substratum roughness into a single index (Statzner 1981).

My results suggest that the assumption of independence may be unrealistic. For example, there is clearly a relationship between velocity and cover in the selection of microhabitats by adult *C. anoterus.* Cover offers the opportunity for animals to move out of the swifter area and minimise energy expenditure, but the high velocities are important in maintaining their food source. Similar behaviour has been described in bigmouth chub, also a riffle-dwelling species (Lobb & Orth 1988), and in drift-feeders (Fausch 1984).

Notwithstanding the concerns of independence, a number of variables have been identified as critical for explaining habitat-discharge relations. Velocity has been nominated as a key variable by Leonard & Orth (1988), since it is more affected by a change in flow than any other hydraulic variable (Kraft 1972; Williams & Winget 1979). They do acknowledge however, that this may not hold true for species associated with cover, such as *C. anoterus.* In contrast, Johnson & Kucera (1984) found that substratum appeared to be the most important habitat parameter affecting the habitat utilisation in subyearling steelhead trout. Moreover, it is likely that the relative importance of these selective pressures varies through space and time (Connell 1975) and after other conditions have been satisfied (Bartholow & Slauson 1990). Such complexities were illustrated by Angermeier (1987) from an examination of spatio-temporal variation in habitat selection by an assemblage of fish. He showed that fish from the same population may exhibit different levels of habitat selectivity in different years, or in different reaches, and some cyprinids showed little fidelity for particular habitat configurations.

Finally, the description of habitat suitability needs to be interpreted in a broader ecological and biological context. The biological response of *C. anoterus* during the drought is a case in point. It is likely that the reduced water velocities, combined with high ambient temperatures, caused conditions that were intolerable for this species (see also Pollard *et al.* 1996). Ultimately, these water quality changes induced extreme physiological stress in animals, evident in the marked increase in parasitic infestations and reduction in recruitment (unpublished data). This demonstrates that the interpretation of habitat use should integrate knowledge on the biological attributes of species if it is to be meaningful.

8.7 CONCLUSIONS

A broad description of habitat use by *C. anoterus* emerged from the IFIM approach to quantifying microhabitat use. Nonetheless, integrating these results into a comprehensive picture of microhabitat use by *C. anoterus* was relatively complex. Given the severe reservations raised regarding the competency of the models, it is not clear that the high logistical and financial investments needed to procure the data, can be justified.

Results from this study corroborate the concerns raised by a number of workers regarding the validity of deriving and presenting habitat use as SI models. Undoubtedly, they provide the empirical mainstay for professional judgement in that there is some degree of quantification over simply describing an animal as a riffle or pool dweller, for example. However, the validity of then using such curves to predict an animal's habitat requirements for management purposes is questionable. These models are considered insufficiently robust to be employed for management when unsupported by additional data that at least corroborates the validity of the curves. Every step in the process is predicated on a number of assumptions that are easily violated and, it is not clear from the literature that habitat-use models are being adequately tested in each study. The danger is that such models are accepted and treated as absolutes and are subsequently used for recommending instream flows (Stanford & Ward 1992). Furthermore, it is the responsibility of researchers to ensure that the dynamic nature of habitats is preserved and the use of single curves makes the management option of interpreting needs as constant, all too easy. The use of a general SI model to describe habitat preferences is repudiated unless there is adequate proof of model homogeneity.

Much of my critique of SI models centres on the description of microhabitat availability since I showed that inaccurate determinations of microhabitat availability can greatly influence the nature and interpretation of the derived preference models. A scrutiny of preference ratings indicates that these values are ambiguous, and hence it is unclear as to what derived models actually demonstrate. Moreover, even if the use habitat availability is correctly quantified, there is an undetermined point beyond which the term "preference" is a misnomer. This was demonstrated during the drought when animals are simply forced into less than ideal conditions. Finally, although the SI curves provided the physical expression of habitat use, understanding the biological effects was equally important.

Table 8.1

Summary of the various sampling strategies, applicable to small rivers that are used in criteria studies (after Bovee 1986). The accounts by Bovee (1986) regarding compatibility with sampling technique are somewhat confusing since for example, he cautions against the use of electrofishing with random sampling but then deems that the use of electrofishing to these techniques "mostly applies". He also fails to explain why some designs are not compatible with certain techniques, such as that of modified cluster sampling and electrofishing. Therefore, comments on compatibility are only offered as guidelines.

METHOD	PREPARATION REQUIRED	DESCRIPTION	ADVANTAGES	DISADVANTAGES	SUITABILITY FOR SINGLE OR MULTI SPECIES STUDIES	COMPATIBILITY WITH SAMPLING STRATEGY
Random sampling	Requires only moderate preparation.	Involves superimposing a grid system over a plan map of the study area and randomly selecting grid numbers which then represent the sample areas.	One of the least biased approaches Only moderate preparation required Reduces pooling problems almost entirely. Highly appropriate for habitat availability	Translation of sample position from map to study area can be difficult Many samples will not contain target biota, thus high field time and large database requirements. Inefficient for single fish species.	Multi species	Adjacent sampling locations often selected and electrofishing in one can bias results of second sample.
Stratified random sampling	Moderate- Scaled site map, delineation of major habitats, determination of area of each.	Discrete habitat types are delineated on the map, each homogeneous unit is then gridded and sampled randomly.	Attempts to ensure that certain habitats are sampled. Relatively simple. Differences amongst sampling locations or times are accounted for.	Can result in inadvertent biaising of data with equal effort being expended in habitats of different sizes. Many samples will not contain target biota, thus high field time and database requirements.	Multi species Can be used for single species	Adjacent sampling locations often selected and electrofishing in one can bias results of second sample.
Proportinal sampling	Very detailed habitat map.	Transects describe the longitudinal variation and verticals across the transects describe the lateral variation. Each cell has a discrete combination of microhabitat variables and those cells with similar variables are grouped into the same habitat category. Samples taken from each habitat category in proportion to the representation of that habitat in the total study area (Bain *et al* 1982).	Attempts to deal with bias. Uses same mapping approach as PHABSIM. Highly appropriate for habitat availability.	High preparation time and logistical effort. Inefficient for single fish species.	Multi species	
Modified cluster sampling	Moderate- Scaled site map, delineation of major habitats, determination of area of each.	Cognisance is taken of habitat types but samples are weighted to reflect the proportions of that habitat in the total study area.	Weights number of samples according to habitat representation. Simpler stratification procedure than that for proportional sampling.		Single species	SCUBA observations fairly efficient as diver spends proportional time in each area.
Systematic or uniform sampling: (A) Blanket (B) Systematic random walk	Least - plan map		Simplest.	Sampling bias can occur (p.113)	Multi species. Can be used for single species.	Electrofishing possible because the problem of adjacent samples is minimal. SCUBA observations inefficient.

Table 8.2

Summary of techniques used in the development of SI curves (Gosse 1982; Bovee 1986; Cheslak & Garcia 1988; Slauson 1988)

TECHNIQUE & DESCRIPTION	DIFFERENCES IN CURVE CONSTRUCTION FOR AVAILABILITY, USE & PREFERENCE	ADVANTAGES	DISADVANTAGES & CONSTRAINTS
Histogram analysis Most frequently used technique for SI curve construction. Plots frequency (abundance or observations) against the measured range of a particular hydraulic variable. A frequency polygon is created by connecting the mid-points of each bar. Class intervals calculated by Sturges equation: $C=\frac{R}{(1+3.222*\log_{10}N)}$ Equation 8.2 where C= the optimal class (interval) size; R = the range of the variable (Xmax - Xmin); N = the number of observations Additional equations given in Slauson (1988).	In the determination of microhabitat availability, the frequency distribution is determined in one of two ways, depending on whether random or proportional sampling was used (Bovee 1986, p122). Bovee (1986) details two options for generating a preference curve from utilisation and availability frequency distributions: 1. Curves are fit to both the utilisation and availability histograms. For each increment over the range of the variable there is a predicted relative frequency. The unormalised preference for the increment is computed as the ratio between these two predicted values. 2. The observed relative frequencies from the utilisation by the availability and then a curve is fit to the resulting preference histogram.	Cheslak & Garcia (1988) concluded that this approach produced the least error. Both the utilisation and availability distributions are derived as relative frequencies, facilitating the conversion to preference criteria (Bovee 1986). Manipulation of class intervals confers flexibility.	The shape of the histogram can be markedly influenced by the choice of class intervals (Mordhardt, *cited in* Cheslak & Garcia 1988). Aggregation of classes tends to be at the expense of accuracy. A major disadvantage is the determination of the position of the curve drawn through the data. Can be improved by accurate class interval determination, smoothing or computation of the residual sum of the squares for curves and use of the curve that minimizes this statistic
Nonparametric tolerance limits Described by Gosse (1982) and Bovee (1986). Involves placing an umbrella over the observed frequency histogram. Measured data of a particular variable are ranked in order of increasing magnitude and contingency tables are used to determine which rank corresponds to an area of 50%, 75%, 90%, 95% and 99%. These ranks describe, at a given confidence level, the range of the variable that will contain a specified proportion of the population regardless of the distribution of the data. Tolerance limits represent integrated areas under the curve rather than relative frequencies (Bovee 1986).	Theoretically, availability and use curves are created in the same way using this approach. Bovee (1986, p. 131) details a procedure for the construction of availability curves based on approximating the relative frequency distribution from the tolerance limits.	Relative ease of use. It is not influenced by irregularities in the data caused by random sampling and does not involve the selection of any particular distribution or curve shape. Recommended by Bovee (1986) for the treatment of small data bases, but not for data exhibiting bimodal distributions. End points are properly addressed.	Curves can be produced irrespective of an instance in which data exhibit a flat species -response distribution. Transition to a preference function is not as simple as that of histogram analysis. The reason for this is that the tolerance limits represent integrated areas under the curve rather than relative frequencies (Bovee 1986). Must have counts/ frequency data and not biomass or density data.

TECHNIQUE & DESCRIPTION	DIFFERENCES IN CURVE CONSTRUCTION FOR AVAILABILITY, USE & PREFERENCE	ADVANTAGES	DISADVANTAGES & CONSTRAINTS
Nonlinear regression Similar to hand -fitting curves described for histogram analysis but an equation is used to fit the curve (Bovee 1986). Univariate/ multivariate approach. Polynomial regression as a way of expressing a species response to a single microhabitat variable. Has been recommended by Slauson (1988) as a method for deriving smooth SI curves from raw data. However, as noted by King & Tharme (1994), inherent assumptions render it less frequently used than other methods. Slauson (1988) reviews two approaches that have been used by instream flow researchers to derive SI curves. Briefly, these include 1. Fitting a species response to a quadratic, cubic or higher degree polynomial of a single environmental variable, or 2. Cumulative frequency distribution of a species response to a variable is fit with a fourth degree polynomial of the habitat variable.	In terms of computing a preference function, Bovee (1986) adds a third option when utilisation and availability equations are derived: the equation for the utilisation can be divided by the availability equation which results in an equation describing preference. This technique is limited to equations of the same type or order. Otherwise the best fit function is obtained for both utilisation and availability and then the respective predicted frequencies are divided to obtain the preference curve.	Employs standard techniques widely available as computer packages. Also enables determination of residuals and goodness-of-fit. (However decisions still have to be made by the researcher, such as which degree polynomial to fit and whether or not to transform the data and how to deal with outliers (King & Tharme 1994)	With polynomials, data are forced to follow a specific distribution; consequently, there is a lack of biological evidence to support the distribution of data. Species response to any microhabitat variable is generally expected to be either monotonic or unimodal and not multimodal (Slauson 1988): thus, the use of higher order polynomials may be questionable. These equations dictate that there will only be one optimum value whereas from a biological perspective, a range of values will be suitable (Milhous, *cited in* King & Tharme 1994). The assumptions of regression, for example that the x and y-axis are unbounded, are often not met. Requires literacy in statistical and computer language.
Running filters Computed by way of a running mean of a specific span (window). Slauson (1988) further suggests a modification on this approach, being that of running medians which is more resistant to outliers and is particularly useful in the case of data infested with odd values. Can be used to construct or smooth a curve. Slauson (1988) notes that particular attention should be paid to the end points since they do not have neighbouring points on one side. In evaluating the efficacy of this approach for smoothing data, Cheslak and Garcia (1988) advocate that the error is controlled more effectively via proper selection of interval size than the application of a running mean. Secondly, they suggest a maximum of two passess since excessive passes can produce a complex, polymodal curve. Slauson (1988) on the other hand, states that a five-compound smoother is possibly the best filter to use as for the construction of SI curves.	Theoretically, availability and use curves treated in the same way.	Filters that are easy to compute; they are free of statistical assumptions (as in frequency and nonparametric methods); calculations of residuals are straightforward and running filters are not overly influenced by outliers and tend not to produce spurious modes, tails or negative values.	The appropriate choice of a filter from a wide variety of options and the influence of outliers which can be treated by wide-spans, but which may in turn overround the data, whilst a too narrow-span may track extremes too closely.

9

Microhabitat Availability for *Chiloglanis anoterus* as Calculated by PHABSIM II

9.1. INTRODUCTION

An overview of the conceptual basis and the sequence of steps involved in IFIM and its associated software PHABSIM II, was given in Chapter 2 and was summarised in Figures 2.1 and 2.2. Essentially, PHABSIM II is an integral part of IFIM and is the model designed to calculate an index of the amount of physical habitat available to the biota at different flows. The principal objectives of PHABSIM II are to transform hydraulic information into a measure of the available habitat, and to derive a habitat-discharge relationship for selected species. To this end, PHABSIM II links (i) hydraulic data (a physical description of the study site) with (ii) "biological" data (a description of microhabitat used or preferred) to simulate the total available habitat at a site, weighted to reflect its suitability for a certain species, at a particular discharge (see Figure 2.2).

This chapter aims to test, and assess, the application of PHABSIM II to the Marite River to determine the amount of suitable habitat for juvenile and adult *Chiloglanis anoterus*. The collection of the hydraulic data was described in Chapter 5 (Sections 5.4 & 5.5), and the "biological" data, in the form of SI curves, was dealt with in the preceding chapter. This chapter will focus on the hydraulic analysis, the linkup with the "biological" data, and the resultant estimates of available habitat for *C. anoterus*.

9.2 THE THEORY OF HYDRAULIC & HABITAT SIMULATION

The typical flow of data through PHABSIM II is shown in Figure 9.1. PHABSIM consists of two distinct analytical components, namely: hydraulic simulation and habitat simulation (Bullock *et al.* 1991). These, together with their associated programmes, form the basis of the following discussion.

An extensive suite of programmes exist within both the Hydraulic and Habitat Simulations Program Groups. In addition to these, there are the Curve Maintenance Programs and Effective Habitat Analysis Programs. The former simply converts the SI data to a form required by the various programmes, and the latter considers habitat as a function of two flows that are considered to be important in combination, such as spawning flows followed by incubation flows. These programmes are detailed in Milhous *et al.* (1989; 1990) and Gan & McMahon (1990), and are summarised in Table 9.1.

The objective of the first component, hydraulic simulation (Figure 9.1), is to predict changes in the depth and velocity for each cell of a transect at a site (see Figure 5.5), over a range of unmeasured discharges

(Milhous *et al.* 1989; see also Gan & McMahon 1990; Bullock *et al.* 1991; Ghanem *et al.* 1996). Milhous *et al.* (1990) recommend that the range of discharges to be simulated, known as "QARDs", do not exceed 0.4 times the lowest calibration discharge, and 2.5 times the highest measured discharge. Model calibration is achieved by linking field data on the cell velocities, depths and substrata from the transects, to the water surface elevations (or WSE), and discharge, of each transect. Then, hydraulic modelling is performed in two steps.

- Firstly, WSEs are simulated as closely as possible to the measured WSEs, using one of three programmes: IFG4, WSP or MANSQ (Table 9.1). The WSEs are simulated using a stage-discharge relationship (see Figure 2.5) from which water depths and cell widths are calculated.
- Once this has been achieved, the velocity distributions across each transect (i.e. at each cell) are simulated using the programme IFG4 (see Figure 2.2).

The outputs of hydraulic simulation are predictions of depth and velocity for each cell for each simulation discharge. Channel index (CI) is not simulated because, theoretically, it is assumed to remain constant although, in reality, it does not (King & Tharme 1994). A third output of hydraulic simulation is the production of two unformatted files, TAPE 3 (transect and reach data) and TAPE 4 (discharge and velocity data), which are used as the hydraulic input files for the habitat simulation programmes. Once cell-specific depths and velocities have been simulated, these data are then used to assess the cells value as microhabitat by comparison to the habitat curves developed for a particular species (see Chapter 8).

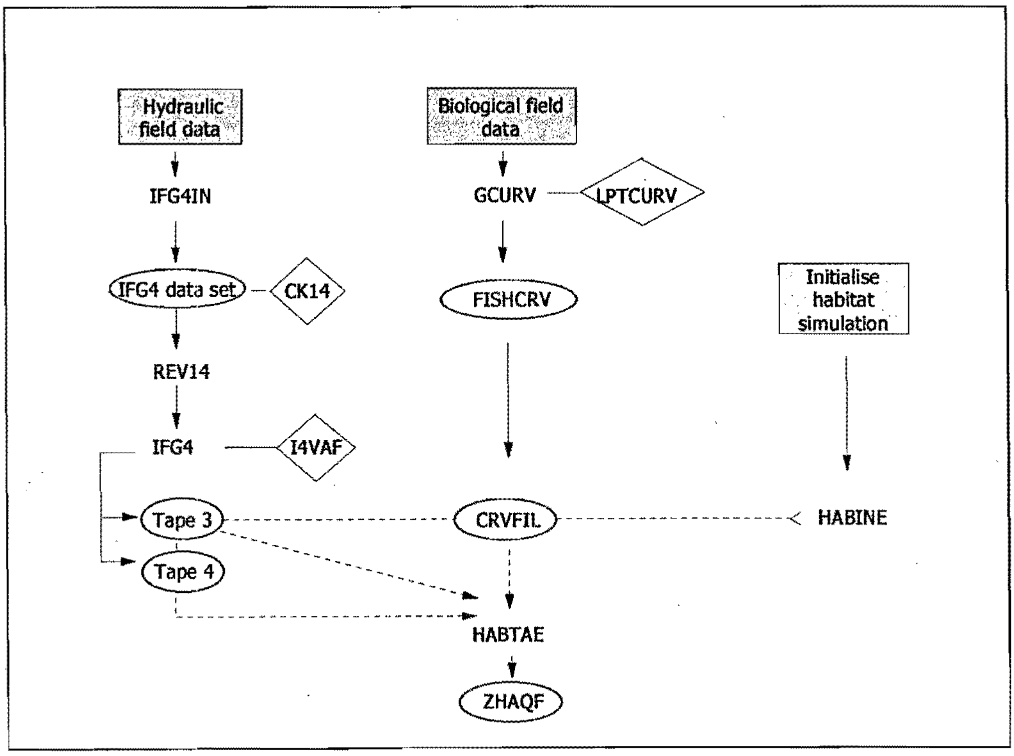


Figure 9.1 Typical flow of data through PHABSIM system (after R.T. Milhous, USFWS, *pers. comm.*). This schematic, which is an abridged version of that presented by Bullock *et al.* (1991), represents the routines used in this study. Table 9.2 provides a description of each routine.

The objective of the second component of PHABSIM, habitat simulation (Figure 9.1), is to quantify the available microhabitat for the selected species, or lifestage, and/ or activity, at a site for unmeasured discharges. To do this, the simulated hydraulic data, together with the habitat suitability data for the target species, or lifestage (SI curves, which are incorporated into an unformatted file called FISHFIL) are used as input to the habitat simulation component of PHABSIM. A range of habitat simulation programmes is available in PHABSIM II, the most important of which are described in Table 9.1.

This simulation produces both an estimate of total available wetted area (ft^2 per 1000 ft) as a function of discharge, as well as species-specific habitat, weighted by its "suitability" for that particular species, lifestage or activity. "Suitability" is derived as a product of the preference indices of depth, velocity and substratum (see Section 8.4). It is expressed as Weighted Usable Area (WUA), or alternatively, Weighted Usable Volume (WUV) or Weighted Usable Bottom Area (WUBA), as appropriate to the species in question. This output is also represented as a measure of area, generally ft^2 per 1000 ft, but the units, and their interpretation, are contentious - an issue which is elaborated later.

Although largely theoretical, the net suitability of a cell can also be expressed as the *geometric mean*, or as a *minimum preference formulation* (Gan & McMahon 1990). The former index is used when the importance of two of the three variables is considered to be high, reducing the effect of the third. Use of the latter index implies that habitat is no better than its minimum component so that the value is weighted to accentuate the importance of the minimum of the three variables.

At increasing spatial scales, the steps involved in determining the WUA (or WUV, or WUBA) include deriving a composite suitability index for each cell along a transect (see Equation 2.1), multiplying these values by the cell area to derive their WUA (see Equation 2.2), summing these for the reach (see Equation 2.3) and finally for the river (see Equation 2.4). A useful example of the derivation of a cell's net suitability is given by Gan & McMahon (1990) for a 10 m^2 cell, as follows. A net suitability of 0.765 would be derived as a product of the value from the SI curves for velocity, depth and CI as: 0.9; 0.85 and 1.0 respectively. This would then be multiplied by the surface area of the cell (10 m^2) to give a WUA of 7.65 m^2. The WUA for the site, at a specified discharge, would be the summation of WUA for all cells.

The final outputs, the habitat-discharge curves (see Figure 2.2), constitute the key information for negotiating IFRs (Bovee 1982). Despite the importance of this step, King & Tharme (1994) point out that there is little guidance on how to objectively assess the point on the curve that may comprise a "minimum recommended flow". Apparently, the inflection point on the curve, where habitat values decline rapidly with discharge, is usually fitted by eye. This approach is contested by Gippel & Stewardson (1998) who developed a method for calculating the breakpoint for various channel shapes mathematically, based on the point of maximum curvature or where the slope equals 1. Theoretically then, the impact of altering flows can be assessed based on the estimated change in WUA by repeating the above computation for each discharge, species and/ or lifestage of interest.

Table 9.1
Summary of the hydraulic and habitat simulation programmes available within PHABSIM II (from Milhous *et al.* 1989,1990; Gan &McMahon 1990; Bullock *et al.* 1991)

PROGRAMME	DESCRIPTION
Hydraulic Simulation Programs Group (WSE simulation) There are three options for the hydraulic analysis of data within PHABSIM II (see Chapter 2, Step 7.1)	
IFG4	Uses a stage-discharge (SQ) relationship to determine WSEs unless they are supplied in the input data. Cross sections are treated independently. The velocities are determined using the techniques based on Manning's equation, which calculates Manning's "n" and velocities are checked against the simulation discharges using a Velocity Adjustment Factor. Manning's "n" is a coefficient of the bed roughness used in calculating water depth (Scott & Shirvell 1985). IFG4 is usually calibrated to at least one set of velocities.
WSP	This programme uses a standard step backwater method to determine WSEs calibrated by adjusting the Manning's roughness given in the data set. Transects are considered as dependent and WSP uses an energy balance model to project WSE from one known SQ relationship to all transects upstream. Cannot predict velocities - must be predicted using IFG4.
MANSQ	MANSQ assumes that the SQ relationship can be calculated using Manning's equation and the model is calibrated with one set of WSEs. Cross-sections are treated independently. This approach assumes that no backwater influences are present (Mr. R. Rowlston, DWAF, *pers. comm.*). Cannot predict velocities - must be predicted using IFG4.
Curve Maintenance Programs Group	
GCURV	Builds a formatted file (FISHCRV) of the SI data
LPTCRV	Checks the above file and graphs data
CRVFIL	Builds an unformatted version of the FISHCRV file for use with habitat simulation
Habitat Simulation Programs Group As part of the suite, commands for habitat simulation (Input-Output Commands) are created using programmes indicated in parentheses.	
HABTAT	Calculates habitat area for the reach. Defines cell boundaries as lying at the verticals of the transect. This is the basic simulation routine. (HABIN; HABINS).
HABTAE	Calculates habitat for each cross-section of the reach. Defines cell boundaries as lying at, or halfway between, the verticals, of the transect. Regarded as the newest and most sophisticated since it calculates Weighted Usable Bed Area or Volume (King & Tharme 1994). (HABINE).
HABTAM	Simulates habitat in situations where biota may migrate laterally across a section in response to changes in velocity. Defines cell boundaries as lying halfway between verticals of the transect. (HABINM).
HABTAV	Calculates habitat under the assumption that the condition in a cell plus the velocity at another point in the cell or in another cell, establishes the worth of a cell. Defines cell boundaries as lying halfway between verticals of the transect. (HABINV).
AVDEPTH & AVPERM	Not strictly habitat simulation programmes. Calculate average cross-section, or reach, hydraulics (wetted width and wetted surface) when SI curves cannot be created.
Effective Habitat Analysis Group	
HABEF	Compares two habitat output files from the habitat simulation.

9.3 RUNNING PHABSIM TO DETERMINE HABITAT AVAILABILITY FOR *Chiloglanis anoterus* AT SITE 3 ON THE MARITE RIVER

Considerable effort was invested in attempts to calibrate the hydraulic data of all three sites on the Marite River. This required the assistance of a hydraulics modeler, Mr. W. Rowlston (Department of Water Affairs & Forestry, Pretoria, South Africa) who had previous experience in running PHABSIM II for another South African project in the Western Cape (see King & Tharme 1994). However, it was finally decided that attempts to model Site 1 (see Figure 5.6 (A)) would be invalid due to the complex channel morphology at that site. In particular, PHABSIM II cannot compute split flows in multiple channels. Site

2 on the other hand, whilst hydraulically less complex (see Figure 5.6 (B)), provided little potential to understand habitat dynamics for the indicator species in that the shallow, homogeneous cobble-riffles are unrepresentative of most the riffles/ rapids that characterise the Marite River (see later discussion in Chapter 11).

Site 3 (see Figure 5.6 (C)) was finally selected for habitat modelling because it represented an intermediate in terms of channel complexity between the simple channel-type of Site 2, and the complexity of Site 1. Furthermore, the riffles, which encompassed a heterogeneous substratum of boulder, bedrock and cobble, were more representative of the broad habitat in which *C. anoterus* occur.

The simulation programmes used for the analysis of microhabitat availability at Site 3, are shown in Figure 9.1 and are described in Table 9.2. All field measurement data (hydraulic and habitat) were converted to imperial units since PHABSIM II cannot read metric data.

Table 9.2
Sequence of hydraulic and habitat routines used to determine microhabitat availability

Hydraulic suite: IFG4	
IFG4IN	created the hydraulic input file
REV14	calibration of the stage-discharge relationship
CK14	checked the quality of the input file
IFG4	ran the hydraulic simulation and produced Tape 3 (transect and reach data) and tape 4 (discharge and velocity data) files
I4VAF	checked velocity adjustment factors
Habitat suite: HABTAE	
GCURV	created the input file of habitat suitability indices
LPTCURV	checked the accuracy of the input data on habitat suitability indices
CRVFIL	converted the GCURV file to an unformatted version
HABINE	created an options (IOC) control file for the HABTAE programme
HABTAE	ran the habitat simulation, linking the unformatted data on Tape 3, Tape4 and CRVFIL files
LPTHQF	produced WUA-Q plots from the HABTAE output files

APPROACH TO HYDRAULIC SIMULATION

The input data required for hydraulic simulation were detailed in Chapter 5. In essence these consist of transect information (identification, location, length, weighting and the stage of zero flow), the bed profile of each transect (x-values), accompanying depth (y-values) and velocity data, the WSE and discharge for each transect at each calibration field trip, and the range of flows (QARDs) to be simulated. The calibration data set (Appendix B) comprised four discharge data sets together with accompanying WSEs and a velocity data set for one discharge (see below).

Of the three options available within PHABSIM (see Table 9.1) for hydraulic analysis, the IFG4 approach was used. Calibration of the stage-discharge relationship was achieved via REV14 (1), based on a log-log function. In order to simulate WSEs for each transect, which are treated independently within IFG4, a stage-discharge relationship was derived from the measured stage and discharge data (see Table 9.1). Two discharges are contained in the model for each calibration discharge: that measured ("given") and that computed by the model ("calculated"). The WSEs of each transect were measured at 0.026, 0.54, 0.68 and 6.3 $m^3 s^{-1}$, although only the WSE of three transects (TR 4,5 and 6) were considered to be sufficiently accurate at the highest discharge of 6.3 $m^3 s^{-1}$.

Based on the recommended range of simulated discharges values (see Section 9.2), the initial discharges included in the simulation run were 0.005, 0.014 and 6.3 $m^3 s^{-1}$. However, the lowest and highest values showed unacceptable differences between measured and calculated WSEs, and were therefore excluded. Ultimately, two additional discharges were simulated, namely 1.4 and 3.4 $m^3 s^{-1}$.. However, some amendments were made to the given discharge data where necessary in order to achieve concurrence between given and calculated data, specifically between those stages for the middle and high discharge values. The rationale for this was that, given that WSEs measurements are more reliable than those of flow rates, the values for WSE were retained whilst changes were made to flow rates. Therefore the final QARD values (those discharge values for which PHABSIM II simulates habitat) were 0.026; 0.54; 0.68; 1.4 and 3.4 $m^3 s^{-1}$. One set of calibration velocities, measured at a discharge of 0.02 $m^3 s^{-1}$, was provided as input to the hydraulic simulation.

APPROACH TO HABITAT SIMULATION

The habitat simulation routine known as HABTAE (see Table 9.1) was used for this analysis since it provides an option to derive WUBA. An estimate of the bottom area for habitat was considered to be most appropriate for the rheophilic *C. anoterus*.

Each of the habitat simulation programmes requires an input options file, and within HABTAE, this file is called HABIN. The creation of the HABIN file is important in that it contains a suite of commands (so-called "input-output commands" or IOC) which specify user preferences. For example, it is within these IOC values that the option to specify mean column velocity, or nose velocity, is contained. Few authors however, report on the IOC options used in habitat runs. Although an attempt was made to choose IOC values prudently, it appeared that the only major difference in results from those delivered by the default IOC options, was that of IOC(1) which produced WUBA (bottom area) rather than WUA. Another option

---

[1] The MANSQ approach was considered inappropriate because the longitudinal plot clearly indicated that Sections TR 1,2,3,4 and 7 (see Figure 5.6 (C)) were influenced by backwaters due to the negative slopes on the river bed for the range of specified flows or QARD values. The WSP approach, which analyses the sections as a continuum using a standard-step method backwater analysis programme, was attempted but late abandoned. This was because a number of dummy sections had to be inserted and changes made to roughness values, and cross-sections, in order to get concurrence with the stage data (Mr. W. Rowlston, *pers. comm.*).

IOC options, was that of IOC(1) which produced WUBA (bottom area) rather than WUA. Another option is that of using "nose velocities" which, in contrast to the default mean column velocity, describes the exact velocity where an organism, such as a benthic or surface dweller, is found. Habitat tends to be underestimated in the case of mean velocity because potential habitat around cover is unaccounted for. Nonetheless, changing the IOC value for nose velocity had little impact on the outputs.

Finally, the relative contribution of riffles, the key habitat of adult and late-juvenile *C. anoterus*, to the total wetted area, was assessed as a function of discharge. This was estimated by summing the wetted areas of riffle transects (TR 3, 3A, 4 and 7), which were derived from the output data of PHABSIM II.

9.4 RESULTS: PHABSIM II OUTPUTS

HYDRAULIC SIMULATION

The stage-discharge relationship for each of the 8 transects describing Site 3 are shown in Figure 9.2. Results for the simulations for the very high flow of 6.4 m^3 s^{-1} were not hydraulically robust and were therefore discounted. The WSEs were reasonably well simulated using the IFG4 approach for the flows between 0.02 and 3.4 m^3 s^{-1}, supporting the range of flows selected for the QARD values in PHABSIM II simulation runs (Mr. Rowlston, *pers. comm.*).

The given and calculated discharges differed notably at transects 3A and 7 (see Figure 5.6 (C)), but given that these are riffle/ rapid sections, these results are not surprising. Likewise, in the computation of velocities at the QARD discharges, transects 3A, 4 and 7 showed large discrepancies between the given and calculated flow rates. Crosschecking the data revealed no problems with the data measurements.

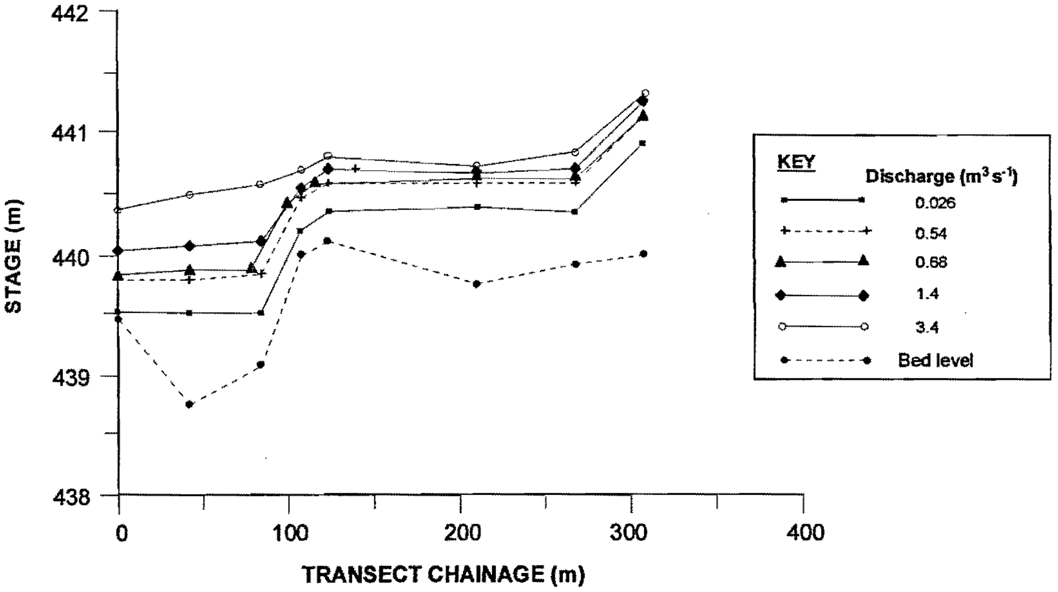


Figure 9.2 Stage-discharge curves for 8 transects at Site 3 over a range of simulated discharges.

HABITAT SIMULATION

The total wetted area at Site 3 (Figure 9.3) increased most sharply between 0.026 and 0.5 m^3 s^{-1} with the addition of about 800 m^2/ 300m (8611 ft^2/ 1000 ft). Thereafter, doubling the discharge resulted in the addition of about 300 m^2/ 300 m (3229 ft^2/ 1000 ft).

Adults and late juveniles occur principally in riffles. The PHABSIM II outputs indicated that the proportional contribution of riffles to the total wetted area of the study reach was relatively low. The estimates varied from 13% of the total wetted area at the lowest discharge, increasing to 23% at a discharge of 3.4 m^3 s^{-1} (Table 9.3).

Table 9.3

PHABSIM simulations of the Weighted Usable Bottom Area or WUBA (m^2) for each transect at Site 3 at five discharges. The proportional contribution of riffles to the total WUBA is calculated from transects 3, 3A, 4 and 7.

TRANSECT	THALWEG (m)	DISCHARGE (m^{3}s^{-1})				
		0.03	0.54	0.68	1.42	3.4
1	0.0	9.3	123.7	143.7	172.1	189.5
2	41.2	1048.3	1089.2	1096.9	1139.1	1228.1
3	83.8	102.8	161.2	165.3	185.2	226.6
3A	109.0	109.8	348.2	363.4	428.7	508.1
4	124.3	117.9	203.7	209.1	233.0	261.5
5	210.5	2721.3	2832.7	2843.8	2864.2	2889.2
6	268.1	101.0	146.3	164.2	175.7	202.1
7	309.1	249.2	317.7	321.4	337.5	380.3
TOTAL WUBA		**4459.6**	**5222.9**	**5307.8**	**5535.6**	**5885.4**
Riffles (% of total WUBA)		13.0	19.7	20.0	21.4	23.4

According to the outputs of WUBA, the available, suitable habitat for early juveniles was highest, and relatively consistent, at low flows but declined after about 1.4 m^3 s^{-1} (Figure 9.4). Assuming that areas of low-velocity (such as the sandy runs in which early juveniles are found) are likely to decrease with increasing discharge, these results are not unexpected. However, Mr.R. Milhous (US Fish & Wildlife Service, Fort Collins, *pers comm.*) cautions that increasing discharges are not necessarily synonymous with increasing velocities, due to changes in the flow patterns. In contrast, the amount of habitat for late juveniles and adults was lowest below about 0.5 m^3 s^{-1}. At higher discharges up to 3.4 m^3 s^{-1}, habitat for both lifestages increased steadily but appeared to level off earlier for juveniles.

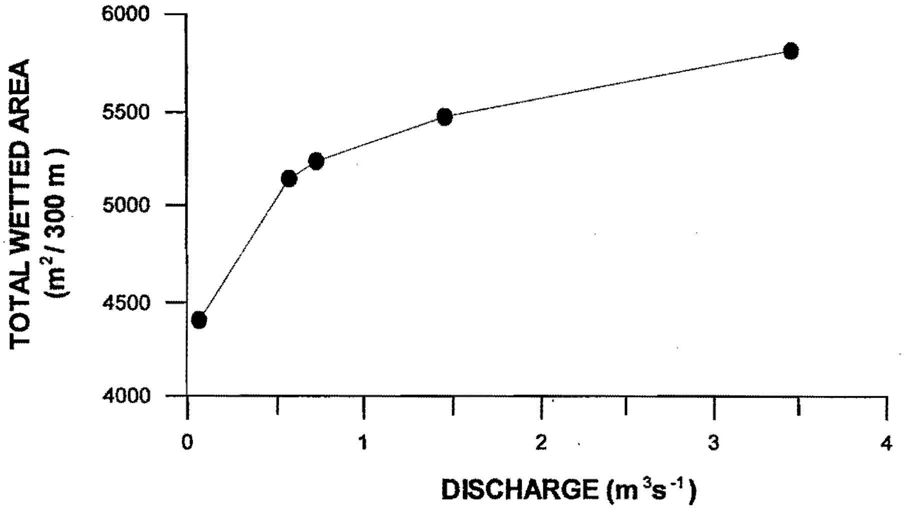


Figure 9.3 PHABSIM II predictions of total wetted area for Site 3 over a range of discharges. See text for discussions on the units of total wetted area.

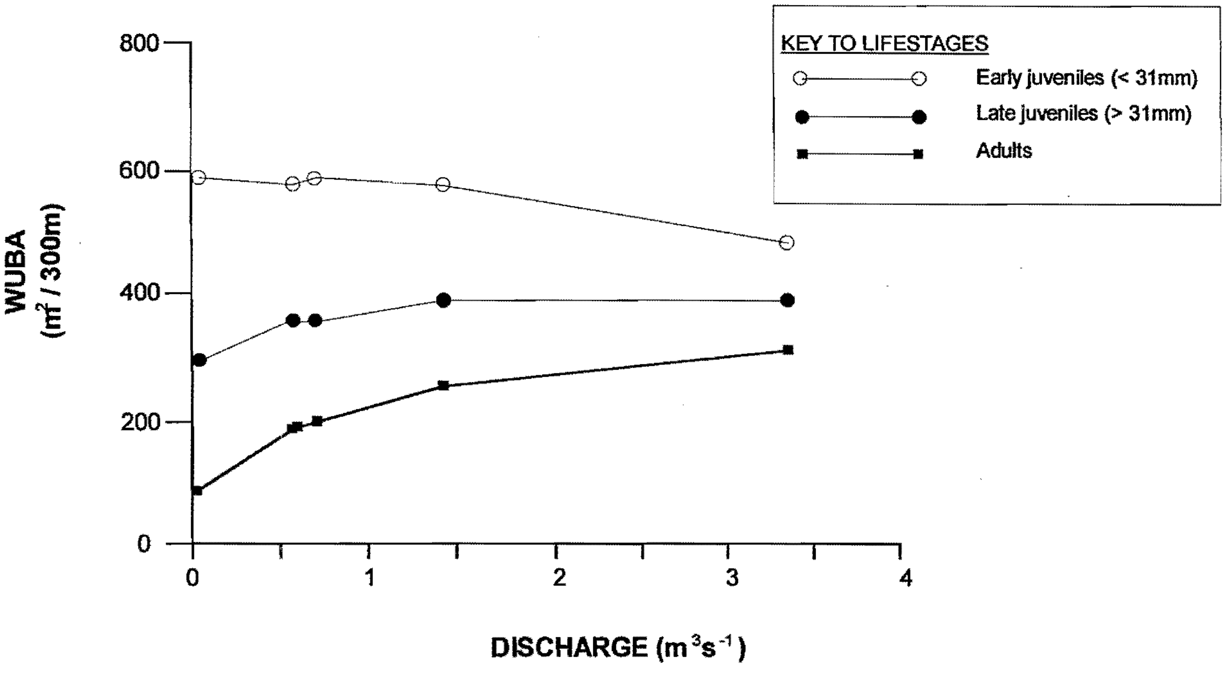


Figure 9.4 PHABSIM II predictions of WUBA (Weighted Usable Bottom Area) for three lifestages of *C. anoterus* over a range of discharges.

Initially, attempts were made to calculate suitable habitat as a proportion of the total potential habitat (wetted area) so as to provide a relative index of habitat availability. Ultimately however, this was not undertaken for two reasons that relate to the nature of PHABSIM. Firstly, the units of WUA and WUBA are not clearly defined in the PHABSIM literature and therefore they may be incompatible. The Wetted Area is assumed to be described in either ft^2, or ft^2 per 1000 ft, and WUBA appears to be delivered as ft^2 per 1000 ft, although even this is inconsistent in the literature (King & Tharme 1994).

Secondly, even if this issue was resolved, Shirvell (1986) provides clear arguments as to why expressing habitat as a percentage, rather than absolute amounts, strongly distorts the habitat-discharge curve. In his example, the "minimum flow" inflection point was 340% lower when WUA was expressed as a percentage of total area, than when WUA was expressed as an absolute area. This is because as stream flow decreases, the width decreases at a faster rate than the absolute area of habitat. For instance, a 1 m^2 area of WUA in 10 m^2, representing 10% of the total, would increase to 20% if the wetted area decreased to 5 m^2, although in real terms habitat has not increased.

Nonetheless it is clear that there is less habitat for adults, presumably because the area of riffles is more limited than that of runs. Furthermore, broad comparisons between total area and suitable habitat (2) indicated that suitable habitat for all lifestages of *C. anoterus* comprised a very low percentage of the total wetted area at all flows modelled. This amounted to between 2 and 5% in the case of adults, and 8 and 13% in the case of early juveniles.

THE CONTRIBUTION OF PHABSIM II OUTPUTS TOWARDS SETTING INSTREAM FLOW RECOMMENDATIONS

Water management recommendations, based on PHABSIM simulations, are normally made on the basis of a notable loss of habitat which then constitutes a minimum flow. Notwithstanding later discussions questioning the validity of this step, the following broad interpretations are provided so as to demonstrate the use of the model outputs.

In making flow recommendations, two stratifications are possible from the habitat-discharge curves shown in Figure 9.4. Firstly, the curve for early juveniles is essentially limited to the dry season since this lifestage has matured by the onset of the rains (see Chapter 7). Secondly, since both late juveniles and adults are almost exclusively restricted to riffles, the curves for these two lifestages are confined to this habitat type.

Given that all three lifestages of *C. anoterus* are present during the dry season, all three habitat-discharge curves would be considered. Whilst the habitat for the early juveniles was maintained at the

---

[2] Coincidentally, the length of Site 3 was approximately 1000 ft (~300 m) and so the outputs could have been expressed as ft^2, or ft^2 per 1000 ft. This did provide the facility to compare proportions since the units of wetted area and WUA were the same.

lowest discharges that typify the dry season, habitat declined in the case of both late juveniles and adults below about 0.5 $m^3 s^{-1}$. In contrast however, at the higher discharges, the habitat of early juveniles declined between 1.4 and 3.4 $m^3 s^{-1}$. Thus presumably the recommended flows for the dry season would be between 0.5 $m^3 s^{-1}$ and about 1.5 $m^3 s^{-1}$ in order to accommodate all three lifestages. Flows above this upper limit would also be likely to flush the early juveniles from the shallow runs. In contrast, appropriate flows for the wet season would consider only the habitat-discharge curves for late juveniles and adults. Again, flows below about 0.5 $m^3 s^{-1}$ resulted in a considerable loss of habitat and, within the PHABSIM approach, this inflection value would therefore constitute the minimum discharge for the wet season.

9.5 ASSESSMENT OF THE OUTPUTS OF PHABSIM II

An overriding consideration that prefaces any discussion of PHABSIM II, is that judgement of the accuracy of outputs is entirely inferential. There are no techniques to validate the results (Gan & McMahon 1990) and so any appraisal of the accuracy, or validity, of outputs can only be arrived at through inferences based on an assessment of the protocol and procedures within PHABSIM II.

Within this context, it is important to recognise that whilst habitat-discharge outputs (WUBA) have been produced for three lifestages of *C. anoterus*, as rigorously as possible and based on biological realism, these could have differed considerably based on different choices of options within the simulation routines. Gan & McMahon (1990) clearly show how wide the scope for variable results is (sometimes in the order of 300%), even with exactly the same data set, by simply using the various options in the habitat simulation programmes. Making the most appropriate choices is not facilitated by the manuals, which are widely regarded as user-unfriendly (King & Tharme 1994).

Modelling available habitat via PHABSIM

A major problem with the initial attempt to model available habitat in the Marite River was the inability of PHABSIM II to handle complex channel morphologies. Indeed, Site 1 was finally discounted for this reason. Whilst sites were chosen objectively, in accordance with the IFIM guidelines, having to discount sites retrospectively highlights that, forewarned, it might be tempting for researchers to choose sites that are amenable to modelling rather than those that meet IFIM criteria. This illustrates the importance of understanding the limitations of PHABSIM at the outset, particularly given the high logistical requirements of a PHABSIM study.

Whilst PHABSIM was run for Site 3, a number of problems were encountered with the hydraulic simulation, particularly for those transects describing pools and backwaters. One of the limitations of PHABSIM II is that pools and backwaters are not accounted for, in that the model assumes that these areas of zero flow are equivalent to no habitat, although in reality they offer important refuge and habitat for certain species (Mr. Milhous, *pers. comm.*). Furthermore, habitat descriptions in pools and backwaters are inaccurate once flow is introduced. These habitats that in reality only fill once the main channel has overtopped, are filled from the bottom by IFG4 as water levels rise in the main channel. Since IFG4 only "sees" a transverse slice of the channel, it assumes that these habitats are part of the active channel and hence are filled from upstream waters rather than from waters backing up from downstream. Consequently, wetted area is overestimated. I chose to excise these sections to mitigate this problem.

Additionally, there was poor concurrence between the calculated discharges (from velocities) and the discharge specified for a number of transects (transects 3A, 4, & 7). Whilst this is most likely because these transects lie in riffle/ rapid sections, which have highly variable velocities in any event, this disagreement is considered to be one of the most significant limitations of this data set (Mr. W. Rowlston, *pers. comm.*). These inconsistencies would have had a bearing on the calculations of available microhabitat for the riffle-dwelling *C. anoterus*, suggesting that outputs for these transects should be interpreted cautiously. This, in turn, raises concerns as to the ability of PHABSIM to accurately model riffle habitats which are regarded to be one of the habitats most sensitive to dewatering (see Chapter 6). Ghanem *et al.* (1996) argued that one-dimensional models, where the stream is viewed as a number of transects, such as those within the hydraulic suite of PHABSIM, cannot be used to simulate complex flow phenomena. Specifically, they questioned the accuracy and value of the simulated velocity distributions which, they contend, influence WUA more than depth simulations. They recommended using a two-dimensional model, which is less data intensive and which better accommodates flow features and unsteady flows.

The suitability of describing habitat via transects has come under scrutiny (see discussions in Locke 1988; Shirvell 1989). In the hydraulic simulation of PHABSIM, these transects are considered to represent a length of river upstream, defined by the user (see Figure 2.3). Since such homogeneity in geomorphological conditions is rarely true in reality, the assumption that hydraulic conditions remain constant within cells has been strongly contested by a number of researchers (e.g. Shirvell 1989; Grossman *et al.* 1995; Bourgeois *et al.* 1996; Lamouroux *et al.* 1998). For instance, the poor relationship found between WUA and spawning habitat of chinook salmon, *Oncorhynchus tshawytscha* was principally ascribed to the inability of PHABSIM to detect heterogeneity between transects (Shirvell 1989). Likewise, Bourgeois *et al.* (1996) found that the heterogeneity between transects was one of the most important parameters that accounted for the variable results of WUA. In their study, Grossman *et al.* (1995) elegantly demonstrated the annual variation in substratum composition in a permanent study reach in North Carolina. Lamouroux *et al.* (1998) contend that the scale at which the hydraulic habitat modelling is undertaken is biologically unsuitable since it does not adequately capture the mosaic nature of habitat and consequently, they chose to model habitat use at the scale of a reach. These concerns also highlight the importance of determining the scale at which scientific enquiry is conducted. A transect across a sandy run for example, may well appear, to the researchers eye, to be homogeneous but to the biota inhabiting that reach, small-scale differences in any of the hydraulic variables may affect habitat suitability. These results and debates suggest that the transect method fails to capture real patterns of habitat heterogeneity at the spatial scales that are important for biota (e.g. Bult *et al.* 1998).

Theoretically within PHABSIM, this could be accommodated by including additional transects but this introduces the constraints, discussed in Chapter 5, that are associated with over-transecting a reach. Overall, the concern is that modelling habitat on the basis of conditions at transects introduces an aspect of constancy to the description of physical habitat that is not only untested, but that also deprives the researcher of opportunities to explore the biological responses to small-scale variability. Whilst the challenge for all models is to ascertain what variability to retain, or relinquish (Levin 1992), the degree to which the modelled conditions at Site 3 depart from those in reality is undefined and uncorroborated. Discussions on the themes of heterogeneity and scale, important considerations in the description of habitat for biota, will be fully explored in the subsequent chapters.

In a similar vein, a certain degree of data "homogenisation" is required in preparing the hydraulic input data for PHABSIM. Although PHABSIM can accept up to four digits for channel index, this results in a large number of permutations with few matches to the coded requirements of the indicator species (King & Tharme 1994). The simplification that is then required may underrate certain physical attributes that are critical for describing habitat. In the case of *C. anoterus*, for example, the nature of the bedrock substratum as smooth, fractured or tilted, which is thought to be an important habitat determinant, was lost once a single code was used.

An important concern that has been spearheaded by King & Tharme (1994), relates to the units and interpretation of the modelling outputs of habitat. Clearly, the suitability of the habitat (see Section 9.2) is more important than simply the total available habitat (wetted area). Within PHABSIM, "suitability" is captured in the output of weighted usable area (WUA), volume (WUV) or bottom area (WUBA). The units appear to be in ft^2 per 1000 ft (King & Tharme 1994), although this is never clarified in any of the manuals, and units given in the literature vary widely from m^2 per 1000 ft, to ft^2 per 1000 ft (see King & Tharme 1994, p. 276).

Even if the units represent a measure of area, this does not appear to clarify the interpretation of WUA. For example, what does a WUA of 7.65 m^2 in a streambed area of 10 m^2 represent? Two interpretations are possible. In accordance with the notion of WUA as an area, the output would imply that 7.65 m^2 is available and is totally (100%) suitable. This interpretation, given by Gan & McMahon (1990) is regarded as the official IFIM stance (King & Tharme 1994) but seems to have little biological rationale. A second interpretation, and one that King & Tharme contend would be more valuable, would be to express WUA in units of suitability or "worth", and not as an area which implies 100% suitability. In other words, all of the 10 m^2 of streambed in the above example, is 76.5 % suitable. They argue that this interpretation has greater ecological value, particularly since there is little evidence to support the concept that habitat is always entirely suitable. It would seem unlikely that "perfect" net suitability could be derived from three indices, all or some of which may be relatively unsuitable.

Comments on the outputs of PHABSIM as a contribution to instream flow recommendations

As noted by Scott & Shirvell (1985), the calculation of WUA does not lead directly to recommendations for a flow regime. Nor does PHABSIM II offer, on its own, a holistic assessment of instream flow requirements, and yet it has been used as such (e.g. Nestler *et al.* 1989). Firstly, it is not an ecological model and therefore can only predict how physical habitat will change in relation to changing streamflow, and **not** how species will react to those. Secondly, if the objective is to determine IFR's for the river system as a whole, and not for single species, it fails to account for the wide range of additional instream flow needs, such as those of the riparian zone, for example. Currently, two such comprehensive methods are being developed in South Africa; the Building Block Methodology (King *et al.* in press), and DRIFT (Brown & King, in prep; see Chapter 1).

PHABSIM outputs are intended to provide an indication of critical losses in habitat. At Site 3, the inflection point of 0.5 $m^3 s^{-1}$ is plausible in that it falls within the range of dry-season discharges between 0.04 and 1 $m^3 s^{-1}$ (50% > 0.4 $m^3 s^{-1}$ in August, see Chapter 4). Nonetheless, it could be argued that, as a minimum discharge, the value is high in that it corresponds to flows that are only exceeded 40% of the time. This could therefore be difficult to defend in the negotiation phase. Likewise, some of the minimum critical flows calculated using PHABSIM for the lower Sabie River (Gore *et al.* 1992), were higher than the average daily baseflow, and would be difficult to justify. Moreover, based on the concerns regarding the conceptual framework of the method, little faith could be placed in these outputs without further validation. Equally concerning is evidence that shows how widely disparate recommendations can emanate from IFIM studies depending on how the model is run and the outputs, interpreted (see earlier discussions regarding the study by Gan & McMahon 1990).

Even if the inflection point is tractable, a major limitation of deriving single figures must be recognised. One of the inherent characteristics of semi-arid sub-tropical river systems is the variability in the summer flows (see Fig 4.3). Although it could be argued that single value outputs should serve simply as a minimum critical flow, experience shows all to well that single values frequently become entrenched as definitive management objectives. Moreover, in a system where flood pulses play an essential role in a number of ecological functions such as cues for the onset of reproduction, ensuring this variability is as important to safeguarding the ecological integrity of the system, as a minimum flow. Thus, the task would still remain to incorporate the additional flow pulses and their characteristics into the flow recommendation. Theoretically, this can be achieved within IFIM, using Habitat Time Series software (Milhous 1986; Milhous *et al.* 1990; Stalnaker *et al.* 1995), although this appears to be an option rarely reported in the literature. Its use was not considered appropriate in this study due to the wide range of concerns pertaining to both the hydraulic and habitat outputs that have been raised.

Broader discussion regarding the validity of assumptions contained within IFIM & PHABSIM will be dealt with in the following chapter, which provides an assessment of the entire methodology as applied to this study.

9.6 CONCLUSIONS

All three sites on the Marite River were chosen according to IFIM guidelines and in particular, without considering their amenability to modelling by PHABSIM II. It was only as modelling was initiated that the limitations became apparent, particularly with regard to sites that included multiple channels, backwaters and channels that fill by overtopping.

The final site that was modelled represented an intermediate in terms of channel complexity, and included rapids in which the indicator species were typically found. The IFG4 programme was used to derive a stage-discharge relationship for each transect. Simulations for high and low discharges had to be discounted and even within the range of discharges that were acceptably simulated, outputs for transects that spanned riffles were considered to be insufficiently robust, due to poor concurrence between measured and calculated data. Although estimates of physical habitat were derived for three lifestages of *C. anoterus*, these constraints suggest that the WUBA outputs should only be viewed as broad, relative descriptions of habitat loss or gain.

Given the high logistical investment required to reach a point at which PHABSIM II could be run, it was felt that little more than indications on broad trends were gained. This conclusion may in part reflect the fact that PHABSIM is not used in South Africa and thus suffers the limitations of being isolated from the network of IFIM/ PHABSIM practitioners in North America. Nonetheless, the difficulty of being able to engage PHABSIM out of this context must, in itself, be recognised as a major shortcoming in terms of model transferability. These issues, and related concepts, are elaborated in the following chapters.

PART IV

The development and application of an alternative approach: The Geomorphological-Biotope Assessment

10

An Assessment of IFIM & PHABSIM and the Conceptual Basis for an Alternative Habitat-assessment Approach

10.1 INTRODUCTION

The objectives of this thesis were to assess the potential effects of flow reductions on fish habitat using a quantitative methodology, namely IFIM and PHABSIM, and to evaluate the validity of using such a methodology within the local context. Furthermore, alternative habitat-assessment methodologies were to be explored based on the outcomes of these discussion(see Chapter 1). Chapters 4 to 9 described the approach and application of IFIM to the Marite River study area, and provided a detailed assessment of the methodology at each step. These assessments challenged the conceptual basis, assumptions and methods of IFIM. For the most part, therefore, IFIM was considered to be unsuitable as a potential habitat-assessment approach for the Marite River.

This chapter will provide a synopsis of the main critiques that relate specifically to the determination of physical habitat. This does not negate the additional constraints evident in the theoretical framework and use of IFIM, but reflects the original thesis objectives. This will be followed by a discussion of key concepts that frame a proposed alternative approach to examining flow-habitat relationships. The application of this approach to the Marite River study area will be detailed in Chapters 11 and 12, and assessed, together with IFIM, in Chapter 13.

Terms used to describe physical habitat

Definitions of the terms applicable to *habitat* were made in Chapter 1 (Section 1.6). In accordance with IFIM convention, the term *microhabitat*, as the smallest scale of habitat, has been used in the preceding work and will be applied in future references to IFIM or PHABSIM. However, with the development of an alternative methodology which follows, the term *hydraulic biotope*, or simply *biotope*, which essentially refers to the same spatial scale as that of microhabitats, will be adopted. This accords with the use of this term within fluvial geomorphological research in South Africa with which my work is closely linked. Wadeson (1996) defined a *hydraulic biotope* as "a spatially distinct in-stream flow environment characterised by specific hydraulic and substrate attributes".

10.2 COMMENTS ON THE USE OF HABITAT-ASSESSMENT APPROACHES TO DETERMINING INSTREAM FLOW REQUIREMENTS

As a preface to the assessment of IFIM and the proposed alternative, the following discussion will briefly contextualise both approaches within some of the key debates regarding habitat-assessment approaches.

To recap, the approaches to defining the flow requirements of riverine biota, involve exploring the links between three key components (see Figure 1.4):

1. FLOW → 2. HABITAT → 3. BIOTA (e.g. fish / invertebrates)

My research has concentrated principally on the relationship between flow and habitat, via the *habitat-modelling* approach of IFIM (see Section 1.4).

One of the major criticisms of IFIM is that it is based on the implicit, but rather doggedly championed assumption that "more habitat equals more animals". However, attempts to correlate microhabitat with standing stocks have met with mixed success (see Orth & Maughan 1982; Marthur *et al.* 1985a; Rimmer 1985; Conder & Annear 1987; Irvine *et al.* 1987). In addition, Grossman *et al.* (1995) point out that habitats with the highest species abundance do not necessarily signify critical habitat per sé. Further, if populations are limited by usable habitat it is assumed that there is a positive, linear relationship between standing stocks and WUA(1) (Orth & Maughan 1982; Shirvell 1986). The benefits of establishing this relationship lie in the ability to use habitat as a surrogate for standing stocks. This tenet has evoked considerable debate in the literature (e.g Orth & Maughan 1982; Orth & Maughan 1983; Mathur *et al.* 1983; 1985a,b; Scott & Shirvell 1985; Orth & Maughan 1986; Orth 1987; Layzer & Madison 1995), principally because it fails to explain why a species may be absent from some stream reaches despite the abundance of suitable microhabitat (see, for example, Bozek & Rahel 1991).

Orth (1987) postulated that the poor correlation is because microhabitat analyses can only explain fish *distributions*, and not abundance, since population size is regulated by a variety of additional factors. When Bozek & Rahel (1991) failed to explain the density of young cutthroat trout by the amount of suitable microhabitat, they explored this using both macro- and micro-habitat approaches. In support of Orth's hypothesis, they showed that fish abundance was limited by "macrohabitat" factors, such as spawning gravels and reach depth, whilst microhabitat influenced the spatial distribution of the species in the reach. Thus, the importance examining the relationship between animal abundance and habitat over a number of spatial scales has been stressed (e.g. Poizat and Pont 1996; Bult *et al.* 1998).

Three key factors emerge from the work that have challenged the "habitat quantity versus standing stock" assumption. Firstly, as argued by Orth & Maughan (1986), the importance of physical habitat as a determinant of abundance may only be valid under specific circumstances, such as during periods of limiting habitat. Secondly, physical habitat itself comprises a more complex array of variables than those nominated in IFIM studies, and the importance of each variable may differ in different regions (see Section 8.7). For example, Bozek & Rahel (1991) showed how morphologically diverse streams all create suitable microhabitat for young cutthroat trout in different ways. Thirdly, habitat is only one of a number of factors that limit or influence populations: that is, IFIM does not take into account biological processes such as predation and behaviour (see Chapters 8 & 13), or wider landscape variables (Pusey *et al.* 2000). However, in response to this, the PHABSIM proponents contend that it is a water management model that is restricted to evaluating the variables most closely affected by altered flows (see Chapter 2).

---

[1] WUA is a term used within IFIM to describe usable habitat for a species (see Chapters 2 and 9).

The lack of a tested ecological linkup with the outputs of IFIM and PHABSIM constitutes a major constraint for IFIM, but equally applies to any habitat-assessment approach. As research into this field gains momentum and understanding, it is clear that the limitations of habitat models need to be clearly recognised and reevaluated. Bearing these broader issues in mind, it is now appropriate to focus on discussions pertaining to physical habitat which, within IFIM, still requires further refinement.

10.3 OVERVIEW OF THE ASSESSMENT OF IFIM & PHABSIM AS IDENTIFIED FROM THE PRECEDING RESEARCH

A prerequisite for undertaking an IFIM or microhabitat study is the completion of two key steps: namely an assessment of catchment equilibrium(2) and the selection of sites (Bovee 1982). They lay the foundation for quantifying the distribution and abundance of habitat, and for decisions as to whether or not this will hold true under future water-development scenarios.

Despite the importance of establishing channel equilibrium, almost no studies report undertaking this step, with a few exceptions (e.g King & Tharme 1994). As stated in Chapter 4, this is not surprising given the inadequate definitions and guidelines, particularly regarding unidirectional (and hence long-term) channel change. Likewise, the protocol for site selection is questionable due to ambiguities in terminologies and scale. Since site-specific results are extrapolated to the entire river, an explicit statement of what these sites represent is required otherwise, clearly, extrapolation cannot be justified. Despite this, only a few authors have addressed this issue (e.g. Maddock & Bird 1996; Maddock 1999). Consequently it would appear that a culture has developed within IFIM studies where there is little peer review, or demand, for either of these steps to be applied. Ultimately, the inadequacies of these steps were ascribed to the failure to define the spatial relations between physical habitat features.

In addition, evidence from research on lowveld river systems in South Africa has shown that their geomorphological characteristics differ significantly from those in which IFIM was developed. This suggests that the guidelines for site selection, as loose as they are, may be inappropriate for East African semi-arid systems. For instance, data for the Sabie system, a bedrock/ alluvial system (see later), indicates that tributaries, which are used in IFIM to identify zones, are not as morphologically significant as in North American temperate systems for which PHABSIM II was developed (Moon *et al.* 1997).

Once macrohabitat and microhabitat sites have been selected, the habitat at a site is described by transects (Chapter 5). Although theoretically straightforward, resolving the placement of transects in complex, multiple channel-types, was problematic, as was their subsequent modelling (see Chapter 9). Moreover, the description of habitat on the basis of transects across "broad habitat features" is

---

[2] Catchment equilibrium *(see* Chapter 4) refers to a situation in which the dynamic catchment factors such as water and sediment yields (and hence microhabitat factors) fluctuate about some steady state.

questioned since it assumes that conditions between transects are homogeneous. Indeed, heterogeneity between transects has been cited as one of the most important parameters influencing the variable outputs of WUA (e.g. Shirvell 1989; Bourgeois *et al.* 1996).

Quantifying the habitat used by a target organism is undertaken as a parallel process to describing habitat availability. With IFIM, the selection of a single, or limited number of species is rationalised on the basis that a comprehensive community analysis is beyond the scope of most research initiatives. The underlying assumption, that the provision of conditions for the selected species will also satisfy the habitat requirements of the remaining species, makes this a critical step. Nonetheless, the guidelines in IFIM do not rigorously link target species selection to the study objectives. To address this, an alternative model for the indicator species selection was proposed in Chapter 6.

The habitat that is both available to, and used by, the target species is expressed within IFIM as Habitat Suitability, or SI curves (Chapter 8). Firstly, representing physical habitat as univariate curves as opposed to an area, with spatial dimensions, appears to have little biological basis and is, conceptually, counterintuitive. These concerns form the basis for much of the following research and will, therefore, be fully discussed below (see also review in Chapter 13). Secondly, these curves are often presented as preference indices which purport to address, and correct for, the lack of "optimal" habitat availability of the species in question. However, major concerns pertaining to the derivation and interpretation of these curves were raised in Chapter 8. Predictions of preference assume that the measurement of microhabitat availability is accurate. I challenged this on the basis of insufficient sample size, the inaccessibility of certain habitat types, and limitations in the development of the availability model itself.

In view of this, I showed that any minor deviation in the data on habitat availability from that of reality causes a major shift in the preference curve and hence their interpretation (see Table 8.11). I also showed that a single preference index value can reflect quite different situations of habitat availability and use (see Table 8.10). Such ambiguities raised concerns as to how robust and relevant the SI curves are, particularly in instances where there appeared to be little biological rationale for results. For example, apparent seasonal differences in the preferred habitat (such as depth), may simply be a function of seasonal differences in the habitat availability. These results suggest that in most studies that SI curves are inadequately validated and can only be regarded as gross representations of the microhabitat variables that a species may use.

Finally, the total microhabitat available for the site in question at different discharges is derived through PHABSIM II. The problems of modelling complex channel morphologies evident in the Marite River have already been raised. In particular, concerns were raised with regard to the ability to model riffles or rapids, as well as secondary channels. With rapids being its primary habitat, these considerations were particularly pertinent in the case of *C. anoterus*.

In concluding, my results suggest that if the sites are incorrectly chosen, or the determination of habitat availability is erroneous, derived suitability curves will be so inaccurate that results can only be viewed with circumspection. Moreover, whilst it may be expedient to present a single habitat use or preference model (rather than seasonal models) for a species, the effect of this is to establish a myth of constancy, thereby obscuring the variable and dynamic nature of habitat use. The dangers of this approach lie in the fact that it makes the management option of interpreting habitat needs as constant, all too easy (see also preceding discussion on the additional factors influencing habitat use). Thus, in spite of warnings from its authors, IFIM may ultimately work at cross purposes to the objectives for which it was intended (Stanford & Ward 1992). It is within this context that an alternative habitat-assessment approach will be developed in the following section.

10.4 TOWARDS AN ALTERNATIVE APPROACH TO THE ASSESSMENT OF HABITAT AVAILABILITY

Motivation for further research

Although the authors of PHABSIM point out that theirs' is a water management model, it was not developed in a vacuum. Indeed, it evolved in response to the needs of ecologists and water managers and shaped the future of habitat-assessments. Nonetheless, given this, it must at least have the capacity to derive outputs that are useful to both user groups. Whilst the relatively simple, single outputs of PHABSIM may be useful to some, ecologists are often unconvinced that these capture, at a meaningful scale, the heterogeneous and dynamic attributes of river systems that influence biotic distribution and abundance. Let us not forget that it is ultimately the biotic response to changing flows that we are trying to understand although this may be approached from a "habitat" slant (see Figure 1.4). Regardless, the challenge for all models is to decide what detail to preserve in order to describe processes that produce patterns, and what detail to omit, not because it is unimportant but because it does not affect these observed patterns (Levin 1992).

I would suggest that many of the constraints of IFIM arise, predominantly, from two key oversights:

- the omission of a clear morphological classification system for rivers (despite their availability) which explicitly describes the spatial relationship between physical features and,
- it's inflexibility in incorporating new and evolving conceptual models.

The following research, therefore, is designed to test the conceptual basis of IFIM/ PHABSIM through the development of an alternative approach to habitat-based assessments. In essence, this research was framed by the need for a conceptual framework that (i) integrates the various spatial scales of habitat and that (ii) describes the mechanisms governing spatial patterns and, (iii) that offers an approach to describing biotope availability in a way that captures the heterogeneous nature of habitat. When one considers that within a full habitat assessment, the management of flow regimes is undertaken at a much larger scale (river basin or study reach) than that of habitat selection by biota, then integrating information across this wide scale differential, is critical. I would argue that this can more readily be achieved by prefacing habitat assessment with a rigorous classification system that links spatial features, and their underlying mechanisms, across spatial scales.

Recognising the potential of a multi-scale, classification system also raises the opportunity to explore habitat patterns, and their variability and underlying influences. A number of key themes and concepts underscore these issues, including *heterogeneity and pattern, the issue of scale, patch dynamics* and *landscape ecology*. These themes and concepts, together with a description of an appropriate classification system, will be reviewed, followed by a statement of the objectives of the research and an overview of a proposed alternative approach.

10.5 KEY CONCEPTS RELATING TO THIS RESEARCH

The themes of heterogeneity, pattern & scale

One of the most important developments in modern ecology is the recognition that heterogeneity(3), or spatial pattern, is a key part of the structure and function of nature (Kolasa & Pickett 1991; Li & Reynolds 1994; Pickett & Rogers 1997; Palmer & Poff 1997, and see discussion in Chapter 13). It is in accepting this challenge that, in instream studies, for example, we can move from the notion of "optimal habitat", embodied in SI curves, to the recognition that it is a *mixture of habitat*, or heterogeneity, at different scales that constitute key habitat attributes. Further, this paves the way for understanding firstly, how the spatial and temporal patterns are developed and maintained and, secondly, for unravelling the ecological consequences of these for populations and ecosystems (see example in Crowl *et al.* 1997; Stevenson 1997). Once patterns are detected, one can look for their determinants and, with an understanding of the mechanisms, one can explore potential change. In other words, one has predictive capacity (Levin 1992).

Central to these patterns is the issue of scale and how the scale of observation influences the descriptions of pattern and variability (Levin 1992). *Scale* is a theme that runs through the majority of habitat studies, even if only implicitly, and yet, as stated by Bult *et al.* (1998), it is poorly resolved in most habitat studies. All ecological systems exhibit heterogeneity and patchiness at a broad range of scales, and this environmental patchiness provides a diverse landscape of resources that is, amongst other things, fundamental to population dynamics. Importantly, no single mechanism explains patterns on all scales (Levin 1992).

These themes of pattern and scale then become fundamental to advances in habitat-assessments. For example, if one takes an ecosystem approach to habitat-assessments, the rationale may be to explore mechanisms first from a catchment perspective and then to trace these through to the finest resolution at which habitat selection operates (see, for example, Richards *et al.* 1996). At the catchment scale, the patterns of topography, rainfall, temperature and geology and land-use will be expressed in the hydrological and geomorphological attributes of the river. This spatial expression provides the architecture of physical habitat. The hydrology then superimposes the dynamic nature of habitat on this physical form. These principles are not new and are being employed for instance, within the broader

---

[3] Defined as the variability in a process or pattern over space or time (Kolasa & Rollo 1991).

discipline of Integrated Catchment Management (see for example Cohen *et al.* 1998; Pollard & Huxham 1998; Krairapanond & Atkinson 1998; Pollard *et al.* 1998; Harper *et al.* 1999). In ecological terms, there are patterns within this broader scale that can be extracted to understand patterns in animal distributions and abundance (see review by Brookes 1994). It is at a much finer scale, however, that habitat is selected and there is a variable scale even within this. Consequently, resolving the issue of scale is critical and a framework is required that integrates habitat information across spatial scales that may differ by orders of magnitude.

The development of an ecologically-significant, geomorphological classification system for South African rivers

An important step forward for ecologists has been a formal recognition that the morphology of stream channels influences the distribution and abundance of instream physical habitats. Characterising and appreciating these spatial patterns falls within the rubric of river classification systems and, already, there is a well-developed body of literature that underscores their importance (see Beschta & Platts 1986; Kershner & Snider 1992; Naiman *et al.* 1992; Petts & Maddock 1994; van Niekerk *et al.* 1995; Wadeson 1996; Rowntree & Wadeson 1996; Pickett & Rogers 1997; Montgomery 1999). In essence, geomorphological classification systems allow for an examination of geomorphic patterns that can be linked, causally, to physical factors regulating instream characteristics and hence, in part, the distribution and abundance of biota (van Niekerk *et al.* 1995).

The last five years of aquatic research in South Africa have seen an increasing integration of interdisciplinary concepts and approaches to lotic-system functioning, particularly in the field of stream-habitat research (see for example van Niekerk 1995; Rowntree 1996; Rowntree & Wadeson 1996). With the evolution of habitat studies in South Africa, three major problems emerged in the description of physical habitat.

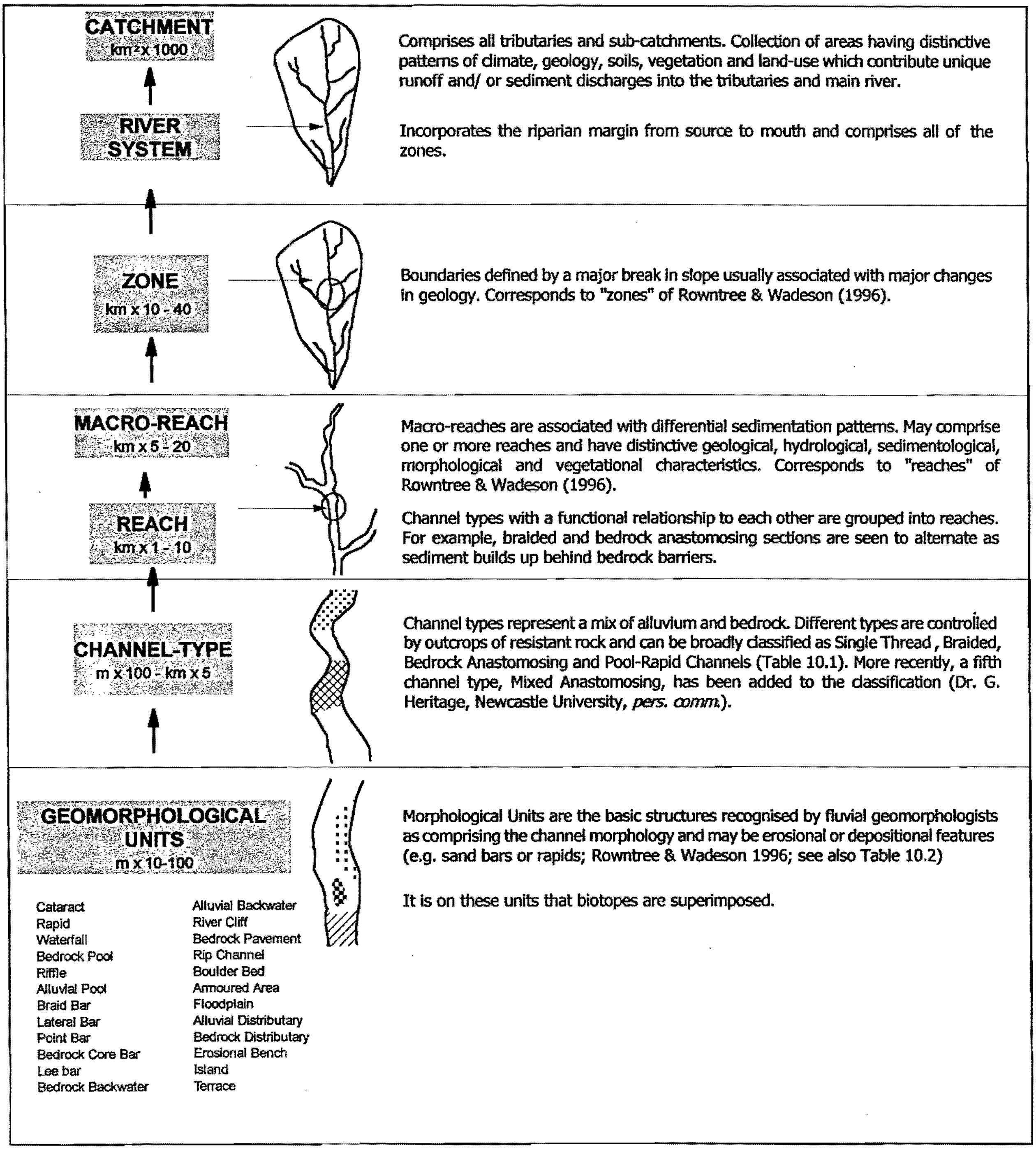
Firstly, there were few collaborative research initiatives between ecologists and fluvial geomorphologists and, hence, there was little common understanding of the respective fields and conceptual frameworks. Geomorphological terms used by ecologists to describe habitat frequently did not conform to conventional definitions and this hampered collaborative research efforts. Ecologists described habitat somewhat intuitively, and inherently included an ecological and temporal bias, whereas geomorphologists regarded morphological features as fixed in space and time (Rowntree & Wadeson 1996). Thus for example, to the ecologist, the amount of "riffle" habitat varied seasonally as the distribution of turbulent flows over cobble varied, whilst geomorphologists defined this as a fixed channel feature irrespective of flow. Secondly, although it was clear that ecologists needed a geomorphological model on which to base their classification of physical habitat, many southern African rivers did not conform to the models developed elsewhere. Thirdly, with ecologists generally working at smaller scales than fluvial geomorphologists, there was a paucity of geomorphological information (the template for habitat) at a scale that was ecologically significant (Rowntree & Wadeson 1996).

These constraints provided the impetus for the development of locally-applicable classification systems for South African rivers at a scale that had ecological significance. Researchers from both fields, as well as hydrologists, embarked on research that integrated these concerns and that developed many of the guiding principles (Wadeson 1994; Heritage & van Niekerk 1994; Wadeson & Rowntree 1994; Heritage *et al.* 1995a,b; van Niekerk *et al.* 1995; Rowntree 1996; Moon *et al.* 1997; Rowntree & Wadeson 1999).

The initial problem in classifying South African rivers concerned their geomorphological nature. Many rivers in South Africa, such as those that flow from the escarpment eastwards towards Moçambique, are known as *bedrock-controlled* rivers, whilst most of the international research had focussed on *alluvial systems.* Alluvial and bedrock systems represent opposite ends of the spectrum in terms of sediment supply and transport capacity (van Niekerk *et al.* 1995). Whilst the characteristics of alluvial features are largely governed by sediment supply and discharge patterns, bedrock features tend to respond more slowly and less predictably to disturbance. The recognition of differences between alluvial and bedrock systems, particularly when assessing the impact of flow alterations on channel morphology, was important for ecologists (Rowntree & Wadeson 1999).

As a point of departure, South African researchers reviewed the different geomorphological classification systems for rivers. Stream classification has a long history and has been reviewed from a geomorphological perspective by Hawkes (1975), Mosley (1987) and Rosgen (1994), whilst the incorporation of ecological concerns has been elegantly addressed by Naiman *et al.* (1992). Although geomorphological in emphasis, the local reviews by Wadeson & Rowntree (1994) and van Niekerk *et al.* (1995) focussed on the importance of a biologically-based classification system. A pervasive theme in recent classification systems has been a hierarchical perspective that centres on the ability to link catchment-scale features to those at the biotope scale. Notable examples include the *nested hierarchy* of Hawkins *et al.* (1993) which was based on the morphological and hydraulic properties of geomorphic units (see later), but which concentrated principally on alluvial systems. The *spatially-nested hierarchy* of Frissel *et al.* (1986) is widely recognised for its valuable contribution to classification systems, but van Niekerk *et al.* (1995) suggested that it is largely unsuitable for the lowveld Sabie system in that it focussed primarily on second- and third- order mountain streams in forested environments.

Importantly for ecologists, two teams in South Africa started to examine the underlying mechanisms controlling the architecture and distribution of instream habitats. Generally, their approaches were mutually supportive but were undertaken for different objectives. To address the inclusion of large rivers, and to incorporate catchment characteristics, Wadeson & Rowntree (1994) modified the Frissel *et al.* classification system to derive a top-down hierarchical classification system for selected rivers throughout South Africa. van Niekerk & Heritage (1993), and van Niekerk *et al.* (1995), on the other hand, concentrated their efforts on semi-arid, mixed bedrock-alluvial systems, using the Sabie River (into which the Marite River flows) as a case study. As a result of the difficulties recognised by Wadeson & Rowntree in classifying rivers at an ecologically-relevant scale using a top-down framework, van Niekerk *et al.* proposed and adopted a bottom-up, *agglomerative hierarchical classification system.* This allowed for the linkage of the catchment scale attributes with that of the microhabitat scale (Figure 10.1).



Comprises all tributaries and sub-catchments. Collection of areas having distinctive patterns of climate, geology, soils, vegetation and land-use which contribute unique runoff and/ or sediment discharges into the tributaries and main river.

Incorporates the riparian margin from source to mouth and comprises all of the zones.

Boundaries defined by a major break in slope usually associated with major changes in geology. Corresponds to "zones" of Rowntree & Wadeson (1996).

Macro-reaches are associated with differential sedimentation patterns. May comprise one or more reaches and have distinctive geological, hydrological, sedimentological, morphological and vegetational characteristics. Corresponds to "reaches" of Rowntree & Wadeson (1996).

Channel types with a functional relationship to each other are grouped into reaches. For example, braided and bedrock anastomosing sections are seen to alternate as sediment builds up behind bedrock barriers.

Channel types represent a mix of alluvium and bedrock. Different types are controlled by outcrops of resistant rock and can be broadly classified as Single Thread, Braided, Bedrock Anastomosing and Pool-Rapid Channels (Table 10.1). More recently, a fifth channel type, Mixed Anastomosing, has been added to the classification (Dr. G. Heritage, Newcastle University, *pers. comm.*).

Cataract
Rapid
Waterfall
Bedrock Pool
Riffle
Alluvial Pool
Braid Bar
Lateral Bar
Point Bar
Bedrock Core Bar
Lee bar
Bedrock Backwater
Alluvial Backwater
River Cliff
Bedrock Pavement
Rip Channel
Boulder Bed
Armoured Area
Floodplain
Alluvial Distributary
Bedrock Distributary
Erosional Bench
Island
Terrace

Morphological Units are the basic structures recognised by fluvial geomorphologists as comprising the channel morphology and may be erosional or depositional features (e.g. sand bars or rapids; Rowntree & Wadeson 1996; see also Table 10.2)

It is on these units that biotopes are superimposed.

Figure 10.1 The hierarchical classification system for mixed bedrock/alluvial rivers in the Lowveld Region as proposed by van Niekerk *et al.* (1995). See also Table 10.1 and Table 10.2. The description of the terms, together with a schematic representation of the spatial features, are taken from both van Niekerk *et al.* (1995) and Rowntree & Wadeson (1996).

In essence, their classification holds that **geomorphological units**[4] combine to form **channel types** (Table 10.1), which are characterised according to the degree of accumulated sediment within the active channel (Heritage *et al.* 1997a,b). Channel types with a functional relationship are grouped into **reaches**. An example of such a relationship is that of alternating sections of braided and anastomosing channel types which are relational in that the bedrock controls cause an increase in deposition upstream and hence the development of braiding. At a higher scale, reaches combine to form **macro-reaches** which have distinct geology, hydrology, sediment and vegetation. Several of these combine to form a **zone**, with boundaries delimited by major breaks in slope. The **river** comprises all the zones and riparian margins and lies within the **catchment**.

A key focus of their research was that of geomorphic units (such as rapids, bars and pools; Table 10.2). These are important features in terms of ecological research in that they represent the smallest spatial scale of the classification and hence are fixed areas, or templates, on which physical habitat is superimposed. From their research, van Niekerk *et al.* (1995) found that the major determinants of habitat structure and distribution in the Sabie system are the sediment and water dynamics which, in conjunction with a highly unpredictable seasonal flow-regime, give rise to a patchy mosaic of geomorphic units. They are formed from the erosion of bedrock and the deposition of alluvium. van Niekerk *et al.* described five channel types for the Sabie River (Table 10.1 a), which are defined according to their assemblage of geomorphic units (Table 10.1 b).

At the same time that these classification systems were evolving, a supportive concept regarding the smallest spatial scale of physical habitat, was developing. This was formulated by Wadeson (1994) in the concept of **hydraulic biotopes** (see Section 10.1). Importantly, since biotopes preserved their spatial reference, they represented a marked departure from the conventional IFIM description of microhabitat as three, independent curves. Essentially, biotopes are delimited through a visual assessment of flow and substratum. Standardised descriptions of both of these attributes (Table 10.3), and of hydraulic biotopes, were developed by a multi disciplinary team at a workshop held in 1995 (see Rowntree 1996). Following this workshop, Rowntree & Wadeson (1999) combined flow type and substratum class into a hydraulic biotope matrix in order to develop an objective method for visually identifying biotopes (see Chapter 11, Table 11.3). In support of this approach, Wadeson & Rowntree (1998) also tested, and provided statistical validation of the flow hydraulics of biotope classes.

---

[4] The term geomorphological unit and its abbreviated (but synonymous) terms, such as morphological unit, morph unit and geomorphic unit, are frequently interchanged in the literature. Henceforth, the term *geomorphic unit* (see also Montgomery 1999) will be used specifically to refer to these geomorphological units of the classification system of van Niekerk *et al.* (1995).

Table 10.1

(a) Description of the five primary channel-types that comprise the Sabie River and, (b) the geomorphic units that are commonly associated with each channel type (after van Niekerk & Heritage 1993; van Niekerk *et al.* 1995).

(A) MAIN CHANNEL TYPES OF THE SABIE RIVER

POOL/ RAPID	BRAIDED	SINGLE THREAD	ANASTOMOSING	
			BEDROCK ANASTOMOSING	ALLUVIAL ANASTOMOSING
• Dominated by bedrock and small-scale erosional features • Typically, rapids are free from sediment • Pools vary from sediment-free bedrock areas to bedrock pools with variety of bar types	• Alluvial systems that exhibit channel splitting and rejoining over a distance of a few channel widths • Consist of ephemeral deposits of sediments • Uncommon in the Sabie River	•Encompass both straight and meandering channels •Develop in alluvial sections •Typically contain features noted in temperate alluvial systems	• First described by van Niekerk & Heritage (1993) • Dominated by bedrock features, particularly bedrock distributaries • Distributaries at different elevations may be active at same flow • Bedrock core bars distinguished by *Breonadia salicina*	•Macro-channel displays multiple alluvial, & occasional bedrock distributaries •Different geomorphological features influenced by differing flows (i.e. not by bankfull flow) • Active channel is relatively stable

(B) GEOMORPHIC UNITS ASSOCIATED WITH EACH CHANNEL-TYPE. P = present; r = rare; x = does not occur, blank = uncertain

GEOMORPHIC UNIT	POOL/ RAPID	BRAIDED	SINGLE THREAD	ANASTOMOSING
Cataract	P	X	X	P
Rapid	P	X	r	P
Waterfall			X	P
Bedrock pool	P	X	P	P
Riffle	X	r	r	X
Alluvial Pool	r	P	P	X
Braid Bar	r	P	r	X
Lateral Bar	P	P	P	X
Point Bar	X	r	P	X
Bedrock Core Bar	P	X	X	P
Lee Bar	P	X	X	P
Bedrock Backwater	P	X	X	P
Alluvial Backwater	X	r	X	
River Cliff		r	r	
Bedrock Pavement	P	X	X	P
Rip Channel		P		
Boulder Bed	P	X	r	P
Armoured Area	P	P		P
Floodplain	P	P	P	P
Alluvial Distributary	r	P	X	r
Bedrock Distributary	P	X	X	P
Island				
Terrace	P	P	P	X

Table 10.2
Description of the geomorphic units found on the Sabie River (after van Niekerk *et al.* 1995; Heritage *et al.* 1995a; Rowntree & Wadeson 1999). Once flow is superimposed on the geomorphic unit, biotopes are derived.

GEOMORPHIC UNIT	DESCRIPTION
Cataract	Step-like succession of small waterfalls, seldom drowned out at high discharges.
Rapid	Steep bedrock sections with concentrated flow, little or no alluvium in the channel. Substratum largely unweathered bedrock (see riffles).
Waterfall	Abrupt vertical discontinuity in channel slope.
Bedrock pool	Deeper areas forming behind bedrock control. May accumulate limited sediment or become scoured.
Bedrock core bar	Accumulation of finer sediment on top of bedrock in bedrock anastomosing areas and rapids (*sensu* van Niekerk & Heritage 1993).
Riffle	Accumulation of coarser, *transported* sediment as a topographic high point.
Lee bar	Accumulation of sediment in the lee of flow obstructions.
Bedrock backwater	Stationary, or near stationary bodies of water in bedrock, morphologically detached side channel which is connected at the lower end to the active channel.
Alluvial pool	Topographic low point in an alluvial channel caused by scour, characterised by finer sediments.
Braid bar	Multiple alluvial bars: Accumulation of sediment in mid-channel causing the flow to diverge over a scale that approximates to the channel width.
Lateral bar	Alluvial bar: Accumulation of sediment attached to the side of the channel, may occur sequentially downstream as alternate bars.
Point bar	Alluvial bar: Accumulation of sediment on the inside of a bend in a sinuous channel.
Alluvial backwater	Stationary, or near stationary bodies of water in alluvium, adjacent to the active channel.
River cliff	Vertical, or near vertical alluvial erosional face.
Bedrock Pavement	Horizontal or sub-horizontal area of exposed bedrock.
Rip channel	High flow distributary channel on the inside of point and lateral bars.
Boulder bed	Accumulation of locally-derived material exceeding 0.25m in diameter.
Armoured area	Accumulation of coarser sediment due to winnowing of finer sediment.
Floodplain	Extensive lateral accumulation of sediment from flood deposition and lateral channel migration.
Alluvial distributary	Individual active channel in an alluvial braided or anastomosing system.
Bedrock distributary	Individual active channel in a bedrock anastomosing system.
Erosional bench	Terrace like feature on macro-channel side resulting from downcutting.
Island	Large mid-channel sediment accumulation that is rarely inundated. Stabilised by vegetation.
Terrace	Relic floodplain or macro-channel floor deposits above the present river level.

Together with the concept of microhabitat as a biotope patch, the development of local classification systems considerably improved our understanding of the importance of the geomorphology in habitat studies. Notably, it signified that catchment-wide morphologies could be linked, at increasing levels of detail, to attributes at the scale of biotopes. Due to its development for the very system into which the Marite River falls, the classification system of van Niekerk *et al.* (1995; Figure 10.1) was regarded as the most appropriate for my research. To this, biotopes (Wadeson 1994) were added to represent the smallest spatial scale of habitat.

Table 10.3
Key attributes of biotopes: the classification of flow-types and substratum classes (Wentworth scale) (from Rowntree 1996)

FLOW TYPES	DEFINITION
No flow	No water movement
Barely perceptible flow	Smooth surface, flow only perceptible through the movement of suspended matter
Smooth boundary turbulence	Water surface remains smooth; streaming flow takes place throughout the water profile; turbulence can be seen as the upward movement of fine suspended particles
Rippled surface	Water surface has regular disturbances which form low transverse ripples across the direction of flow; degree of disturbance may vary from faint to strong ripples
Undular standing waves	Standing waves form at the surface but there is no broken water
Broken standing waves	Standing waves present which break at the crest
Free falling	Water falls vertically without obstruction
Chaotic flow	Complex mixture of continually varying flow types associated with unsteady, pulsating flow; common at high flows.
Boil	Direction of flow is predominantly vertical with strong eddies or boils forming on the surface of the water
SUBSTRATUM CLASS	**PARTICLE DIAMETER (mm)**
Silt	< 0.0625
Sand	0.0625 - 2
Gravel	2 - 64
Cobble	64 -256
Boulder	>256
Fractured bedrock	Bedrock with significant cracks and crevasses which afford some cover
Smooth bedrock	Bedrock lacking cracks and crevasses
Cliff	A vertical bedrock face

Theories of patch dynamics and landscape ecology

Inherently related to the hierarchical classification system of rivers are the unifying concepts of *patch dynamics* and *landscape ecology*. In fact, the above classification of van Niekerk *et al.* (1995) is an example of the various nested scales of patchiness where small, spatially explicit patches combine to form the next hierarchical level (Pickett & Rogers 1997). This section therefore aims to outline the key concepts of patch dynamics and landscape ecology.

A *patch* is simply a recognised area on the surface of the earth that contrasts with adjacent areas and has definite boundaries (Kotliar & Wiens 1990). The origin of the term is difficult to trace, but conceptually the idea was first introduced in 1947 by Watt (Levin 1992). Importantly, a patch is a spatial unit only as determined by the organism since, clearly, patch boundaries differ amongst organisms (Pringle *et al.* 1988).

Patch dynamics, reviewed by Pickett & Rogers (1997), and for lotic systems by Pringle *et al.* (1988) and Townsend (1989), focusses on the mechanisms behind patch change and the interaction between patches. Conceptually, it is the recognition in modern ecology of the universal heterogeneity in nature. In essence, patch dynamics holds that the physical environment, organisms and other ecological objects have complex spatial diversity, and together, comprise a heterogeneous mosaic or patchy landscape (see for example, Bell *et al.* 1991; Wiens 1995). It goes further in that these spatial patterns (i.e.

heterogeneity) are considered to be a key component of the structure and functioning of ecological systems (Pickett & White 1985). It is important to note, however, that parity between major paradigms such as the RCC and nutrient spiralling (see Chapter 1), and patch dynamics still needs to be addressed (Cummins 1992). Pringle *et al.* (1988) for example, suggest that patch dynamics can be integrated into the paradigms of RCC and nutrient spiralling but Townsend (1989) suggests otherwise.

Patch dynamics, as a discipline, has evolved from one of a simplistic interpretation of patches as discrete and internally homogeneous entities at one scale, to a more complex view in which mosaics of patches occur within other patches at a number of scales. The latter view was first recognised as early as 1976 by Wiens and has subsequently been developed into a hierarchical classification of patches at multiple scales (Kotliar & Wiens 1990). The key features of patches are summarised in Table 10.4.

Table 10.4
Key characteristics of patches

- Patches can refer to *abiotic or biotic* components (e.g. a geological patch; a temperature patch; a woodland patch).
- Patches can apply to individual organisms, populations, communities, behavioural (or other) guilds, ecosystems or landscapes (Kolasa & Pickett 1991).
- The structure and functioning of patches may change in space and time. Patches may be *dynamic and mutable* (reflecting either natural or anthropogenic processes).
- Patches are parts of *hierarchies* and the concept of patches may be applied at *many spatial scales* (Wiens 1989). Patches at one scale may be composed of smaller-scale patches that influence the functioning of the larger patch (Pickett & Rogers 1997). Further, specific patterns and dynamics can characterise a particular scale.
- Organisms usually require an ample *mixture* of patches to fulfil behavioural, diurnal, seasonal or lifestage requirements, rather than a single optimal patch-type. It is often therefore the combination of patches that is important.
- Patch mosaics comprise *elements that change at different rates* (Pickett & Rogers 1997).
- Patches have a *multi dimensional structure* (Pickett & Rogers 1997). For example, in rivers, the habitat architecture reflects depth, substratum topography, channel form and velocity, amongst other factors.
- The *edge* between contrasting patches is important in that their resistance or permeability determines the flow of characteristics, such as nutrients or organisms, between patches (see review by Wiens *et al.* 1985).
- *Disturbance* is less likely to spread over a spatially heterogeneous area (i.e. high patch diversity) than through a homogeneous landscape (Pringle *et al.* 1988).

Patch dynamics has two important implications for ecological concepts. Firstly, since biological diversity reflects environmental heterogeneity, patchiness is inherently linked to biodiversity (Pickett 1996). Pringle *et al.* (1988) suggest, for example, that the declines in fish diversity in the rivers of the central plains of North America may reflect the decrease in habitat mosaics through human disturbance. Secondly, patches generate and control the flow of materials, energy, information and organisms through the environment (Wiens *et al.* 1985; Breen *et al.* 1988; Pringle *et al.* 1988; Wiens 1992). How organisms for instance, move between patches is predicated on the quality of patches and their locational relationships within mosaics, such as shape, size, arrangement and connectedness (Wiens *et al.* 1993).

Kotliar & Wiens (1990) argue eloquently for applying a hierarchical approach to patches and suggest that investigators rarely consider using diverse patch types at multiple scales to test theories. They go on to apply this argument to foraging theory and suggest that deviations from theoretical predictions in many field tests may be due to the failure to include the complexities introduced by additional levels of patchiness. A simple illustrative example is that of a species using certain patch types in which to forage. Decisions to move from one patch to another will be influenced by both the features of the patch it uses as well as those that it encounters. Thus its movements through the landscape are contingent not only on the quality of the local patch but on its location within the mosaic of patches (size, shape, arrangement and connectedness). How these patches are located, as well as their attributes, will be influenced at a broader scale by biotic and abiotic factors.

There have been a number of approaches to exploring the occurrence of patchiness: the island approach, the shifting mosaic approach and the landscape approach, and these are reviewed by Pickett & Rogers (1997). In brief, the island approach is formulated in the theory of island biogeography (MacArthur & Wilson 1967). Here, islands (patches) are open to the influence of outside fluxes, which is reflected in colonisation and extinction processes. A constraint of this theory is that it assumes a fixed template of patches in an essentially uniform matrix (Pickett & Rogers 1997). The shifting mosaic approach (*sensu* Borman & Likens 1979) emphasizes that patches are bounded by other patches to form a mosaic, which may itself change through time. This approach unifies population, community and landscape ecology. The landscape approach (Forman & Godron 1986; Turner *et al.* 1990; McDonnell & Pickett 1993) recognises the importance of patches influenced by humans (occupied or created), both in historical and contemporary terms (Pickett *et al* 1989; McDonnell & Pickett 1993; Pickett & Rogers 1997).

Key features of measuring habitat patches include their shape and size; the position and relationship of patches relative to other similar or dissimilar patches; the hierarchical relationship between patches (how large and small scale patches influence each other) and the species composition of patches. The spatial pattern of patches has been expressed by Wiens *et al.* (1993) in several measures of mosaic structure (Figure 10.2; Table 10.5). Pringle *et al.* (1988) also suggest examining patch durations and mechanisms affecting patch formation.

Whilst *patch dynamics* considers the relationship of patches within a mosaic and from a hierarchical perspective, *landscape ecology* is the discipline devoted to the study of the ecological consequences of patch heterogeneity (Kotliar & Wiens 1990; see also Wiens *et al.* 1985; Turner & Gardner 1991; Pickett & Cadenasso 1995). According to Wiens *et al.* (1993) landscape ecology focuses on the *effects* of explicitly spatial patterns and interactions, primarily at the scale of kilometres (although they state that a coherent paradigm for landscape ecology has yet to emerge). Within the remit of landscape ecology, Richards *et al.* (1996) showed how landscape attributes (principally geologic and land-use) affect macroinvertebrate assemblages.

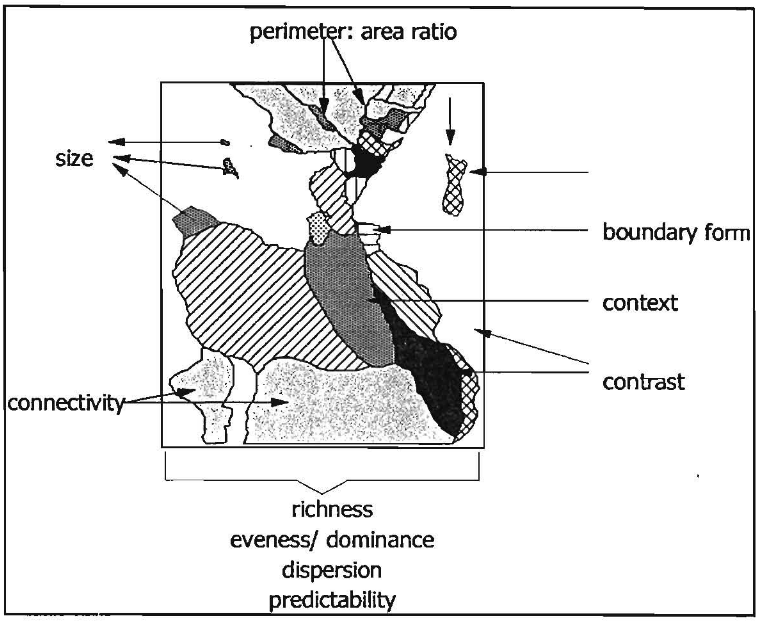


Figure 10.2 An example of a landscape-mosaic map, showing patch parameters that may be measured (after Wiens *et al.* 1993).

Table 10.5
Measurable features of landscape mosaics (from Wiens *et al.* 1993)

FEATURE	DESCRIPTION
Size distribution	Frequency distribution of sizes of patches of a given type
Boundary Form	Boundary thickness, continuity, linearity, length
Perimeter :area ratio	Relates patch area to boundary length; reflects patch shape
Patch orientation	Position relative to a directional process (e.g. water flow, passage of migrants)
Context	Immediate mosaic-matrix in which a patch of a given type occurs
Contrast	Degree of difference in a variable across a given boundary between patches (Kotliar & Wiens 1990)
Connectivity	Degree to which patches of a given type are joined by corridors into a lattice of nodes and links
Richness	Number of different patch types in a given area
Dominance/ Evenness	Degree of dominance by one or a few patch types (modified from Wiens *et al.* 1993)
Dispersion	Distribution pattern of patch types over an area
Predictability	Spatial autocorrelation; the degree to which knowledge about features at a given location reduces uncertainty about variable values at other locations

According to both these concepts then, geomorphic units are fixed patches that provide the template architecture for instream physical habitats. The smallest scale of these habitats is biotopes, which are spatially and temporally defined patches that reflect both the geomorphic architecture as well as the flow types occurring over that patch.

The lack of attention to the characteristics and dynamics of patches (habitat, in this case), and an appropriate classification framework, within the conceptual framework of IFIM, has therefore prompted me to develop an alternative conceptual model which will now be described.

10.6 A FRAMEWORK FOR AN ALTERNATIVE APPROACH: THE GEOMORPHOLOGICAL-BIOTOPE ASSESSMENT

My central focus is to understand the significance of catchment-wide geomorphic characteristics and processes and how these are ultimately expressed at the scale of biotopes. The proposed approach for this, and the description of habitat in rivers, is one that I have formulated as the Geomorphological-Biotope Assessment, or the GBA.

The GBA is best described as an approach to understanding and describing the distribution and abundance of physical habitat based on a locally-appropriate, hierarchical classification systems for rivers. It draws on the themes of scale and pattern (specifically heterogeneity), integrated through the key concepts of patches (habitat) and patch dynamics (habitat changes and interactions). The GBA recognises the smallest scale of habitat as the biotope which, as a patch, has spatial dimension and reference. Nonetheless, the plasticity of habitat at this scale is recognised, depending on the organism and objective at hand. The conceptualisation of the channel (i.e. site) through the GBA, is given in Figure 10.3.

The GBA inherently responds to the scalar attributes of habitat. In other words, the hierarchical, morphological classification for rivers not only recognises the multiple scales of habitat, but also describes their spatial pattern, and their underlying determinants. These are the water and sediment dynamics (at a broader catchment scale) which are expressed in the geomorphology of the river. The temporal patterns of habitat are given by flow. The recognition of spatial attributes offers key advantages. First, it preserves the spatial distribution of habitat, which may be important in that similar outputs on habitat availability may have very different spatial distributions (Cooper *et al.* 1997). Second, it preserves key attributes of patches, such as spatial isolation and diversity (see Table 10.5). Third, by integrating the information within a GIS application, the location of specific points and additional ground-based measurements is facilitated (Hardy 1998). As with IFIM, biotope use can be expressed as numbers (frequencies) of animals per biotope type, but with the introduction of patch area, expressing use as the density of animals per patch-type is an option.

For semi-arid river systems in southern Africa, the spatial patterns of habitat and their underlying mechanisms, are provided for in the hierarchical classification system of van Niekerk *et al.* (1995). Added to this are biotopes - the smallest scale of physical habitat (Wadeson 1994).

Technically, the sequence of steps of the GBA, outlined in Figure 10.4, are not unlike those of IFIM (see Figure 2.1) in that the study area is defined, sites are selected in which both biotope availability and use are quantified at different flows, and these results are then extrapolated to the study area. However the key differences between them, which are elaborated in Chapter 13, lie principally in (a) the classification framework, which is used to describe the relationship between the various spatial features of the river

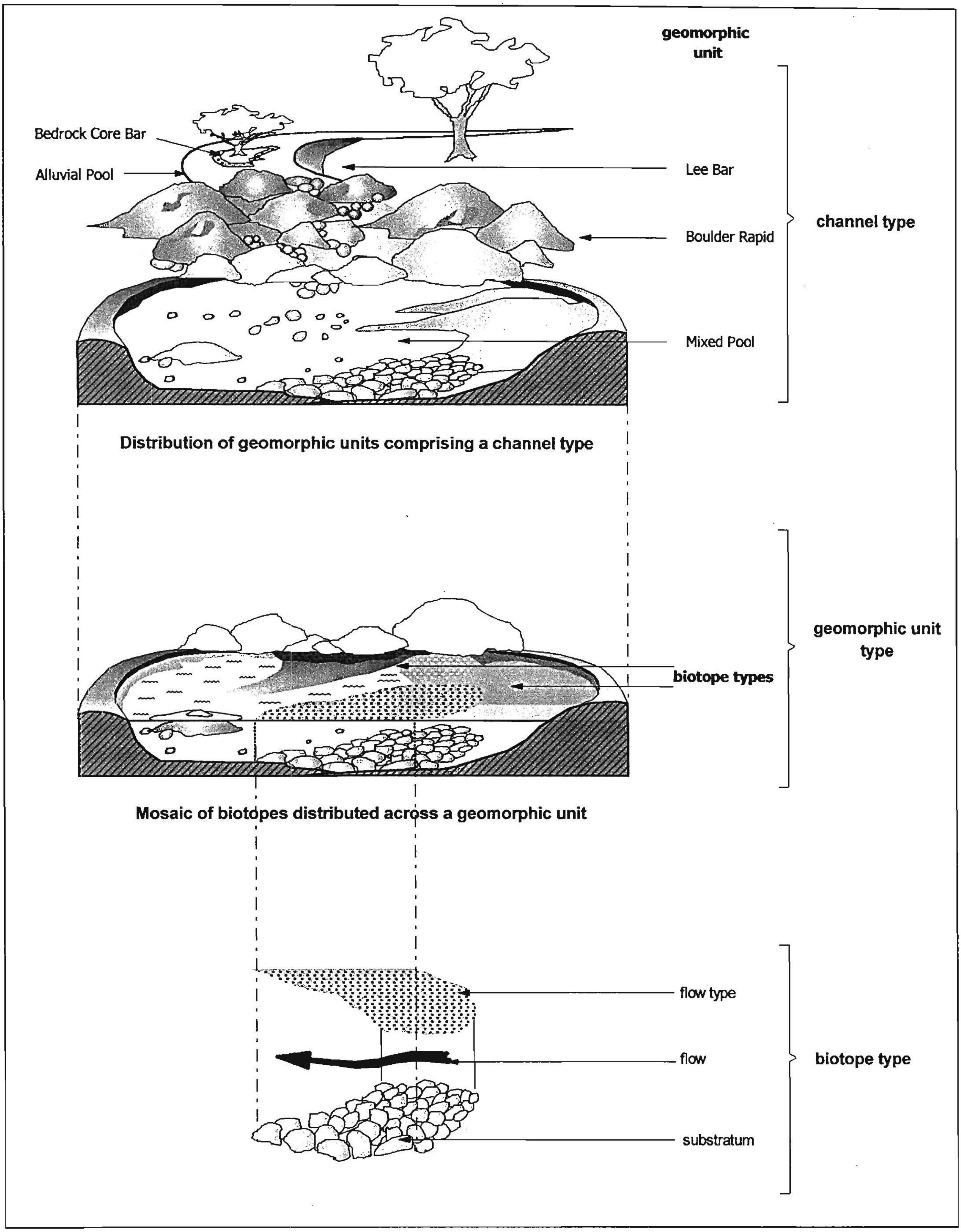


Figure 10.3 The GBA conceptualisation of the river channel as a mosaic of geomorphic units. Biotopes are superimposed on these, as a function of flow. Compare this to the IFIM conceptualisation in Figure 5.5.

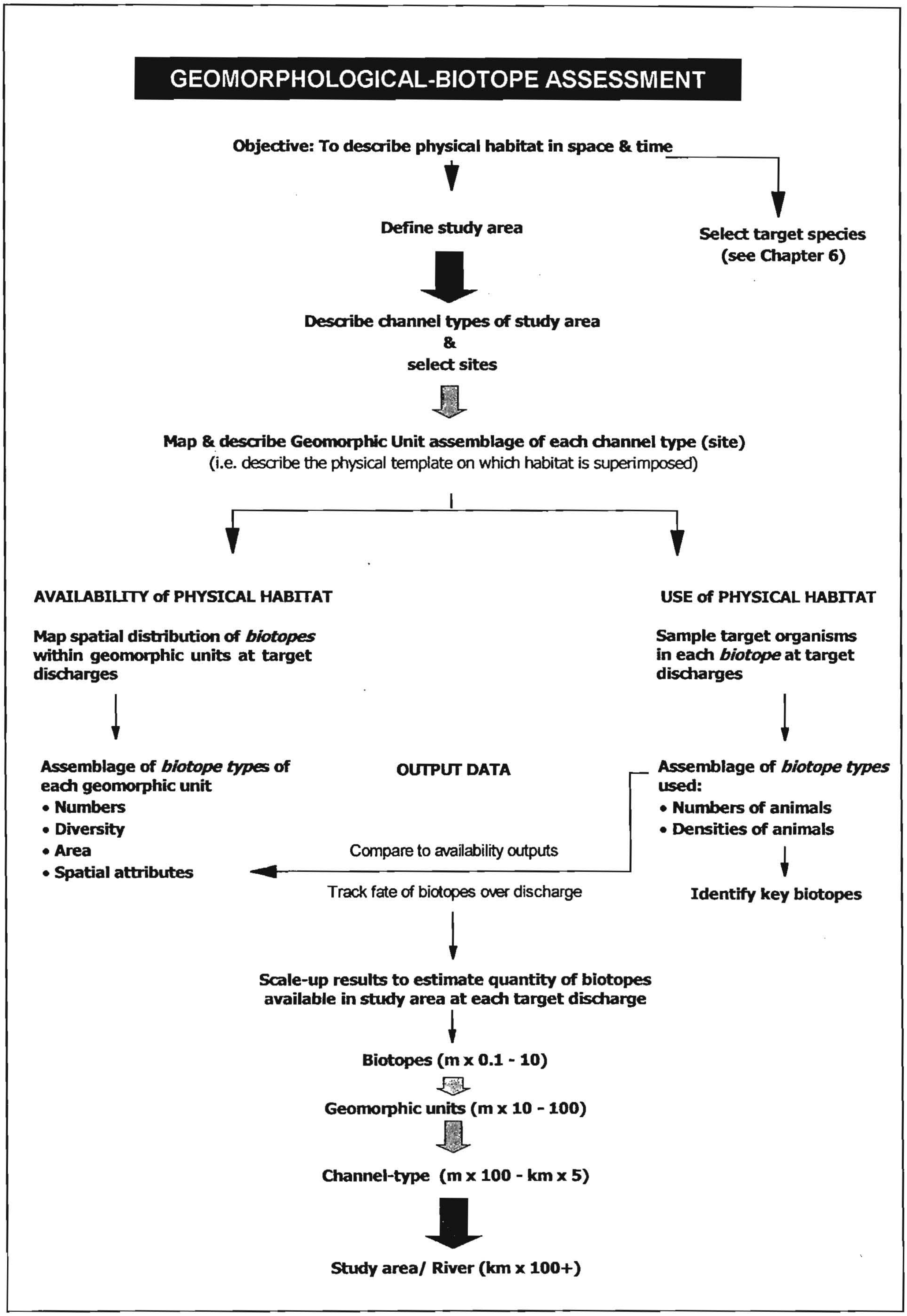


Figure 10.4 Flow diagram of the overall framework of the proposed Geomorphological-Biotope Approach for the assessment of physical habitat.

at different scales, and which guides site selection and, (b) the approach, and units, for describing the smallest scale of habitat - the biotope. Thus, the GBA supports the tenet, raised by van Niekerk *et al.* (1995) and Wadeson & Rowntree (1998), that *the geomorphology provides the physical template on which biotope availability, as a function of flow, is superimposed.* It is postulated that as flows vary, the distribution and abundance of biotopes will change on a temporal and spatial scale, and that these changes are a function of the geomorphic units and hence, channel type (Heritage *et al.* 1996; Rowntree & Wadeson 1996; 1999). Finally, with a hierarchical classification in place, site-specific results can be extrapolated to the study area.

10.7 SUMMARY STATEMENT OF THE PROPOSED APPROACH

The GBA will provide the framework against which to address the final objective outlined in Chapter 1; namely, to "explore an alternative approach to determining the hydraulic habitat of a selected species as a contribution to refining IFR recommendations". The proposed research seeks to address the inherent assumptions in the determination of available physical habitat according to the IFIM approach, that

- sites are truly representative of the river, according to some predetermined criteria, and hence site-specific data can be empirically extrapolated to the length of the river and,
- the determination of available hydraulic habitat approach is accurate.

This will be considered by addressing the steps in the proposed GBA but with a specific focus on an assessment of biotope *availability* as a function of flow, within the Marite River. The proposed research will examine the tenet that the geomorphic units form the template on which biotopes are distributed in space and time as a function of changing flows. Additionally, the outputs of PHABSIM II for a specific discharge under current conditions can be verified.

10.8 CONCLUSIONS

The use of IFIM and PHABSIM is not without controversy due to a number of conceptual and logistical constraints, which were detailed in the preceding chapters and summarised in this chapter. Specifically, methods within IFIM for both site selection and channel stasis were raised as major concerns by my research. Inaccurate or erroneous results from both of these have severe implications for the subsequent determination of both the site-specific and study-wide habitat availability and use for a selected species. However, even if finally refuted for South African conditions, the methodological approach of IFIM provided ecologists with a solid basis from which to unravel the importance of channel structure in defining the characteristics of physical habitat.

On the basis of these concerns, an alternative habitat-assessment approach, the GBA, is proposed. Conceptually, this approach is rooted within locally-developed geomorphological classification systems for rivers, as well as drawing on the concepts of patch dynamics, heterogeneity, pattern, scale and landscape ecology.

11

An Alternative Approach to Determining the Availability of Hydraulic Biotopes in The Marite River

11.1. INTRODUCTION

Together with PHABSIM, IFIM is designed only to predict the *physical habitat availability* for selected species at different flows (Nestler *et al.* 1989). In the previous chapter, I suggested that it may not do this very satisfactorily, particularly in the case of complex channel morphologies. Moreover, the assumption of homogeneity between transects is questionable. Whilst their use might be technically sound, I supported the concerns of other authors that these had little biological rationale and were, therefore, conceptually problematic. Further, as I showed in Chapter 8, inaccuracies in the measurement of availability markedly influenced the resultant microhabitat preference(1) models, which are open to ambiguous interpretations in any event. An additional concern was the framework for extrapolating site-specific data to represent habitat availability for the study area as a whole. I concluded that this was also unsatisfactory, largely due to the inadequate guidelines for site selection.

These concerns pointed to the need for (i) a more rigorous approach to site selection based on a sound conceptual framework, coupled to (ii) an approach for describing habitat availability that both captures spatial and temporal heterogeneity, and that is supported by appropriate theoretical models.

Consequently, an alternative approach to site selection and to the quantification of *biotope*(2) availability, namely the *geomorphological-biotope assessment*, or GBA, is to be explored in this chapter. Chapter 10 reviewed of the conceptual underpinnings of this approach (see Figure 10.3) and the key steps (see Figure 10.4). As a framework for site selection, a geomorphological approach to river classification was described. Based on this, the extent, patterns and processes that influence the architecture of habitat can be examined. The conceptual support is provided through the themes of heterogeneity, pattern and scale which are integral to the models of patch dynamics and landscape ecology. Collectively, these have the potential to contribute to an improved understanding of the distribution and abundance of physical habitat. As a final step in Chapter 12, biotope availability will be linked to the biotope use by the indicator species.

---

[1] Preference models (see Section 8.5) are derived from data on both habitat availability (A) and habitat use (U), so that Preference, P = U/A.

[2] In accordance with the nomenclature used by researchers in habitat studies in South Africa (see Section 1.6), the abbreviated term *biotope* now replaces the term *microhabitat*, and refers to *hydraulic habitat*.

11.2 OBJECTIVES

The overall goal of this chapter is to understand and quantify the availability of biotopes, and their spatial and temporal attributes, based on the hierarchical classification developed for semi-arid rivers in southern Africa by van Niekerk *et al.* (1995) and the concept of habitat as biotopes (Wadeson 1994).

This research is guided by three objectives which attempt to integrate the various scales that pervade the geomorphology of the Marite River system. Thus, it is hoped that the broad morphological characteristics at the scale of the river channel (Objective 1) can be linked to the small scale characteristics that are ecologically meaningful (Objective 2), so as to provide a biotope characterisation of the study area as a whole (Objective 3). The three objectives are as follows.

1. To describe the channel types of the Marite River, and their assemblages of geomorphic units(3) (see Table 10.1 and Figure 10.1), according to the hierarchical classification of van Niekerk *et al.* (1995). This will provide the basis for (a) an assessment of the IFIM sites as representative of the study area, (b) the selection of sites for the quantification of biotope availability and for, (c) extrapolation (see Objective 3).
2. To describe the biotope availability of pool and rapid geomorphic units on a spatial and temporal scale. They were selected for detailed analyses for two reasons. Firstly, pools were the dominant and the most ubiquitous of geomorphic units found in the Marite River, comprising an estimated 40% of the total river. Secondly, since rapids constitute the primary habitat for the target species *C. anoterus,* outputs could be compared with those of PHABSIM (see Chapter 9).
3. To develop a framework for extrapolating site-specific (i.e. channel type) information on biotope availability up to the study area.

Since the third objective is contingent on the outcomes of the first two objectives, the format of this chapter will be to describe, separately, the approach to, and outcomes of each objective. The analysis of channel types will be followed by a description of their geomorphic assemblages, and an analysis of the biotopes that occur within these. Finally, a framework will be provided to address the issue of extrapolation.

11.3 OVERALL APPROACH

To recap, the overall approach, summarised in Figure 11.1, reflects the central tenet of the hierarchical classification of van Niekerk *et al.* (1995) for semi-arid, bedrock-controlled rivers (see Figure 10.1). This holds that the interaction of channel morphology, and flow, influences the distribution and abundance of available habitat: that is, *the geomorphology provides the physical template on which biotope availability, as a function of flow, is superimposed in space and time* (see Figure 10.3 and Section 10.6).

---

[3] The river comprises geomorphic units nested within channel types, which are recognised by their distinctive assemblage of geomorphic units.

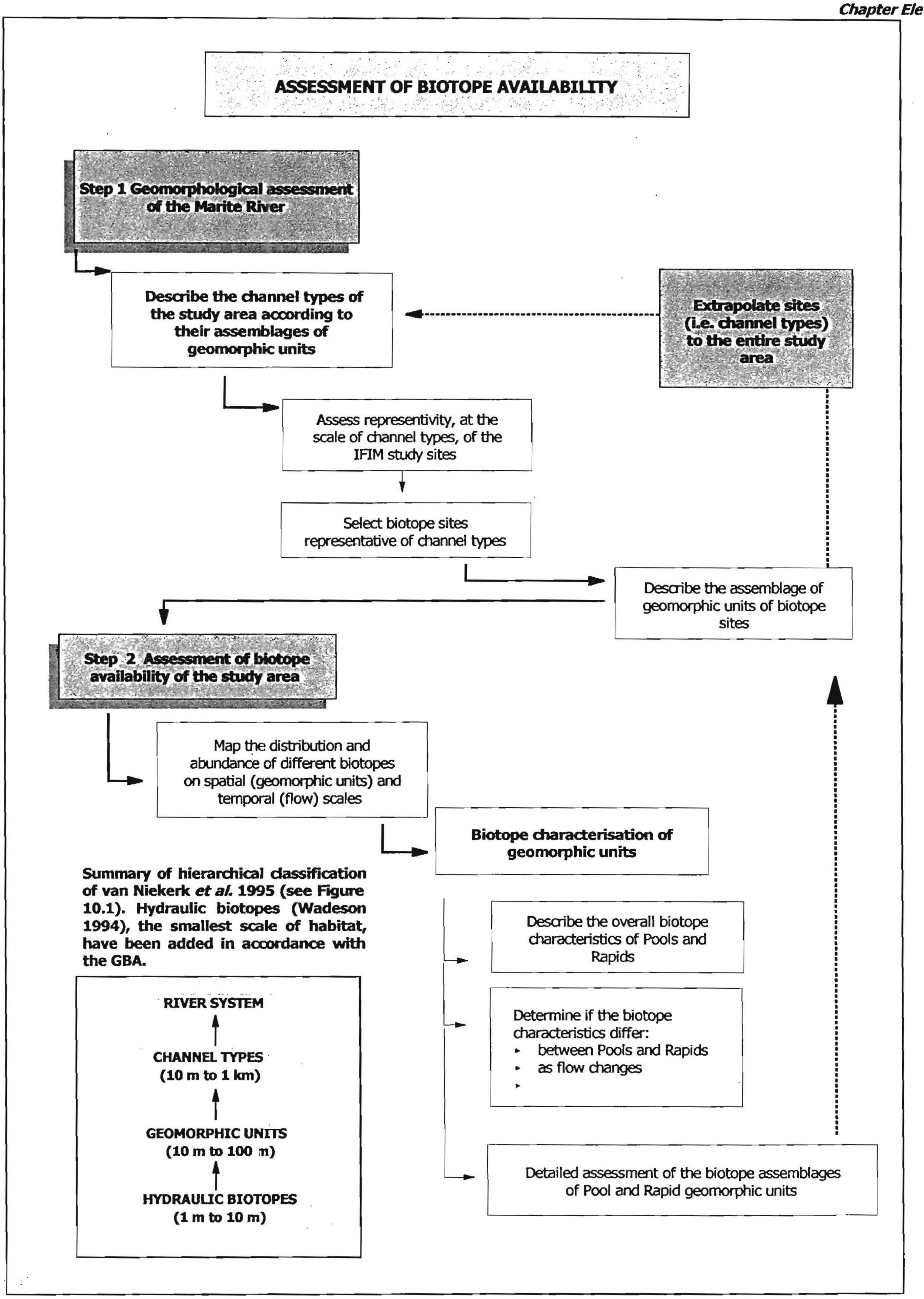


Figure 11.1 Flow diagram of approach used to describe the biotope availability in the Marite River. The box in the lower, left-hand corner provides a summary of the hierachical classification for semi-arid bedrock rivers developed by van Niekerk *et al.* (1995) which provides the overall framework for this research (see Section 10.5 for details).

By establishing the relationship between channel types and geomorphic units, and geomorphic units and biotopes, I hope to show that the availability of biotopes down the length of the river at different flows can be described. Additionally, the outputs of PHABSIM II for a specific discharge, under current conditions, can be verified.

The overall approach to meeting the above three objectives involved two key steps, namely a geomorphological assessment of the study area, and a biotope assessment of each site (Figure 11.1). The *geomorphological assessment* was designed to address Objective 1. Using the approach and definitions of van Niekerk *et al.* (1995) for the Sabie River, it provided an overview of the channel morphology of the Marite River. This, in turn, allowed for a more detailed characterisation of the channel types based on their geomorphic assemblages. The purpose of this step was given under Objective 1.

The subsequent *assessment of biotope availability* (Objective 2) was undertaken through detailed biotope mapping at sites over a range of discharges. This generated a biotope map of each site, which allowed for an analysis of the biotope characteristics (see Section 11.5), and assemblages, of each type of geomorphic unit as a function of flow.

There are two inherent assumptions in this approach:

1. The geomorphology of the system (semi-arid, mixed bedrock/ alluvial) controls the distribution of biotopes.
2. A description of the physical biotope implicitly includes hydraulic variables of velocity and depth (Rowntree & Wadeson 1999). This is given in the sediment size and surface-flow character. However, depths and velocities will be measured for each biotope in order to verify this assumption.

11.4 GEOMORPHOLOGICAL ASSESSMENT: CHANNEL TYPES, GEOMORPHIC ASSEMBLAGES AND SITE SELECTION

BACKGROUND AND METHODOLOGY

In accordance with the classification system of van Niekerk *et al.* (1995), quantifying the availability of physical habitat (biotopes) is predicated on understanding the geomorphology of the system and, in particular, of *channel types* and *geomorphic units* (see Section 10.5 for details). The river comprises different channel types which are classified according to their distinctive assemblages of geomorphic units (see Table 10.1). Importantly, the rationale behind site selection for habitat assessments, which is conducted at the scale of channel types, is that the biotope conditions of a site can be scaled-up to the study area according to the channel type that they represent (Figure 11.1).

A description of the channel types of the Marite River was based on the classification of the geomorphic assemblages that define the five channel types found in the Sabie River (van Niekerk *et al.* 1995). From an assessment of video footage, and subsequent field validation, channel types were marked on 1:10000 maps and the length of each channel type was measured (Figure 11.2). All descriptions were corroborated by a fluvial geomorphologist, Dr. G. Heritage (Department of Geography, Salford University, UK, *pers. comm.*).

The geomorphic assemblage of each channel type was quantified so as to provide a geomorphological characterisation that was specific to the Marite River. To do this, as many sections of each channel type that could be accessed, or adequately viewed on video, were used. This amounted to 19 of a total of 36 sections, which represented changes in channel types (see Figure 11.2). Of the total number of sections of each channel type, indicated in parentheses, the numbers that were described, were:

- Alluvial Single Thread = 3 (4);
- Mixed Single Thread = 4 (5);
- Mixed Pool Rapid = 6 (14);
- Mixed Anastomosing = 4 (10)
- Bedrock Anastomosing = 2 (3).

In each section, the total number of each type of geomorphic unit was computed and the proportional contribution of each to the channel type in question was then calculated. Data were examined to see if any of the sections appeared to house unusual geomorphic unit assemblages. The final biotope sites were chosen from this assessment.

RESULTS

Channel types of the marite river

The Marite River study area comprises five channel types: Alluvial Single Thread (AST), Mixed Single Thread (MST), Mixed Pool Rapid (MPR), Mixed Anastomosing (MAN) and Bedrock Anastomosing (BAN) (Figure 11.2; Table 11.1). The dominant channel type, MPR, is followed by MST, which together account for 83%, or 27 km of the total length of the 30.5 km of study area. This amounts to approximately 1.8 km of rapids and 11 km of pools. Both AST and BAN channels were rare.

All three of the IFIM sites traversed more than one channel type, as follows: Site 1 - AST and MPR; Site 2 - MPR and MST; Site 3 - MPR and MAN (see Plates 4.1, 4.2 and 4.3). Two channel types, AST and BAN (Plates 11.1 and 11.2 respectively), were not represented in the original IFIM site selection. Although they do not comprise a major part of the study area, very little is known about the biotopes that they house, the response of these to changes in discharge, or the response of these channel types to long-term flow modifications.

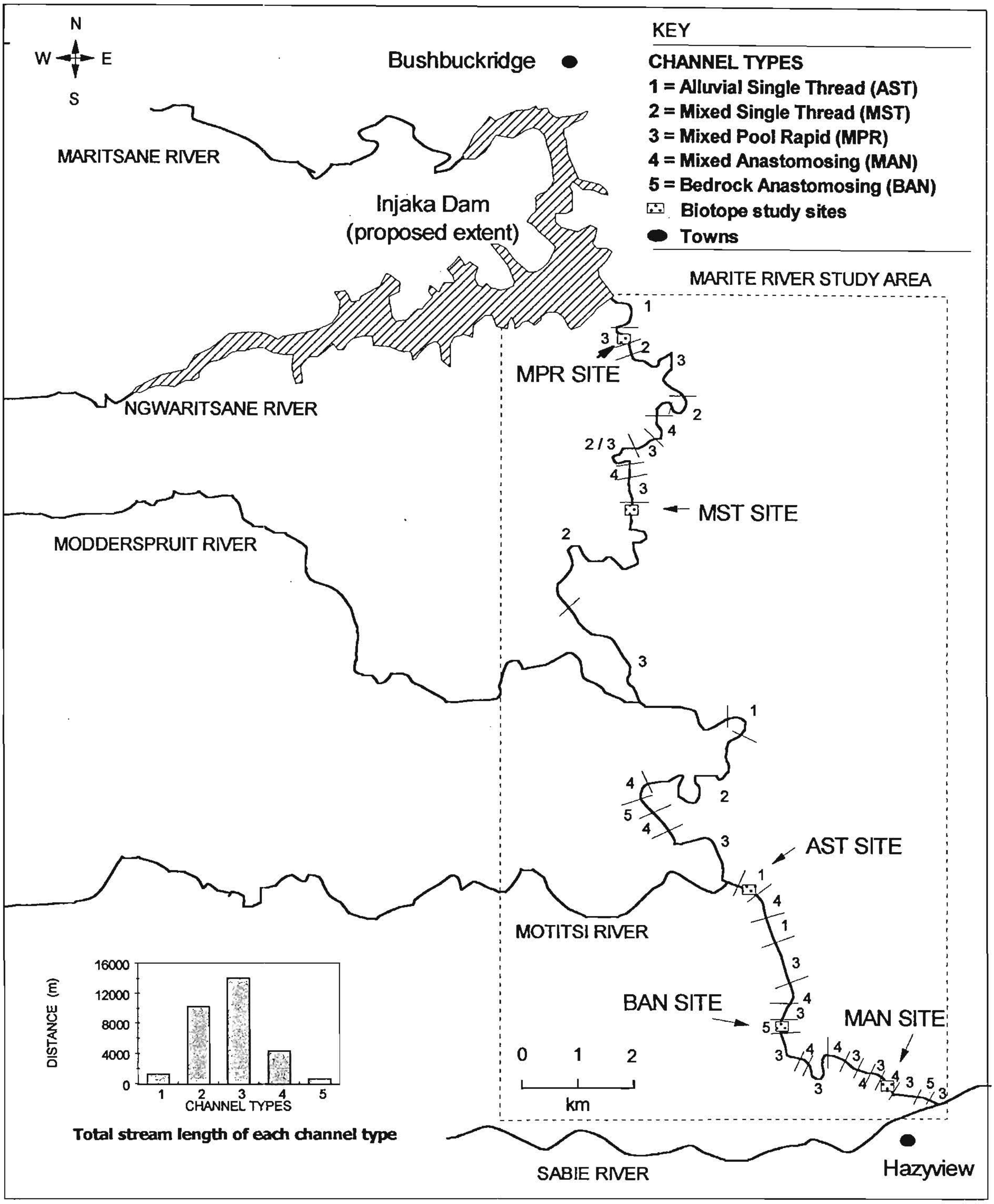


Figure 11.2 Channel types (1 - 5), and corresponding biotope study sites, represented within the study area of the Marite River. Compare these study sites to the original PHABSIM II microhabitat study sites (see Figure 4.6). Note the addition of two study sites, representing Alluvial Single Thread (1) and Bedrock Anastomosing (5) channel types which were not represented by the PHABSIM II study sites.

Plate 11.1 Typical section of an Alluvial Single Thread (AST) channel of the Marite River. This channel type was omitted in the IFIM site selection process. The key geomorphic features (see Table 10.2) are indicated.

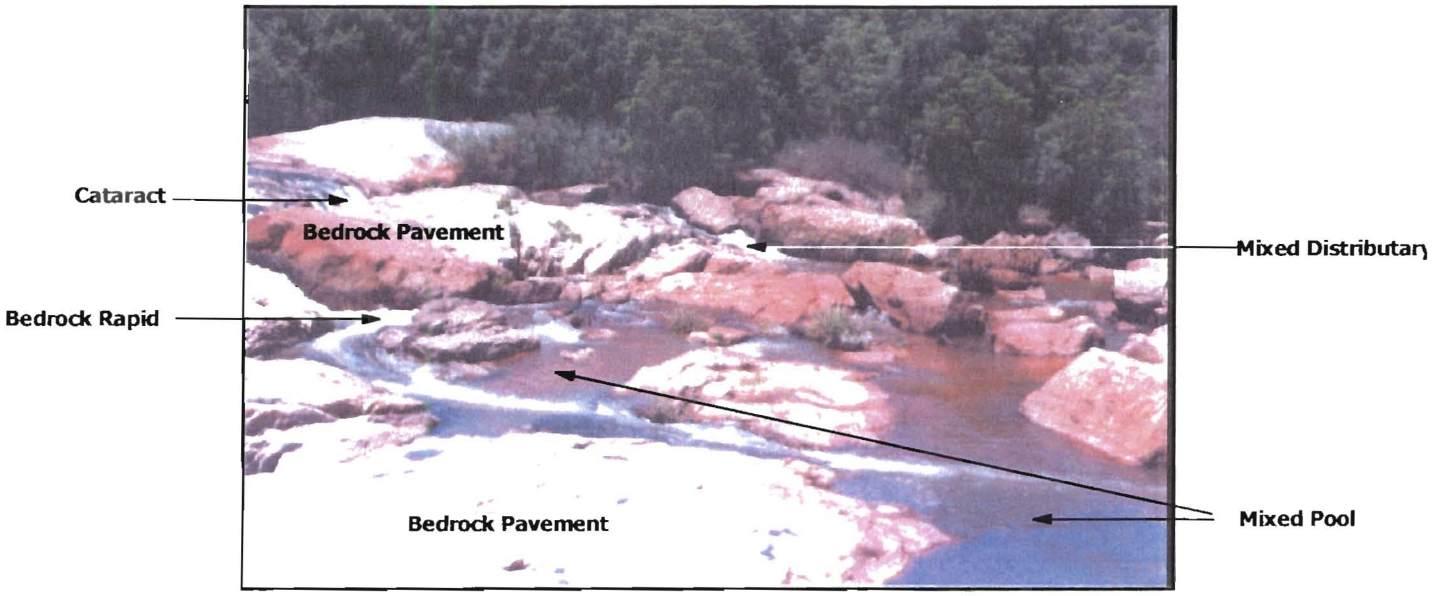


Plate 11.2 Typical section of a Bedrock Anastomosing (BAN) channel of the Marite River. This channel type was omitted in the IFIM site selection process. The key geomorphic features (see Table 10.2) are indicated.

Table 11.1
Channel types, distances and relative proportions of each channel type comprising the Marite River study area (see also Figure 11.2)

CHANNEL TYPE	CODE	TOTAL DISTANCE (km)	PERCENTAGE OF TOTAL	COMMENT
Alluvial Single Thread	AST	1.3	4.2	Not represented in IFIM sites
Mixed Single Thread	MST	10.5	34.3	Long contiguous stretches found in middle reaches
Mixed Pool Rapid	MPR	14.0	45.9	Dominant channel type
Mixed Anastomosing	MAN	4.1	13.5	Only found in lower reach of study area
Bedrock Anastomosing	BAN	0.7	2.1	Rare, not represented in IFIM sites
TOTAL		30.6	100	

Geomorphic assemblages of the five channel-types

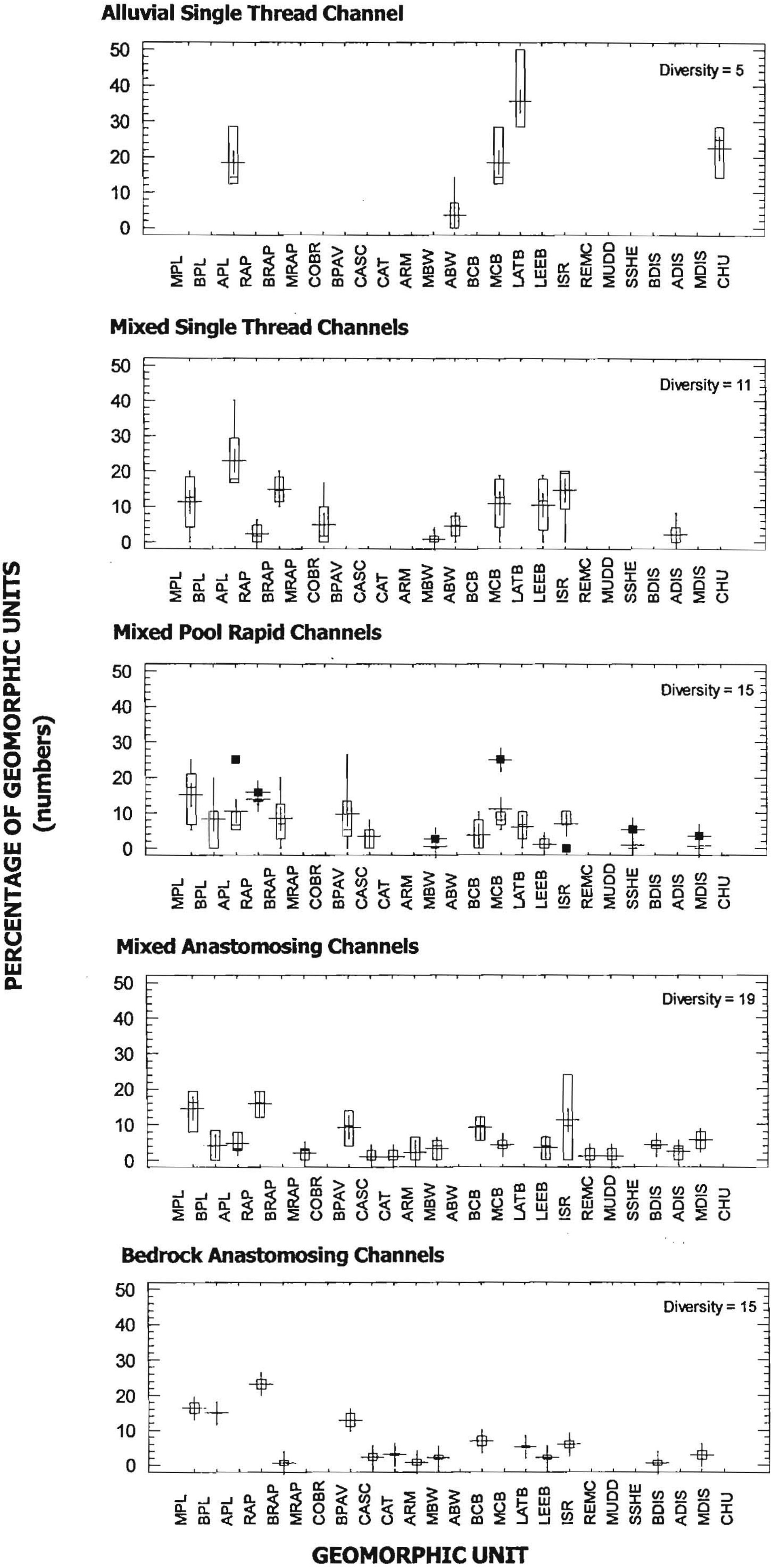
Some 25 types of geomorphic units were recorded in the Marite River. On a trajectory of simple to complex channel types, the single-thread sections (AST and MST) were the least diverse, followed by MPR and BAN, and lastly MAN (Figure 11.3). The increased diversity was accounted for by the addition of (a) Mixed and Bedrock Pools which were restricted to the anastomosing and MPR sections, and (b) a number of geomorphic units that were unique to the anastomosing sections, such as Bedrock and Mixed Distributaries and Cataracts. Pools were found in all channel types. Rapids occurred in all channel types with the exception of AST, and true cobble riffles only occurred in MST channels.

Biotope sites and their geomorphic assemblages

Based on the geomorphological assessment, five sites, representative of the five channel types were chosen for the detailed biotope mapping. An examination of the geomorphic assemblages of the channel types (Figure 11.3), indicated that none of the IFIM sites was unusual in its composition of geomorphic units. Thus for consistency, portions of the previous IFIM sites were retained as representative of three different channel types as follows: Site 1: MPR; Site 2: MST; Site 3: MAN. In addition, two randomly selected sites were also included to represent AST and BAN channels (see Figure 11.2).

The mapping of a detailed geomorphic template was undertaken at the five sites (see Figure 11.2) in August 1996, which is the winter low-flow season. Detailed maps were prepared by means of differential leveling, as described in Chapter 4 for transect profiles. This involved mapping of the perimeter of each geomorphic unit as well as any major feature within each unit, such as boulder or bedrock outcrops. Each geomorphic unit was given a unique number (Figures 11.4 & 11.5).

Of the 25 types of geomorphic units recorded, those comprising the study sites are illustrated in Figures 11.4 and 11.5. Their contribution to each site, in terms of numbers and area, is shown in Table 11.2. Pools comprised a major proportion of the area in AST, MPR and BAN channel types. Rapids, on the other hand, comprised only a small proportion of the total area, ranging between 2% and 13% of channel area (Table 11.2).



Alluvial Single Thread Channel

Mixed Single Thread Channels

Mixed Pool Rapid Channels

Mixed Anastomosing Channels

Bedrock Anastomosing Channels

Figure 11.3 Assemblages of geomorphic units (percentages) of the five channel types that comprise the Marite River. Box indicates the median, mean and interquartiles and whiskers show the range. Diversity refers to the number of types of geomorphic units. Full terms for abbreviations of geomorphic units are given in Table 11.2.

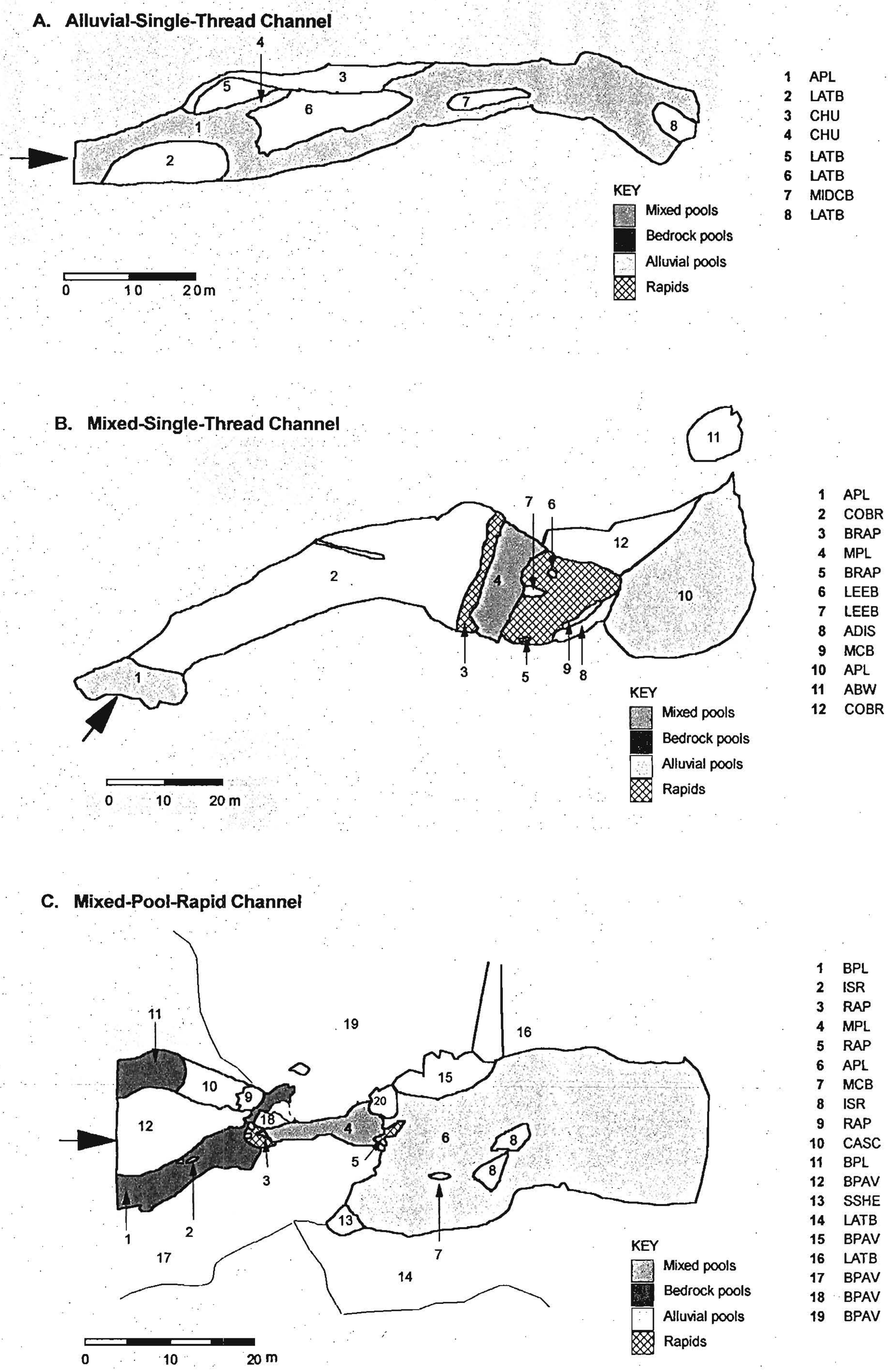
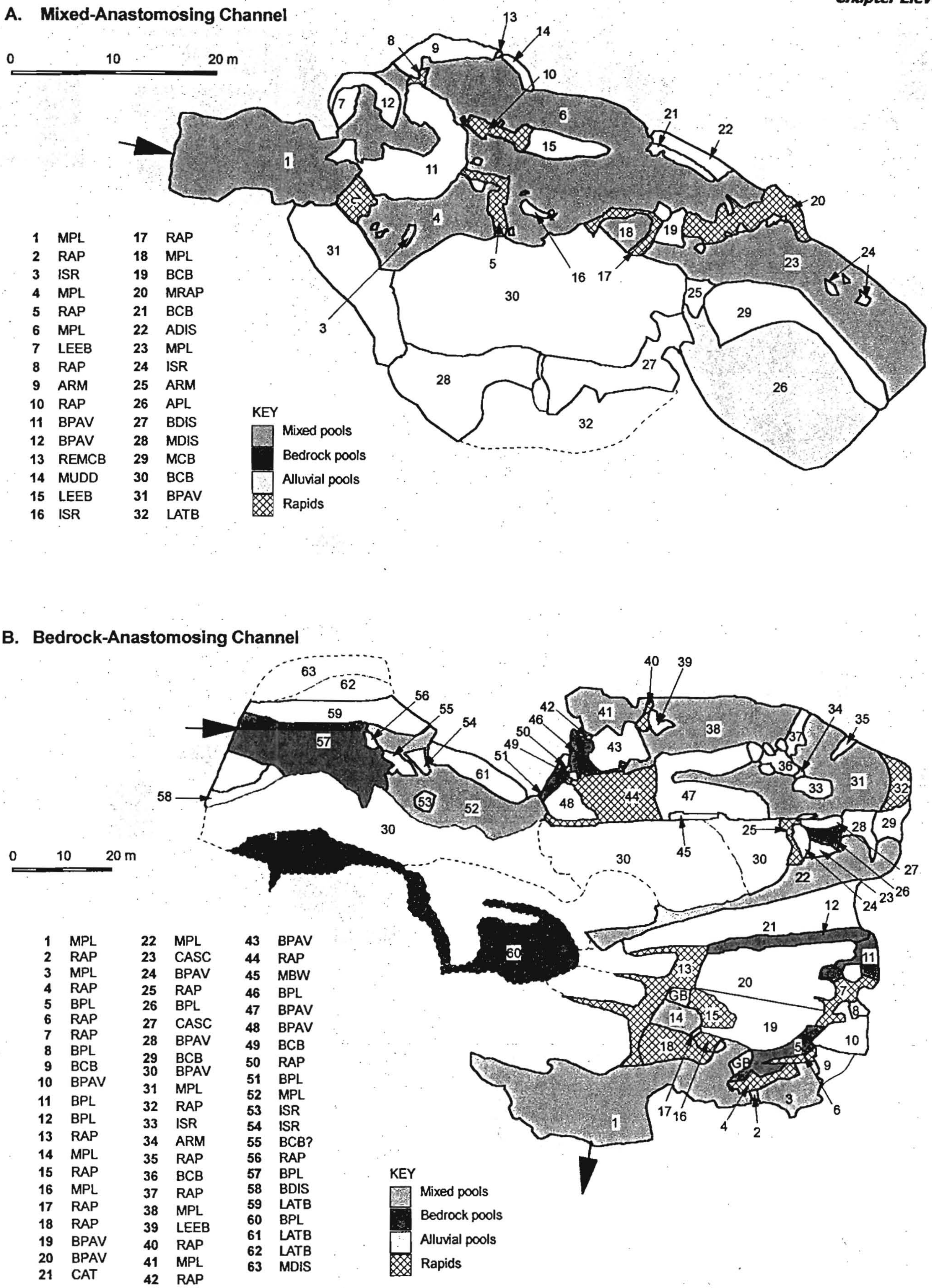


Figure 11.4 Site maps detailing the geomorphic units associated with the Single Thread and Mixed Pool Rapid channels. Full terms for abbreviations are given in Table 11.2. Filled polygons highlight pools and rapids, the focus of this study. Large arrows indicate the direction of flow.



1	MPL	17	RAP
2	RAP	18	MPL
3	ISR	19	BCB
4	MPL	20	MRAP
5	RAP	21	BCB
6	MPL	22	ADIS
7	LEEB	23	MPL
8	RAP	24	ISR
9	ARM	25	ARM
10	RAP	26	APL
11	BPAV	27	BDIS
12	BPAV	28	MDIS
13	REMCB	29	MCB
14	MUDD	30	BCB
15	LEEB	31	BPAV
16	ISR	32	LATB

1	MPL	22	MPL	43	BPAV
2	RAP	23	CASC	44	RAP
3	MPL	24	BPAV	45	MBW
4	RAP	25	RAP	46	BPL
5	BPL	26	BPL	47	BPAV
6	RAP	27	CASC	48	BPAV
7	RAP	28	BPAV	49	BCB
8	BPL	29	BCB	50	RAP
9	BCB	30	BPAV	51	BPL
10	BPAV	31	MPL	52	MPL
11	BPL	32	RAP	53	ISR
12	BPL	33	ISR	54	ISR
13	RAP	34	ARM	55	BCB?
14	MPL	35	RAP	56	RAP
15	RAP	36	BCB	57	BPL
16	MPL	37	RAP	58	BDIS
17	RAP	38	MPL	59	LATB
18	RAP	39	LEEB	60	BPL
19	BPAV	40	RAP	61	LATB
20	BPAV	41	MPL	62	LATB
21	CAT	42	RAP	63	MDIS

Figure 11.5 Site maps detailing the geomorphic units associated with the anastomosing channels. Full terms for abbreviations are given in Table 11.2. Filled polygons highlight pools and rapids, the focus of this study. Dashed lines indicate units that are only wet at the highest flows. Large arrows indicate the direction of flow.

Table 11.2
The assemblage of geomorphic units found at the biotope study sites, which represent the different channel types that occur in the Marite River. Figures represent the percentage contribution as numbers, and as area (hatched columns). Asterisks indicate additional geomorphic units that were represented at other sites of the channel type in question.

GEOMORPHIC UNIT AND ABBREVIATION						**CHANNEL TYPE**					
		Alluvial Single Thread		Mixed Single Thread		Mixed Pools Rapid		Mixed Anastomosing		Bedrock Anastomosing	
		% of total		% of total		% of total		% of total		% of total	
		number	area	number	area	number	area	number	area	number	area
Mixed pool	MPL			8.3	7.5	5.3	4.5	16.1	30.5	14.8	40.2
Bedrock pool	BPL					10.5	12.5	*		14.8	13.7
Alluvial pool	APL	11.1	57.6	16.7	31.6	5.3	59.9	3.2	5.6		
Bedrock rapid	RAP			*		15.8	1.8	16.1	2.5	24.6	11.7
Boulder rapid	B-RAP			16.7	13.1	*					
Mixed rapid	MRAP							3.2	1.6		
Cobble riffle	COBR			16.7	42.1						
Bedrock pavement	BPAV					26.3	11.0	9.7	21.1	14.8	19.3
Cascade	CAS					5.3	3.1	*		3.3	1.1
Cataract	CAT							*		3.3	5.8
Armoured area	ARM							6.5	2.4	1.6	0.1
Mixed Backwater	MBW			*		*		*		1.6	0.4
Alluvial Backwater	ABW	*		8.3	3.5						
Bedrock Core Bar	BCB					*		9.7	16.8	8.2	2.0
Mid Channel bar	MCB	22.2	2.0	8.3	0.5	5.3	0.2	3.2	8.7	*	
Lateral Bar	LATB	44.4	26.9			10.5	5.3			4.9	3.4
Lee Bar	LEEB			16.7	0.4	*		6.5	1.3	1.6	0.4
Isolated Rock	ISR			*		10.5	0.6	9.7	0.3	4.9	1.0
Remnant Core Bar	RCB							3.2	0.0		
Mud Drape	MUDD							3.2	0.2		
Sand Sheet	SSHE					5.3	1.0				
Bedrock Distributary	BDIS							3.2	4.5		
Alluvial Distributary	ADIS			8.3	1.4			3.2	0.4		
Mixed Distributary	MDIS					*		3.2	4.0	1.6	0.9
Chute	CHU	22.2	13.5								
POOLS: % TOTAL		**11.1**	**57.6**	**25.0**	**39.1**	**21.1**	**77.0**	**19.4**	**36.1**	**29.5**	**53.9**
RAPIDS: % TOTAL		**0**	**0**	**16.7**	**13.1**	**15.8**	**1.8**	**19.4**	**4.2**	**24.6**	**11.7**

11.5 BIOTOPE AVAILABILITY IN THE MARITE RIVER

This section will address the second and third objective which, together, aim to (i) describe the spatial (geomorphic units) and temporal (discharge) attributes of biotope availability and, (ii) to illustrate how such data can be extrapolated up to the study area. A number of questions, which reflect increasing scales of resolution, circumscribe the second objective. These relate to:

a. The overall biotope characteristics of all geomorphic units:

- What are the overall biotope characteristics (numbers and diversity) of each type of geomorphic unit?

b. The overall biotope characteristics of pools and rapids:

- What biotope characteristics typify pool and rapid geomorphic units?
- Do these differ between flows and between geomorphic units?

c. The detailed biotope assemblages of pools and rapids:

- What biotope assemblages (i.e. biotope types) characterise pool and rapid geomorphic units?
- Do these differ with flow?

The biotope characteristics were described by three of the features listed by Wiens *et al.* (1993) for characterizing patch attributes (see Table 10.5). These were (i) biotope numbers (mean number per geomorphic unit), (ii) richness or diversity (mean number of biotope types per geomorphic unit) and, (iii) size (m^2). A fourth feature was added, namely (iv) density (mean number per unit area of geomorphic unit). This incorporates the variation in the area of the geomorphic units. "Diversity" refers to the biotope types, classified according to their flow and substratum characteristics (see later).

BACKGROUND AND METHODOLOGY

The description of channel types, through representative sites, was based on a *low-flow classification* system (van Niekerk & Heritage 1993). Thus, the geomorphic units that comprise a site are regarded as fixed physical features irrespective of flows. Changing flows are then accounted for through the descriptions of biotopes which are superimposed on each geomorphic unit as a function of flow (see Figure 10.3). In terms of the ecological relevance, it is postulated that as flows vary, the distribution and abundance of biotopes will change on a temporal and spatial scale (Stalnaker *et al.* 1996), and that these changes are a function of the geomorphic units and hence, channel type (Dr. G. Heritage, *pers. comm*; Wadeson 1994).

Accordingly, biotope distributions were then mapped on the geomorphic-template map (see Figures 11.4 and 11.5) for each site at four different discharges between October 1997 and February 1998. They represented a low flow (0.2 $m^3 s^{-1}$); two intermediate flows (0.9 and 1.5 $m^3 s^{-1}$) which characterise the dry season and start of the wet season respectively; and a high flow (1.9 $m^3 s^{-1}$) which represents the mean daily flow for the wet season (see Figure 4.3). Attempts to include a higher flow of 5.4 $m^3 s^{-1}$ were unsuccessful as only two sites could be adequately mapped due to limited access. However, the focus of this study is on low flows and it was felt that these had been adequately covered by the four discharges. All discharge measurements were taken from gauging station no: X3H011 (see Figure 3.2).

Each biotope was given a unique numbering code which indicated the parent geomorphic unit, and a sequential number. For example, a number of 2.01 at Site 1 (Figure 11.4) would indicate that this was the first biotope in geomorphic unit number 2 (a lateral bar). In accordance with Rowntree (1996), biotopes were delimited through a visual assessment of flow, and substratum, and coded using a hydraulic biotope matrix which describes 62 potential biotope types (Table 11.3; see discussions in Section 10.5). Although the hydraulic variables of velocity and depth are implicit in the biotope codes, both of these variables were measured on the first two sampling occasions to delimit the velocity and depth parameters of each biotope type. Finally, each biotope map was digitised in ArcView to facilitate calculations of geomorphic unit and biotope area.

It is necessary at this point to make a distinction between the terminologies that are used to describe geomorphic units and biotopes to avoid confusion. Even in the most recent literature, the same terms such as riffles, backwaters and pools, are used to describe both spatial features (see for example Rowntree & Wadeson 1996; 1999; Newson & Newson 2000). Nonetheless, given the history of confusing terminologies, I have chosen to limit the above terms to geomorphic units *only*, whilst biotopes will only be referred to by their codes (see Tables 11.3; 11.4).

Table 11.3

Matrix of hydraulic biotopes, derived as a combination of substratum and flow conditions. This table was adapted both from the outcome of a workshop on hydraulic biotopes (see Rowntree 1996), and a later matrix of hydraulic biotopes developed by Rowntree & Wadeson (1999) to include algae and instream vegetation. Whilst not strictly geomorphological, in ecological terms they offer an important component of physical habitat. Additionally, although the above authors named some of the biotopes, many of the terms are the same as those used for geomorphic units and hence have not been used. Thus, in this study, biotopes have only been referred to by codes which indicate their flow (integer) and substratum (decimal) types. Descriptions of flow and substratum types are given in Table 10.3.

		SUBTRATUM TYPE									
		Algae	Instream Veg.	Silt	Sand	Gravel	Cobble	Boulder	Fractured Bedrock	Smooth Bedrock	Stepped Bedrock
FLOW TYPE	**CODE**	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	0.10
		RESULTANT HYDRAULIC BIOTOPE-TYPE									
Near zero	1	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	/
Barely perceptible	2	2.1	2.2	2.3	2.4	2.5	2.6	2.7	2.8	2.9	/
Smooth boundary	3	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8	3.9	/
Accelerating	4	4.1	4.2	4.3	4.4	4.5	4.6	4.7	4.8	4.9	/
Rippled	5	5.1	5.2	/	5.4	5.5	5.6	5.7	5.8	5.9	/
Standing waves	6	6.1	6.2	/	/	6.5	6.6	6.7	6.8	6.9	/
Broken standing waves	7	7.1	7.2	/	/	7.5	7.6	7.7	7.8	7.9	/
Chaotic	8	8.1	8.2	8.3	8.4	8.5	8.6	8.7	8.8	8.9	/
Boil	9	9.1	9.2	9.3	9.4	9.5	9.6	9.7	9.8	9.9	/
Free fall	10	/	/	/	/	/	/	10.7	10.8	10.9	10.10

DATA ANALYSIS

The presentation of the data analyses reflects each of the key questions given at the start of Section 11.5.

General characteristics of geomorphic units

The initial focus was on a general description of the biotope characteristics of all 25 geomorphic-unit types. These were determined from the mean number, and diversity, of biotopes per geomorphic-unit type (wetted) over all discharges.

Comparison of biotope characteristics of Pools and Rapids

Three types of pools and four types of rapids (including cobble riffles) occur in the study area (see Table 11.2). So as to develop a meaningful description of patch characteristics and to make statistical inferences, data were grouped. This was important since not all types of geomorphic units were represented across all channel types, nor did all biotope types occur in all geomorphic units, leading to an imbalanced design for statistical validation. Groupings were informed by field experience, the research findings of van Niekerk & Heritage (1993), van Niekerk *et al.* (1995) and Heritage *et al.* (1997b), and through exploratory data analyses. Pools were grouped into Mixed Pools, with a heterogeneous substratum, and Simple Pools, with a homogeneous substratum (Alluvial and Bedrock Pools). All Rapids were grouped because they were considered to be insufficiently different to warrant separation, and due to insufficient data at all sites. Site 1 (AST) was excluded since rapids did not occur in this channel type. Cobble riffles were rare and hence were excluded. Thus, the three categories used for the data analysis were: Mixed Pools (n=16), Simple Pools (n=14) and Rapids (n=27).

The effect of discharge on biotope characteristics

The effect of flow on the overall biotope characteristics was examined by calculating the mean biotope number, size, diversity and density for each geomorphic-unit type, at each discharge. Then, for each of the three geomorphic-unit types, each biotope characteristic was compared, individually, among the four different discharges as follows. First, data were tested for normality. Since samples were taken in the same place at each discharge, they could not be regarded as independent as flow changed. Thus a generalised linear model of repeated measures was used (GLM Repeated Measures, SPSS. Version 7.5 1996) to examine the effects of discharge. This provides an analysis of variance when the same measurement is made several times (at different discharges) on the same subject (geomorphic units) (Sokal & Rohlf 1995). Separate models were developed for each geomorphic-unit type.

The effect of geomorphic-unit type on biotope characteristics

In order to compare biotope characteristics between pools and rapids at each measured discharge, the following approach was taken. Data were stratified according to the four discharges. At each discharge, the biotope characteristics (see above) were compared among the three types of geomorphic-units. Data were tested for significant differences by one-way analysis of variance (ANOVA, SPSS), and subjected to a post-hoc Bonferroni test to elucidate any internal differences between geomorphic-unit types. Separate models were developed for each biotope characteristic.

Biotope assemblages of Pools and Rapids at different discharges

In terms of biotope availability, the third focus was to (i) develop a detailed biotope profile (based on biotope types) of Mixed Pools, Simple Pools and Rapids, and (ii) to examine the internal variations of each biotope profile as a function of discharge.

The overall biotope assemblage of each of the three geomorphic units was described according to three characteristics, namely; mean number, density and size of biotopes within each category of biotope type. To develop a more meaningful investigation of biotope patterns, the 62 biotope types described in Table 11.3 were grouped into 24 new biotope types (Table 11.4). These data were examined at two scales of resolution. First, the mean numbers, and size, of each of the 24 biotope types were examined via frequency histograms. This produced a description of the overall biotope assemblage for each of the three geomorphic-unit types.

Secondly, the variations in the internal biotope patterns as a function of flow, was examined. For coherency, data were further grouped into six categories of biotope types according to their flow type. Similar flow types are indicated by the integer in the codes shown in Table 11.4. These six categories reflected combinations of flow types as follows: near-zero + barely perceptibly flow; smooth-boundary flow; accelerating + rippled flow; standing + broken waves; chaotic flow + boils; and free fall. These groups were informed by exploratory data analysis which indicated similarities in their depth and velocity conditions, and from professional judgement (Prof. K. Rowntree, Department of Geography, Rhodes University, *pers. comm.*). Substrata were also combined into five broad categories: algae + instream vegetation; silt + sand; gravel + cobble; boulders + fractured bedrock; and smooth bedrock + stepped bedrock. These groupings were informed by the categories of substrata that are used by *C. anoterus.* Mean biotope numbers, density and size were then calculated for each biotope group at each discharge, and compared.

Table 11.4
A recoded matrix of the biotope types given in Table 11.3. The new codes are defined by flow (integer) and substratum (decimal) type. This two-digit code was used for the analysis of biotope diversity.

	SUBSTRATUM TYPE								
FLOW TYPE	Instream vegetation	Silt	Sand	Gravel	Cobble	Boulder	Fractured Bedrock	Smooth Bedrock	Stepped Bedrock
	Final code for 24 categories of biotope types (Flow + Substratum type)								
Near zero	1.2	1.3	1.3	1.5	1.5	1.7	1.7	1.9	
Barely perceptible	1.2	1.3	1.3	1.5	1.5	1.7	1.7	1.9	
Smooth boundary	3.2	3.3	3.3	3.5	3.5	3.7	3.7	3.9	
Accelerating	4.2		4.4	4.5	4.5	4.7	4.7	4.9	
Rippled	4.2		4.4	4.5	4.5	4.7	4.7	4.9	
Standing waves			6.4	6.5	6.5	6.7	6.7	6.9	6.9
Broken standing waves			6.4	6.5	6.5	6.7	6.7	6.9	6.9
Chaotic			8.5	8.5	8.5	8.7	8.7	8.9	10.7
Boil					8.5	8.7	8.7	8.9	10.7
Free fall						10.7	10.7	10.9	10.7

The development of a framework for extrapolating information up to the study area

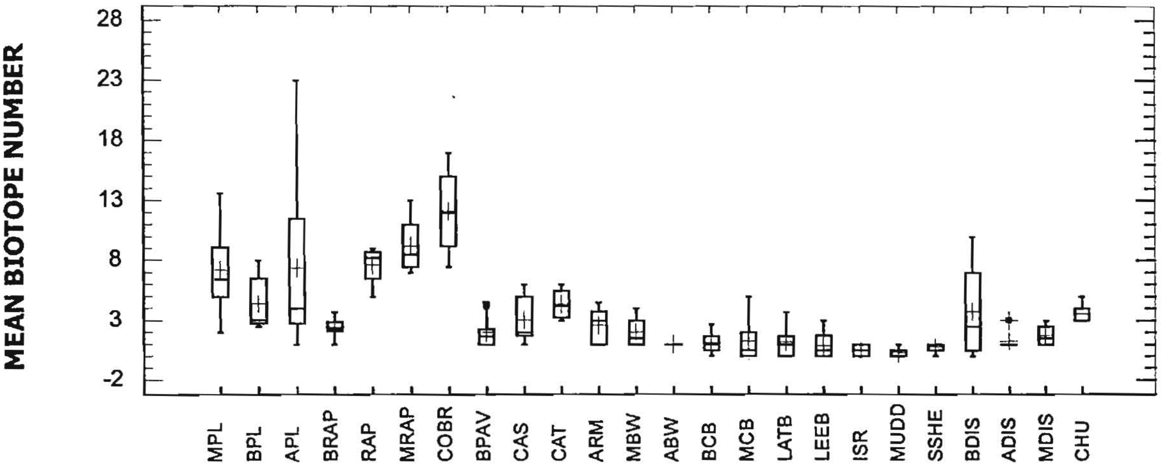
As part of the GBA, a framework was developed for extrapolating information from scales that are ecologically important, the biotope and geomorphic unit, to that of the study area. The preceding information on the biotope assemblages of Rapids was used to demonstrate how this framework could be applied to estimate the amount of available habitat in the Marite River (see Appendix C).

RESULTS

General characteristics of geomorphic units

With the exception of Bedrock Rapids and Bedrock Pools, the highest diversity and numbers of biotopes occurred in rapids, followed by pools (Figure 11.6). Relatively high numbers were also evident in cataracts, bedrock distributaries and chutes. In contrast, the lowest numbers occurred in alluvial backwaters, mud drapes and sand sheets. The lowest biotope diversity was found in lateral bars, mud drapes and sand sheets. The simplest channel type, AST is composed of geomorphic units with limited substratum and flow types (near-zero flows to smooth boundary turbulence over silt, sand, cobble and organic detritus).

A. Biotope numbers



B. Biotope diversity

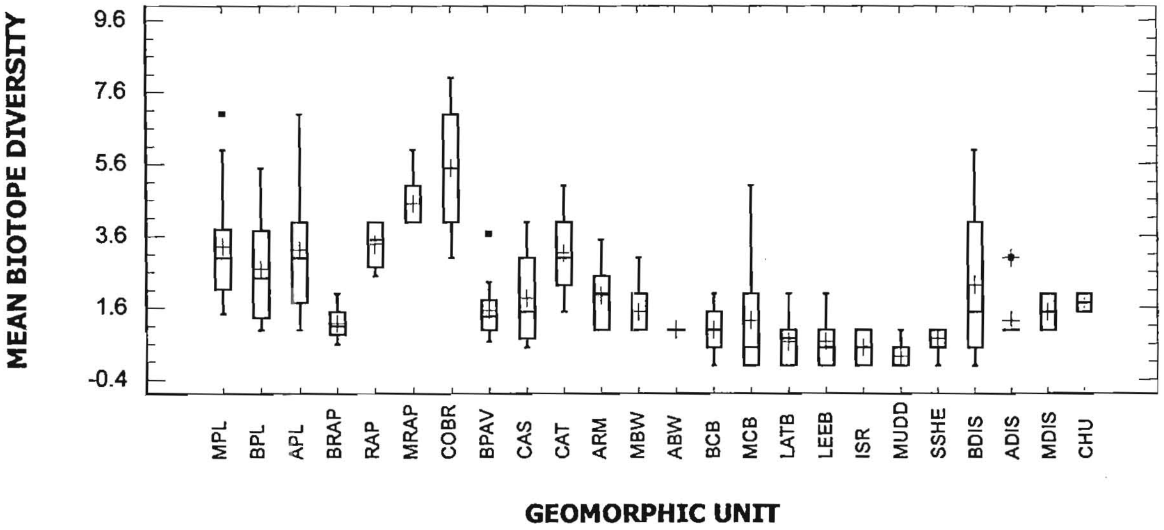


Figure 11.6 Box-and-whisker plots, across all discharges, of mean biotope numbers and diversity of the geomorphic units represented in the study area. Box indicates the median, mean and interquartiles and whiskers show the range. A full description of the abbreviations of geomorphic units is given in Table 11.2.

Biotope characteristics of Pools and Rapids

The effect of discharge

The range of discharges that were mapped did not significantly alter ($p \leq 0.05$) the overall mean number, diversity or density of biotopes in any of the three geomorphic-unit types, namely; Mixed Pools, Simple Pools or Rapids (Table 11.5; Figure 11.7). However, although discharge did not affect biotope size in both types of pools, the mean size of biotopes within Rapids differed significantly as flow changed. Specifically, the size of biotopes decreased by 50% (from an average of 9.8 m^2 to 4.8 m^2) as flows dropped to the lowest discharge of 0.2m^3 s^{-1}.

Table 11.5

Summary of the F values and probabilities from the generalised linear model of repeated measures, regarding the effects of discharge on biotope characteristics within three geomorphic units (GU): Mixed Pools (MPL), Simple Pools (SPL) and Rapids (RAP). p = probability, * indicates a significant effect ($\leq$ 0.05). See also Figure 11.7.

GU type	BIOTOPE CHARACTERISTIC											
	MEAN NUMBERS			MEAN SIZE			MEAN DIVERSITY			MEAN DENSITY		
	f ratio	df	P ($\leq$0.05)	f ratio	df	P ($\leq$0.05)	f ratio	df	P ($\leq$0.05)	f ratio	df	P ($\leq$0.05)
MPL	0.507	16	0.684	1.5	16	0.265	0.496	16	0.691	2.01	16	0.162
SPL	0.988	14	0.43	0.716	14	0.563	0.926	14	0.461	0.727	14	0.557
RAP	0.954	27	0.431	5.906	27	* 0.007	0.227	27	0.877	1.118	27	0.361

The effect of geomorphic-unit type on biotope characteristics

Significant differences ($p \leq 0.05$) were evident in the mean number, size, diversity and density of biotopes between all three geomorphic-unit types, at each discharge, with the exception of biotope size at a discharge of 1.5 m^3 s^{-1} (Table 11.6). Significantly higher biotope numbers, and diversities occurred in Mixed Pools than in Rapids (Figure 11.7). The two pool types, Simple Pools and Mixed Pools only differed in their mean numbers and diversity at the lowest and highest discharges (Table 11.6). In contrast, Rapids always housed significantly higher densities of biotopes than Mixed Pools, and than Simple Pools at the lower discharges (0.2 m^3 s^{-1} and 0.9 m^3 s^{-1}). On average Simple Pools contained larger biotopes than Rapids, except at a discharge of 1.5 m^3 s^{-1}.

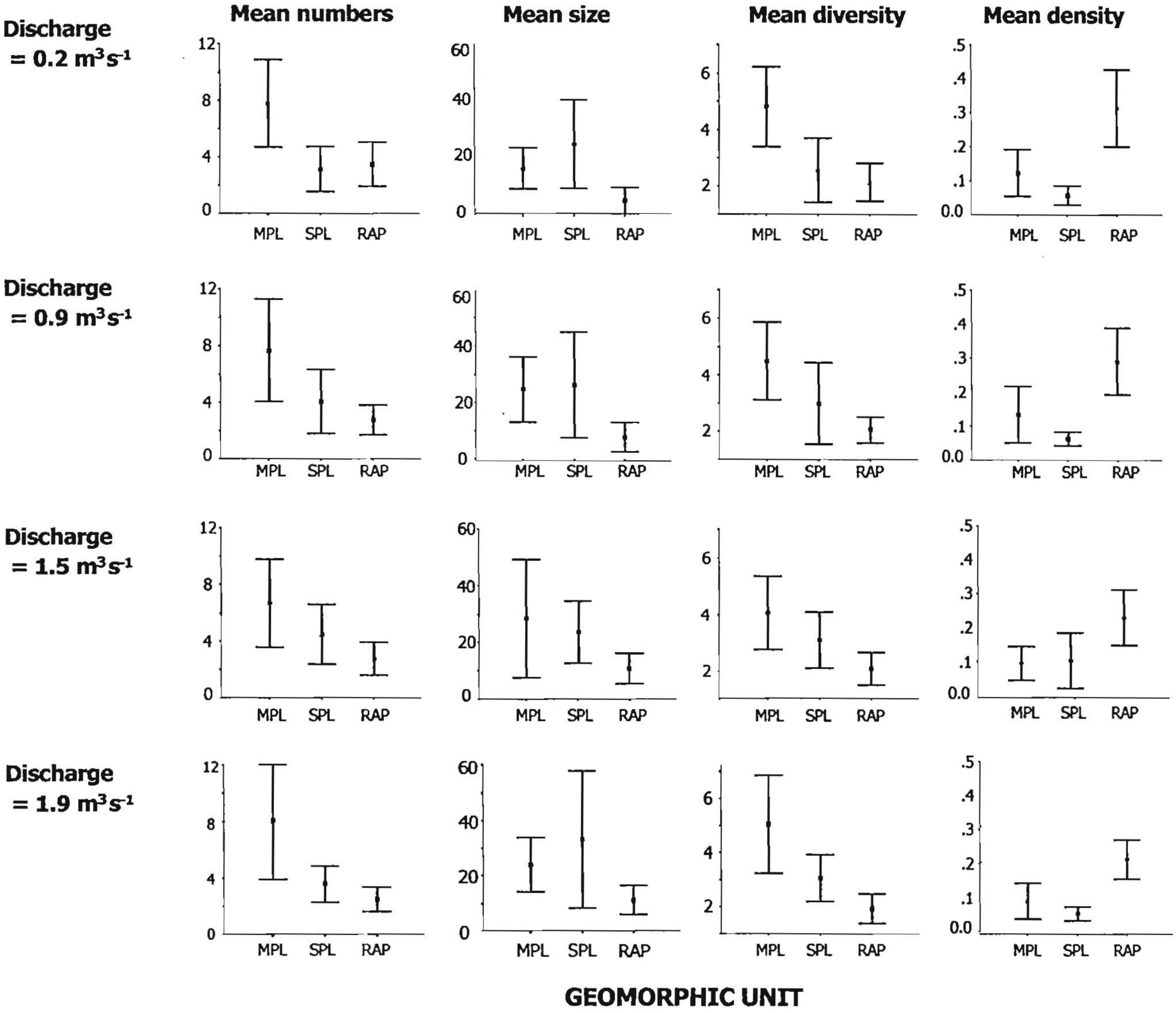


Figure 11.7 The effect of discharge (Table 11.5) and geomorphic-unit type (Table 11.6) on the mean numbers, size, diversity and density of biotopes at each measured discharge. Results are presented in table form with discharge as rows and columns as biotope characteristics. Error bars represent 95% confidence intervals. The GU types are abbreviated as follows: Mixed Pools = MPL; Simple Pools = SPL; Rapids = RAP

Table 11.6

Summary of the F values and probabilities of the one-way analysis of variance, comparing biotope characteristics between Mixed Pools (MPL), Simple Pools (SPL) and Rapids (RAP) at four different discharges. The internal differences (Bonferroni) among the three geomorphic-unit (GU) types are indicated (see also Figure 11.7). * indicates significant effect ($p \leq 0.05$).

DISCHARGE	BIOTOPE CHARACTERISTIC (mean per GU type)	F-ratio	df	Probability ($\leq$0.05)	DIFFERENCES BETWEEN EACH GU type Probability ($\leq$0.05)		
					MPL - SPL	MPL -RAP	SPL - RAP
0.2 $m^3 s^{-1}$	Numbers	6.012	54	* 0.014	* 0.004	* 0.008	1
	Size	5.992	54	* 0.005	0.542	0.153	* 0.004
	Diversity	8.724	54	* 0.001	* 0.014	* 0.000	1
	Density	8.087	54	*0.001	1	* 0.019	* 0.002
0.9 $m^3 s^{-1}$	Numbers	6.158	54	* 0.004	0.093	* 0.003	1
	Size	4.558	55	* 0.015	1	0.053	* 0.042
	Diversity	7.328	54	* 0.002	0.139	* 0.001	0.502
	Density	7.585	54	* 0.001	0.927	* 0.036	* 0.002
1.5 $m^3 s^{-1}$	Numbers	4.57	54	* 0.015	0.455	* 0.012	0.626
	Size	2.804	54	0.07	1	0.089	0.372
	Diversity	5.969	54	* 0.005	0.469	* 0.004	0.297
	Density	4.004	54	* 0.024	1	* 0.050	0.103
1.9 $m^3 s^{-1}$	Numbers	7.868	54	* 0.001	* 0.027	* 0.001	1
	Size	3.355	53	* 0.043	1	0.417	* 0.04
	Diversity	10.436	54	* 0.001	* 0.046	* 0.000	0.347
	Density	3.837	54	* 0.028	0.054	* 0.047	* 0.05

Biotope assemblages of Pools and Rapids at different discharges

In terms of their biotope assemblages (Figure 11.8), Mixed Pools contained the greatest diversity of biotope types (23) compared to Simple Pools and Rapids (19). Numerically, these were fairly evenly represented by near-zero, smooth-boundary- and accelerating-flow biotopes, with a range of substratum types. In contrast, both Simple Pools and Rapids were dominated by biotopes in only two flow categories. In Simple Pools, almost 40% of the biotope types were accounted for by near-zero and smooth-boundary flows over sand and vegetation. Rapids contained few zero-flow or smooth-flow biotope-types and were dominated by accelerating, or turbulent, flows over boulders and bedrock (40%).

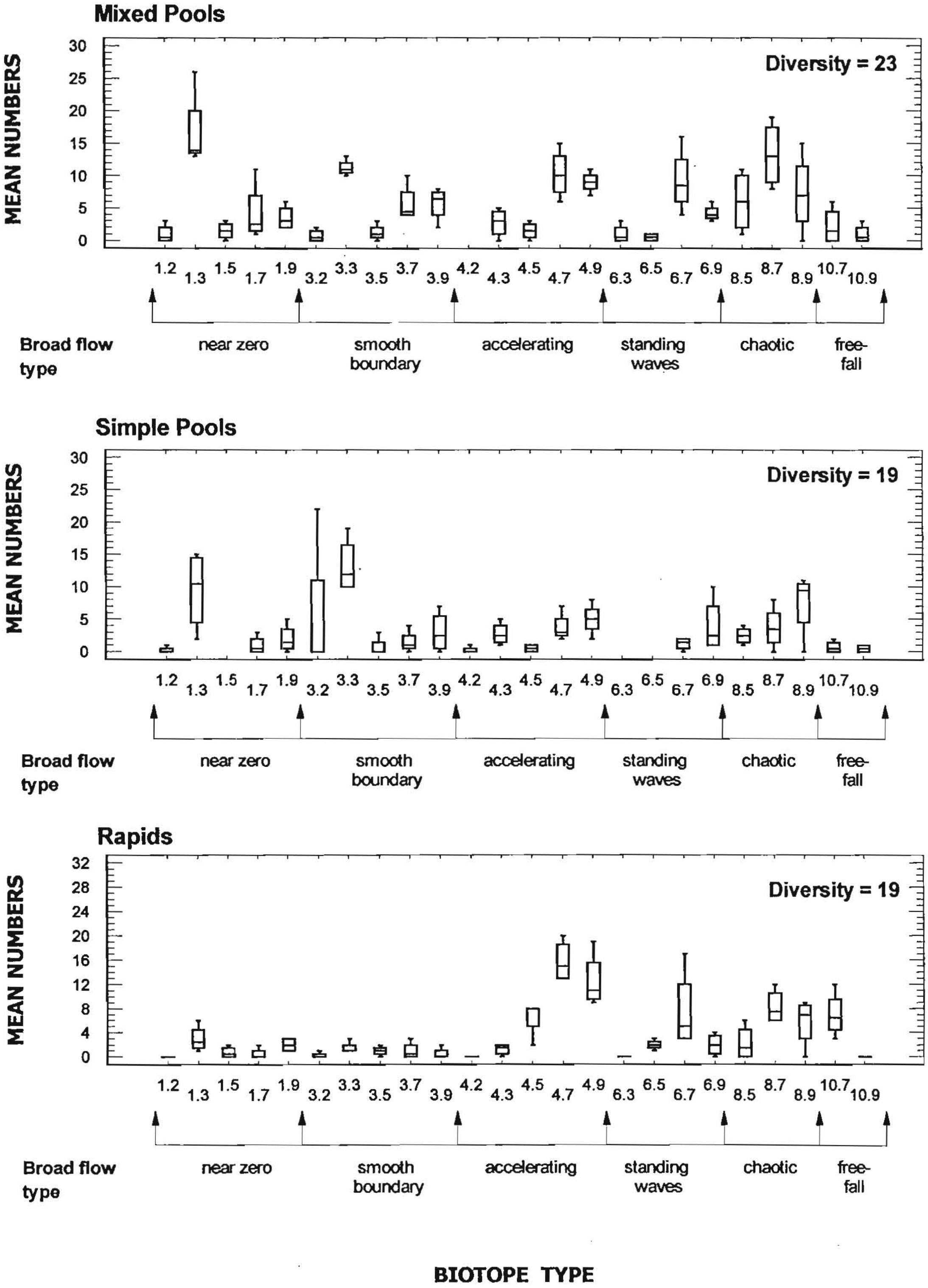


Figure 11.8 Box-and-whisker plots of the biotope assemblages (mean numbers) of Pools and Rapids, across four discharges. Box indicates the median, mean and interquartiles and whiskers show the range. The biotope type, shown as a code along the x-axis, comprises a combination of flow-type (the integer), described below the x-axis, and substratum (the decimal) which is coded as follows: 0.2 = instream vegetation; 0.3 = silt/ sand; 0.5 = gravel/ cobble; 0.7 = boulder/ fractured bedrock and 0.9 = smooth bedrock (see Table 11.4). Diversity figures exclude single occurrences of a biotope type.

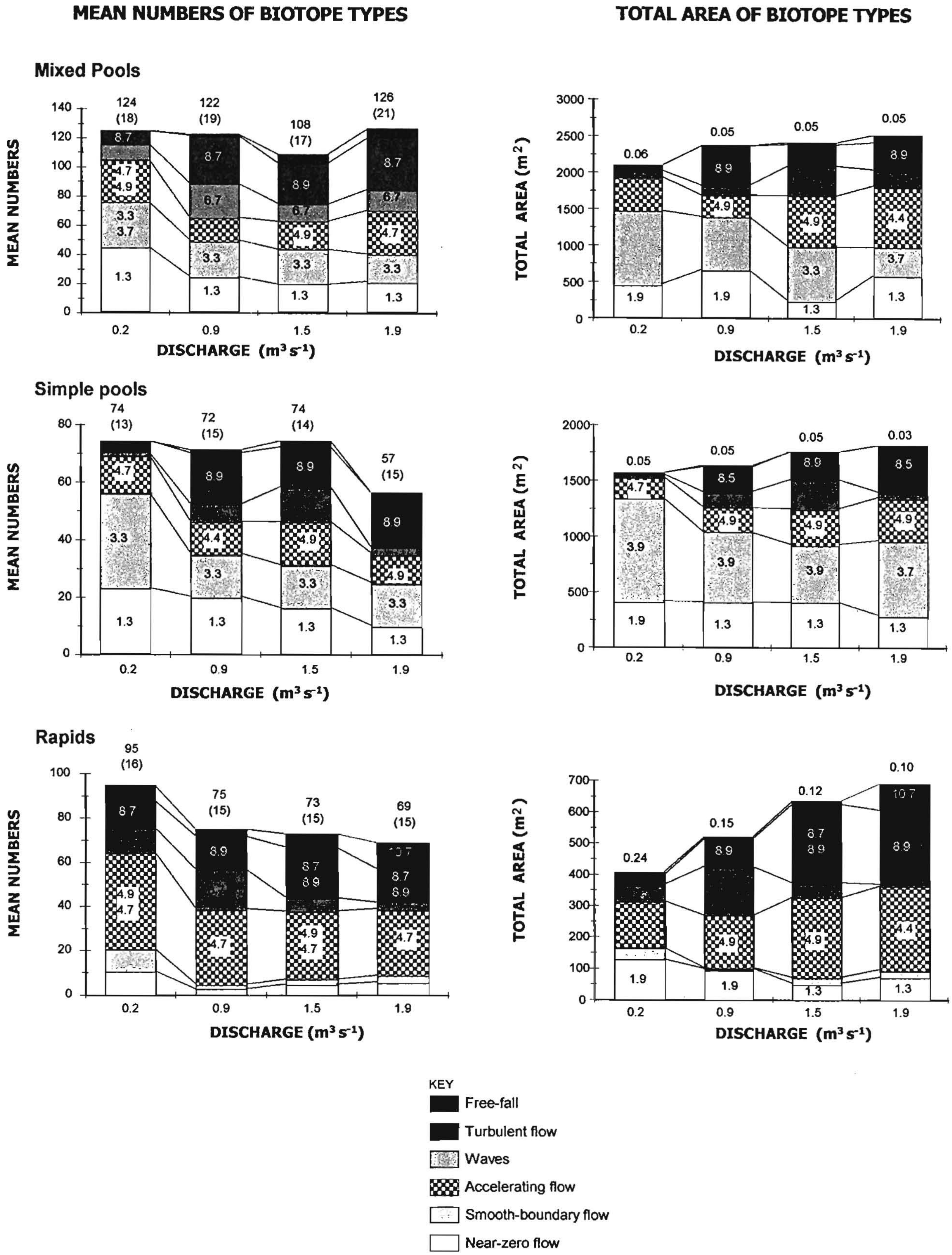


Figure 11.9 Summary of the mean numbers and total area of biotope types, grouped into categories of flow types, for pools and rapids at each discharge. Graphs in the left-hand column represent mean numbers. Figures within the bars are the dominant biotope-type within that category. The total number of biotopes is shown above each bar and the biotope diversity (ie. number of biotope types) is given in parenthesis. Graphs in the right-hand column represent the total area of each category of biotope type. Figures within the bars represent the largest biotope type within that category. Numbers above the bars indicate the average density of biotopes at that discharge. The details of biotope codes are given in Table 11.4.

Figure 11.9 provides a summary of the internal variation of biotope categories in each type of geomorphic unit with increasing discharge. The following patterns emerged.

Mixed Pools: At the lowest discharge, biotopes within the near-zero flow category dominated numerically. Smooth-boundary flow and accelerating-flow biotopes contributed equally, and turbulent-flow biotopes were rare. The largest area was covered by smooth-boundary flow biotopes. As discharge increased, turbulent-flow biotopes dominated numerically with relatively equal contributions by other biotope categories. Smooth-boundary flow and accelerating-flow biotopes made up the largest area. The overall wetted area of Mixed Pools increased by 17% across the four discharges.

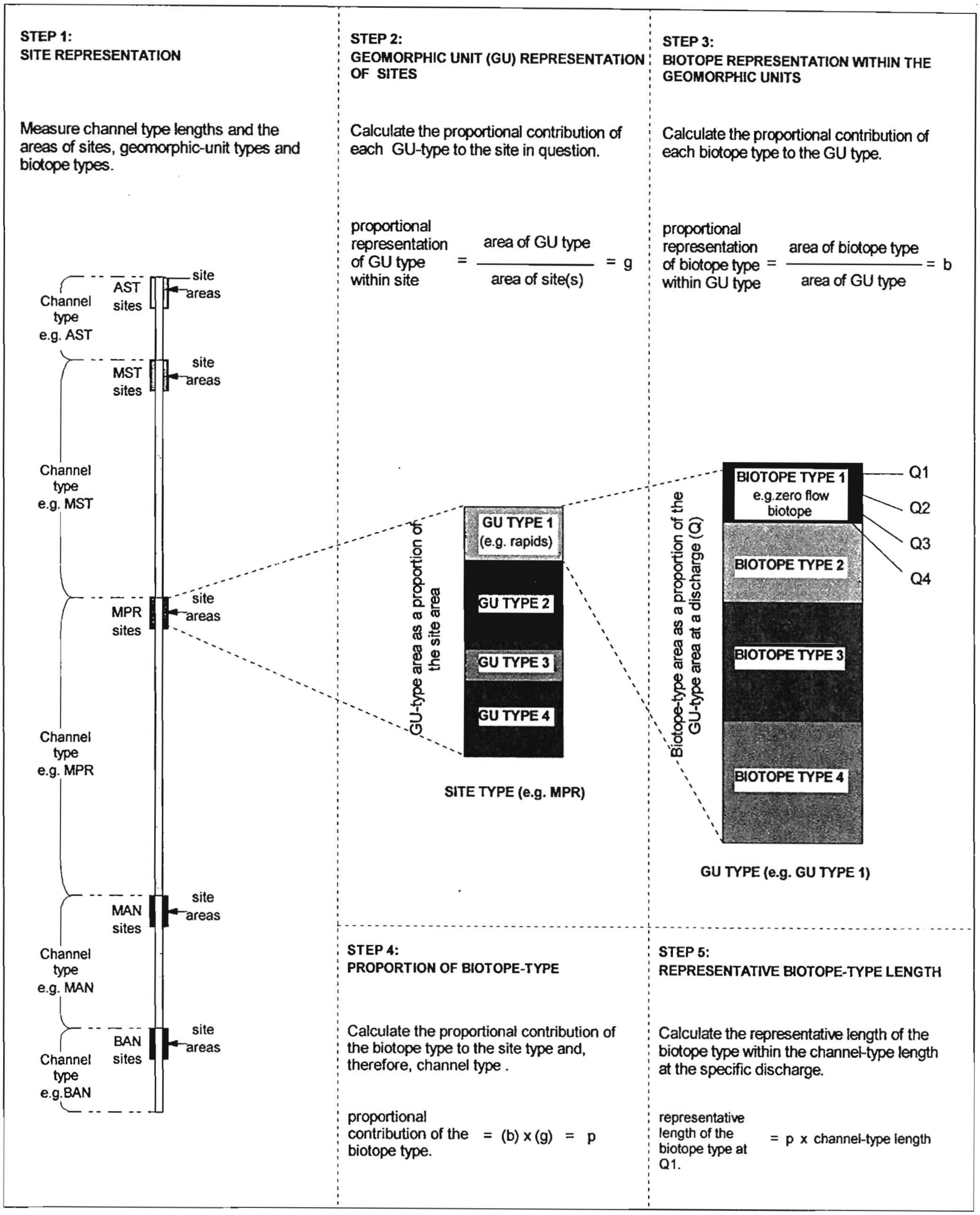
Simple Pools: Smooth-boundary flow biotopes dominated at the lowest discharges and turbulent-flow biotopes were rare. Although not dominant until the highest discharge, turbulent-flow biotopes contributed substantially to the overall biotope numbers, and area, thereafter. Smooth-boundary flow biotopes covered the largest area at all discharges. The total wetted area of Simple Pools increased by 14% across the four discharges.

Rapids: This geomorphic unit was always dominated, numerically, by accelerating-flow biotopes. These, together with near-zero flow biotopes, covered the largest area at the low discharges. Together with turbulent biotopes, they also comprised the largest area at all other flows. As discharge increased, there was a decrease in zero-flow biotopes, and a marked increase in the numbers and area of turbulent-flow biotopes, which peaked at a discharge of 1.5 $m^3 s^{-1}$. A notable proportion of free-fall biotopes was also evident at the highest discharge. The total wetted area of Rapids increased by 42% across the four discharges.

Extrapolating information up to the study area

The framework for extrapolating information is outlined in Figure 11.10, and comprises five key steps. These involve using information from the previous steps and analyses (see Figure 11.1) regarding the (1) length of each channel type, (2) the proportional contribution of each type of geomorphic unit to the site, and (3) the proportional contribution of each biotope-type to each geomorphic-unit type at the discharge of interest. These data are then used to calculate (4) the proportional contribution of each biotope type to each channel type and finally (5) the length of each biotope type in each the channel type (and hence, study area).

Rapids were used to demonstrate the application of the method. Details of the data used and calculations are given in Appendix C. From this, it was estimated that Rapids comprised approximately 1800 m, or 6%, of the total length (30.5 km) of the study area (Figure 11.11). The composition of biotope types that make up this total varied as a function of discharge. For example, zero-flow biotopes accounted for about 32% of the total length of rapids at the lowest discharge whilst turbulent-flow biotopes comprised just 8%. At the highest discharge, there was a fourfold increase in the amount of turbulent-flow biotopes and these percentages were reversed.



STEP 1:
SITE REPRESENTATION

Measure channel type lengths and the areas of sites, geomorphic-unit types and biotope types.

STEP 2:
GEOMORPHIC UNIT (GU) REPRESENTATION OF SITES

Calculate the proportional contribution of each GU-type to the site in question.

$$\text{proportional representation of GU type within site} = \frac{\text{area of GU type}}{\text{area of site(s)}} = g$$

STEP 3:
BIOTOPE REPRESENTATION WITHIN THE GEOMORPHIC UNITS

Calculate the proportional contribution of each biotope type to the GU type.

$$\text{proportional representation of biotope type within GU type} = \frac{\text{area of biotope type}}{\text{area of GU type}} = b$$

STEP 4:
PROPORTION OF BIOTOPE-TYPE

Calculate the proportional contribution of the biotope type to the site type and, therefore, channel type .

$$\text{proportional contribution of the biotope type.} = (b) \times (g) = p$$

STEP 5:
REPRESENTATIVE BIOTOPE-TYPE LENGTH

Calculate the representative length of the biotope type within the channel-type length at the specific discharge.

$$\text{representative length of the biotope type at Q1.} = p \times \text{channel-type length}$$

Figure 11.10 A proposed framework for extrapolating biotope information from sites (i.e. channel types) to the study area. A theoretical example of the calculations of the length of biotopes within rapids is given in Appendix C

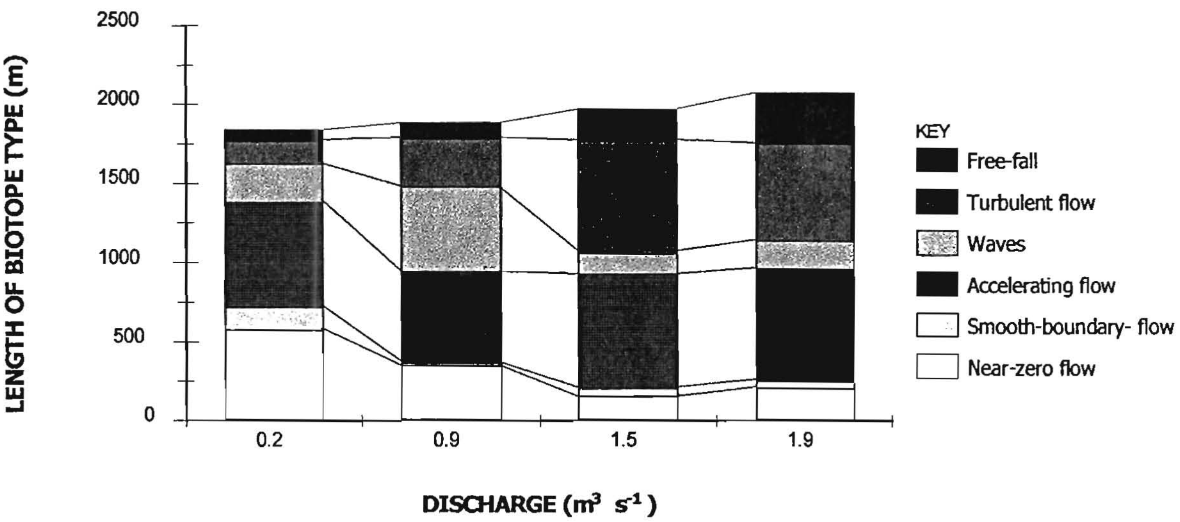


Figure 11.11 Example of the results of extrapolating site-specific information up to the scale of the study area. The graph represents Rapids, and their composition of biotope types (see Table 11.4), at four discharges.

11.6 DISCUSSION

An alternative approach to estimating habitat availability has been described based on the geomorphic and biotope assessments of the GBA. Results of these, together with the approach to extrapolation will be discussed. The discussion will conclude with a brief assessment of this approach which will be elaborated in Chapter 13.

Geomorphic attributes and the quantification of biotope availability

This research supported the findings of van Niekerk & Heritage (1993) from the Sabie River which showed that mixed channel types (MPR and MAN) represent a complex assemblage of geomorphic units. In contrast, the single thread sections comprised limited geomorphic diversity. Such differences are important in that these geomorphic units form different templates for biotope availability. In addition, my results revealed further details regarding the relationship between geomorphic units and biotopes. First, the highest numbers and diversity of biotopes were found in pools and rapids, followed by cataracts and bedrock distributaries. Second, the focus on pools and rapids indicated that they each exhibit a distinctive biotope "fingerprint" (see, for example, Figure 11.8). This refers to the biotope assemblage, with its own inherent characteristics of biotope numbers, size and density. It is postulated that these assemblages can be further characterised in terms of the spatial and temporal attributes of biotopes. Furthermore, it is likely that each type of geomorphic unit will display a characteristic biotope fingerprint.

The geomorphological assessment indicated that the PHABSIM sites excluded two channel types, AST and BAN, amounting to about 6% of the study area. Furthermore, each PHABSIM site straddled two channel types. The implications of this are that habitat would have been inaccurately depicted by

PHABSIM. For instance, alluvial pools which dominate AST channels, and Rapids, which are common in BAN channels, would have been under represented. Consequently, it appears that the approach proffered by IFIM to extrapolate site-specific results to the study river may be inappropriate insofar as it does not encompass the full suite of physical conditions present in the river.

The influence of discharge on biotope characteristics

Interestingly, discharge had no significant influence on the overall biotope numbers, density or diversity of pools and rapids. The only biotope characteristic that was significantly affected by increasing discharge was the size of biotopes in Rapids, particularly between 0.2 and 0.9 $m^3 s^{-1}$. Their increase in size probably reflects the sharp increase (42%) in the wetted area of Rapids as discharge increased, compared to a 16% increase in the size of pools. Nonetheless, these results represent only a selected window of the discharges that occur and, in all likelihood, lower or higher discharges would significantly influence the overall biotope characteristics. This would reflect changes in the relationship between channel morphology and hydrology in that the patterns of filling and bank-overtopping will differ within, and between, channel types.

Importantly, however, discharge altered the internal patterns of biotope assemblages. For example, a common feature of all three geomorphic units was an increase in the numbers, and area, of turbulent-flow biotopes as flow increased. These results suggest that, at the discharges measured, flow exerts its major influence on the *biotope makeup* of geomorphic units. Further, given that each type of geomorphic unit has a distinctive biotope fingerprint, these internal patterns will display different responses to changes in flow.

Biotope patterns at low discharges

Of particular interest to this study was the fate of habitat at low flows. Rapids, the primary habitat of adult *C. anoterus,* were distinguished by three key features at the lowest discharge: (i) a dramatic reduction in their overall size (wetted area), (ii) a reduction in the size of the biotopes and (iii) changes in the biotope assemblage, with near-zero/ stagnant-flow biotopes replacing turbulent and accelerating-flow biotopes. The reduction in the area of pools was far less dramatic, and the areas of both pool types were dominated by smooth-boundary flow biotopes whereas rapids were dominated by accelerating-flow biotopes. Like Rapids, there was a substantial reduction in turbulent-flow biotopes in both pool types.

From my data it appears that habitat (biotopes) in Rapids is characterised by a dramatic decline below some "minimum" flow and any slight increase above this point increases habitat considerably (see similar discussion by Heggenes *et al.* 1996). Although physical habitat loss appeared to be less dramatic in Pools, I would suggest that an important issue is the drawdown from vegetated pool margins, which offer an important habitat, but which have not been considered in this study.

Extrapolation: Biotope availability for the study area

One of the challenges of the GBA methodology is to develop, and rationalise, an approach to extrapolating information from a scale that is ecologically meaningful (biotopes) to the study area. The links for this are provided for in the hierarchical classification of van Niekerk *et al.* (1995): from biotopes, through to geomorphic units and channel types which, in turn, constitute the study river. For example, using this approach, it was estimated that the study area comprised about 1.8 km of rapids, and 11.4 km of pools. Whilst these are estimates, I would argue that they do offer a far more rational approach than that provided through PHABSIM. A more thorough discussion of the two approaches, and the implications of using sites as a proxy to represent an entire study area, follows in Chapter 13. Maddock & Bird (1996) and Maddock (1999) have proposed a similar approach to extrapolation that recognises the spatial links between physical features. Their approach advocates for a rapid assessment of physical features, principally mesohabitats, which dovetail with the scale of geomorphic units in the GBA but which, in contrast, includes flow characteristics.

Overviews for the river as a whole, such as that provided for Rapids (see Figure 11.11) are of limited value if they are interpreted in isolation. They do not, for example, provide any spatial reference which may be important to understand in relation to the anticipated project impacts. This would be provided by the information on the distribution of geomorphic units and channel types. Clearly, then, the approach to extrapolation will depend on the project objectives so that for instance, increased abstraction down the river course may require a different approach to that needed if the construction of a dam is the issue at hand.

Assessment of the GBA

Although a complete assessment of the GBA will follow in Chapter 13, it is valuable at this point to highlight some of the key advances offered by the GBA in terms defining habitat availability, as well as areas of this approach that require further refinement.

An overriding asset of the GBA is the preservation of spatial reference, which is given in the hierarchical classification of van Niekerk *et al.* (1995) and which, specifically, addresses the mechanisms controlling biotope architecture, distribution and abundance. Two key advantages of this relate to the formal recognition of the intermediate scale of geomorphic units, and to the option to retain attributes of habitat heterogeneity. The inclusion of geomorphic units not only reflects their geomorphological importance, but also responds to the needs of ecologists who have consistently incorporated this scale of habitat (see discussion in Section 13.2). In this regard, I would suggest that they better reflect reality than the transect approach used in IFIM. Since they are static geomorphological features, not only can availability then be compared between geomorphic units, and at different discharges, but this can be readily interpreted at the scale of channel types. Additionally, it is through geomorphic units, that extrapolation is undertaken. With the exception of work by Maddock & Bird (1996) and Maddock (1999), suitable approaches have, to date, remained obscure.

Recent work on ecosystems characteristics, and discussed further in Chapter 13, advocates for approaches that retain, rather than obscure, heterogeneity. My premise is that if ecosystem heterogeneity is regarded as a key attribute, then retaining the spatial attributes of the smallest scale of habitat, the biotope, as a patch, that more closely approximates reality is a significant step forward for habitat studies. This offers opportunities to explore key features of habitat heterogeneity which may provide key advances in understanding habitat use. For example, are biota responding to patch numbers, their size, their dispersion or their connectivity, or a combination of these? Furthermore, does the current suite of hydraulic parameters adequately describe physical habitat?

In this regard, and as I suggested in the preceding chapter, both habitat availability and use may be better characterised as *assemblages of patch types* which capture variability, as opposed to the single-peak curves produced by PHABSIM for the entire site. Holding heterogeneity as a main theme, however, does require incorporating new analytical approaches since conventional analytical constraints inevitably necessitate grouping data. This undermines the very challenge of capturing attributes of heterogeneity. The incorporation of new analytical techniques (see Chapter 13) and simulation routines that can handle large databases would advance developments in habitat studies.

Finally, once the distribution and abundance of biotopes are understood, a major challenge for future research is to accommodate this approach into a formal simulation model which allows one to predict biotope availability under different flow conditions.

11.7 CONCLUSIONS

The seminal work by researchers on the geomorphological determinants of habitat, and on the characterisation of habitat as patches which have spatial reference, has provided the essential elements required to develop a new approach, the GBA, to describing the availability of physical habitat in rivers.

First, in terms of validating PHABSIM, this approach revealed that two channel types had been omitted in the IFIM site selection. Additionally, each IFIM site straddled two channel-types. Secondly, in contrast to the transect approach of PHABSIM, I suggest that the geomorphic units used by the GBA provide a more useful and objectively defined scale at which to model habitat. The GBA presents the smallest scale of habitat as the *biotope*, and holds that each geomorphic unit comprises a distinctive assemblage of biotopes. As representative of channel types, the study site then, is depicted as a patchy mosaic of different biotope types nested within a mosaic of geomorphic units. This picture of habitat availability more closely matches that of reality than the outputs of PHABSIM. The description of habitat as biotopes, as opposed to cells between transects, offers the potential to explore the key attributes of habitat heterogeneity such as the number of patches, the diversity, the size, and the area that they cover.

It was only through the use of the geomorphological classification system that the link for extrapolating site-specific data up to the scale of the study area, was provided. A framework for extrapolation, together with recommendations for further refinement, has been provided.

12

Making the Ecological Link in the GBA - A Framework for Determining Biotope Use

12.1 INTRODUCTION AND OBJECTIVES

The preceding chapters have presented two habitat assessment approaches, IFIM and the proposed alternative, the Geomorphological-Biotope Assessment, or GBA. Both approaches have delivered, as one of their outputs, an assessment of the availability of physical habitat. Whilst the models for available habitat and "ecological" (habitat use) have been linked within IFIM (Chapter 8), this linkup must still be made within the GBA. This chapter proposes to develop, and demonstrate, an approach to coupling the biotope-use data with that of biotope availability, as outlined in the overall framework for the GBA in Chapter 10. The challenge is to link the ecological data (biotope use) with that of biotope availability so as to track the fate of biotopes that are used by the target species at low discharges. The discussion will then focus on potential output models of biotope use. This will provide the basis for a comparison, and assessment, of the outputs of both IFIM/ PHABSIM and the GBA which will be undertaken in Chapter 13.

The purpose of this chapter, therefore, is to:

1. demonstrate an approach to linking biotope use models with those of availability. This will be illustrated by using data collected for adult *C. anoterus* and to,
2. compare the utility of the outputs for adult *C. anoterus* from PHABSIM and the GBA.

12.2 APPROACH TO LINKING BIOTOPE-AVAILABILITY MODELS WITH THOSE OF HYDRAULIC HABITAT-USE

The proposed approach follows the protocol outlined for the GBA in Figure 10.4. Firstly, samples of fish or invertebrates are located on the same geomorphic-template map (e.g. Figure 11.4) used for describing biotope availability, over the range of target discharges. Then, so as to develop models of biotope use commensurate with those of availability, the *assemblages* of biotope types that are used within each type of geomorphic unit are derived using the same methodology outlined in Section 11.5. In contrast to IFIM, biotope use can be presented not only as numbers of animals per biotope type but, with the inclusion of biotope area, also as animal densities. The distributional patterns of use can also be represented as spatially explicit data. Finally, these data can be compared to that of biotope availability.

In order to demonstrate this approach, the habitat-use (or so-called "ecological") data collected for PHABSIM, were needed. The IFIM and GBA data were collected and described in different ways, and clearly, in order to make the linkup, the data sets had to be comparable. Within the GBA, physical habitat availability is depicted at the scale of biotopes, which represent a combination of flow-type and substratum. IFIM, on the other hand, depicts both the availability and use of physical habitat as three independent, univariate SI curves of depth, velocity and substratum. Consequently, the IFIM data were reorganised to represent the IFIM data by the same parameters that describe biotopes.

Moreover, the IFIM protocol does not require that the broad habitat-types, or geomorphic units, in which fish were sampled, be recorded. This scale is explicit in the GBA since biotopes are described as assemblages nested within these geomorphic units (see Figure 10.3 and Section 11.5). Since adult *C. anoterus* are found almost exclusively in Rapids (as a geomorphic unit) identifying the appropriate IFIM data set for adult *C. anoterus* was relatively straightforward. However, it was not possible to isolate the appropriate biotope-availability data for juvenile fish in any meaningful way since they used a mosaic of geomorphic units, including both pools and rapids (see discussions below).

Nonetheless the intention of this chapter is to support the proposed GBA framework by demonstrating how links can be made between the hydraulic information and the biotope-use data, as outlined in Chapter 10. The intended product is a framework, and a demonstration of potential outputs, rather than an empirical model of biotope use for *C. anoterus, per se.* In light of this, adult *C. anoterus* will constitute the main focus to illustrate a model for the ecological linkup.

12.3 DATA ANALYSES

Data were analysed at the spatial scale of geomorphic units. A number of data sets was prepared to meet different analytical objectives (Table 12.1). Broadly, these were aimed at deriving outputs at two spatial scales:

1. Composite-biotope use profiles which combined biotope use from all sites (i.e. across all channel types). Accordingly, biotope-use profiles were developed for all three lifestages, as an alternative to the outputs of IFIM.
2. Biotope-use profiles at the scale of channel type, in order to compare site-specific outputs with composite outputs (see above). Further, to compare biotope use with that available, biotope-availability and use profiles were developed for adult *C. anoterus* at this scale. The biotope availability was represented by rapids, the primary habitat of adults.

The profiles for biotope use were derived from the data collected for IFIM (Chapter 8), as described below. Biotope availability profiles were derived from the biotope data set (Chapter 11). Although the IFIM and GBA data were collected at different times, their collection was sufficiently consistent in terms of site and discharge that a subset of habitat-use data could be identified for the linkup.

Data were stratified according to the discharges measured during the biotope survey (0.2, 0.9; 1.5 and 1.9 $m^3 s^{-1}$). Only biotope-use data that fell within this discharge range were extracted from the IFIM database. Where discharges were not identical, IFIM data were assigned to the nearest GBA discharge category. For example, IFIM data for discharges of 0.3 $m^3 s^{-1}$ were assigned to the GBA category of 0.2$m^3 s^{-1}$. Data for discharges of 0.5 $m^3 s^{-1}$ and 1.2 $m^3 s^{-1}$ were excluded since they fell midway between two values. The numbers of fish for which data were analysed were 244 early juveniles, 299 late juveniles and 879 adults.

Then, so as to express biotope-use at the same scale and units as those used for the analysis of biotope availability (see Section 12.2), data were organised in the following way:

- The original substratum types (see Table 8.4) were reassigned codes that corresponded to those used in the GBA (see Table 11.4).
- A flow-type was then assigned to each sample by considering the depth and velocity conditions for each IFIM habitat-use sample. These codes were crosschecked both with notes made during the IFIM field surveys, which recorded flow conditions for each sample, and from velocity and depth ranges associated with each flow-type, developed from the biotope data set (Pollard, unpubl. data).
- The substratum and flow-type codes were then combined to assign a code of biotope type to each sample, in accordance with Table 11.4.
- Data sets were developed of biotope use for the three key lifestages identified in Chapter 8, namely early juveniles (<31mm SL), late juveniles (31 - 38mm SL) and adults (>38mm SL).

Frequency histograms were then developed of (i) composite biotope-profiles for all three lifestages, and for biotope availability in Rapids and (ii) biotope-profiles of availability and use by adult *C. anoterus* in the Mixed Anastomosing Channel-type (MAN, see Chapter 11). This site was chosen because it was the IFIM site for which PHABSIM was used. Finally, the area of the biotopes that were used in MAN channels was calculated from the GIS data at all four discharges.

Lastly, estimates of the total amount of habitat used in the entire study area were made, using data for adult *C. anoterus* to illustrate this. To do this, the same process that was undertaken in estimating the amount of biotope availability was applied (see Section 11.5 and Appendix C). First, this was undertaken for each channel-type. Then, knowing the proportional contribution of each channel type to the entire study river, these estimates were scaled-up to produce estimates of the used biotopes for the entire river, as a function of discharge. This information was compared to the total wetted area so as to (a) estimate the proportional biotope area that was used by adult *C. anoterus* and, (b) to see if comparisons with the outputs of PHABSIM could be made.

Table 12.1
Summary of the data analyses undertaken to describe biotope use for *C. anoterus*

OBJECTIVE	APPROACH TO DATA ANALYSES	
	BIOTOPE AVAILABILITY	BIOTOPE USE
Lifestage: Adults within Rapids		
1. Derive a composite profile (across channel-types) so as to compare biotope availability and use.	1.1 Data from three of the GBA sites that corresponded to the IFIM sites (MPR, MAN, BAN - see Chapter 11) were aggregated. Temporal attributes preserved and represented as four discharges between 0.2- 2 m^3 s^{-1}.	1.2 Aggregated data from the three IFIM sites, but restricted to discharges for which biotope availability data were collected, namely: 0.2 to 2 m^3 s^{-1}. Temporal attributes preserved and represented as four discharges between 0.2 and 2 m^3 s^{-1}.
2. Derive comparative biotope use, and availability, profiles that preserve the spatial scale of channel types, so as to (a) provide a detailed analysis of biotope use and availability as a framework for future work and, (b) provide comparative data with those of the PHABSIM outputs for the same site.	2.1. Subset of data focussing on the MAN channel-type (GBA). Temporal (discharge) attributes preserved.	2.2 Subset of data focussing on IFIM Site 3, which corresponds to the GBA site of MAN. Restricted to four discharges between 0.2 and 2 m^3 s^{-1}. Temporal (discharge) attributes preserved.
Lifestage: Juveniles		
3. Provide a composite profile (across channel types) of biotope use so as to (a) compare the habitat-use outputs of the GBA and IFIM, for juveniles (b) compare biotope-use patterns, derived from the GBA, between adult and juvenile fish	Early-juvenile *C. anoterus* use both Pools and Rapids and, as stated above, the information on biotope use could not be isolated from the IFIM data set so as to derive complimentary biotope-availability data.	3.2 Aggregated data from the 3 IFIM sites, restricted to discharges for which biotope data were collected, namely 0.2 to 2 m^{3}s^{-1}. Temporal attributes preserved as four discharges between 0.2 - 2 m^{3}s^{-1}.

12.4 RESULTS

PRESENTING OUTPUTS AS SITE-COMPOSITE, HABITAT-USE PROFILES FOR EACH LIFESTAGE

The composite biotope-use profiles (i.e. across all sites) for all three lifestages of *C. anoterus* are shown in Figures 12.1 to 12.3. Late juveniles were not found at a discharge of 1.9 m^3 s^{-1}. Overall, all three lifestages utilised 14 biotope types, but the biotope assemblages differed between lifestages. In general, the biotope-use patterns for the two lowest discharges (0.2 and 0.9 m^3 s^{-1}) were similar within a lifestage. Also, curves for the higher discharges exhibited a relative increase in faster-flow biotope types.

Biotope use by juveniles

At low discharges, almost all of the early-juvenile fish (90%) occurred in biotopes with near-zero or smooth-boundary flows over sand, or smooth bedrock (Figure 12.1). This was the only lifestage in which the use of sand was recorded, accounting for 30% of the substrata used at low discharges. As discharge increased, the maturing juveniles shifted almost exclusively to biotopes of smooth-boundary flows over gravel/ cobble or boulders/ bedrock. The first notable evidence of the use of turbulent-flow biotopes was at 1.5 $m^3 s^{-1}$ (the highest flows in which early juveniles were recorded). Early juveniles were almost always found in association with attached algae or bryzoans (Pollard, unplubl. data), which offer overhead and hydraulic cover.

Late juveniles occurred almost exclusively in biotopes of smooth-boundary, or accelerating flows (80 - 100%) over mixed substrata (gravel/ cobble; boulder and bedrock; Figure 12.2). As discharge increased, juveniles increasingly used accelerating-flow and turbulent-flow biotopes.

Two issues warrant mentioning at this point. Firstly, when examining the graphs, it should be noted that the seasonal increase in discharge parallels the increasing maturity of young *C. anoterus*⁽¹⁾ (see Chapters 7 & 8). Thus, at higher discharges, the habitat use of late juveniles would be expected to more closely resemble that of adults. Secondly, the formal recognition through the GBA, of the use of multiple geomorphic units by juveniles, is important and is an issue that I will return to in the discussion.

Adult biotope use and biotope availability

The composite output of biotope availability in Rapids (Figure 12.3) indicated that

- a diversity of 16 biotope types was consistently represented at all discharges,
- this assemblage was fairly consistent at all four discharges, although near-zero and smooth-boundary flows declined with increasing discharge when wave, and turbulent flow-types increased (the latter doubled to 20% of the total),
- biotopes characterised by accelerating flows were dominant at all discharges,
- boulders and fractured bedrock were the dominant substrata.

In terms of biotope-use, more than 50% of all adult *C. anoterus* occurred in biotopes with accelerating flows (Figure 12.3). At the lowest discharges this was followed by biotopes with smooth-boundary flows (15%) but this decreased to an almost negligible contribution at the highest discharge, when turbulent biotopes were the next most utilised (35%). Boulder and fractured-bedrock substrata dominated all biotopes used throughout (Figure 12.3).

In summary, the biotope-use profiles indicated that:

- most early juveniles occurred in smooth-boundary flows and in all substratum types,
- most late juveniles occurred in smooth-boundary, and accelerating flows, and in all substratum types with the exception of sand and,
- most adults occurred in accelerating flows and in all substratum types, with the exception of sand.

---

[1] In brief, breeding takes place in rapids during the rainy season. Then, as discharge decreases and stabilises, I suggested that fry move out to the slower-flowing areas such as pools where they remain through the dry season and as they mature. With the onset of rains, the young move back into rapids and use habitats more akin to that of adults.

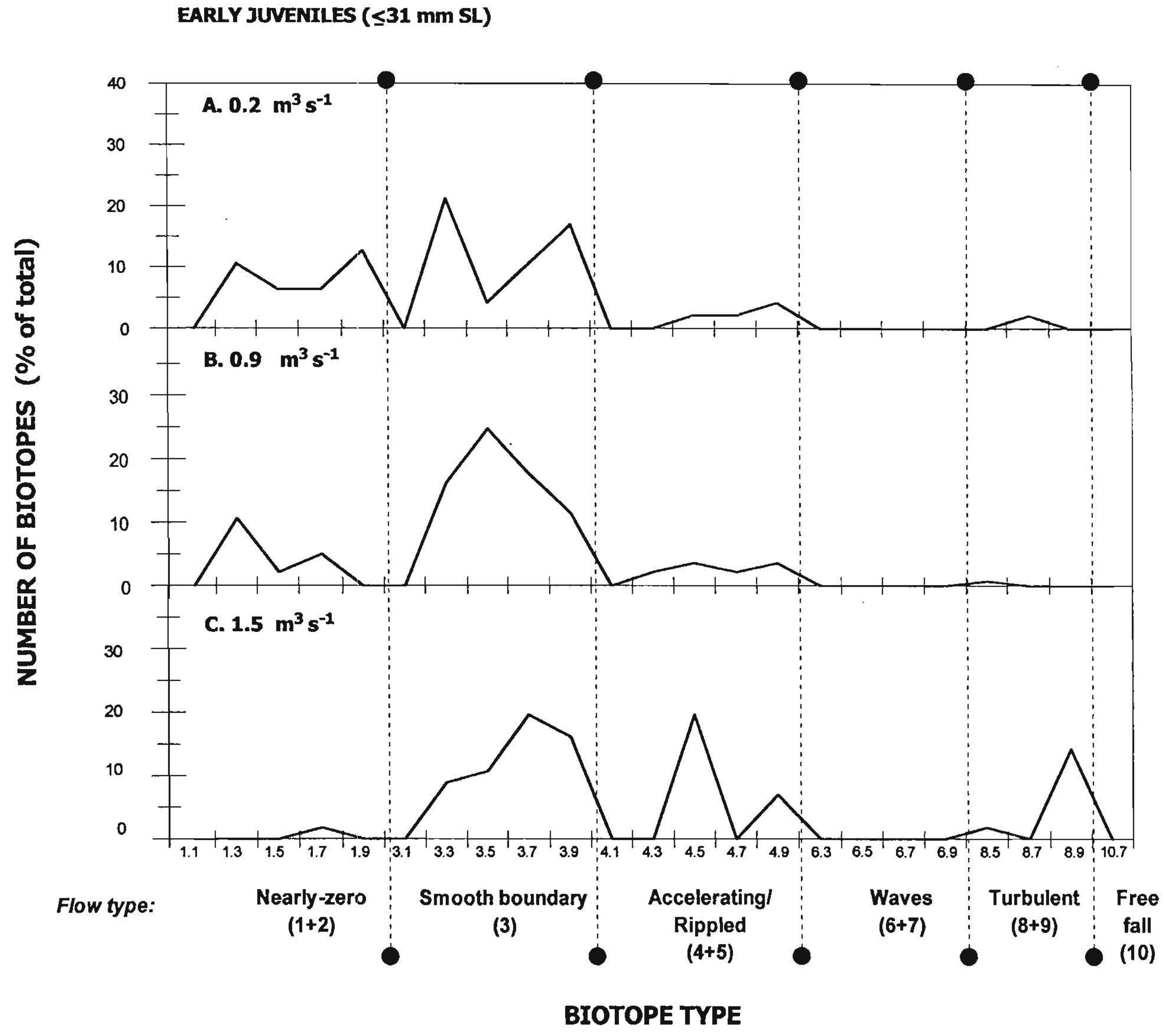


Figure 12.1 Composite curves of the biotope assemblages used by early juvenile *C. anoterus* at four discharges. The biotope type, shown as a two digit code along the x-axis, comprises a combination of flow type (the integer), described below the x-axis, and substratum (the decimal) which is coded as follows: 0.1 = instream vegetation; 0.3 = silt/ sand; 0.5 = gravel/ cobble; 0.7 = boulder/ fractured bedrock and; 0.9 = smooth bedrock. A comparison of this output to that produced for IFIM (see for example Figure 8.1) indicates that the GBA produces habitat use as (a) a biotope patch, which encompasses a number of hydraulic variables, rather than univariate curves and, (b) an assemblage of biotope types rather than as a single curve (see text for discussions).

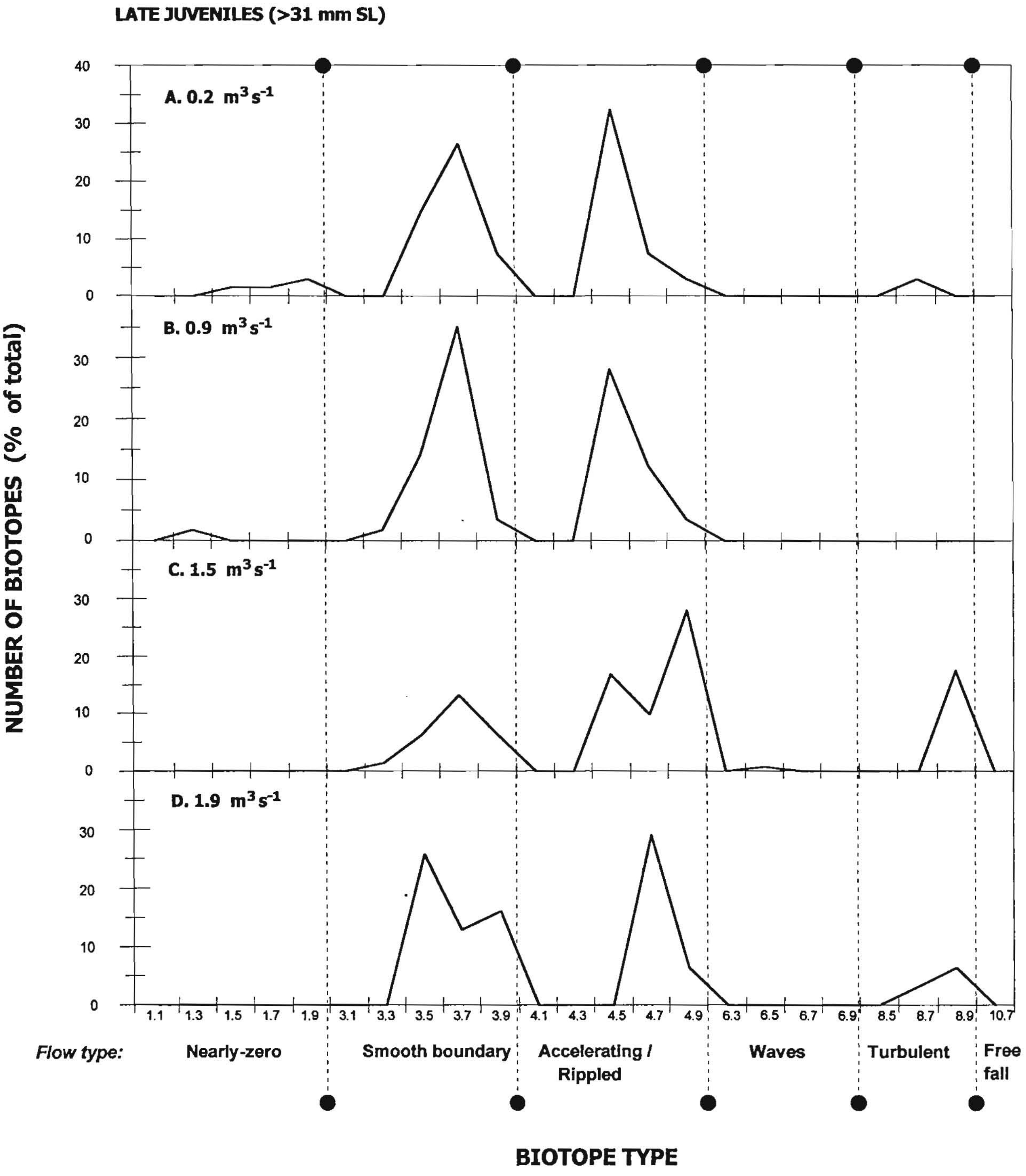


Figure 12.2 Composite curves of the biotope assemblages used by late juvenile *C. anoterus* at four discharges. The biotope type, shown as a two digit code along the x-axis, comprises a combination of flow-type (the integer), described below the x- axis, and substratum (the decimal) which is coded as follows: 0.1 = instream vegetation; 0.3 = silt/ sand; 0.5 = gravel/ cobble; 0.7 = boulder/ fractured bedrock and; 0.9 = smooth bedrock.

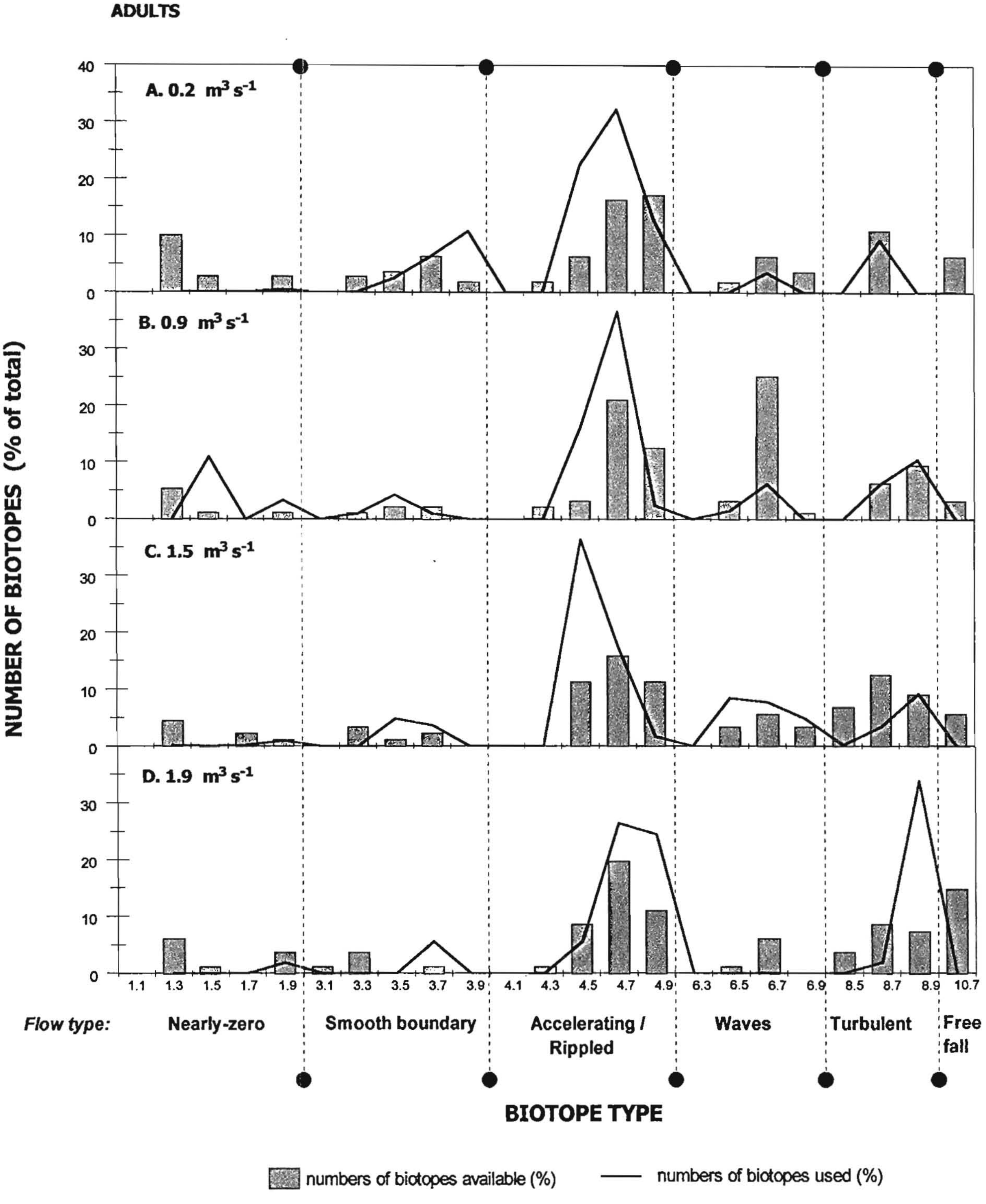


Figure 12.3 Composite curves of the biotope assemblages available in Rapids, and those used by adult *C. anoterus* at four discharges. The biotope type, shown as a two digit code along the x-axis, comprises a combination of flow type (the integer), shown below the x-axis, and substratum (the decimal) which is coded as follows: 0.1 = instream vegetation; 0.3 = silt/ sand; 0.5 = gravel/ cobble; 0.7 = boulder/ fractured bedrock and; 0.9 = smooth bedrock.

CAPTURING THE SPATIAL SCALE OF PHYSICAL HABITAT: BIOTOPE AVAILABILITY, AND USE, WITHIN MIXED ANASTOMOSING CHANNELS (IFIM SITE 3)

The profiles of biotope availability within Rapids, where adult *C. anoterus* occur, represented as (a) numbers of biotope types (Figure 12.4) and (b) areas of biotope types (Figure 12.5) were very similar. These outputs indicated that:

- consistently, a diversity of 7 biotope types was available at all discharges,
- near-zero and smooth-boundary flows were only represented at the lowest discharge,
- accelerating-flow biotopes were dominant at all discharges and,
- the sub-dominant biotopes were those with turbulent flows (see Table 12.2),
- boulders and fractured bedrock were the dominant substrata.

Differences were evident between the composite and site-specific profiles of biotope availability (Figures 12.3 and 12.4, respectively). Firstly, the diversity of biotopes within the MAN channel-type was less than half of that found when all sites were aggregated. Secondly both near-zero, and smooth-boundary flow biotopes were consistently represented in the composite profile, albeit in very low numbers, whereas in MAN channels they were absent at all discharges except for the lowest.

Turning to the biotopes used, *C. anoterus* adults generally used most of the available biotope types (Figure 12.4). The highest numbers of fish (60%) were consistently found in biotopes comprising accelerating flows over boulder/ fractured bedrock (i.e. code 4.7). Importantly, biotope 4.7 was consistently the *most numerous, and largest, available biotope type* (Table 12.2). Turbulent flows over bedrock (code 8.9) also dominated at the highest discharge (Table 12.2). Biotope 8.9 was not available at discharge of 0.2 $m^3 s^{-1}$, but when it was, it dominated in terms of fish density at 1.5 $m^3 s^{-1}$ and fish numbers at 1.9 $m^3 s^{-1}$.

However, the pattern of biotope use was reversed when the output was derived as fish density (Figure 12.5). The highest densities of fish occurred in turbulent flow biotopes at all flows, except the highest, when, together with turbulent biotopes, those with accelerating flows (i.e. code 4.9) dominated (Table 12.2). Generally, the biotopes housing the highest densities of fish were also the smallest (8.7, 8.9 and 4.9). At 1.9 $m^3 s^{-1}$, the highest densities of fish occurred in biotope type 4.9. Although 4.9 was available at the lowest flows, was more numerous and larger than at 1.9 $m^3 s^{-1}$, no fish occurred there. It is possible that this reflects the fact that at low flows, the depth of water over smooth bedrock offers little overhead cover. In contrast, the turbulent flows and boulders associated with 8.7, in which the highest fish numbers and densities occurred at low flows, would do so.

To summarise, the following key findings emerged (Table 12.2):

Table 12.2

Summary of the biotope availability (dark shading) and biotope use (light shading) by adult *C. anoterus* in Rapids in a Mixed Anastomosing channel-type at four discharges. Numbers in the table indicate the dominant (1) and sub-dominant biotopes (2) at each discharge. Availability is expressed in biotope numbers (no.) and area. Biotope use is expressed as fish numbers (no.) and density (dens).

BIOTOPE TYPE and CODE		Discharge 0.2 m^3 s^{-1}				Discharge 0.9 m^3 s^{-1}				Discharge 1.5 m^3 s^{-1}				Discharge 1.9 m^3 s^{-1}			
		AVAILABILITY		USE		AVAILABILITY		USE		AVAILABILITY		USE		AVAILABILITY		USE	
		no.	area	no.	dens	no.	area	no.	dens	no.	area	no.	dens	no.	area	no.	dens
Near zero on sand	1.3	▓	▓	░	░	▓	▓										
Smooth boundary flow on boulder/ fractured bedrock	3.7	▓	▓	░	░												
Accelerating flow on gravel/ cobble	4.5	▓	▓	░	░ 2					▓	▓	░	░ 2				
Accelerating flow on boulder/ fractured bedrock	4.7	▓ 1	▓ 1	░ 1	░	▓ 1	▓ 1	░ 1	░ 2	▓ 1	▓ 1	░ 1	░	▓ 1	▓ 1	░ 2	░
Accelerating flow on smooth bedrock	4.9	▓ 2	▓ 2			▓	▓	░	░	▓	▓	░ 2	░	▓	▓	░	░ 1
Waves on gravel/ cobble	6.5													▓	▓		
Waves on boulder/ fractured bedrock	6.7	▓	▓			▓	▓ 2	░ 2	░					▓	▓		
Turbulent flow on gravel/ cobble	8.5									▓	▓			▓	▓		
Turbulent flow on boulder/ fractured bedrock	8.7	▓ 2	▓	░ 2	░ 1	▓ 2	▓	░	░ 1	▓ 2	▓ 2	░	░	▓ 2	▓ 2	░	░
Turbulent flow on smooth bedrock	8.9					▓	▓			▓	▓	░	░ 1	▓	▓	░ 1	░ 2
Freefall on boulder/ fractured bedrock	10.7					▓	▓			▓	▓			▓	▓		

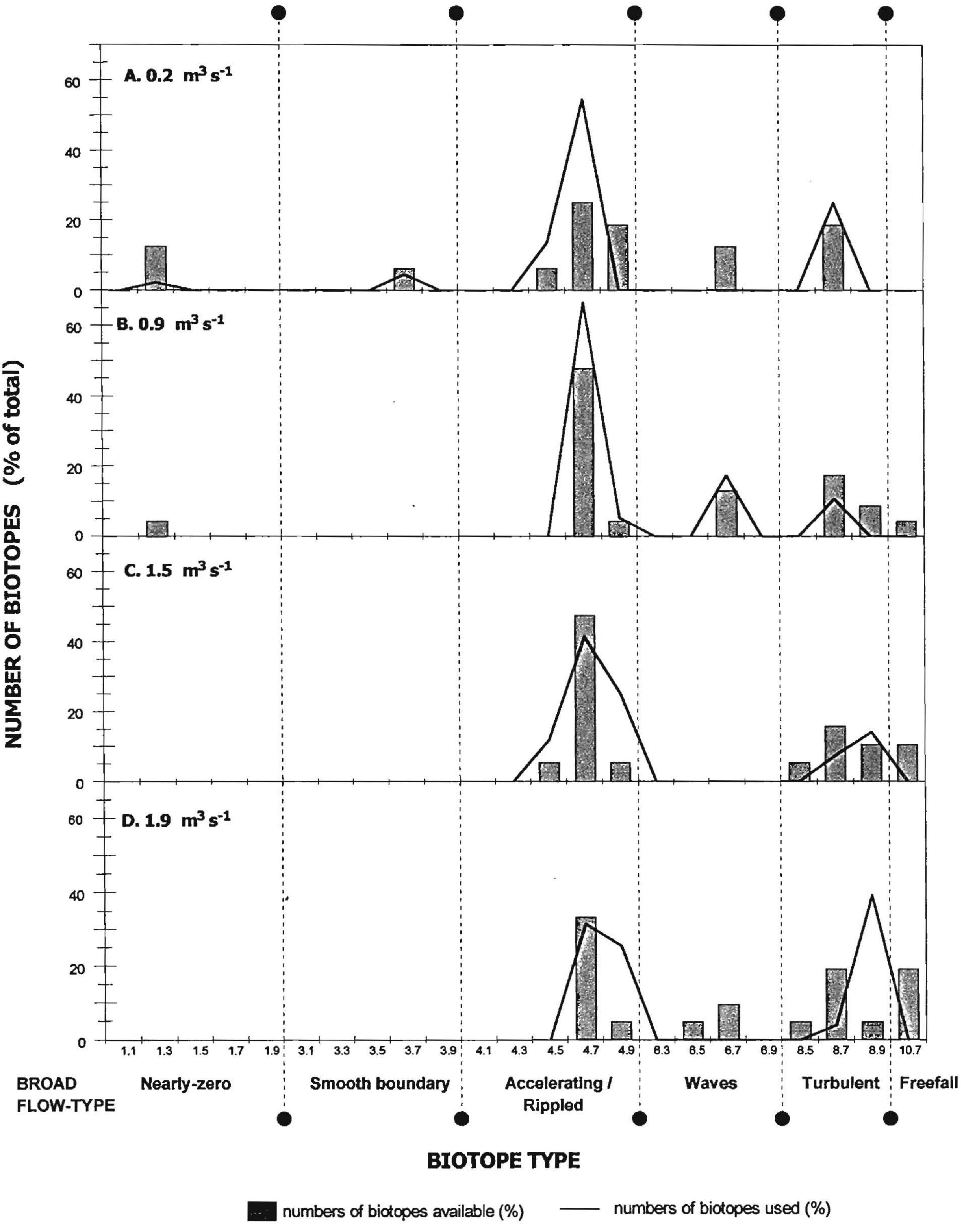


Figure 12.4 Site-specific curves of the biotope assemblages available in Rapids, and those used by adult *C. anoterus* in Mixed Anastomosing channels, at four discharges. The biotope type, shown as a code along the x-axis, comprises a combination of flow type (the integer), shown below the x-axis, and substratum (the decimal) which is coded as follows: 0.1 = instream vegetation; 0.3 = silt/ sand; 0.5 = gravel/ cobble; 0.7 = boulder/ fractured bedrock and; 0.9 = smooth bedrock.

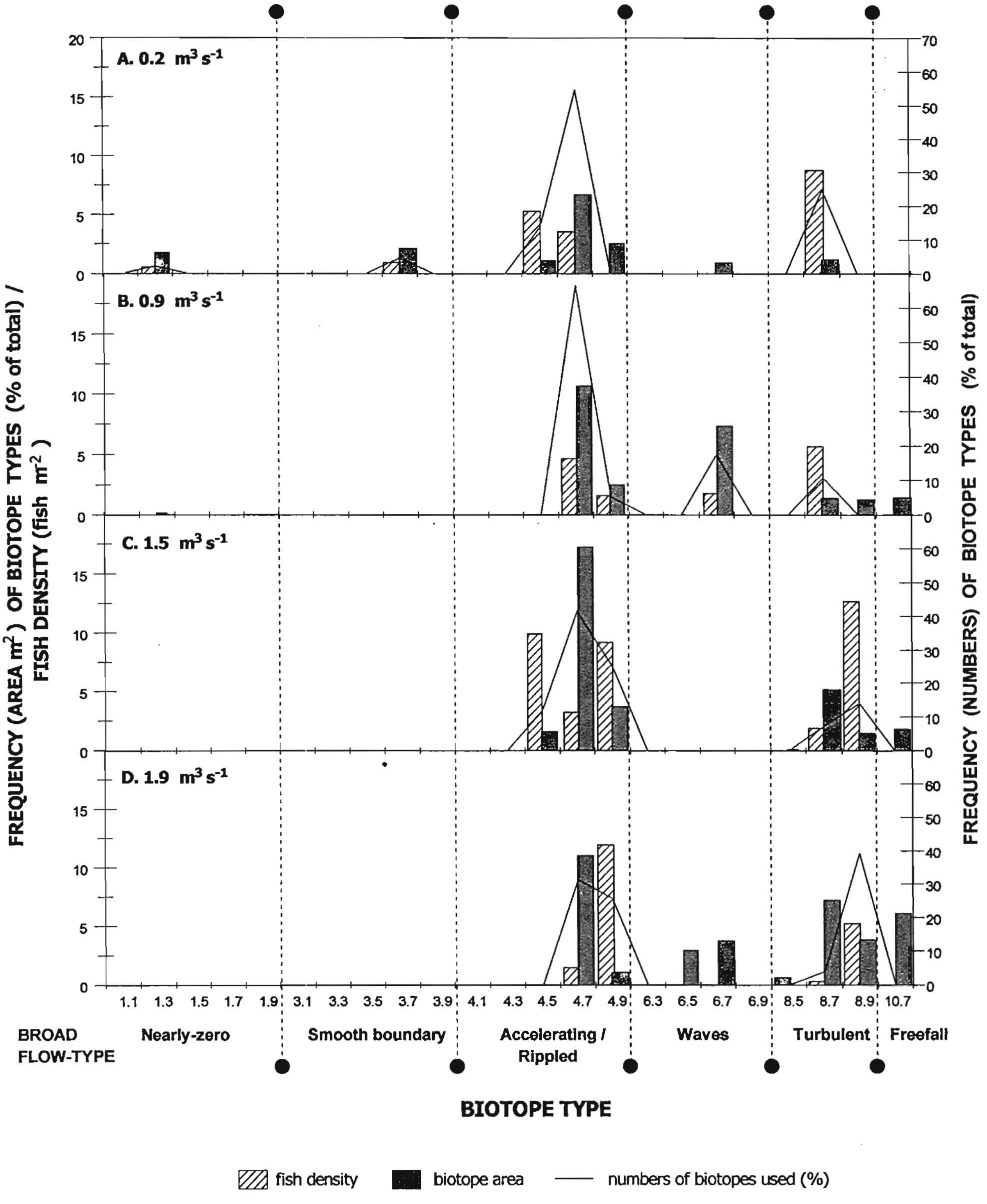


Figure 12.5 Area (m^2) of available biotopes in Mixed Anastomosing Channels at four discharges, and corresponding biotope use by adults *C. anoterus* expressed as: (a) density (fish m^{-2}) and, (b) numbers of biotopes (%). Biotope type comprises flow-type (see above) and substratum, coded as follows: 0.1 = instream vegetation; 0.3 = silt/ sand; 0.5 = gravel/ cobble; 0.7 = boulder/ fractured bedrock and; 0.9 = smooth bedrock. The profile of biotope use in numbers (see Figure 12.4) is included to facilitate comparison between fish density and numbers.

In terms of biotope availability,

- biotopes within the accelerating-flow category dominated (numerically and size) throughout, but at the highest discharge, their proportional contribution decreased and turbulent- flow biotopes increased and,
- biotope 4.7 (accelerating flow over boulder or fractured bedrock), was the most numerous biotope type and accounted for the largest area at all discharges.

The outputs on the use, in numbers, of biotopes indicated that

- biotopes within the accelerating-flow category dominated numerically throughout but, at the highest discharge, their proportional contribution decreased and turbulent-flow biotopes increased,
- biotope 4.7 (accelerating flow over boulder or fractured bedrock) was the dominant biotope used, except at a discharge of 1.9 m^3 s^{-1}, when biotope 8.9 (turbulent flow over bedrock) dominated and,
- turbulent-flow biotopes (8.7 at low discharges, and 8.9 at the highest discharge) were the next most utilised (and available) biotope types

The outputs of biotope use represented by fish densities (Figure 12.5) indicated that

- fish densities were highest in turbulent biotopes at the lowest discharges (8.7 at 0.2 and 0.9m^3s^{-1}; 8.9 at 1.5 m^3 s^{-1}), and in accelerating-flow biotopes (4.9) at 1.9 m^3 s^{-1}.

As stated, additional outputs of the GBA include maps which how the spatial distribution of biotopes, at the scale of either (a) geomorphic units or (b) channel types. An example of the first output, is given in Figure 12.6, which shows the spatial distribution of biotopes within Rapids only, the geomorphic unit in which *C. anoterus* occur. This output provides a range of possibilities for exploring patch characteristics such as patch size, patch diversity and patch isolation (see Table 10.5 and discussions in Chapter 13). An example of the second output is presented in Figure 12.7 which shows the distribution of available biotopes within the Mixed Anastomosing channel-type. For clarity, only biotopes within the category of accelerating flows, which feature consistently in the biotope-use profile of *C. anoterus*, are presented. From this it is evident that the demographics of all broad categories of biotopes differ on a spatial and temporal scale, as suggested by Cooper *et al.* (1997). For instance, at high discharges, patches of biotope 4.7 have a higher connectivity (see Table 10.5).

OVERALL ESTIMATES OF HABITAT AVAILABILITY

Adult *C. anoterus* were found almost exclusively in Rapids which amounted to between 6% and 7% of the total length of the study area (see Chapter 11). Within these, adult *C. anoterus* utilised almost the entire area of the Rapid, with the exception of zero-flow and free-fall biotopes. This utilised habitat amounted to an estimated 1186 m at the lowest discharge and increased to 1550 m at the highest discharge (or between 4 and 5 % of the river length). Similar estimates of between 3 and 4% of the total site length were obtained for the MAN channel alone (Table 12.3). These figures cannot be compared to the absolute amounts of habitat calculated by PHABSIM for a number of reasons discussed below.

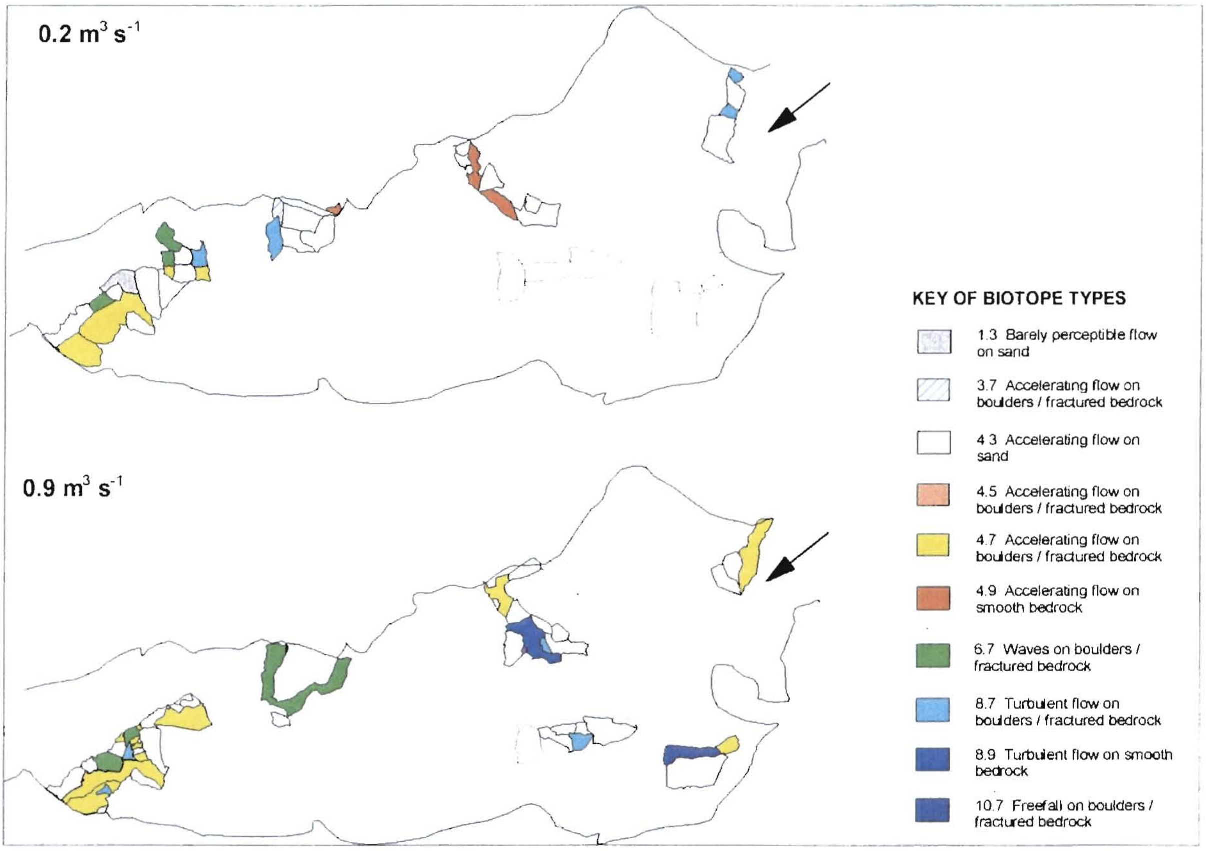


Figure 12.6 An example of the output of the GBA at the scale of geomorphic units. Here, the spatial distribution and extent of biotope types within Rapids at two discharges, in the Mixed Anastomosing (MAN) channel type, is shown (see also Figure 12.4). The Rapids found in MAN sites comprised Mixed Rapids and Bedrock Rapids (see Table 11.2).

Table 12.3
Estimated area of biotopes used by adult *C. anoterus* in Mixed Anastomosing channels

DISCHARGE ($m^3 s^{-1}$)	TOTAL WETTED AREA (m^2)	TOTAL WETTED AREA of RAPIDS (m^2)	AREA OF BIOTOPES USED (m^2)	% of TOTAL WETTED RAPID AREA USED	% of TOTAL WETTED AREA USED
0.2	470	16	15.1	94	3
0.9	574	25.4	21.7	85	4
1.5	648	28.83	26.9	93	4
1.9	725	36.52	23.1	64	3

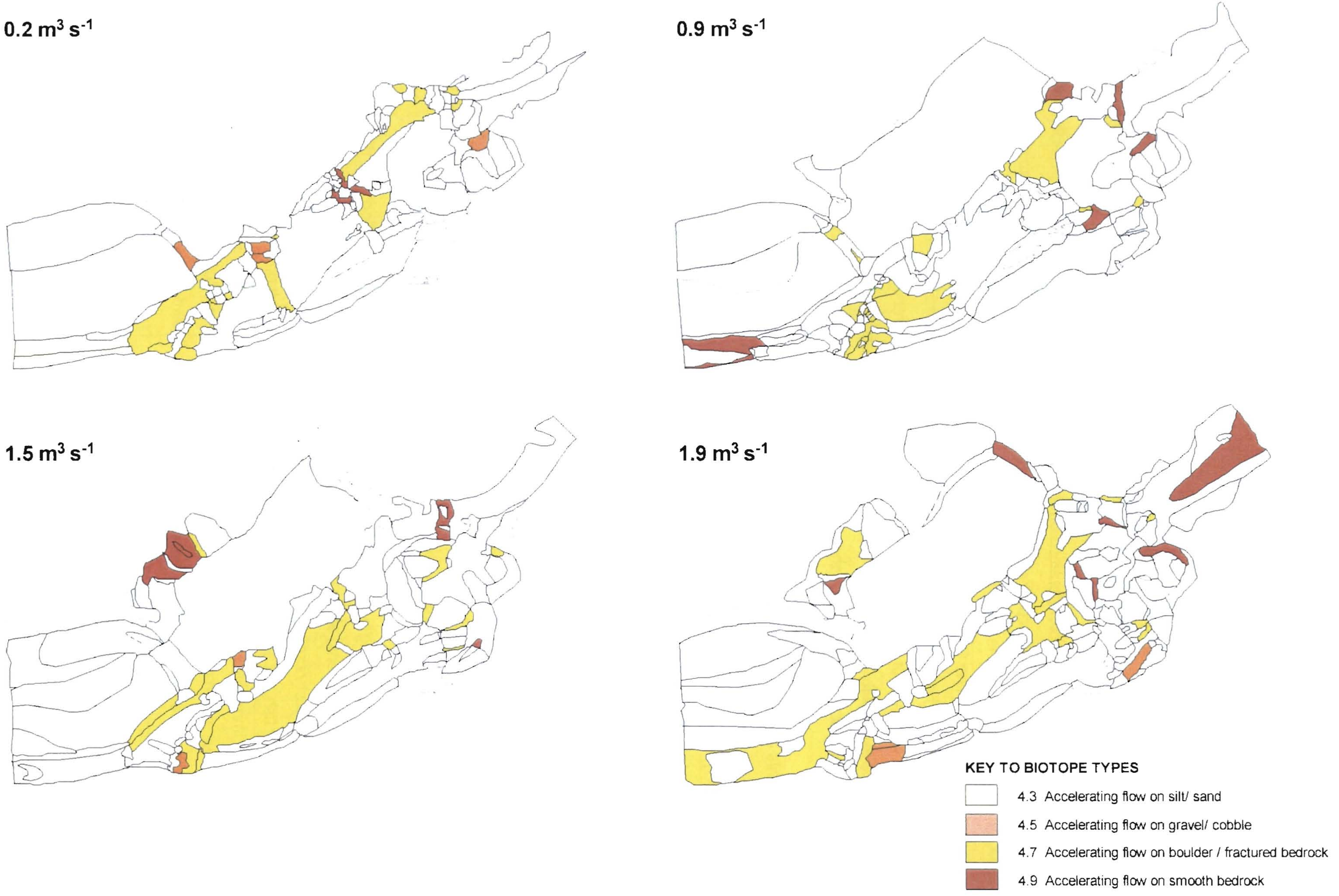


Figure 12.7 An example of the output of the GBA at the scale of channel type. Here, the distribution and extent of biotopes at four discharges, that fall within the biotope category of *accelerating flows* within the Mixed Anastomosing channel-type, is shown.

12.5 DISCUSSION OF THE HABITAT-USE OUTPUTS FROM THE GBA

Habitat use can only be satisfactorily modelled if it is adequately understood. Thus, this discussion will focus primarily on whether or not the GBA provides an improved understanding of the use of physical habitat by *C. anoterus*.

What do the outputs of the GBA contribute to understanding habitat?

I hope to have demonstrated that through a formal recognition of the themes of scale and heterogeneity, the GBA offers new opportunities for exploring and understanding habitat. To this end, I would suggest that one of the most significant contributions offered by the GBA is the inclusion of the intermediate scale of geomorphic units (see also discussion in Chapter 11). In the outputs of PHABSIM, suitable habitat, or WUA, is described either at the scale of the study site, or between two transects, on the basis of three independent variables. The GBA, on the other hand, presents habitat use as biotopes nested within geomorphic units. Furthermore, the outputs are retained as two-dimensional habitat patches and not disaggregated into curves of single variables which have no spatial reference, as is the case in PHABSIM. As with biotope availability (see Chapter 11), the patterns, and differences, in the biotope use can then be explored at this scale, and in a way that captures and preserves heterogeneity.

By adopting this approach, my research revealed that (i) the three lifestages of *C. anoterus* occurred in different proportions in each type of geomorphic unit, where (ii) they used distinct assemblages of biotopes which, (iii) displayed some internal variation as discharge changed, particularly in the case of juveniles. Of particular interest was the use of multiple geomorphic units (Pools and Rapids) by early juveniles, in comparison to the limited distribution of adults to Rapids. Potential reasons for this emerged when the distribution and abundance of the biotopes used were compared to those of availability. The dominant biotope types that were used by both early juveniles (1.3 and 1.7) and late juveniles (3.7) were rare in Rapids but more common in Mixed Pools (see Figure 11.9). This suggests that even though *C. anoterus* may hatch in Rapids, their dispersal to geomorphic units other than Rapids, could be explained, partly, by their different hydraulic requirements, described *collectively* by biotopes. Within PHABSIM there would be no way of knowing that the spatial distribution of habitat was important since, individually, the hydraulic characteristics would be likely to occur in Rapids as well.

These data provided interesting insights into habitat use specifically within Rapids. Consider the following patterns. With few exceptions, almost all of the area of Rapids was used, particularly at low flows. The biotope with the highest number of patches and that covered the largest area (4.7), also housed the highest numbers of fish, except at the highest discharge. Moreover, a small proportion of animals (15%) occurred in areas immediately adjacent to Rapids at the very low discharges. This suggests that under extreme low-flows, when the wetted area of rapids declined by more than 40% (see Chapter 11), adults moved into adjacent areas. It is likely that conditions such as overcrowding, or a reduction in cover or food, may force adults to seek alternative habitats. Area, does therefore appear to be an important attribute of habitat use in the case of *C. anoterus*. However, habitat volume may in fact the key factor, as suggested by Angermeier & Schlosser (1989). They found that habitat volume was a better predictor of species richness than habitat area in their study on species-area relationships. The current descriptions of biotopes do not adequately describe volume and this would warrant further investigation. Furthermore, this movement into adjacent habitats by *C. anoterus* would support the argument that there is certain degree of plasticity in habitat use (Angermeier 1987; Heggenes & Saltveit 1990; Heggenes *et al.* 1996). These authors contend that fish can adapt to a wide variety of habitat conditions, within ranges.

Further questions were raised around measures of habitat when the spatial pattern of biotopes was considered. Although *C. anoterus* adults were restricted to Rapids and within these, used certain biotopes (such as 4.7 and 8.7), by preserving the spatial scale it was evident that these biotope types are also found in other geomorphic units (see Figure 12.7). What then constrains adult *C. anoterus* to Rapids, given that the biotopes that they use occur outside of Rapids? There are a number of possible reasons for this. Firstly, It is likely that habitat selection is made on the basis of a far more complex array of attributes, both abiotic and biotic, than physical habitat alone. Secondly, physical habitat encompasses a more complex suite of hydraulic variables than those conventionally used in habitat assessments. Both of these issues have been raised by other researchers (see discussions in Chapter 8). Thirdly, the current descriptions of biotopes require testing and refinement to validate hydraulic conformity within a biotope type, particularly in different geomorphic units. In other words, are the current hydraulic descriptions of biotopes too coarse to be transferred between geomorphic units? These possibilities, and studies on the distributional patterns of biotopes, would constitute a useful direction for future research if the impacts of altered flow regimes on organisms are to be fully understood.

In a marked departure from IFIM, the GBA presents biotope use as an *assemblage of biotope types* as opposed to the optima of univariate curves. It is suggested that not only does this offer a more useful interpretation of reality, but it also offers a starting point for addressing the issues of *"utilised" versus "preferred"* habitat (see Chapter 8). Although ecologists are still grappling to find an acceptable measure of "preference", I proposed that, within IFIM, the derived preference indices are insufficiently robust to provide meaningful insights into habitat selectivity. Nonetheless, as the GBA stands, the interpretation of "preference" versus "use" is still limited to a qualitative, descriptive output. This would require a formal integration of the complex array of characteristics of habitat availability (such as patch numbers and area), and those of habitat use (such as numbers and densities of fish).

In this regard, biotope use has been expressed not only as numbers of fish, but also as density per unit area. The relationship between biotope area, biotope use and biotope selection warrants further investigation. In my research for instance, the highest densities of fish occurred in accelerating-flow biotopes (4.9) at a discharge of 1.9 $m^3 s^{-1}$. Despite the fact that this biotope type occurred at the lower discharges, they did not contribute to the biotopes used in any notable way. Could these patterns provide some indication of habitat selection, governed by cover or food, for example (but see concerns raised regarding the use of density as a measure of preference in Chapter 8)? If so, how could this be formally quantified? Such questions may offer guidance for new research initiatives.

In terms of estimates of total habitat, the final outputs of PHABSIM and the GBA are not directly comparable for three reasons. Firstly, PHABSIM models so-called "suitable" habitat, which represents a composite ratio of the habitat available and that used. In my case, habitat availability and use were described as separate models. Secondly, the PHABSIM site spanned two channel types whilst the GBA focussed on single channel types. Thirdly, as previously noted, the outputs as biotopes are not comparable with the univariate curves of PHABSIM.

The final comments pertain to issues of model transferability. The biotope-diversity for a single channel-type (i.e. MAN, see Figure 12.4) was only half of that evident in the composite profile (Figure 12.3). This was because the MAN channel-type did not contain Boulder Rapids which comprised an array of additional biotope types. This suggests that using a single model to represent habitat availability or use may be inappropriate. Moreover, these results lend support to the GBA approach to site selection which is undertaken at the scale of the channel type.

12.6 CONCLUDING REMARKS ON THE OUTPUTS OF THE GBA

A framework for the development of biotope-use models, commensurate with those of biotope availability, was outlined and demonstrated for *C. anoterus*.

The potential outputs on habitat-use within the GBA were discussed. These outputs provided a level of information that was not available from those of IFIM, and which, it is suggested, contributed to an improved understanding of habitat use by *C. anoterus*. The focus on geomorphic units, as the intermediate scale of habitat between sites and biotopes, provided invaluable insights into the use of multiple habitats by juvenile *C. anoterus*. It is also on the basis of geomorphic units that biotope availability and use were compared and further, that enabled the extrapolation of site-specific data to the study river.

Notably, the spatial dimensions of physical habitat were conserved through presenting habitat as biotopes rather than three univariate and independent curves. Furthermore, biotope use was represented as an assemblage of biotope types which, it was argued, more closely approximates reality. In future work, this provides the basis for examining key biotope attributes that may be important determinants of biotope use. Whilst the composite output might provide an overview of biotope availability and use, I demonstrated that there are shortcomings associated with aggregating data. These relate to the inaccurate representation of the biotope-diversity, and the loss of spatial reference. I would argue that this obscures the spatial and temporal attributes of habitat which may be equally as important to understand in habitat assessments, as the general descriptions of habitat loss or gain.

The description of biotope availability and use at this spatial scale raised concerns regarding the ability of habitat assessments that are based purely on physical conditions, or at least on those conventionally used, to adequately explain the distribution and abundance of organisms. This issue underscores the need for complimentary ecological data within habitat-assessment approaches and critically, in species or generations that display multiple habitat use (Lancaster & Belyea 1997, see Chapter 13).

13

Conclusions: An Appraisal of the GBA and IFIM and the Future of Habitat Assessments

13.1 INTRODUCTION AND OBJECTIVES

In terms of the thesis objectives (Section 1.7), the overall appraisal challenged a number of key concepts and assumptions of IFIM and PHABSIM, and concluded that it was unsuitable as a potential habitat-assessment approach for the Marite River. The main concerns centred on the difficulties in defining and measuring habitat-availability and, as a corollary, habitat-use, principally due to weaknesses in the conceptual framework and the methodologies used. Resolving these limitations provided the basis for developing a proposed alternative approach, formulated as the Geomorphological-Biotope Assessment or GBA (see Chapter 10; Figure 10.3). In developing the GBA, the main focus was to test this approach to quantifying habitat availability (Chapter 11). In order to consolidate the key steps of the proposed model, a framework for integrating the models of habitat availability with those of habitat use was addressed in the last chapter (Chapter 12).

Given these outputs, this chapter concludes discussions with an integrated, comparative assessment of the IFIM/ PHABSIM and GBA approaches, through an evaluation of their frameworks, approaches and outputs. This will also provide directives for future research needs that are required to refine the GBA, and concluding comments on the future of habitat assessments. The objectives of this chapter are, therefore:

1. to appraise the strengths and weaknesses of both approaches and,
2. to make recommendations for future developments.

The following discussion will centre specifically on issues pertaining to *physical habitat* and not on the additional concerns that habitat is circumscribed by a far wider range of abiotic and biotic factors. This broader debate, and its resolution, is beyond the scope of this thesis but was discussed in Chapter 10.

13.2 ASSESSMENT OF THE TWO APPROACHES

In order to contextualise and facilitate the assessment of both approaches, the following discussion will refer to Figure 13.1 which provides an overview of their main steps. Generally, habitat-assessments can include a hierarchy of objectives that cover a wide scale from a description of physical habitat in space and time, through to river management objectives. Essentially, their aim is to assess the consequences of altered flow regimes on physical habitat and to recommend a flow regime that will minimise habitat loss.

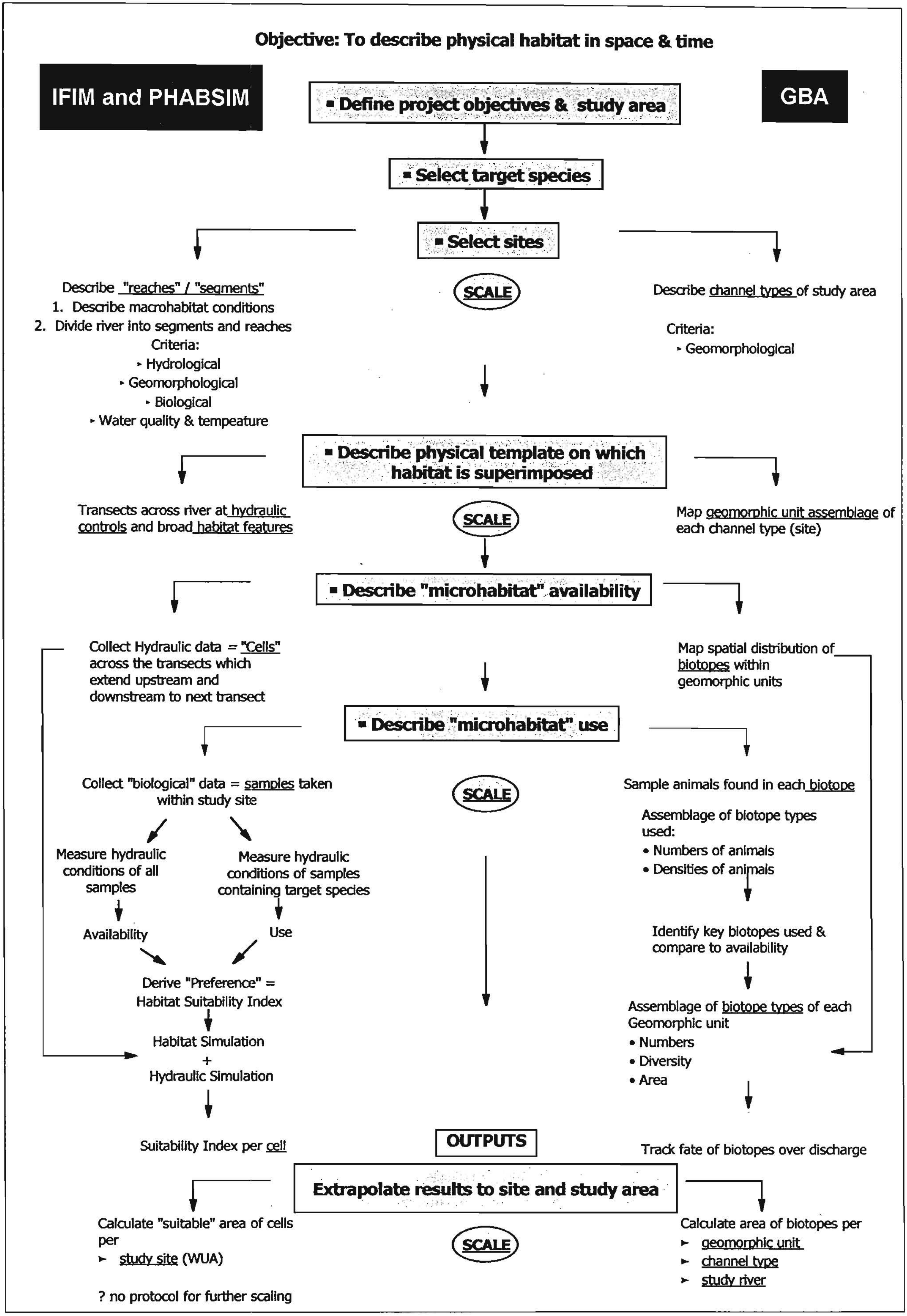


Figure 13.1 Schematic of the two alternative approaches to habitat assessments, IFIM/ PHABSIM and the GBA , indicating the overall framework for both approaches and highlighting the spatial scales of each step.

Whilst the objectives and overall steps of both the PHABSIM and the GBA approaches are similar, they differ in three key areas, which will direct the following discussion. These are

- the conceptual framework underlying the two methodologies,
- the process by which site-specific data are extrapolated to represent the study area in question and,
- the approach to describing habitat availability and use at a site, i.e. the model inputs and outputs.

The case for a scale-dependent hierarchical framework

Concerns regarding the conceptual context of IFIM were discussed in Chapter10. I proposed that many of the problems could be traced almost entirely to the issues of scale and spatial pattern and these formed the cornerstones of an alternative approach. Initially, therefore, both approaches will be examined in the context of scale. I hope to have demonstrated that an overarching advantage of the GBA is the preservation of spatial reference which, for semi-arid rivers, is given in the hierarchical classification of van Niekerk *et al* (1995). This framework provides the essential elements for describing biotope availability, and use, as well as for linking various spatial scales, in a way that was not possible through PHABSIM. Specifically, it does not neglect the mechanisms controlling biotope architecture, distribution and abundance (see Chapter 11).

One of the major consequences of this is seen at the scale of site selection, which is the first point of departure between the two approaches (Figure 13.1). Site selection should be guided by a description of *what the sites represent*, since this lays the foundation for extrapolating site-specific results to the study area (see discussion in Chapter 11; and Maddock 1999). Yet, within IFIM, this is unclear due to the lack of a clear formulation and framework that defines the relationship between spatial features in the study river. In my assessment of PHABSIM, I could only find a somewhat oblique reference to the use of a hierarchical framework (e.g. Bovee 1982). I argued that for this reason, almost no studies undertaken under the PHABSIM banner ever report on this process (with the exception of King & Tharme 1994) and that this must throw into question the premise that site-specific information is representative of the river in question (see Chapter 4).

Within the GBA, understanding the geomorphology of the system is key since the central tenet holds that the geomorphology of the river provides the physical template upon which the smaller-scale physical habitats, used by biota, are superimposed. Thus, in contrast to IFIM, site selection is carried out at the scale of *channel types* since, collectively, these comprise the river. The criteria used for site selection are specifically geomorphological as opposed to PHABSIM, where site selection is approached from a mixture of hydrological, geomorphological and, at times, ecological perspectives.

At a finer scale of resolution, the spatial scale of geomorphic units is central (Figure 13.1). Not only do they define channel types, and hence facilitate site selection but most notably, I would argue, they provide an objective basis on which to quantify habitat availability and use. Ecologists have intuitively appreciated the importance of this scale because the broad distributional patterns of biota tend to match the extent of habitat features at this scale and, hence, they provide the template for microhabitat distribution. Despite calls for its characterisation based on objective criteria (e.g. Kershner & Snider 1992), this spatial scale has received inadequate attention until recently and nonetheless, most descriptions still incorporate a mixture of qualitative assessment with empirical measurement (Maddock & Bird 1996). The repercussion has been a plethora of terms (and their definitions) such as "mesohabitat" (e.g. Kershner & Snider 1992; Maddock 1999; Vadas & Orth 1998; Cohen *et al.* 1998), "channel units" (Bisson *et al.* 1988), "functional habitats" (Harper *et al.* 1992) or "habitat type" (e.g. Bourgeois *et al.* 1996; Lancaster & Belyea 1997), but which all refer to the same spatial scale.

The only formal recognition of this scale by PHABSIM appears to be in the placement of transects across "broad habitat features", which lose their spatial reference once modelling proceeds. Although these features appear to dovetail with that of geomorphic units (Figure 13.1), the difference between them lies in their definition. Within the GBA, this scale comprises geomorphic, and *not* hydrological units, as suggested within IFIM, and therefore does not include flow as one of the defining variables. Using the latter approach, studies corfront the problem of trying to accommodate transforming "mesohabitats" as flow changes, such as instances in which "a rapid becomes a pool" (see for example Vadas & Orth 1998). In contrast, once described within the GBA, a geomorphic unit remains fixed in space and time, irrespective of flows - "once a rapid, always a rapid", so to speak. For the same reason, I would argue that recent attempts to define this scale (e.g. Cohen *et al.* 1998; Vadas & Orth 1998; Wood *et al.* 1999; Kemp *et al.* 1999), may still prove unsatisfactory because the dynamic nature of habitat, namely flow, is introduced at too broad a scale (within IFIM this is done at the scale of segments). In the GBA, flow is introduced at the smallest scale of habitat, namely that of biotopes. Furthermore, the value of geomorphic units as static geomorphological features is that not only can biotope availability (and use) then be compared between geomorphic units, and at different discharges, but this can be readily interpreted at the scale of channel types. This spatial reference also offers new avenues for resolving the issue of extrapolation (see below).

Turning to the determination of habitat availability (Figure 13.1), the scale at which this is undertaken is governed by the scale at which habitat is modelled. PHABSIM describes the smallest scale of habitat - microhabitat - as "cells" between transects. The assumption that the hydraulic conditions of a cell remain unchanged to the next transect has been repeatedly questioned and, hence, appropriate scales at which to model habitat have been examined (see discussions in Chapter 9). In contrast to the transects, I proposed that the geomorphic units provide a more useful and objectively defined scale for this. The GBA presents the smallest scale of habitat as the *biotope*, and my evidence suggests that each geomorphic unit comprises a distinctive assemblage of biotopes (see Chapter 11). The study site then, is presented as a patchy mosaic of biotope types nested within a mosaic of geomorphic units. The value of representing the smallest scale of habitat as biotopes will be discussed in the following section.

An important issue that recording habitat at the scale of geomorphic units raised, relates to the contention that a description of physical habitat fails to adequately explain the distribution and abundance of organisms in streams (see for example Orth & Maughan 1982; Mathur *et al.* 1985a,b; Weshe *et al.* 1987; Hubert & Rahel 1989; Shirvell 1989). There is increasing support for the concept that animal distribution, and particularly abundance, is influenced by a far more complex suite of variables than those used in IFIM. It is suggested that the GBA goes some way to addressing the concerns regarding distribution. For example, by formally incorporating the scale of geomorphic units, the dispersal to, and use of, a wider array of geomorphic units by early-juveniles in comparison to adults appeared to be explained, at least partly, by the distribution of the biotopes used (Chapter 12). This level of detail was not possible to detect using IFIM.

Finally, one of the key values of subscribing to a rigorous classification system, is that such an hierarchy provides the basis for resolving the second issue raised regarding the extrapolation of data to the study area (see also Maddock & Bird 1996; Maddock 1999). Because the GBA is based on a nested, hierarchical model, the information derived at the level of biotopes can be extrapolated to the study area, from biotopes, to geomorphic units, to channel-types and then the entire study area (see Figure 10.1). Notwithstanding the debates on appropriate approaches to habitat-assessments, this issue remains to be resolved within PHABSIM (Maddock & Bird 1996).

Describing the habitat availability at sites: Inputs and outputs of the two approaches

A further issue that distinguishes the GBA from IFIM and PHABSIM, is the nature of input data, and consequently the outputs (Figure 13.1). The distinction here between IFIM and PHABSIM is intentional because, irrespective of their intended linkup to PHABSIM, most habitat studies describe habitat use according to the IFIM precedent. Within IFIM, both habitat-availability and use are described on the basis of three hydraulic variables (depth, velocity and substratum) that are typically regarded as independent, and therefore "microhabitat" is represented as univariate curves (see Chapter 8). This assumption of independence has come under scrutiny and has been directly refuted by a number of studies (e.g. Orth & Maughan 1982; Mathur *et al.* 1985a,b; Shirvell 1989; and see Chapter 8) since it is the combination of hydraulic characteristics that define habitat suitability (see, for example, Rowntree & Wadeson 1996). I would suggest that this represents a conceptual "dead-end" in that, ultimately, it has little biological rationale. The fact that ecologists intuitively recognise habitat as a patch, with spatial dimensions, is evident from the literature (e.g Angermeier & Schlosser 1989; Maddock & Bird 1996), and yet, PHABSIM constrains the logical expression of this. Although PHABSIM starts with a "cell", which at least has some spatial dimensions, this is not preserved as the description of microhabitat proceeds.

There are two further major limitations of modelling physical habitat as independent variables. One of the most serious and tangible consequences is that it divorces the researcher from the river in that, by virtue of the nature of the information, it cannot be spatially explicit. Conceptually, it is impossible to transform an array of values of these different variables into a three-dimensional picture of habitat availability (or use) that matches the physical reality of the river. Consequently, as modelling proceeds within PHABSIM, the river, which contains a mosaic of physical habitats, is disaggregated into three curves and reaggregated into "cells" of suitable habitat, which no longer have any spatial reference. One potential shortfall of this was illustrated in Chapter 12 with regard to habitat for *C. anoterus* adults. Once the utilised biotopes were represented spatially, it was evident that whilst *C. anoterus* were limited to Rapids, the biotopes that they used were found over a much wider range of geomorphic units and raised questions as to what constrains the distribution of this species (see Chapter 12, Section 12.5).

A further limitation relates to the theme of heterogeneity that was raised earlier. The use of disaggregated, univariate habitat curves within IFIM is a case in point. By their nature, the inputs, and hence outputs of PHABSIM, average the physical description of the river, thereby eliminating the possibility of capturing the very attributes that characterise physical heterogeneity. Recent discussions point to the central role that these attributes play in understanding the true nature of habitat in space and time (see Table 10.4). By obscuring heterogeneity, IFIM assumes that it is simply the overall loss, or gain, of habitat that is important. Nonetheless, the thesis that it is the attributes of heterogeneity that are equally as important, requires examination.

As suggested by Palmer & Poff (1997), our empirical approaches need to be reconsidered so that measures of heterogeneity have relevance to ecological entities and are not simply absolute, and sometimes arbitrary, measurements. This is not a new concern and I have highlighted debates in the literature regarding heterogeneity previously (see Chapter 10). Nonetheless, it has such critical implications that these warrant mentioning in relation to the outputs of PHABSIM. If the SI curves of IFIM (see Chapter 8) are fully interrogated, it is clear that they imply an average physical condition, not only at the PHABSIM site but throughout the macrohabitat zone that the site is said to represent. Importantly, Li & Reynolds (1994) suggest that the ability to detect (human-induced) changes in the ecosystem depends on our ability to quantify natural heterogeneity, particularly given the links with biodiversity (Pickett 1996). Furthermore, environmental heterogeneity appears to affect the way that animal assemblages recover from stress (Stevenson 1997; Svensson 1999). Clearly, the averaged output of IFIM offers little potential to explore the links between habitat heterogeneity, the implications of this for species distribution and, hence, the potential effects of anthropogenic disturbance.

My premise is that if ecosystem heterogeneity is regarded as a key attribute, then retaining the smallest scale of habitat, the biotope, as a patch with spatial characteristics and reference, more closely approximates reality and represents a significant step forward for habitat studies. This offers opportunities to explore key features of habitat patches such as their number, size and context (see also Section 10.6). Importantly, it may be in this biotope characterisation that the key links with habitat use are provided. For example, are biota responding to patch numbers, their size, their dispersion or their connectivity, or a combination of these?

As our understanding of habitat improves, it is clear that these patch attributes affect the patterns of distribution and abundance of organisms and recent literature offers some interesting insights into this. For example, McIntyre & Wiens (1999) showed that the landscape used by darkling beetles *Eleodes obsoleta*, varied in response to patch size, an outcome which led them to suggest that not only the total amount of habitat, but also the sizes of habitat patches may therefore affect habitat suitability. Additionally, a number of authors (e.g. Grossman *et al.* 1995; Palmer & Poff 1997; Pusey *et al.* 2000) have highlighted that not only do abiotic and biotic processes operate simultaneously to generate biotic patterns, but also, abiotic heterogeneity influences biotic heterogeneity, and *vice versa*. This complexity was described by Flecker (1997) who demonstrated that biotic processes (fish foraging) influenced the distribution of abiotic (sediment) heterogeneity, and this in turn influenced resource distribution (algal patches) and, hence, community structure. Additionally, the extent to which sediment distributions were controlled by fish foraging was variable across habitats such as pools and riffles. A similar cascade of heterogeneous interactions was suggested by Poff & Nelson-Baker (1997) who modelled the distribution of algal biomass. Their models suggested that algal distibution is dependent on a complex interaction between grazer density, physical habitat heterogeneity and stream velocity. Likewise, similar consideration needs to be given to the interactions between heterogeneity in, and between, different types of Rapids, algal grazing by *C. anoterus* and biotope heterogeneity.

Fortunately, the recent literature bears testimony to a major shift in ecological thought, which focusses on trying to preserve, rather than to collapse, this variability. Li & Reynolds (1995) encouraged the collection and analyses of detailed long-term spatial distributions of habitat and animal distributions, using techniques that allow for the quantification of heterogeneity. Within this paradigm, a range of analytical tools has been developed that provide new approaches to meeting the "variability challenge".

In recognition of this, a workshop hosted by the North American Benthological Society, held ecological heterogeneity as its main theme. Authors explored the linkages in multiple spatial and temporal scales, the interaction between abiotic and biotic heterogeneity and ways to embrace variance (Palmer & Poff 1997). The most compelling case for this was presented by Palmer *et al.* (1997) who suggested that the key to understanding biotic patterns and process of spatial heterogeneity was to focus on the variance rather than the mean. In conjunction with this, Cooper *et al.* (1997) offered interesting options for deconstructing heterogeneity, and reviewed tools for analysis of variance, especially the geostatistical analyses of spatial data and heterogeneity (e.g. spatial autocorrelation and spectral analysis). Crowl *et al.* (1997) and Palmer *et al.* (1997) both used the coefficient of variation (C_v) as a means to explore the variance in faunal abundances in relation to abiotic and biotic variances. Whilst the Cv describes the amount of variation, the spatial arrangement of variation is captured through the Relative Patchiness Index developed by Li & Reynolds (1994). Lamouroux *et al.* (1998) provided an interesting approach to address the inherent variability of local habitat. Instead of describing fish habitat as a mean, univariate value, as with the IFIM approach, they measured a frequency distribution of physical variables in the reach and described habitat with a multivariate habitat-use model. This was then coupled with statistical hydraulic models to estimate habitat suitability. Importantly, all of these approaches provide new and innovative opportunities to embrace the multi-scale heterogeneity that the habitat assessment approaches aspire to describe and quantify.

Finally, within the broad theme of heterogeneity, I would reiterate the proposals regarding appropriate outputs of biotope availability and use that were developed in Chapters 11 and 12. With better biological rationale than the single peak curves of PHABSIM for the entire site, I suggested that habitat availability (and hence, use) may be better characterised as *assemblages of patch types* which capture variability. Furthermore, it would be valuable to explore the concept that it is this *mixture* of biotope types that constitutes "optimal" habitat for biota (see Chapter 12).

13.3 CRITIQUE OF THE GBA AND RECOMMENDATIONS FOR FUTURE DIRECTIONS

As an alternative habitat-assessment approach, the GBA requires further testing. The preceding work has highlighted specific areas of this approach that require refinement, and the following recommendations are provided in the hope that they could usefully guide future work.

1. Links to broader approaches

The true value of the GBA, or indeed of any habitat-assessment approach, lies in its potential for incorporation within broader Instream Flow Assessments. As it stands, for example, the GBA cannot provide a comprehensive recommendation for an instream flow regime but, by providing an assessment of habitat changes, it can complement broader methods. Two such methods (see Chapter 1) are currently being developed in South Africa - the Building Block Methodology (King *et al.* in press), and DRIFT (Brown & King in prep.). Both these methodologies incorporate a range of issues including abiotic and biotic, instream and offstream factors, into a comprehensive analysis of desired flows. Recent research elucidating the role of landscape determinants (e.g. Grossman *et al.* 1995; Pusey *et al.* 2000) also offer exciting new advances. Thus, complementing and responding to the needs of these broader methodologies must constitute a priority research directive.

2. Temporal considerations and the use of the GBA in high flows

The GBA is an approach which developed in response to scenarios of discharge reductions, which dominate the South African water-resource situation. The implications of incorporating conditions of extremely high flows, such as floods, have not been explored. For example, recognising the geomorphic units that underlie biotopes may be extremely difficult under these conditions and the applicability of this approach, as it stands, would require careful consideration.

3. Capturing heterogeneity

Currently, the challenge of capturing environmental heterogeneity in descriptions of habitat is lost due to the constraints of the conventional analytical tools and to what can be conceptually tracked. This problem was highlighted once the biotope types were spatially represented when, for instance, two adjoining biotopes that were distinctive in the field, were categorised within the same class on the map.

Moreover, I have argued that the "usefulness" of summarising data into aggregated models reflects the needs of the researcher rather than the organisms in question. In doing so, the spatial or temporal habitat heterogeneity is collapsed into a picture of averages, thereby creating a myth of constancy that is evident in many habitat studies. I would propose that only once data have been thoroughly tested, and homogeneity identified as a real attribute of habitat, should the composite outputs be considered.

Recent advances in the spatial representation of data and analytical tools for capturing environmental heterogeneity offer innovative ways of embracing heterogeneity (see previous discussions). These need to be incorporated into future research initiatives.

4. Exploring biotope assemblages of geomorphic units

I would suggest that data on biotope use should be collected as a function of geomorphic units and there should be a continued characterisation of the biotope assemblages to test the outputs from my research. For example, further investigation of the differences or similarities in the biotope assemblages, or biotope fingerprint, of different geomorphic units is needed. I was able to derive a biotope profile for Pool and Rapid geomorphic units, yet it remains to be seen, for example, whether or not differences exist between different types of Pools, or Rapids. I focussed on these two categories of geomorphic units but other key geomorphic units may be key in providing physical habitat.

5. Ecological links to habitat

Without adequate ecological data, full explanations of animal distributions are likely to remain largely theoretical. For example, the restriction of adult *C. anoterus* to Rapids could not be explained by a similar spatial restriction in the biotopes that they used, which were distributed over a variety of geomorphic units. Clearly, insights into the ecology of the animals in question may provide directions for explaining such issues.

6. Resolution on the link between habitat availability and habitat use

Although a broad framework for coupling the habitat-use information with that of habitat availability was provided, with a variety of potential outputs (Chapter 12), this needs refinement. Habitat selection, described through an index such as "preference", warrants consideration since there is merit in being able to quantify the use of sub-optimal habitats if the optimal habitat is limited. Despite this, I would contend that the approach used by IFIM is flawed (Chapter 8) and alternative approaches, such as those used by terrestrial ecologists, may prove more fruitful. Moreover, it may prove more biologically meaningful, and rational, to explore the concept that it is the *assemblage* of biotope types that constitutes "optimal" habitat, rather than a single value as suggested by IFIM.

7. Interdisciplinary approaches

As a theme, the role of interdisciplinary research in linking phenomena, approaches and conceptual tools has recently received formal recognition (see for example Cummins 1992; Stanford & Ward 1992; Pickett *et al.* 1999; Turner & Carpenter 1999). The importance of these linkages for instream studies requires no review. Understanding the functional role of geomorphology in providing the physical template, and of hydrology in providing the dynamic nature of the system, has been critical for ecologists to examine habitat in any depth. This integrative work would further benefit by a focus in the following areas:

- The inclusion and testing of additional variables that may comprehensively capture physical habitat should be considered. My data suggested that habitat volume, for example, may be a key habitat determinant for *C. anoterus* but the current descriptions of biotopes do not capture patch volume and warrant further investigation (see, for example, Angermeier & Schlosser 1989). Also, it may be useful, although challenging, to incorporate elements such as algal cover and vegetation in that, from an ecological perspective, biotopes are quite distinctive based on their occurrence.
- A refined understanding of the hydraulic characteristics of different flow types would advance our knowledge of biotope characteristics. This work has been initiated by two teams in South Africa (Dr. King, Freshwater Research Unit, University of Cape Town) and Prof. Rowntree (Department of Geography, Rhodes University) as well as in the UK (Newson & Newson 2000). Furthermore, hydraulic conformity within biotope types needs to be further explored (see Chapter 12).
- Conceptually, it is important to recognise that the finest scale of resolution namely, the biotope, may depend on the objectives at hand, in that their spatial dimensions may only be appropriate to certain organisms and under certain conditions.
- Whilst most comparisons between habitat availability and use are based on data collected at the same time, given the constraints of limited resources, the transferability of habitat-use models is increasingly compelling (e.g. Loar 1985; Bourgeois *et al.* 1996).
- My data suggested that the biotope characteristics within a geomorphic-unit type were consistent across all channel types, with the exception of the BAN channels. Here, the areas of geomorphic units appeared to be larger relative to other channel types. If this is true, this could influence the biotope characteristics, such as biotope size and number. Thus, the influence of channel type on the attributes of geomorphic units (types), warrants verification.
- The current framework for extrapolation, did not take account of the channel width, and hence area, of each channel type, but should be considered in future studies.
- Finally, a key challenge for future research is to accommodate this approach into a formal simulation model which allows one to predict biotope availability under different flow conditions.

8. Investigating long-term channel change

Even if PHABSIM II outputs are regarded as accurate, they stand as a description of present conditions and cannot be applied to the river once a development is in place, unless there is proof that the catchment characteristics and, hence, channel characteristics, will not change significantly. The importance of such issues has been highlighted by the recent floods in the study area. For example, the geomorphological changes in the river have been dramatic and whilst the effects on physical habitat remains to be seen, the Marite and Sabie Rivers, which were undergoing progressive alluviation appear to have been scoured of sediments (personal observation and Prof. K. Rogers, Centre for Water & the Environment, University of Witwatersrand, South Africa, *pers. comm.*).

In this regard, proponents of PHABSIM recommend assessing "catchment equilibrium" and channel dynamics (see Chapter 4). Nonetheless, few studies ever describe undertaking this step. In all probability this reflects the same reasons given for the failure to extrapolate site-specific data up to the entire study area (see Section 13.2).

Table 13.1
A proposed framework for assessing channel change with a water development in place

OBJECTIVE	METHOD	OUTPUT	COMMENT
1. Hydrological Assessment: Comparing current and future hydrology	**1.1** Assessment of the current hydrology of the river (e.g. see Chapter 5).	Pre-development hydrological profile.	Hydrological profile, indicating normal, wet and dry periods.
	1.2 Assessment of the post-development hydrological scenario (e.g. daily dam release flows).	Post-development hydrological profile.	Profile of post-development hydrology. Compare to pre-development scenarios.
2. Geomorphological Assessment: Examining areas of the river that are likely to reflect deposition or erosion	**2.1** Assessment of present geomorphology (see chapter 11).	Profile of pre-development channel morphology.	Description of the present morphology of the study river at the scale of channel-type and geomorphic units (geomorphic assemblages of channel types).
	2.2 Assess long-term channel equilibrium.	Assessment of areas of channel change. Specifically, a description of the channel types of the river that are prone to erosion or deposition, or likely to remain stable.	Pool-rapid areas on the Sabie River lowveld have been shown to undergo progressive alluviation through the development of lee bars and braid bars, followed by lateral bars and bedrock core bars (Dr G. Heritage, Department of Geography, Salford University, U.K. *pers. comm.*).
	2.2.1 Assess channel slope and derive description of the energy of the system.	Areas of likely morphological change.	Presented at the scale of channel types.

The same rationale would apply in terms of the predictive capabilities within the GBA. Therefore a broad framework for assessing channel change, currently being developed (Heritage & Pollard in prep.) is offered for future work in this area (Table 13.1). The overall approach is based on the inherent assumption that certain channel types manifest differential responses (i.e. some channel types are inherently unstable) to charges in the hydrology. That is, certain channel types are more or less prone to erosional or depositional processes and this can be assessed with the future water development in place. This would involve an assessment of the present and future hydrology and channel morphology and, by linking this information to that of biotope distributions, an assessment of the degree to which biotope proportions may change in unstable sections of the river.

13.4 CONCLUDING REMARKS ON THE FUTURE OF HABITAT ASSESSMENTS: INTEGRATING KEY THEMES

Habitat assessments, which strive to understand the nature of habitat, the mechanisms that structure it, its influence on the distribution and abundance of organisms and, hence, the consequences of habitat change, or loss, are a critical component of Instream Flow Assessments and should be viewed as tools in constant evolution. PHABSIM certainly changed the face of habitat-based assessments and cemented the disparate data that pointed to a functional link between the geomorphology and physical habitat of a river. The development of IFIM and PHABSIM was not undertaken in a vacuum but rather evolved in response to the needs of ecologists and managers. In itself, it has provided the framework against which limitations are raised and resolved.

However, the discussions of the preceding chapters point to a certain inflexibility within PHABSIM to respond to, and to incorporate, new and evolving concepts and this must stand as one of the major constraints of this methodology. Aside from the "technical" inflexibility, this also partly reflects a reluctance to change and adapt on the part of PHABSIM proponents. For example, in a discussion on the recent advances offered by two-dimensional models, one of the authors of PHABSIM anticipated resistance to these developments by PHABSIM users (Bovee 1996).

The proposed GBA, as an alternative habitat-assessment approach, goes some way towards addressing these concerns. Its development has attempted to incorporate pertinent conceptual models, and specifically to take cognisance of the concerns raised in the use of IFIM and PHABSIM. Most important, its development has been guided by the belief that for models to be accurate, useful and consistently validated, they need to reflect, and not obscure, reality.

The real strength of any conceptual model and framework lies in its adaptability. For example, recent theoretical and empirical developments have suggested that the study of heterogeneity and its ecological consequences requires new and more complex conceptual frameworks and empirical approaches (Kolasa & Rollo 1991). In conclusion, it is worth reiterating some of these key conceptual advances that require integration into habitat-based assessments, within the broad discipline of "instream flows", if they are truly to contribute to our understanding of rivers.

Firstly, it is important to ask if any spatial and temporal patterns in physical habitat exist, are these scale dependent and what mechanisms underlie these patterns? The work of Frissel *et al.* (1986), and others, clearly focussed attention on the functional role of geomorphology in providing the underlying mechanisms that control the architecture and distribution of instream habitats. Their work provided the basis for a classification system for rivers within which the multiple scales that circumscribe habitat could be developed. In South Africa, the focus on locally-appropriate river classification systems required defining the scale at which ecologists, hydrologists and geomorphologists were working and exposed gaps that required interdisciplinary efforts to integrate information. In this regard, the pivotal work of a number of research teams (King & Tharme 1994; Wadeson 1994; Heritage *et al.* 1995a; van Niekerk *et al.* 1995; Rowntree & Wadeson 1996, amongst others) provided the fundamental groundwork for developing and reorientating approaches to habitat assessments.

In parallel, another key challenge was to confidently find ways of representing and quantifying the attributes of habitat as spatio-temporal mosaics. Within the PHABSIM approach, the methods for describing habitat are somewhat crude, not in the intensive work that they require, but in the depiction of habitat as linearly-delineated blocks, the attributes of which are disaggregated as modelling proceeds. Drawing habitat back into the "real world" of mosaics of three-dimensional patches, cannot be laid at a single door. The option tc preserve this characteristic was embraced in the concept of *hydraulic biotopes* of Wadeson (1994; see also Rowntree 1996) and synonymously, in the *physical biotopes* of Padmore (1997). Once this foundation had been laid, the potential to explore key features of habitat patches was realised, supported by a range of conceptual and thematic developments.

Landscape ecology, patch theory, the studies of heterogeneity, pattern and scale(1) all contribute significantly to the conceptual frameworks that should underpin instream studies, but which seem to have been subsumed by the technical limitations of engineering models. The increased profile that heterogeneity has received in the last decade has signified a major shift in ecological thinking. With these frameworks, the possibility of addressing the concerns of ecologists around capturing habitat complexity received the theoretical support it required and opened up new avenues for habitat assessments. Furthermore, technical advancements in the last decade have offered analytical tools that capture heterogeneity in a way that was previously not possible.

The real future and strength of habitat assessments, as tools, lies in their conceptual adaptability and potential for evolution, and our ability to recognise this. As researchers in the discipline of instream studies, it may be our role to represent the needs of the river, but to do so judiciously, we need periodically to review the intended purpose, and the actual consequence, of the tools we use. If our efforts to mitigate the increasing pressures on the world's water resources are to meet with success and if we are to ensure the integrity and sustainability of the rivers that we purport to represent, then the real test for habitat assessments lies in our own capacity for innovation and adaptability.

---

[1] These conceptual frameworks and their development can be attributed to various researchers and, for expediency, are not re-listed here. See Chapter 10 for relevant references.

References

Acocks J.P.H. 1988. Veld Types of South Africa. *3rd Ed. Mem. Bot. Surv. S. Afr.* 57: 1-92.

Alexander, W.J.R. 1985. Hydrology of low latitude Southern Hemisphere land masses. *Hydrobiologia* 125: 75-83.

Allanson, B.R., R.C. Hart, J.H. O'Keeffe and R.D. Robarts. 1990. *Inland Waters of Southern Africa: An Ecological Perspective.* Kluwer Academic Publishers, Netherlands.

Allredge, J.R. and J.T. Ratti. 1986. Comparison of some statistical techniques for analysis of resource selection. *J. Wildl. Mgmt.* 50(1): 157-165.

Anderson, C.S. and R.B. Nehring. 1985. Impacts of stream discharge on trout rearing habitat and trout recruitment in the South Platte River, Colorado. Pp. 59-64. *In:* F.W. Olson and R.H. Hamre. Eds. *Proceedings of the Symposium on Small Hydropower and Fisheries.* Am. Fish. Soc. Bethesda, MD.

Angermeier, P.L. 1987. Spatiotemporal variation in habitat selection by fishes in small Illinois streams. 52-60. *In:* W. J. Mathews and D.C. Heins. Eds. *Community and Evolutionary Ecology of North American Streams.* University of Oklahoma Press.

Angermeier, P.L. and J.R. Karr. 1983. Fish communities along gradients in a system of tropical streams. *Envir. Biol. Fishes* 9(2): 117-135.

Angermeier, P.L. and I.J. Schlosser. 1989. Species-area relationships for stream fishes. *Ecology* 70(5): 1450-1462.

Armitage, P.D. 1979. Stream regulation in Great Britain. Pp. 165-82. *In:* Ward, J.V. and J.A. Stanford. Eds. *The Ecology of Regulated Streams.* Plenum Press, NY.

Armitage, P.D. 1994. Prediction of biological responses. Pp. 254-275. *In:* P. Calow and G.E. Petts. Eds. *The Rivers Handbook: Hydrological and Ecological Principles.* Blackwell Sci. Pubs., Oxford.

Armitage, P.D. and M. Ladle. 1989. Habitat preferences of target species for application in PHABSIM testing. Pp. 87-122. *In:* A. Bullock, A. Gustard and E.S. Grainger. Eds. *Instream Flow Requirements of Aquatic Ecology in Two British Rivers.* Rpt. No. 15. Inst. Hydrology, Oxon, U.K.

Armour, C.L., R.J. Fisher and J.W. Terrell. 1984. *Comparison of the Use of the HEP and IFIM in Aquatic Analyses.* U.S. Fish & Wildlife Service FWS/OBS-84/11. Washington, DC.

Arthington, A.L., J.M. King, J.H. O'Keeffe, S.E. Bunn, J.A. Day, B.J. Pusey, D.R. Bluhdhorn and R.E. Tharme. 1992. Development of an holistic approach for assessing environmental water requirements of riverine ecosystems. Pp. 69-76. *In:* J.J. Pigrham and B.P. Hooper. Eds. *Water Allocation for the Environment - Proceedings of An International Seminar and Workshop.* Armidale, Australia.

Bagnenal, T.B. 1967. A short review of fish fecundity. Pp. 89-111. *In:* S.D. Gerking. Ed. *The Biological Basis of Freshwater Fish Production.* Blackwell, Oxford.

Bagenal, T.B. 1978. Aspects of fish fecundity. pp 75-101.*In:* S.D. Gerking. Ed. *Ecology of Freshwater Fish Production.* Blackwell, U.K. 45 Pp.

Bagenal, T.B. and E. Braum. 1971. Eggs and early life history. Pp. 166-198. *In:* Ricker, W.E. Ed. *Methods for the Assessment of Fish Production in Fresh Waters.* IBP Handbook No. 3. Blackwell Scientific Publications. Oxford. 307 Pp.

Bagenal, T.B. and W. Nellen. 1980. Sampling eggs, larvae and juvenile fish. Pp. 13-36. *In:* T. Backiel and R.L. Welcomme. Eds. *Guidelines for Sampling Fish in Inland Waters.* FAO, European Inland Fisheries Advisory Commission, Techn. Paper 33. Rome, Italy.

Bain, M.B. 1988. An evaluation of sampling methods and study designs for quantifying habitat utilisation by stream fish. Pp. 58-67. *In:* K. Bovee and J.R. Zuboy. Eds. *Proceedings of A Workshop on the Development and Evaluation of Habitat Suitability Criteria.* U.S. Fish and Wildlife Service. Biol. Rpt. 88(11).

Bain, M.B. and J.M. Boltz. 1989. *Regulated Streamflow and Warmwater Stream Fish: A General Hypothesis and Research Agenda.* U.S. Fish and Wildlife Service, Biol. Rep. 89(18). Washington, D.C. 28 Pp.

Bain, M.B., J.T. Finn and H.E. Booke. 1988. Streamflow regulation and fish community structure. *Ecology* 69(2): 382-392.

Bain, M.B., J.T. Finn, L.J. Gerardi, Jr., M.R. Ross and W.P. Saunders, Jr. 1982. *An Evaluation of Methodologies for Assessing the Effects of Flow Fluctuations on Stream Fish.* Massachusetts Cooperative Fishery Research Unit Contribution No. 78. University Mass., Amherst. FWS/OBS-82-63.

Baldridge, J.E. and D. Amos. 1981. *A Technique for Determining Fish Habitat Suitability Criteria: A Comparison Between Habitat Utilization and Availability.* Symposium on Acquisition and Utilization of Aquatic Habitat Inventory Information. Am. Fish. Soc. Portland, Oregon. 57 Pp.

Balon, E.K. 1975. Reproductive guilds of fishes: A proposal and definition. *J. Fish. Res. Brd. Can.* 32(6): 821-864.

Balon, E.K. 1984. Patterns in the evolution in reproductive styles in fishes. 35-53. *In:* G.W. Potts and R.J. Wooton. Eds. Fish *Reproduction, Strategy and Tactics.* Academic Press, Inc., NY. 410 Pp.

Balon E.K. 1985. Additions and amendments to classification of reproductive styles in fish. Pp. 59-72. *In:* E.K. Balon. Ed. *Early Life Histories of Fish.* Junk Publ.

Barmutta, L.A. and P.S. Lake. 1982. On the value of the river continuum concept. *N. Z. J. Mar. Fresh. Res.* 16:227-231.

Bartholow, J.M. and W.L. Slauson. 1990. Questions on habitat preference. *N. Am J. Fish. Mgmt.* 10(3): 352.

Bayley, P.B. 1991. The flood pulse advantage and the restoration of river-floodplain systems. *Reg. Riv. Res. Mgmt.* 6: 75-86.

Bell, S. S., E.D. McCoy and H.R. Mushinsky. Eds. 1991. *Habitat Structure: the Physical Arrangements of Objects in Space and Time.* Chapman & Hall, NY.

Bell-Cross, G. and J.L. Minshull. 1988. *The Fishes of Zimbabwe.* Trustees of the National Museums and Monuments of Zimbabwe. Harare. 294 Pp.

Benade, C. and S.J. van Vuuren. 1993. Ecological Management of Riverine Water Resources: The Case of the Orange River System, South Africa. *Proceedings of the Conference on Water: the Lifeblood of Africa.* July, Zimbabwe.

Beschta, R.L. and W.S. Platts. 1986. Morphological features of small streams: significance and function. *Wat. Res. Bull.* No. 86006. 369-379.

Biggs, B.J. 1982. The effects of low flow regulation on river water quality and biology. A case study. Pp. 28-44. *In:* R.H.S. McColl. Ed. *River Low Flows: Conflicts of Water Use.* Water and Soil Misc. Publ. 47.Wellington, NZ.

Birkhead, A.L., B.W. Olbrich, C.S. James, K.H. and Rogers. 1996 a. *Developing an Integrated Approach to Predicting the Water Use of Riparian Vegetation.* Water Research Commission Rpt. No. 474/1/96.

Birkhead, A.L., G.L. Heritage, H. White and A.W. van Niekerk 1996 b. Ground-penetrating radar as a tool for mapping the phreatic surface, bedrock profile, and alluvial stratigraphy in the Sabie River, Kruger National Park. *J. Soil Water Cons.* 51(3): 234-240.

Bisson, P.A., J.L. Nielsen, R.A. Palmason and L.E. Grove. 1982. A system of naming habitats in small streams with examples of habitat utilisation by salmonids during low stream flow. Pp. 62-73. *In:* N.B. Armandtrout. Ed. *Acquisition and Utilisation of Aquatic Habitat Information.* West. Div. Am. Fish. Soc. Portland, Or.

Bisson, P.A.; K. Sullivan and J.L. Nielsen. 1988. Channel hydraulics, habitat use, and body form of juvenile Coho salmon, steelhead and cutthroat trout. *Trans. Am. Fish. Soc.* 117: 262-273.

Bourgeois, G., R.A. Cunjak, D. Caissie and N. El-Jabi. 1996. A spatial and temporal evaluation of PHABSIM in relation to measured density of juvenile Atlantic salmon in a small stream. *N. Am. J. Fish. Mgmt.* 16: 154-166.

Bovee, K.D. 1974. *The Determination, Assessment, and Design of "Instream Value" Studies for the Northern Great Plains Region.* N. Great Plain Resources Program. 204 Pp.

Bovee, K.D. 1978. The incremental method of assessing habitat potential for coolwater species, with management implications. *Am. Fish. Soc. Spec. Publ.* 11: 340-346.

Bovee, K.D. 1982. *A Guide to Stream Habitat Analysis Using the Instream Flow Incremental Methodology.* U.S. Fish & Wildlife Service FWS/OBS-82/86. Washington, D.C.

Bovee, K.D. 1986. *Development and Evaluation of Habitat Suitability Criteria for Use in Instream Flow Methodology.* U.S. Fish and Wildlife Service, Biological Report 86(7). Washington, DC.

Bovee, K. 1996. Perspectives on two-dimensional river habitat models: the PHABSIM experience. *Proc. 2nd IAHR Int. Symp. Hydr. Hab.* Quebec City, June 11 -14, 1996.

Bovee, K.D. and T. Cochnauer. 1977. *Development and Evaluation of Weighted Criteria, Probability-of-use Curves for Instream Flow Assessments: Fisheries.* Instream flow information paper No. 3. U.S. Fish and Wildlife Service FWS/OBS-77/63 Fort Collins, Colorado.

Bovee, K.D. and R. Milhous. 1978. *Hydraulic Simulation in Instream Flow Studies: Theory and Techniques. Instream Flow Information Paper 5.* U.S. Fish and Wildlife Service FWS/OBS-78/33: 130 Pp.

Bovee, K. and J.R. Zuboy. Eds. 1988. *Proceedings of A Workshop on the Development and Evaluation of Habitat Suitability Criteria.* U.S. Fish and Wildlife Service, Biol. Rpt. 88(11).

Bozek, M.A. and F.J. Rahel. 1991. Assessing habitat requirements of young Colorado cutthroat trout by use of microhabiat and microhabitat analysis. *Trans. Am. Fish. Soc.* 120: 571-581.

Bozek, M.A. and F.J. Rahel. 1992. Generality of microhabitat suitability models for young Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) across sites and among years in Wyoming streams. *Can. J. Fish. Aquat. Sci.* 49: 552-564.

Breen, C.M., J.A. Cambray, F.M. Chutter, J.A. Day, F.C. de Moor, J. Heeg, J.H. O'Keeffe and K.F. Walker. 1984. Stream regulation. Pp. 33-63. *In:* R.C. Hart and B.R. Allanson. Eds. *Limnological Criteria for Management of Water Quality in the Southern Hemisphere.* S. Afr. Nat. Sci. Prog. Rpt. No. 93.

Breen, C.M. K.H. Rogers and P.J. Ashton. 1988. Vegetation processes in swamps and flooded areas. Pp. 223-247. *In:* J.J. Symoens. Ed. *Vegetation of Inland Waters.* Kluwer, Dordrecht.

Broadhurst, L.J., G.L., Heritage, A.W, van Niekerk, C.S. James, and K.H. Rogers. 1996. *Translating Local Discharge Into Hydraulic Conditions on the Sabie River: An Assessment of Channel Flow Resistance.* Water Research Commission Rpt. 474/2/96.

Brookes, A. 1994. River channel change. Pp. 55-75. *In:* P. Calow and G.E. Petts. Eds. *The Rivers Handbook: Hydrological and Ecological Principles.* Blackwell Sci. Pubs., Oxford.

Brown, C. A. and J.M. King. In prep. *Environmental Flow Assessments for Rivers: The DRIFT Process.* Southern Waters Information Report. Cape Town.

Bruton, M.N. 1979. The breeding biology and early development of *Clarias garienpinus* (Pisces: Clariidae) in Lake Sibaya, South Africa, with a review of breeding in species of the subgenus *Clarias (Clarias). Trans. Zool. Soc. Lond.* 35: 1-45.

Bruton, M.N. 1989. The ecological significance of alternative life-history styles. Pp. 503-553. *In:* M.N. Bruton. Ed. *Alternative Life History Styles of Animals.* Kluwer Academic Publ., Netherlands.

Bruton, M.N., P.B.N. Jackson and P.H. Skelton. 1982. *Pocket Guide to the Freshwater Fishes of Southern Africa.* Centaur Pubs., Cape Town. 88 Pp.

Bruton, M.N. and H.M. Kok. 1980. The freshwater fishes of Maputaland. Pp. 210-244. *In:* M.N. Bruton and K.H. Cooper. Eds *Studies of the Ecology of Maputaland.* Rhodes University and Natal Branch of Wildlife Society of Southern Africa.

Bullock, A., A. Gustard and E.S. Grainger. 1991. *Instream Flow Requirements of Aquatic Ecology in Two British Rivers.* Rpt. No. 15. Inst. Hydrology. Oxon, U.K.

Bult, T.P., R.L. Haedrich and D.C. Schneider. 1998. New technique describing spatial scaling and habitat selection in riverine habitats. *Reg. Riv. Res. Mgmt.* 14: 107-118.

Burgess, W.E. 1989. *An Atlas of Freshwater and Marine Catfishes. A Preliminary Survey of the Siluriformes.* T.F.H. Publications, Inc., Neptune City, New Jersey, USA. 784 Pp.

Bye, V.J. 1984. The role of environmental factors in the timing of reproductive cycles. Pp. 187-206. *In:* G.W. Potts and R.J. Wootton. Eds. *Fish Reproduction. Strategies and Tactics.* Academic Press Inc., London.

Byers, C. R. and R.K. Steinhorst. 1984. Clarification of a technique for analysis of utilisation-availability data. *J. Wildl. Mgmt.* 48(3): 1050-1053.

Byren, B.A. and B.R. Davies. 1989. The effects of stream regulation on the physico-chemical properties of the Palmiet river, South Africa. *Reg. Riv. Res. Mgmt* 3: 107-121.

Cada, G.F., M.J. Sale, R.M. Cushman and J.M. Loar. 1983. Pp. 1305-1313. test of a biological assumption of instream flow models. *Waterpower '83. Conference Proceedings.* Vol. 3. Knoxville, Tennessee.

Cambray, J.A. 1991. The effects of fish spawning and management implications of impoundment water releases in an intermittent South African river. *Reg. Riv. Res. Mgmt.* 6: 39-52.

Campbell, R.F. and J.H. Neuner. 1985. Seasonal and diurnal shifts in habitat utilized by resident rainbow trout in western Washington Cascade Mountain streams. Pp. 39-48. *In:* F.W. Olson and R.H. Hamre. Eds. *Proceedings of the Symposium on Small Hydropower and Fisheries.* Colorado. Am. Fish. Soc. Bethesda, MD.

Carling, P.A. and C.P. McCahon. 1987. Natural siltation of brown trout (*Salmo trutta* L.) spawning gravels during low-flow conditions. Pp. 229-244. *In:* J.F. Craig and J.B. Kemper. Eds. 1985. *Regulated Streams: Advances in Ecology.* Plenum Press, NY.

Carter, A.J. and K.H. Rogers. 1988. Phragmites reedbeds in the Kruger National Park: The complexity of change in river bed state. Pp. 339-346. *In:* S. Kienzle and H. Maaren. Eds. *Proc. 4th S. Afr. Nat. Hydrol. Symp.* University of Pretoria.

Casado, C., D. Garcia de Jalon, C.M. Del Olmo, E. Barcelo and F. Menes. 1989. The effects of irrigation and hydroelectric reservoir on its downstream communities. *Reg. Riv. Res. Mgmt.* 4: 275-284.

Cassidy, R.A. 1989. Water temperature, dissolved oxygen, and turbidity control in reservoir releases. Pp. 27-62. *In:* J.A. Gore and G.E. Petts. Eds. *Alternatives in Regulated River Management.* CRC Press Inc., Boca Raton, Fl.

Cavendish, M.G. and M.I. Duncan. 1986. Use of Instream Flow Incremental Methodology: a tool for negotiation. *Envir. Impact Assess. Rev.* 6347-363.

Cerri, R.D. and D.F. Fraser. 1983. Predation and risk in foraging minnows: balancing conflicting demands. *Am. Nat.* 121: 552-561.

Chapman, L.J. and D. Kramer. 1991 a. The consequences of flooding for the dispersal and fate of poeciliid fish in an intermittent tropical stream. *Oecologia* 87: 299-306.

Chapman, L.J. and D. Kramer. 1991 b. Limnological observations of an intermittent tropical dry forest stream. *Hydrobiologia* 226: 153-166.

Cheshire, P. 1996. *Geology and Geomorphology of the Sabie River, Kruger National Park and its Catchment Area.* Water Research Commission Rpt. 376/2/96.

Cheslak, E.F. and J.C. Garcia. 1988. An evaluation of the effects of various smoothing and curve-fitting techniques on the accuracy of suitability functions. Pp. 259-283. *In:* K. Bovee and J.R. Zuboy. Eds. *Proceedings of A Workshop on the Development and Evaluation of Habitat Suitability Criteria.* U.S. Fish and Wildlife Service. Biol. Rpt. 88(11).

Chunnett, Fourie and Partners. 1990. *Water Resources Planning of the Sabie River Catchment.* Vol. 1-10.

Chutter, F.M. 1963. Hydrobiological studies of the Vaal River in the Vereeninging area. Part 1. Introduction, water chemistry and biological studies on the fauna of habitats other than muddy bottom sediments. *Hydrobiologia.* 21: 1-65.

Chutter, F.M. 1967. *Hydrobiological Studies of the Vaal River and Some of its Tributaries, Including An Introduction to Simulium in its Lower Reaches.* Unpubl. Ph.D. thesis. Rhodes University, Grahamstown. Two volumes.

Chutter, F.M. 1969. The effects of silt and sand on the invertebrate fauna of streams and rivers. *Hydrobiologia* 34: 57-76.

Chutter, F.M. 1973. An ecological account of the past and future of South African rivers. *Newsl. Limnol. Soc. S. Afr.* 21: 22-34.

Cohen, P. H. Andriamahefa and J.G. Wasson. 1998. Towards a regionalisation of aquatic habitat: distribution of mesohabitats at the scale of a large basin. *Reg. Riv. Res. Mgmt.* 14: 391-404.

Coke, M. and R. Pott. 1970. *The Pongolo Floodplain Pans. A Plan for Conservation.* Natal Parks Board. Unpubl. report.

Conder, A.L. and T.C. Annear. 1987. Test of weighted usable area estimates derived from a PHABSIM model for instream flow studies on trout streams. *N. Am. J. Fish. Mgmt.* 7: 339-350.

Connell, J.H. 1975. Some mechanisms producing structure in natural communities. Pp. 460-490. *In:* M. Cody and J.M. Diamond. Eds. *Ecology and Evolution of Communities.* Harvard University Press, Cambridge, Mass.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science.* 199: 1302-1310.

Conner, L.L. and O.E. Maughan. 1984. Changes in invertebrate and fish populations, and water chemistry in a small stream above and below two impoundments. *Virg. J. Sci.* 35(4): 240-247.

Connigarth Consultants. 1994. *Sabie-Sand River Water Resources Development: Macro-economic and Cost-benefit Analyses with Reference to the Proposed Injaka Dam.* Internal report prepared for the Sabie Steering Committee, South Africa.

Conover, D.O. 1985. Field and laboratory assessment of patterns in fecundity of a multiple spawning fish: the Atlantic silverside *Menidia menidia. Fish. Bull.* 83(3): 331-341.

Coon, T.G. 1987. Responses of benthic riffle fishes to variation in stream discharge and temperature. Pp. 77-85. *In:* W.J. Mathews and D.C. Heins. Eds. *Community and Evolutionary Ecology of North American Stream Fishes.* University Oklahoma Press.

Cooper, S.D., L. Barmuta, O. Sarnelle, K. Krantz and S. Diehl. 1997. Quantifying spatial heterogeneity in streams. *J. N. Am. Benthol. Soc.* 16(1):174-188.

Copp, G.H. 1990. Effect of regulation on 0+ fish recruitment in the Great Ouse, a lowland river. *Reg. Riv. Res. Mgmt.* 5: 251-263.

Crass, R.S. 1964. *The Freshwater Fishes of Natal.* Shuter and Shooter, Pietermaritzburg. 167 Pp.

Crisp, D.T. 1985. Thermal "resetting" of streams by reservoir releases with special reference to effects of salmonid fishes. Pp. 163-182. *In:* J.F. Craig and J.B. Kemper. Eds. *Regulated streams: Advances in Ecology.* Plenum Press, NY.

Crisp, D.T., R.H.K. Mann and P.R. Cubby. 1984. Effects of impoundments upon fish populations in different streams at Cow Green Reservoir. *J. Appl. Ecol.* 21: 739-756.

Crowl, T.A., C. Townsend, N. Bouwes and H. Thomas. 1997. Scales and causes of patchiness in instream invertebrate assemblages: top-down predator effects? *J. N. Am. Benthol. Soc.* 16(1): 277-285.

Cummins, K.W. 1992. Catchment characteristics and river ecosystems. Pp. 125-135. *In:* P.J. Boon, P. Calow and G.E. Petts. Eds. *River Conservation and Management.* John Wiley & Sons Ltd, NY.

Cummins, K.W., G.W. Minshall, J.R. Sedell, C.E. Cushing and R.C. Peterson. 1984. Stream ecosystem theory. *Verh. Internat. Verein. Limnol.* 22: 1818-1827.

Dallas, H.F. and J.A. Day. 1993. *The Effect of Water Quality Variables on Riverine Ecosystems: A Review.* Water Research Commission Rpt. TT 61/93. 240 Pp.

Davies, B.R. 1979. Stream regulation in Africa: A review. Pp. 113-140. *In:* J.V. Ward and J.A. Stanford. Eds. *The Ecology of Regulated Streams.* Plenum Press, NY.

Davies, B.R. and J.A. Day. 1998. *Vanishing Waters.* University of Cape Town Press, Cape Town. 487 Pp.

Davies, B.R., J.H. O'Keeffe and C.D. Snaddon. 1993. *A Synthesis of the Ecological Functioning, Conservation and Management of South African River Ecosystems.* Water Research Commission Rpt. TT 62/93. 232 Pp.

Davies, B.R., J.H. O'Keeffe and C.D. Snaddon. 1995. River and stream ecosystems in South Africa: predictably unpredictable. Pp. 537-599. *In:* C.E. Cushing, K.W. Cummins and G.W. Minshal. Eds. *River and Stream Ecosystems.* Elsevier.

Davies, B.R., R.W. Palmer, J.H. O'Keeffe and B.A. Byren. 1989. The effects of impoundments on the flow and water quality of two contrasting southern African river systems. Pp. 260-268. *In:* S. Kienzle and H. Maaren. Eds. *Proc. 4th S. Afr. Nat. Hydrol. Symp.* University Pretoria.

Davies, B.R., C.D. Snaddon, M.J. Wishart, M.C. Thoms and M. Meador. 2000. A biogeographical approach to interbasin transfers: implications for river conservation. Pp. 431-444. *In:* P.J. Boon, B.R. Davies and Petts. Eds. *Global Perspectives on River Conservation. Science, Policy and Practice.* John Wiley & Sons, NY.

Davies, B.R.D., M. Thoms and M. Meador. 1992. Viewpoint: An assessment of the ecological impacts of inter-basin water transfers, and their threats to river basin integrity and conservation. *Aq. Cons. Mar. Freshw. Syst.* 2: 325-349.

Davies, B.R. and K.F. Walker. 1986. *The Ecology of River Systems*. Monogr. Biolog. 60. Dr. W. Junk. Dordrecht. 793 Pp.

de Villiers, P. 1991. *The Biology and Culture of Chiloglanis Pretoriae (Pisces: Mochokidae)*. Unpubl. M. Sc. Thesis, Rhodes University, Grahamstown. 184 Pp.

Decamps, H.,Capblanq, J., Casanova, H. and Tourenq, J.M. 1979. Hydrobiology of some regulated rivers in south-west France. Pp. 273-88. *In:* J.V. Ward and J.A. Stanford. Eds. *The Ecology of Regulated Streams*. Plenum Press, NY.

DeGraaf, D.A. and L.H. Bain. 1986. Habitat use by and preference of juvenile Atlantic salmon in two Newfoundland rivers. *Trans. Am. Fish. Soc.* 115: 671-681.

DeMartini, E. E. 1991. Annual variations in fecundity, egg size, and the gonadal and somatic conditions of queenfish *Seriphus politus* (Sciaenidae). *Fish. Bull.* 89(1): 9-18.

DeMartini, E.E. and R.K. Fountain. 1981. Ovarian cycling frequency and batch fecundity in the queenfish, *Seriphus politus*: attributes representative of serial spawning fishes. *Fish. Bull.* 79(3): 547-560.

Department of Water Affairs. 1986. *Management of the Water Resources of South Africa*. Govt. Printer. Pretoria. 1031 Pp.

Department of Water Affairs and Forestry. 1991. *Operational Procedures for the Injaka Dam*. Internal Report. Department of Water Affairs and Forestry, Pretoria. 24 Pp.

Department of Water Affairs and Forestry. 1996. *Starter Document: Sabie -Sand IFR Workshop*. Aan de Vliet. 18-22 August 1996. Department of Water Affairs and Forestry, Pretoria. 92 Pp.

Department of Water Affairs and Forestry. 1998. *Final Workshop Report: Sabie -Sand IFR*. Aan de Vliet. Department of Water Affairs and Forestry, Pretoria. 197 pp.

Development Bank of South Africa. 1989. *Development Information Region G*. DBSA. Midrand.

Dufford, R.G., H.J. Zimmerman, L.C. Cline and J.V. Ward. 1985. Responses of epilithic algae to regulation of rocky mountain streams. Pp. 373-383. *In:* J.F. Craig and J.B. Kemper. Eds. *Regulated Streams: Advances in Ecology*. Plenum Press, NY.

Dodge, D.P. Ed. 1989. Proceedings of the International Large River Symposium (LARS). *Spec. Publ. Can. J. Fish. Aquat. Sci.* 106. Pp. 629.

Ehrlich, P. and A. Ehrlich. 1981. *Extinction*. Ballantine Books, NY.

Estes, C.C. and J.F. Osborn. 1986. Review and analysis of methods for quantifying instream flow requirements. *Wat. Res. Bull.* 22: 389-398.

Faush, K.D. 1984. Profitable stream positions for salmonids: Relating specific growth rate to net energy gain. *Can. J. Zool.* 64: 441-451.

Fisher, S.G. 1983. Succession in streams. Pp. 7-27. *In:* J.R. Barnes and G.W. Minshall. Eds. *Stream Ecology- Applications of General Ecological Theory*. Plenum Press, NY.

Fisher, S.G. and N.B. Grimm. 1991. Streams and disturbance: are cross-ecosystem comparisons useful? Pp. 196-221. *In:* J. Cole. Ed. *Comparative Analysis of Ecosystems: Patterns, Mechanisms and Theories*. Springer, NY.

Flecker, A.S. 1997. Habitat modification by tropical fishes: Environmental heterogeneity and the variability of interaction strength. *J. N. Am. Benthol. Soc.* 16(1): 286-295.

Forman, R.T.T. and M. Godron. 1986. *Landscape ecology.* John Wiley & Sons, NY.

Frissell, C.A., W.J. Liss, C.E. Warren and M.D. Hurley. 1986. A Hierarchical framework for stream habitat classification: viewing streams in a watershed context. *Envir. Mgmt.* 10(2): 199-214.

Gaigher, I.G. 1969. *Aspekte Met Betrekking Tot Die Ekologie, Geografie En Taksonomie Van Varswatervisse in Die Limpopo- En Incomati Riviersisteem.* Unpubl. D.SC. Thesis. Rand Afrikaans University, Johannesburg. 268 Pp.

Gaigher, I.G. 1973. *The Habitat Preferences of Fishes From the Limpopo River System, Transvaal and Moçambique. Koedoe* 16: 103-116.

Gale, W.F. and G.L. Buynak. 1982. Fecundity and spawning frequency of the fathead minnow- a fractional spawner. *Trans. Am. Fish. Soc.* 111: 35-40.

Gale, W.F. and C.A. Gale. 1977. Spawning habits of spotfin shiner (*Notropis spilopterus*)- a fractional, crevice spawner. *Trans. Am. Fish. Soc.* 106(2): 170-177.

Gan, K. and T. McMahon. 1990. Variability of results from the use of PHABSIM in estimating habitat area. *Reg. Riv. Res. Mgmt.* 5: 233-239.

Gatz, A.J. 1979. Community organisation in fishes as indicated by morphological features. *Ecology* 60: 711-718.

Ghanem, A; P. Steffler; F. Hicks and C. Katapodis. 1996. Two-dimensional hydraulic simulation of physical habitat conditions in flowing stream. *Reg. Riv. Res. Mgmt.* 12: 185-200.

Gilvear, D.J. 1987. Suspended solid transport within regulated rivers experiencing periodic reservoir release. Pp. 245-125. *In:* Craig, J.F. and J.B. Kemper. Eds. 1985. *Regulated streams: Advances in Ecology.* Plenum Press, NY.

Gippel, C.J. and M.J. Stewardson. 1998. Use of wetted perimeter in defining minimum environmental flows. *Reg. Riv. Res. Mgmt.* 14: 53-67.

Gordon N.D., T.A. McMahon and B.L. Finlayson. 1992. *Stream Hydrology. An Introduction for Ecologists.* John Wiley & Sons Ltd, NY.

Gore, J.A. 1978. A technique for predicting instream flow requirements of benthic macroinvertebrates. *Freshw. Biol.* 8: 141-151.

Gore, J.A. 1987 a. Predictive models of benthic macroinvertebrate density for use in instream flow studies and regulated flow management. *Can. J. Fish. Aquat. Sci.* 38: 1363-1370.

Gore, J.A. 1987 b. Development and applications of macroinvertebrate instream flow models for regulated flow management. Pp. 99-115. *In:* J.F. Craig and J.B. Kemper. Eds. 1985. *Regulated streams: Advances in Ecology.* Plenum Press, NY.

Gore, J.A. 1989. Models for predicting benthic macroinvertebrate habitat suitability under regulated flows. Pp.253-265. *In:* J.A. Gore and G.E. Petts Eds. *Alternatives in Regulated River Management.* CRC Press Inc., Boca Raton, Fl.

Gore, J.A. and R.D. Judy. 1981. Predictive models of benthic macroinvertebrate density for use in instream flow studies and regulated flow management. *Can. J. Fish. Aquat. Sci.* 38: 1363-1370.

Gore, J.A. and J.M. King. 1989 a. An introduction to the Instream Flow Incremental Methodology. Pp. 1-2. *In:* S. Kienzle and H. Maaren. Eds. *Proc. 4th S. Afr. Nat. Hydrol. Symp.* University Pretoria.

Gore, J.A. and J.M. King. 1989 b. Application of the revised physical habitat simulation (PHABSIM II) to minimum flow evaluations of South African rivers. Pp. 289-296. *In:* S. Kienzle and H. Maaren. Eds. *Proc. 4th S. Afr. Nat. Hydrol. Symp.* University Pretoria.

Gore, J.A., J.B. Layzer and I.A. Russell. 1992. Non-traditional applications of instream flow techniques for conserving habitat of biota in the Sabie River of southern Africa. Pp. 161-177. *In:* P.J. Boon, P. Calow and G.E. Petts Eds. *River Conservation and Management.* John Wiley & Sons Ltd, NY.

Gore, J.A. and J.M. Nestler. 1988. Instream flow studies in perspective. *Reg. Riv. Res. Mgmt.* 2: 93-101.

Gorman, O.T. 1987. Habitat segregation in an assemblage of minnows in an Ozark stream, 33-41. *In:* W.J. Mathews and D.C. Heins. Eds. *Community and Evolutionary Ecology of North American Stream Fishes.* University of Oklahoma Press.

Gorman, O.T. 1988. The dynamics of habitat use in a guild of Ozark minnows. *Ecol. Monogr.* 58: 1-18.

Gorman, O.T. and J.R. Karr. 1978. Habitat structure and stream fish communities. *Ecology* 59(3): 507-515.

Goulding, M. 1980. *The Fishes and the Forest.* University of California Press, Berkeley, CA. 280 Pp.

Graham, R.J. and D.J. Orth. 1986. Effects of temperature and streamflow on time and duration of spawning by Smallmouth bass. *Trans. Am. Fish. Soc.* 115: 693-702.

Grande, M. and S. Anderson. 1990. Effect of two temperature regimes from a deep and surface water release on early development of salmonids. *Reg. Riv. Res. Mgmt.* 5: 355-360.

Gray, L.J. and J. V. Ward. 1982. Effects of sediment releases from a reservoir on stream macroinvertebrates. *Hydrobiologia* 96: 177-184.

Grossman, G.D. and M.C. Freeman. 1987. Microhabitat use in a stream fish assemblage. *J. Zool. Lond.* 212: 151-176.

Grossman, G.D.; J. Hill and J.T. Petty. 1995. Observations on habitat structure, population regulation, ans habitat use with respect to Evolutionary significant units: A landscape perspective for lotic systems. *Am. Fish. Soc. Symp.* 17: 381-391.

Hamilton, K. and P.C. Nelson. 1984. *Habitat Suitability Index Models and Instream Flow Suitability Index Curves: White Bass.* U.S. Fish and Wildlife Service Biol. Rep. 82(10.89). 35 Pp.

Hannan, H.H. 1979. Chemical modifications in reservoir-regulated streams. Pp.75-94. *In:* Ward, J.V. and J.A. Stanford. Eds. *The Ecology of Regulated Streams.* Plenum Press, NY.

Hannan, H.H. and W.J. Young. 1974. The influence of deep storage reservoirs on the physicochemical limnology of a central Texas river. *Hydrobiologia* 44: 177-207.

Hardy, T.B. 1998. The future of habitat modelling and instream flow assessment techniques. *Reg. Riv. Res. Mgmt.* 14: 405-420.

Harper, D.M., C.D. Smith and P.J. Barham. 1992. Habitats as the building blocks for river conservation assessment. Pp. 312-319. *In:* P.J. Boon, P. Calow and G.E. Petts. *River Conservation and Management.* John Wiley & Sons Ltd, NY.

Harrison, A.D. 1965. River Zonation in South Africa. *Arch. Hydrobiol.* 61: 387-394.

Harrison, A.D. and J.F. Elseworth. 1958. Hydrobiological studies on the Great Berg River, Western Cape Province, Part 1. General description, chemical studies and main features of the flora and fauna. *Trans. Roy. Soc. S. Afr.* 35: 125-226.

Harrison, A.D., P. Keller and W.A. Lombard. 1963. Hydrobiological studies on the Vaal River in the Vereeniging area. Part 2. The chemistry, bacteriology and invertebrates of the bottom muds. *Hydrobiologia* 21: 66-89.

Harvey, B.C. 1987. Susceptibility of young-of-the-year fishes to downstream displacement by flooding. *Trans. Am. Fishes. Soc.* 116: 851-855,

Hauer, F.R. and J.A. Stanford. 1982. Ecological consequences of hydropsychid caddisflies to stream regulation. *Can. J. Fish. Aquat. Sci.* 39: 1235-1242.

Hauer, F.R., J.A. Stanford and J.V. Ward. 1989. Serial discontinuities in a rocky mountain river. II. Distribution and abundance of Trichoptera. *Reg. Riv. Res. Mgmt.* 3: 177-182.

Hawkes, H.A. 1975. River zonation and classification. Pp. 312-374. *In:* B.A. Whitton. Ed. *River Ecology.* Blackwell, London.

Hawkins, C.P., J.L. Kershner, P.A. Bisson, M.D. Byrant, L.M. Decker, S.V. Gregory, D.A. McCullough, C.K. Overton, G.H. Reeves, R.J. Steedman and M.K. Young. 1993. A hierarchical approach to classifying stream habitat features. *Fisheries* 18 (6): 3-12.

Hearne, J., I. Johnson and P. Armitage. 1994. Determination of ecologically acceptable flows in rivers with seasonal changes in the density of macrophyte. *Reg. Riv. Res. Mgmt.* 10: 9: 177-184.

Heeg, J. And C.M. Breen. 1982. *Man and the Pongola Floodplain.* S.A. Nat. Sci. Prog. Rpt. 56. 117 Pp.

Heggenes, J., A. Brabrand and S.J. Saltveit. 1990. A comparison of three methods for studies of stream habitat use by brown trout and Atlantic salmon. *Trans. Am. Fish. Soc.* 119: 101-111.

Heggenes, J. and S.J. Saltveit. 1990. Seasonal and spatial microhabitat selection and segregation in young Atlantic salmon (*Salmo salar* L.) and brown trout (*S.trutta* L.) in a Norwegian river. *J. Fish. Biol.* 36: 707-720.

Heggenes, J., A, S.J. Saltveit and O. Lingaas. 1996. Predicting fish habitat use to changes in water flow: modelling critical minimum flows for Atlantic salmon, *Salmo salar*, and brown trout, *S. trutta.* *Reg. Riv. Res. Mgmt.* 12: 331-344.

Heins, D.C. 1991. Variation in the reproductive investment among populations of the longnose shiner, *Notropis longirostris*, from contrasting environments. *Copeia* 3: 736-744.

Hempel, G. 1979. *Early Life History of Marine Fish.* University of Washington Press. Seattle. 70 Pp.

Heritage, G.L. and A.W. van Niekerk. 1994. Morphological response of the Sabie River to changing flow and sediment regimes. Pp. 389-402. *In: Proceedings: 50 Years of Water Engineering in South Africa.* S. Afr. Inst. Civ. Eng. Johannesburg.

Heritage, G.L. and A.W. van Niekerk. 1995. Drought conditions and sediment transport in the Sabie River. *Koedoe* 38(2): 1-9.

Heritage, G.L., van Niekerk, A.W., B.P. Moon and K. Kapur. 1995a. The influence of contemporary flow regime on the geomorphology of the Sabie River, South Africa. Paper delivered at *Proc. 7th S. Afr. Nat. Hydr. Symp. Hydrology and Water Resources in South Africa.* Grahamstown. 23 Pp.

Heritage, G.L., van Niekerk, A.W., B.P. Moon. 1995b. Classifying bedrock influenced semi-arid river systems: extending the continuum concept. *Symp. Int. Ass. of Geomorph.*, Singapore. September.

Heritage, G.L., A.W. van Niekerk and D.C. Weeks. 1996. A model of fish assemblage response to hydraulic and fluvial geomorphological change in a pool-rapid channel type. *Proc. 2nd IAHR Int. Symp. Hydr. Hab.* Quebec City, June 11 -14, 1996.

Heritage, G.L., A. W. van Niekerk and B.P. Moon.1997a. A comprehensive hierarchical classification system. *Geoöko plus.* 4: 75-84.

Heritage, G.L., A.W. van Niekerk, B.P. Moon, L.J. Broadhurst, K.H. Rogers and C.S. James, C.S. 1997b. *The Geomorphological Response to Changing Flow Regime of the Sabie and Letaba River Systems.* Water Research Commission Rpt. 376/1/96.

Heritage, G.L. and S.R. Pollard. In prep. A framework for assessing channel change within the context of habitat-assessments: a case study of the Marite River, South Africa.

Horowitz, R.J. 1978. Temporal variability patterns and the distributional patterns of stream fishes. *Ecol. Monogr.* 48: 307-321.

House, R.A. and P.L. Boehne. 1985. Evaluation of instream enhancement structures for salmonid spawning and rearing in a costal Oregan stream. *N. Am. J. Fish. Mgmt.* 5: 283-295.

Hubert and Rahel. 1989. Relations of physical habitat abundance to nongame fishes. *N. Am. J. Fish. Mgmt.* 9(3): 332-340.

Hunter, J.R. and S.R. Goldberg. 1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax. Fish. Bull.* US 77: 641-652.

Hunter, J.R. and B.J. Macewicz. 1980. Sexual maturity, batch fecundity, spawning fecundity, and temporal pattern of spawning for the northern anchovy, *Engraulis mordax*, during the 1979 spawning season. Calif. Coop. Oceanic Fish. Invest. Rep. 21: 139-149.

Hynes, H.B.N. 1970. *The Ecology of Running Waters.* Liverpool University Press.

Hynes, H.B.N. 1975. The river and its valley. *Verh. Int. Ver. Theor. Ang. Limn.* 17: 1-15.

Illies, J. and L. Botosaneanu. 1963. Problèmes et méthodes del la classification et de la zonation écologique des eaux couantes, considerées surtout du point de vue faunistique. Mitt. *Int. Ver. Limnol.* 12. 57 Pp. Cited in Ward 1986.

Infraplan. 1989. *Mhala Regional Planning Study.* Infraplan, Pretoria. 92 pp.

Irvine, J.R., I.G. Jowett and D. Scott. 1987. A test of the Instream Flow Incremental Methodology for underyearling rainbow trout (*Salmo gairdneri* Richardson) in man-made New Zealand streams. *N. Zeal. J. Mar. Freshw. Res.* 21: 35-40.

Ivlev, V.S. 1961. *Experimental Ecology of Feeding Fishes*. Yale University Press, Connecticut. 302 Pp.

Jackle, M.D. and P.J. Barrett. 1988. A statistical approach to determining sample size for species habitat preference curves. Pp. 21-70. *In:* K. Bovee and J.R. Zuboy. Eds. *Proceedings of A Workshop on the Development and Evaluation of Habitat Suitability Criteria*. U.S. Fish and Wildlife Service. Biol. Rpt. 88(11).

Jackson, P.B.N. 1989. Prediction of regulation effects on natural biological rhythms in south-central African freshwater fish. *Reg. Riv. Res. Mgmt.* 3: 205-220.

Jacobs, J. 1974. Quantitative methods of food selection: a modification of the forage ratio and Ivlev's electivity index. *Oecologia* 14: 413-417.

Jezewski, W.A. and C.P.R. Roberts. 1986. *Estuarine and Lake Freshwater Requirements*. DWA Tech. Rpt. No. TR 129. Govn. Printer Pretoria. 22 Pp.

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61(1): 65-71.

Johnson, R.A. 1981. Application of the guild concept to environmental impact analysis of terrestrial vegetation. *J. Envir. Mgmt.* 13: 205-222.

Johnson, B.L., W.B. Richardson and T.J. Naimo. 1995. Past, present, and future concepts in large river ecology. *Bioscience* 45(3): 134-141.

Johnson, D.L. and L.A. Nielsen. 1983. Sampling considerations. Pp. 1-21. *In:* L.A. Nielsen and D.L. Johnson. Eds. *Fisheries Techniques*. Am. Fish. Soc. Bethesda, MD.

Johnson, J.H. and P.A. Kucera. 1984. Summer-autumn habitat utilisation of sub-yearling steelhead trout in the tributaries of the Clearwater River, Idaho. *Can. J. Zool.* 63: 2283.

Jowett, I.G. 1982. The incremental approach to studying stream flows: New Zealand case studies. Pp. 9-15. *In:* R.H.S. McCall. Ed. *River Low Flows: Conflicts of Water Use*. Ministry of Works and Development, NZ Water and Soil Misc. Public. 47.

Jowett, I.G. 1997. Instream flow methods: a comparison of approaches. *Reg. Riv. Res. Mgmt* 13: 115-127.

Jowett, I.G. and J. Richardson. 1990. Microhabitat preferences of benthic invertebrates in a New Zealand river and the development of in-stream flow-habitat models for *Deleatidium* spp. *N.Z. J. Mar. Freshw. Res.* 24: 19-30.

Jowett, I.G., J. Richardson, B.J.F. Biggs, C.W. Hickey and J.M. Quinn. 1991. Microhabitat preferences of benthic invertebrates and the development of generalised *Deleatidium* spp. habitat suitability curves, applied to four New Zealand rivers. *N.Z. J. Mar. Freshw. Res.* 25: 187-199.

Jubb, R.A. 1967. Freshwater fishes of Southern Africa. Balkema, Cape Town. 248 Pp.

Junk, W.J., P.B. Bayley and R.E. Sparks. 1989. The flood-pulse concept in river floodplain systems. Pp. 110-127. *In:* D.P. Dodge. Ed. Proceedings of the International Large River Symposium (LARS). *Spec. Publ. Can. J. Fish. Aquat. Sci.* 106.

Karim, K., M.E. Gubbels and I.C. Goulter. 1995. Review of determination of instream flow requirements with special application to Australia. *Wat. Res. Bull.* 31(6): 1063-1077.

Karr, J.R. and D.R. Dudley. 1981. Ecological perspectives on water quality goals. *Envir. Mgmt.* 5: 55-68.

Kemp, J.L., D. M. Harper and G.A. Crosa. 1999. Use of 'functional habitats' to link ecology with morphology and hydrology in river rehabilitation. *Aq. Cons. Mar. Freshw. Ecos.* 9: 159-178.

Kershner, J.L. and W.M. Snider. 1992. Importance of habitat-level classification system to design instream flow studies. Pp. 180-193. *In:* P.J. Boon, P. Calow and G.E. Petts. *River Conservation and Management.* John Wiley & Sons Ltd, NY.

King, J.M., J.A. Day, B.R. Davies and M.P. Henshall-Howard. 1987a. Particulate organic matter in a mountain stream in the southwestern Cape, South Africa. *Hydrobiologia* 154: 165-187.

King, J.M., M.P. Henshall-Howard, J.A. Day and B.R. Davies and 1987b. Leaf pack dynamics in a South African mountain stream. *Can. J. Fish. Aquat. Sci.* 45: 2168-2181.

King, J.M. and J.H. O'Keeffe. 1989. Looking to the future- South Africas' requirements. *S.A. Nat. Sci. Rep.* No. 162: 110-116.

King, J.M. and D. Louw. 1995. *Development and Use of the Building Block Methodology for Assessing Instream Flow Requirements.* Southern Waters Report. Cape Town.

King, J.M. and R.E. Tharme. 1994. *Assessment of the Instream Flow Incremental Methodology and Initial Development of Alternative Instream Flow Methodologies for South Africa.* Report to Water Research Commission. No. 295/1/94.

King, J.M., R.E. Tharme and M.S. Devilliers. Eds. In press. *Environmental Flow Assessments for Rivers: Manual for the Building Block Methodology.* Water Research Commission Rpt.. Pretoria.

Kleynhans, C.J. 1984. *Die Verspreiding En Status Van Sekere Seldsame Vissorte Van Die Transvaal En Die Ekologie Van Sommige Spesies.* Unpubl. D.Sc. Dissertation. University of Pretoria. 265 Pp.

Kleynhans, C.J. 1986. The distribution, status and conservation of some fish species of the Transvaal. *S.Afr. J. Wildl. Res.* 16(4): 135-144.

Kleynhans, C.J. 1991. *Voorlopige Riglyne Vir Die Klassifisering Van Die Transvaalse Inheemse Vissorte in Die Sensitiwieteitsklasse.* Rpt. for Sensitive fish species Workshop, Skukuza, 23-25 Sept.

Kleynhans, C.J. and J.S. Engelbrecht. 1988. *A Preliminary Assessment of the Conservation Status and Fish Populations of the Olifants River (Limpopo System),* Transvaal. TPA Report, Pretoria.

Kolasa, J. and S.T.A. Pickett. 1991. Eds. *Ecological heterogeneity.* Springer- Verlag, NY.

Kolasa, J. And C.D. Rollo. 1991. Introduction: the heterogeneity of heterogeneity. A glossary. Pp. 1-23. *In:* J. Kolasa and S.T.A. Pickett. Eds. *Ecological heterogeneity.* Springer- Verlag, NY.

Kotliar, N.B. and J.A. Wiens. 1990. Multiple scale of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59: 253-260.

Kozel, S.J. and W.A. Hubert. 1989. Testing of habitat assessment models for small trout streams in the medicine Bow national Forest, Wyoming. *N. Am. J. Fish. Mgmt.* 9: 458-464.

Kraft, M.E. 1972. Effects of controlled flow reduction on a trout stream. *J. Fish. Res. Brd. Can.* 29: 1405-1411.

Krairapanond, N. and A. Atkinson. 1998. Watershed management in Thailand: Concepts, problems and implementation. *Aq. Cons. Mar. Freshw. Ecos.* 14: 485-498.

Kramer, D.L. 1978. Reproductive seasonality in the fishes of a tropical stream. *Ecology* 59(5): 976-985.

Lancaster, J. and L.R. Belyea. 1997. Nested hierarchies and scale dependence of mechanisms of flow refugium use. *J. N. Am. Benthol. Soc.* 16(1): 221-238.

Lamouroux, N., H. Capra and M. Pouilly. 1998. Predicting habitat suitability for lotic fish: Linking statistical hydraulic models with multivariate habitat use models. *Reg. Riv. Res. Mgmt.* 14: 1-11.

Landres, P.B. 1983. Use of the guild concept in environmental impact assessment. *Envir. Mgmt.* 7(5): 393-398.

Landres, P.B., J. Verner and J.W. Thomas. 1988. Ecological uses of vertebrate indicator species: A critique. *Cons. Biol.* 2(4): 316-328.

Lanka, R.P. and W.A. Hubert. 1987. Relations of geomorphology to stream habitat and trout standing stock in small rocky mountain streams. *Trans. Am. Fish. Soc.* 116: 21-28.

Lauth, R.R. 1988. Seasonal spawning cycle, spawning frequency, and batch fecundity of the cabezon, *Scorpaenichthys marmoratus*, in Puget Sound, Washington. *Fish. Bull.* 87: 145-154.

Layzer, J.B. and L.M. Madison. 1995. Microhabitat use by freshwater mussels and recommendations for determining their instream flow needs. *Reg. Riv. Res. Mgmt.* 10: 329-345.

Leopold, L.B., M.G. Wolmanand J.P. Miller. 1964. *Fluvial processes in geomorphology.* Freeman, San Francisco. 522 Pp.

Leonard, P.M., D.J. Orth and C.J. Goudreau. 1986. *Development of A Method for Recommending Instream Flows for Fishes in the Upper James River,* Virginia. Bull. 152. Virginia Water Resources Research Center. Virginia Poly. Ins. and State University.

Leonard, P.M. and D.J. Orth. 1988. Use of habitat guilds of fishes to determine instream flow requirements. *N. Am. J. Fish. Mgmt.* 8: 399-409.

Le Roux. P. and L. Steyn. 1968. *Fishes of the Traansvaal.* S.A. Breweries Inst. Pretoria. 108 Pp.

Levin 1992. The problem of pattern and scale in ecology. *Ecology* 73(6): 1943-1967.

Li, H. and J.F. Reynolds. 1994. A simulation experiment to quantify spatial heterogeneity in categorical maps. *Ecology* 75: 2446-2455.

Lillehammer, A. and Saltveit, S.J. 1984. Eds. *Regulated Rivers. Proc. 2nd Int. Symp. Reg. Riv.* Oslo University Press, Oslo. 540 Pp.

Loar, J.M., M.J. Sale, G.F. Cada, D.K. Cox, R.M. Cushman, G.K. Eddlemon, J.L. Elmore, A.J. Gatz, P. Kanciruk, J.A. Solomon and D.S. Vaughan. 1985. *Application of Habitat Evaluation Models in Southern Appalachian Trout Streams.* Oak Ridge Nat. Lab., Envir. Sci. Div., No. 2383. 310 Pp.

Lobb, D.M. and D.J. Orth. 1988. Microhabitat use by the bigmouth chub *Nocomis platyrhynchus* in the New River, West Virginia. *Am. Midl. Nat.* 120(1): 32-40.

Lobb, D.M. and D.J. Orth. 1991. Habitat use by an assemblage of fish in a large warmwater stream. *Trans. Am. Fish. Soc.* 120: 65-78.

Local Government Bush Buckridge Region South. 1998. *Local Development Objectives Report.* Internal document. South Africa. 94 Pp.

Locke, A. 1988. IFIM- microhabitat criteria development: data pooling considerations. Pp. 31-54. *In:* K. Bovee and J.R. Zuboy Eds. 1988. *Proceedings of A Workshop on the Development and Evaluation of Habitat Suitability Criteria.* U.S. Fish and Wildlife Service. Biol. Rpt. 88(11).

Lovejoy, T.E., J.M. Rankin, R.O. Bierregaard, K.S. Brown, L.H. Emmons and M. van der Voort. 1984. *Ecosystems Decay in Amazon Forest Remnants.* Pp. 45-78. *In:* M.H. Niteki. Ed. Extinctions. University of Chicago Press, Chicago.

Lowe-McConnell, R.H. 1979. Ecological aspects of seasonality in fishes of tropical waters. *Symp. Zool. Soc. Lond.* 44: 219-241.

Lowe-McConnell, R.H. 1987 a. *Ecological Studies in Tropical Fish Communities. Responses of Fish to Conditions in Tropical Waters.* University Press, Cambridge.

Lowe-McConnell, R.H. 1987 b. *Ecological Studies in Tropical Fish Communities. The African Fish Fauna.* University Press, Cambridge.

Maheshwari, B.L., K.F. Walker and T.A. McMahon. 1995. Effects of regulation on the flow regime of the River Murray, Australia. *Reg. Riv. Res. Mgmt.* 10:15-38.

MacArthur, R.H. and E.O. Wison. 1967. *The Theory of Island Biogeography.* Princeton University Press, Princeton.

Maddock, I. 1999. The importance of physical habitat assessment for evaluating river health. *Freshw. Biol.* 41: 373 - 391.

Maddock, I. and D. Bird. 1996. The application of habitat mapping to identify representative PHABSIM sites on the River Tavy, Devon, U.K. *Proc. 2nd IAHR Int. Symp. Hydr. Hab.* Quebec City, June 11 -14, 1996.

Mahon, R. 1984. Accuracy of catch-effort methods for estimating fish density and biomass in streams. *Biol. Fish.* 5(4); 343-360.

Mancy, K.H. 1979. The environmental impact of the Aswan High Dam. *In:* E.E. Driver and W.O. Wunderlich. Eds. *Environmental Effects of Hydraulic Engineering Works.* Tennessee Valley Authority, Knoxville, Tennessee. P. 422-434.

Mason SJ. 1994. *Climatic change over the lowveld of South Africa.* Climatology Research Group Paper, University of the Witwatersrand, Johannesburg. 53 Pp.

Mathur, D., W.H. Bason and J. Downing. 1983. Discussion. "Estimated flow requirements for the fishes of the Washita river below Foss Reservoir, western Oklahoma," by Donald J. Orth and O. Eugene Maughan. *Wat. Res. Bull.* 19(3): 499-502.

Mathur, D., W.H. Bason, E.J. Purdy, and C.A. Silver. 1985 a. A critique of the Instream Flow Incremental Methodology. *Can. J. Fish. Aquat. Sci.* 42:825-831.

Mathur, D., W.H. Bason, E.J. Purdy, and C.A. Silver. 1985 b. Reply to "In defence of the Instream Flow Incremental Methodology" by D.J. Orth and O.E. Maughan. 198? *Can. J. Fish. Aquat. Sci.* 43: 1093-1094.

McClendon, D.D. and C.F. Rabeni. 1987. Physical and biological variables for predicting population characteristics of smallmouth bass and rock bass in an Ozark stream. *N. Am. J. Fish. Mgmt.* 7: 46-56.

McCully, P. 1996. *Silenced Rivers. The Ecology and Politics of Large Dams.* Zed Books. London.

McDonnell, M. J. and S.T.A. Pickett. Eds. 1993. *Humans As Components of Ecosystems: the Ecology of Subtle Human Effects and Populated Areas.* Springer-Verlag, NY.

McIntyre, N.E. and J.A. Wiens. 1999. How does habitat patch size affect animal movement? An experiment with darkling beetles. *Ecology* 80(7). 2261-2270.

Merron, G.S. and M.N. Bruton. 1993. Implications for water release from the Pongolapoort dam for the fish and fishery of the Pongolo floodplain, Zululand. *S. Afr. J. Aq. Sci.* 19: 1/2: 35-49.

Mérigoux, S. and D. Ponton. 1999. Spatio-temporal distribution of young fish in tributaries of natural and flow-regulated sections of a neotropical river in French Guiana. *Freshw. Biol.* 42: 177-198.

Middaugh, D.P. amd M.J. Hemmer. 1992. Reproductive ecology of the inland silverside, *Menidia beryllina*, (Pisces: Atherinidae) from Blackwater Bay, Florida. *Copeia* 1992(1): 53-61.

Milhous, R.T. 1982. *The Application of the Physical Habitat Simulation System to Natural Resources Management.* Summer Computer Simulation Conference. Fort Collins.

Milhous, R.T. 1986. Development of a habitat time series. *J. Water Resources Plan. Mgmt.* 112(1): 145-148.

Milhous, R.T., D.L. Wegener and T. Waddle. 1984. *Users Guide to the Physical Habitat Simulation System (PHABSIM).* U.S. Fish & Wildlife Serv., Instream Flow Info Paper. 11. FWS/OBS-81/43. Washington, D.C.

Milhous, R.T., M. Updike and D. Schneider. 1989. *User's Guide to the Physical Habitat Simulation (PHABSIM)- Version II.* U.S. Fish and Wildlife Service, Biol. Rep. Instream Flow Info. Paper 26.

Milhous, R.T., J.M. Bartholow, M.A. Updike and A.R. Moos. 1990. *Reference Manual for Generation and Analysis of Habitat Time Series- Version Ii.* U.S. Fish and Wildlife Service, Biol. Rep. 90(16).

Milton, D.A. and S.J.M. Blaber. 1991. Maturation, spawning seasonality, and proximate spawning stimuli of six species of tuna baitfish in the Solomon Islands. *Fish. Bull., US.* 89: 221-237.

Minckley, W.L. and J.E. Deacon. 1968. Southwestern fishes and the enigma of 'endangered' species. *Science.* 159: 1424-1432.

Minshall, G.W. 1984. Aquatic insect-substratum relationships. Pp. 358-400. *In:* V.H. Resch and D.M. Rosenberg. Eds. *The Ecology of Aquatic Insects.* Praeger, NY.

Minshall, G.W. 1988. Stream ecosystem theory: a global perspective. *J. N. Am. Benthol. Soc.* 7(4): 263-288.

Minshall, G.W., K.W. Cummins, R.C. Peterson, C.E. Cushing, D.A. Bruns, J.R. Sedell and R.L. Vannote. 1985. Developments in stream ecosystem theory. *Can. J. Fish. Aquat. Sci.* 42: 1045-1055.

Montgomery, D.R. 1999. Process domains and the river continuum. *J. Am. Water Res. Ass.* 35(2): 397-410.

Moon, B.P., A.W. van Niekerk, G.L. Heritage, K.H. Rogers and C.S. James. 1997. A geomorphological approach to the management of rivers in the Kruger National Park: The case of the Sabie River. *Trans. Inst. Brit. Geogr.* 22: 31-48.

Morantz, D.L., R.K. Sweeney, C.S. Shirvell and D.A. Longard. 1987. Selection of microhabitat in summer by juvenile Atalntic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* 44: 120-129.

Mordhart, J.E. 1986. *Instream Flow Methodologies.* Report of research project 2194-2. Electric Power Research Institute, Palo Alto, Ca. 86 Pp.

Morin, A., P. Harper and R.H. Peters. 1986. Microhabitat- Preference Curves of Blackfly larvae (Diptera: Simuliidae): A comparison of three estimation methods. *Can. J. Fish. Aquat. Sci.* 43: 1235-1241.

Mosley, M.P. 1985. River channel inventory, habitat and instream flow assessment. *Prog. Phys. Geogr.* 9(4): 491-523.

Mosley, M.O. 1987. The classification and characterisation of rivers. Pp. 342-380. K. Richards. Ed. *River Channels Environment and Process.* Blackwell, Oxford.

Mosley, M.P. and I.G. Jowett. 1985. Fish habitat analysis using river flow simulation. *N.Z. J. Mar. Freshw. Res.* 19: 293-309.

Moyle, P.B. and D.M. Baltz. 1985. Microhabitat use by an assemblage of California stream fishes: developing criteria for instream flow determinants. *Trans. Am. Fish. Soc.* 114: 695-704.

Moyle, P.B. and B. Vondracek. 1985. Persistence and structure of the fish assemblage in a small california stream. *Ecology* 66(1): 1-13.

Muncy, R.J., G.J. Atchison, R.V. Bulkley, B.W. Menzel, L.G. Perry and R.C. Summerfelt. 1979. *Effects of Suspended Solids and Sediment on Reproduction of Early Life History Stages of Warmwater Fishes: A Review.* US. Environmental Protection Agency, Corvallis, Oregon. EPA 600/3-79-042.

Naiman, R.J. and H. Décamps. Eds. 1990. *The Ecology and Management of Aquatic-terrestrial Ecosystems.* UNESCO , Paris and Parthenon Publ. Group, UK.

Naiman, R.J., D.G. Lonzarich, T.J. Beechie and S.C. Ralph. 1992. General principles of classification and the assessment of conservation potential in rivers. Pp. 93-123. *In:* P.J. Boon, P. Calow and G.E. Petts. *River Conservation and Management.* John Wiley & Sons Ltd, NY.

Newson, M.D. and C.L. Newson. 2000. Geomorphology, ecology and river channel habitat: mesoscale approaches to basin-scale challenges. *Prog. Phys. Geogr.* 24: 195-217.

Neel, J.K. 1963. Impact of reservoirs. Pp. 575-593. *In:* D.G. Fey. Eds. *Limnology in North America.* University of Wisconsin Press, Wisconsin. USA.

Nestler, J.M. 1990. *Considerations in Applying IFIM to Warmwater Streams. Pp. 34-35. In:* M. B. Bain. Ed. *Ecology and Assessment of Warmwater Streams; Workshop Synopsis.* U.S. Fish and Wildlife Service, Biol. Rep. 90(5).

Nestler, J.M., R.T. Milhous and J.B. Layzer. 1989. Instream habitat modelling techniques. Pp. 295-315. *In:* J.A. Gore and G.E. Petts. Eds. *Alternatives in Regulated River Management.* CRC Press Inc., Boca Raton, Fl.

Nestler, T.P., R.T. Muth and A.F. Wasowicz. 1988. Evidence for baseline flow spikes as spawning cues for Colorado squawfish in the Yampa River, Colorado. *Am. Fish. Soc. Symp.* 5: 68-79.

Neu, C.W. C.R. Byers and J.M. Peek. 1974. A technique for analysis of utilisation-availability data. *J. Wildl. Mgmt.* 38: 541-545.

Neves, R.J. and P.L. Angermeier. 1990. Habitat alteration and its effects on native fishes in upper Tennessee. *J. Fish. Biol.* Supp. A: 45-52.

Newbold, J.D., R.V. O'Neill, J.W. Elwood and W. van Winkle. 1982. Nutrient spiralling in streams: implications for nutrient limitation and invertebrate activity. *Am. Nat.* 120: 628 652.

Ni, I-H. and E.J. Sandeman. 1984. Size at maturity for Northwest Atlantic Redfishes (Sebastes). *Can. J. Fish. Aquat. Sci.* 41: 1753-1762.

Nikolsky, G.V. 1963. *The Ecology of Fishes.* Acad. Press. London. 352 Pp.

Northcote, T.G., M.S. Arcifa and O.Froehlich. 1985. Effects of impoundment and drawdown on the fish community of a South American river. *Verh. Internat. Verein. Limnol.* 22: 2704-2711.

Odum, E.P. 1971. *Fundamentals of Ecology.* Saunders, Philadelphia.

O'Keeffe, J.H. 1990. A review of river research in southern Africa since 1900. Pp. 96-163. *In:* B.R. Allanson, R.C. Hart, J.H. O'Keeffe and R.D. Robarts. *Inland Waters of Southern Africa: An Ecological Perspective.* Kluwer Academic Publishers. Netherlands.

O'Keeffe, J.H. and B.R. Davies. 1991. Conservation and management of the rivers of the Kruger National Park: suggested methods for calculating instream flow needs. *Aquat. Conserv. Mar. Freshw. Ecos.* 1: 1-17.

O'Keeffe, J.H., B.R. Davies, J.M. King and P.H. Skelton. 1989 a. The conservation status of South African Rivers. *In:* B.J. Huntley. Ed. *Biotic Diversity in Southern Africa.* Oxford University Press, Cape Town.

O'Keeffe, J.M. King, J.A. Day, O. Roussouw, D.W. van der Zel and R. Skoroszewski. 1989 b. Pp. 41-56. *In:* A.A. Ferrar. Ed. *General Concepts and Approaches to Instream Flow Assessment.* S. Afr. Nat. Sci. Prog. Rep. No. 162.

O'Keeffe, J.H., R.W. Palmer, B.A. Byren and B.R. Davies. 1990. The effects of impoundments on the physicochemistry of two contrasting Southern African river systems. *Reg. Riv. Res. Mgmt.* 5: 97-110.

O'Keeffe JH, D.C. Weeks, A. Fourie and BR Davies. 1996. *The Effects of Proposed Impoundments and Management Recommendations. A Pre-impoundment Study of the Sabie Sand River System, Eastern Transvaal with Special Reference to the Predicted Impacts on the Kruger National Park.*

Vol. 3. Pp 111. Water Research Commission Rpt. 294/3/96.

Olofin, E.A. 1988. Monitoring the impact of dams on the downstream physical environment in the tropics. *Reg. Riv. Res. Mgmt.* 2: 167-174.

Orth, D.J. 1987. Ecological considerations in the development and application of instream flow-habitat models. *Reg. Rivers: Res. Manag.* 1: 171-181.

Orth, D.J. and P.M. Leonard. 1990. Comparison of discharge methods and habitat optimization for recommending instream flows to protect fish habitat. *Reg. Riv. Res. Mgmt.* 5: 129-138.

Orth, D.J. and O.E. Maughan. 1981. Estimated flow requirements for fishes of the Washita river below Foss Reservoir, western Oklahoma. *Wat. Res. Bull.* 17(5): 831-843.

Orth, D.J. and O.E. Maughan. 1982. Evaluation of the incremental methodology for recommending instream flows for fishes. *Trans. Am. Fish. Soc.* 111: 413-445.

Orth, D.J. and O.E. Maughan. 1983. Reply to "Discussion by D. Mathur, W.H. Bason and J. Downing. `Estimated flow requirements for fishes of the Washita river below Foss Reservoir, western Oklahoma'". *Wat. Res. Bull.* 9(3): 501.

Orth, D.J. and O.E. Maughan. 1986. In defence of the Instream Flow Incremental Methodology. *Can. J. Fish. Aquat. Sci.* 43: 1092.

Padmore, C.L., M.D. Newson and M.E. Charlton. 1996. Instream habitat in gravel bed rivers: identification and characterisation of biotopes. *Proc. IV Gravel Bed Rivers Workshop.* University of Oregon.

Padmore, C.L. 1997. *Physical Biotopes in Representative River Channels: Identification, Hydraulic Characterisation and Application.* Unpubl. Ph.D. Thesis, University of Newcastle upon Tyne.

Palmer, C.G. 1991. *Benthic Assemblage Structure, and Feeding Biology of 16 Macroinvertebrate Taxa From the Buffalo River, Eastern Cape, South Africa.* Unpubl. Ph.D. thesis. Rhodes University, Grahamstown. 257 Pp.

Palmer, M., C.C. Hakenkamp and K. Nelson-Barker. 1997. Ecological heterogeneity in streams: Why variance matters. *J. N. Am. Benthol. Soc.* 16(1): 189-202.

Palmer, M. and N.L. Poff. 1997. Heterogeneity in streams. The influence of environmental heterogeneity on patterns and processes in streams. *J. N. Am. Benthol. Soc.* 16(1): 169-173.

Palmer, R. and J.H. O'Keeffe. 1990 a. Downstream effects of impoundments on the water chemistry of the Buffalo River (eastern Cape), South Africa. *Hydrobiologia* 202:71-83.

Palmer, R. and J.H. O'Keeffe. 1990 b. Transported material in a small river with multiple impoundments. *Freshw. Biol.* 24: 563-575.

Pearce, F. 1992. *The Dammed. Rivers, Dams and the Coming World Water Crisis.* The Bodley Head, London.

Peters, J.C. 1982. Effects of river and streamflow alteration on fishery resources. *Fisheries.* 7(2): 20-22.

Petitjean, M.O.G. and B.R. Davies. 1988. Ecological impacts of inter-basin transfer: some case studies, research requirements and assessment procedures in southern Africa. *S. Afr. J. Sci.* 84:819-828.

Petts, G.E. 1980. Longterm consequences of upstream impoundments. *Envir. Conserv.* 7: 325-332.

Petts, G.E. 1984. *Impounded Rivers.* Wiley, Chichester. 326 Pp.

Petts, G.E. and I. Maddock. 1994. Flow allocation for in-river needs. Pp. 289-307. *In:* P. Calow and G.E. Petts. Eds. *The Rivers Handbook: Hydrological and Ecological Principles.* Blackwell Sci. Pubs., Oxford.

Pickett, S.T.A. 1996. Natural processes. Pp. 1-22. *In:* P.A. Opler. Ed. *National Status and Trends of Our Living Resources.* National Biological Service. Washington, DC.

Pickett, S.T.A. and M.L. Cadenasso. 1995. Landscape ecology: spatial heterogeneity in ecological systems. *Science* 269: 331-334.

Pickett, S.T.A. and K.H. Rogers. 1997. Patch dynamics: the transformation of landscape structure and function. Pp. 101-127. *In:* J.A. Bisonette. *Wildlife and Landscape Ecology.* Springer-Verlag, NY.

Pickett, S.T.A. and P.S. White. Eds. 1985. *The Ecology of Natural Disturbance and Patch Dynamics.* Academic Press, Orlando, Florida, USA.

Pickett, S.T.A., W.R. Burch and J.M. Grove. 1999. Interdisciplinary research: Maintaining the constructive impulse in a culture of criticism. *Ecosystems:* 2: 302 - 307.

Pickett, S.T.A., J. Kolasa, J.J. Armesto and S.L. Collins. 1989. The ecological concept of disturbance and its expression at various hierarchical levels. *Oikos* 54: 129-136.

Pienaar, D.J., J. du P. Bothma and G.K. Theron. 1992. Landscape preferences of the white rhinoceros of the southern Kruger National Park. *Koedoe* 35(1): 1-7.

Pienaar, U. de V. 1978. *The Freshwater Fishes of the Kruger National Park.* National Parks Board of South Africa. 91 Pp.

Pienaar U. de V. 1985. Indications of progressive desiccation of the Transvaal lowveld over the past 100 years, and implications for the water stabilisation programme of the Kruger National Park. *Koedoe* 28: 93-165.

Pitchford, R.J. and P.S. Visser. 1975. The effects of large dams on river water temperature, with special reference to bilharzia and the Verword Dam. *S. Afr. J. Sci.* 71: 212- 213.

Platts, W.S., R.J. Torquemada, M.L. McHenry and C.K. Graham. 1989. Changes in salmon spawning and rearing habitat from increased delivery of fine sediment to the South Fork Salmon River, Idaho. *Trans. Am. Fish. Soc.* 118: 274-283.

Poff, N.L. and K. Nelson-Barker. 1997. Habitat heterogeneity and algal-grazer interaction in stream: explorations with a spatially explicit models. *J. N. Am. Benthol. Soc.* 16(1): 263-276.

Poizat, G. and D. Pont. 1996. Multi-scale approach to species-habitat relationships: juvenile fish in a large river section. *Freshw. Biol.* 36: 611-622.

Polis, G.A. 1984. Age structure component of niche and width and intraspecific resource partitioning: can age groups function as ecological species? *Am. Nat.* 123: 541-564.

Pollard, P. and M. Huxham. 1998. The European water directive framework: a new era in the management of aquatic ecosystems health? *Aq. Cons. Mar. Freshw. Ecos.* 8: 773-792.

Pollard, S.R. and J.Juritz. In prep. The selection of instream habitats: physical variables that define suitable microhabitat for the pennant-tailed catlet, *Chiloglanis anoterus.*

Pollard, S.R., Weeks, D.C., and A.Fourie. 1996. *Effects of the 1992 Drought on Fish and Invertebrates of the Sabie- Sand Rivers.* Vol. II. Water Research Commission Rpt. 294/2/96. 135 Pp.

Pollard, S.R.; J.C. Perez de Mendiguren; A. Joubert; C.M. Shackleton; P. Walker; T. Poulter and M. White. 1998. *Save the Sand: Phase I. Feasibility Study: The Development of A Proposal for A Catchment Plan for the Sand River Catchment.* Department of Water Affairs and Forestry; Department of Agriculture and Land Affairs. 280 Pp.

Power, M.E. 1984a. Depth distributions of armoured catfish: predator-induced resource avoidance? *Ecology* 65: 523-528.

Power, M.E. 1984b. Habitat quality and the distribution of algae-grazing catfish in a Panamanian stream. *J. Anim. Ecol.* 53: 357-374.

Power, M.E. 1987. Predator avoidance by grazing fishes in temperate and tropical streams: importance of stream depth and prey size. Pp. 333-353. *In:* W.C. Kerfoot and A. Sih. Eds. *Predation: Direct and Indirect Impacts on Aquatic Communities.* University of New England Press, New Hampshire.

Pringle, C.M. 2000. River conservation in tropical versus temperate latitudes. Pp. 371-384. *In:* P.J. Boon, B.R. Davies and Petts. Eds. *Global Perspectives on River Conservation. Science, Policy and Practice.* John Wiley & Sons Ltd, NY.

Pringle, C.M., R.J. Naiman, G. Bretschko, J.R. Karr, M.W. Oswood, J.R. Webster, R.L. Welcomme and M.J. Winterbourn. 1988. Patch dynamics in lotic systems: the stream as a mosaic. *J. N. Am. Benthol. Soc.* 7(4): 503 - 524.

Prochazka, K. B.A. Stewart and B.R. Davies. 1991. Leaf litter retention and its implications for shredder distribution in two headwater streams. *Arch. Hydrobiol.* 120: 315-325.

Pusey, B.J., M.J. Kennard and A.H. Arthington. 2000. Discharge variability and the development of predictive models relating stream fish assemblage structure to habitat in northeastern Australia. *Ecol. Freshwater Fish* 2000: 30-50.

Ractliffe, G. 1991. *The Influence of Discharge on Bank Litter in Langrivier, A South-western Cape Stream.* Unpubl. B.Sc. (Hons.) thesis. Freshwater Research Unit, University of Cape Town. 27 Pp.

Raleigh, R.F. and L.D. Zuckerman. 1986. *Habitat Suitability Index Models and Instream Flow Suitability Curves: Brown Trout.* U.S. Fish and Wildl. Ser. Biological Report 82(10.124).

Ramadan, F. 1979. The environmental impact of the Aswan High Dam. Pp. 446-458. *In:* E.E. Driver and W.O. Wunderlich. Eds. *Environmental Effects of Hydraulic Engineering Works.* Tennessee Valley Authority, Knoxville, Tennessee.

Republic of South Africa. 1996. The constitution of South Africa (Act 108 1996). *Govn. Gaz.* South Africa.

Republic of South Africa. 1996. The Water Act. (Act 36. 1998). *Govn. Gaz.* South Africa.

Republic of South Africa. 1997. White Paper on national water policy (Act 92 1997). *Govn. Gaz.* South Africa.

Resh, V.H., A.V. Brown, A.P. Covich, M.E. Gurtz, H.W. Li, G.W. Minshall, S.R. Reice, A.L. Sheldon, J.B. Wallace and R.C. Wissmar. 1988. The role of disturbance in stream ecology. *J. N. Am. Benthol. Soc.* 7(4): 433-455.

Richards, C., L.B. Johnson and G. E. Host. 1996. Landscape-scale influences on stream habitats and biota. *Can. J. Fish. Aquat. Sci.* 53(1): 295-311.

Richardson, B.A. 1986. Evaluation of instream flow methodologies for freshwater fish in New South Wales. Pp. 42-58. *In:* I.C. Cambell. Ed. *Stream Protection. The Management of Rivers for Instream Uses.* Water Studies Centre. Chisholm Ins. Tech. Australia.

Rimmer, D.M. 1985. Effects of reduced discharge on the production and distribution of age-0 rainbow trout in semi-natural channels. *Trans. Am. Fish. Soc.* 114: 388-396.

Rimmer, D.M., U. Paim and R.L. Saunders. 1984. Changes in the selection of microhabitat by juvenile Atlantic salmon (*Salmo salar*) at the summer-autumn transition in a small river. *Can. J. Fish. Aquat. Sci.* 41: 469-475.

Rogers, K.H. 1980. The vegetation of the Pongola floodplains: Distribution and utilisation. Pp. 69-77. *In:* M.N. Bruton and K.H. Cooper. Eds. *Studies on the Ecology of Maputaland.* Rhodes University and the Natal Branch, Wildl. Soc. S. Afr.

Rosgen, D.L. 1994. A classification of natural rivers. *Catena* 22 (194) 169-199.

Roberts, C.P.R. 1983. Environmental constraints on water resources development. Pp. 16-23. *Proc. S. Afr. Inst. Civil Eng.* Cape Town.

Root, R.B. 1967. The niche exploitation pattern of the blue-grey gnatcatcher. *Ecol. Monogr.* 37: 317-350.

Rowntree, K.M. 1996. *The Hydraulics of Physical Biotopes: Terminology, Inventory and Calibration.* Report of a workshop held in Citrusdal, 4 - 7 February 1995. Water Research Commission Rpt. KV84/96. Pretoria.

Rowntree, K.M. and R.A. Wadeson. 1996. Translating channel morphology into hydraulic habitat: application of the hydraulic biotope concept to an assessment of discharge related habitat changes. *Proc. 2nd IAHR Int. Symp. Hydr. Hab.* Quebec City, June 11 -14, 1996.

Rowntree, K.M. and R.A. Wadeson. 1999. *A Hierarchical Geomorphological Model for the Classification of Selected South African Rivers.* Water Research Commission Rpt. 497/1/99, Pretoria. 334 Pp.

Rulifson, R. and C.S. Manooch. 1990. Recruitment of juvenile stripped bass in the Roanoke river, North Carolina, as related to reservoir discharge. *N. Am. J. Fish. Mgmt.* 10: 397-407.

Russell, I.A. and K.H. Rogers. 1989. The distribution and composition of fish communities in the major rivers of the Kruger National Park. *In:* S. Kienzle and H. Maaren. Eds. *Proc. 4th S. Afr. Nat. Hydrol. Symp.* University Pretoria.

Rutherford, M.C. and R.H. Westfall. 1986. Biomes of South Africa- An objective categorisation. *Mem. Bot. Surv. S. Afr.* 54: 1-98.

Saltveit, S.J. and A. Babrand. 1985. Predicting the effects of possible temperature increase due to stream regulation on the eggs of whitefish (*Coregonus laveretus*)- a laboratory approach. Pp. 219-228. *In:* J.F. Craig and J.B. Kemper. Eds. *Regulated streams: Advances in Ecology.* Plenum Press, NY.

Scarnecchia, D.L. and E.P. Bergersen. 1987. Trout production and standing crop in Colorado's small streams, as related to environmental features. *N. Am. J. Fish. Mgmt.* 7(3): 315-330.

Schlosser, I.J. 1982 a. Fish community structure and function along two habitat gradients in a headwater stream. *Ecol. Monogr.* 52(4): 395-414.

Schlosser, I.J. 1982 b. Trophic structure, reproductive success, and growth rate of fishes in a natural and modified headwater stream. *Can. J. Fish. Aquat. Sci.* 39: 968-978.

Schlosser, I.J. 1985. Flow regime, juvenile abundance, and the assemblage structure of stream fishes. *Ecology* 66:1484-1490.

Schlosser, I.J. 1987. The role of predation in age- and size-related habitat use by stream fishes. *Ecology* 68: 651-659.

Schlosser, I.J. 1990 a. Environmental variation, life history attributes and community structure in stream fishes: implications for environmental management and assessment. *Envir. Mgmt.* 14(5): 621-628.

Schlosser, I.J. 1990 b. A pluralistic view of factors influencing warmwater stream fishes: Implications for environmental management. Pp. 14-15. *In:* M.B. Bain. Ed. *Ecology and Assessment of Warmwater Streams; Workshop Synopsis.* U.S. Fish and Wildlife Service, Biol. Rep. 90(5).

Schlosser, I.J. and K.K. Ebel. 1989. Effects of flow regime and cyprinid predation on a headwater stream. *Ecol. Monogr.* 59: 41-57.

Scott, D. and C.S. Shirvell. 1985. A critique of Instream Flow Incremental Methodology and observations on flow determination in New Zealand. Pp. 27-46. Craig, J.F. and J.B. Kemper. Eds. 1985. *Regulated streams: Advances in Ecology.* Plenum Press, NY.

Scullion, J. 1983. Effects of impoundments on downstream bed materials of two upland rivers in mid-Wales and some ecological implications of such effects. *Arch. Hydrobiol.* 96(3): 239-344.

Severinghaus, W.D. 1981. Guild theory development as a mechanism for assessing environmental impact assessment. *Envir. Mgmt.* 5: 187-190.

Shackleton, C.M. 1993. Demography and dynamics of the dominant woody species in a communal and protected area of the eastern Transvaal lowveld. *S. Afr. J. Bot.* 59: 569-574.

Sheppard, J.D. and J.H. Johnson. 1985. Probability-of-use for depth, velocity and substrate by subyearling coho salmon and steelhead in Lake Ontario tributary streams. *N. Am. J. Fish. Mgmt.* 5: 277-282.

Sheppe, W.A. 1985. Effects of human activities on Zambia's Kafue Flats ecosystem. *Envir. Conserv.* 12: 49-57.

Shirvell, C.S. 1986. Pitfalls of physical habitat simulation in the Instream Flow Incremental Methodology. *Can. Tech. Rep. Fish. Aquat. Sci.* No. 1460.

Shirvell, C.S. 1989. Ability of PHABSIM to predict chinook salmon spawning habitat. *Reg. Riv. Res. Mgmt.* 3: 277-289.

Shirvell, C.S. and R.G. Dungey. 1983. Microhabitats chosen by brown trout for feeding and spawning in rivers. *Trans. Am. Fish. Soc.* 112(3): 355-367.

Shirvell, C.S. and D.L. Morantz. 1983. Assessment of the Instream Flow Incremental Methodology for Atlantic Salmon in Nova Scotia. *Trans. Can. Elect. Assoc., Eng. Oper. Div.,* 22: 83-H-108: 22 Pp.

Shrode, J.B. and S.D. Gerking. 1977. Effects of constant and flucruating temperatures on reproductive performance of a desert pupfish, *Cyprinodon n. nevadensis. Physiol. Zool.* 50: 1-10.

Simons, D.B. 1979. Effects of stream regulation on channel morphology. Pp. 95-111. *In:* J.W. Ward and J.A. Stanford. Eds *The Ecology of Regulated Streams.* Plenum Press, NY. 398 Pp.

Skelton, P.H. 1987. *South African Red Data Book- Fishes.* S. Afr. Nat. Sci. Prog. Rpt. No. 137. FRD, CSIR.

Slauson, W.L. 1988. Constructing suitability curves from data. Pp. 225-255. *In:* K. Bovee and J.R. Zuboy. Eds. 1988. *Proceedings of A Workshop on the Development and Evaluation of Habitat Suitability Criteria.* U.S. Fish and Wildlife Service. Biol. Rpt. 88(11).

Slauson, W.L. 1990. *Problems with Preference.* Internal Report. TGS technology, Inc., Fort Collins, Colorado. 30 Pp.

Smith, R.E. and D.F. Scott. 1992. The effects of afforestation on low flows in various parts of the catchment. *Water SA* 18(3): 185-194.

Snaddon, C.D., B.A. Stewart and B.R. Davies. 1992. The effects of discharge on two headwater streams. *Arch. Hydrobiol.* 125: 109-120.

Snyder, D.E. 1983. Fish eggs and larvae. Pp. 165-197. *In:* L.A. Nielsen and D.L. Johnson. Eds. *Fisheries Techniques.* Am. Fisheries Society. Bethesda, MD.

Snyder, D.E. 1990. Fish larvae- ecologically distinct organisms. Pp. 20-23. *In:* M.B. Bain. *Ed. Ecology and Assessment of Warmwater Streams; Workshop Synopsis.* U.S. Fish and Wildlife Service, Biol. Rep. 90(5).

Sokal, R.R. and F.J. Rohlf. 1995. *Biometry.* 3rd edition. Freeman, NY. 859 Pp.

Soltero, R.A., Wright, J.C. and Horpestad, A.A. 1973. Effects of impoundments on water quality of Bighorn River. *Water Res.* 7: 343-354.

Southwood, T.R.E. 1988. Tactics, strategies and templets. *Oikos* 52: 3-18.

Spence, J.A. and H.B.N. Hynes. 1971. Differences in fish populations upstream and downstream of a mainstrean impoundment. *J. Fish. Res. Brd. Can.* 28: 45-46.

Spence, J.A. and H.B.N. Hynes. 1971. Differences in benthos upstream and downstream of a mainstrean impoundment. *J. Fish. Res. Brd. Can.* 28: 35- 43.

SPSS. 1996. *SPSS Inc., Version 7.5.* Philadelphia. 1996.

Stalnaker, C.B. 1979. The use of habitat structure preferenda for establishing flow regimes necessary for the maintenance of fish habitat. Pp. 321-337. *In:* J.W. Ward and J.A. Stanford. Eds *The Ecology of Regulated Streams.* Plenum Press, NY. 398 Pp.

Stalnaker, C.B. 1981. Low flow as a limiting factor in warmwater streams. Pp. 192-199. *In:* L.A. Krumholz. Ed. *Warmwater Streams Symposium.* Am. Fish. Soc. Bethesda, MD.

Stalnaker, C.B. 1982. Instream flow assessments come of age in the decade of the 1970's. *In:* W.T. Mason and S. Iker. Eds. *Research on Fish and Wildlife Habitat.* U.S. Envir. Prot. Agency. EPA-600/8-82-002.

Stalnaker, C.B. 1990. Minimum flow is a myth. Pp. 31-33. *In:* M.B. Bain. Ed. *Ecology and Assessment of Warmwater Streams; Workshop synopsis.* U.S. Fish and Wildlife Service, Biol. Rep. 90(5).

Stalnaker, C.B. 1994. Evolution of Instream Flow Habitat Modelling. Pp. 276- 286. *In:* P. Calow and G.E. Petts. Eds. *The Rivers Handbook: Hydrological and Ecological Principles.* Blackwell Sci. Pubs. Oxford.

Stalnaker, C.B. and S.C. Arnette. 1976. *Methodologies for the Determination of Stream Resource Flow Requirements: An Assessment.* US Fish and Wildlife Services, Office of Biological Services Western Water Association. 199 Pp.

Stalnaker, C.B., K.D. Bovee and T.J. Waddle. 1996. Importance of the temporal aspects of habitat hydraulics to fish population studies. *Reg. Riv. Res. Mgmt.* 12: 145-153.

Stalnaker, C., B.L. Lamb, J. Henriksen, K. Bovee and J. Bartholow. 1995. *The Instream Flow Incremental Methodology: A Primer for IFIM.* Biol. Rpt. Nat. Biol. Serv. US Dept. Int. 29: 1-44.

Stanford, J.A. 1989. *Flow Alteration and Ecosystem Stability in the Gunnison River, Colorado: A Perspective.* Open file report 105-89. Flathead Lake Biological Station, University of Montana. Montana.

Stanford, J.A. and J.V. Ward. 1984. The effects of regulation on the limnology of the Gunnison River: A North American case history. Pp. 467-480. *In:* A. Lillehammer and S.J. Saltveit. Eds. *Regulated Rivers. Proc. 2nd Int. Symp. Reg. Riv.* Oslo University Press, Norway.

Stanford, J.A. and J.V. Ward. 1986. Fishes of the Colorado system. Pp. 385-402. *In:* B.R. Davies and K.F. Walker. Eds. *The Ecology of River Systems.* Monogr. Biolog. 60. Dr. W. Junk. Dordrecht. 793 Pp.

Stanford, J.A. and J.V. Ward. 1988. The hyporheic habitat of river ecosystems. *Nature* 335: 64-66.

Stanford, J.A. and J.V. Ward. 1992. Management of aquatic resources in large catchments: Recognising interactions between ecosystem connectivity and environmental disturbance. Pp. 91-124. *In:* R.J. Naiman. Ed. *Watershed Management.* Springer-Verlag, NY. 542 Pp.

Statzner, B. 1981. The relation between "hydraulic stress" and microdistribution of benthic macroinvertebrates in a lowland running water system, the Schierenseebrooks (North Germany). *Arch. Hydrobiol.* 91(2): 192-218.

Statzner, B. and B. Higler. 1985. Questions and comments on the River Continuum Concept. *Can. J. Fish. Aquat. Sci.* 42: 1038-1044.

Statzner, B. and B. Higler. 1986. Stream hydraulics as a major determinant of benthic zonation patterns. *Freshw. Biol.* 16: 127-139.

Statzner, B., Gore, J.A. and Resh, V.H. 1988. Hydraulic Stream Ecology: observed patterns and potential applications. *J. N. Am. Benthol. Soc.* 7(4): 307-360.

Stearns, S.C. and R.E. Crandall. 1984. Plasticity for age and size at sexual maturity: A life history response to unavoidable stress. Pp. 13-34. *In:* G.W. Potts and R.J. Wooton. Eds. *Fish Reproduction, Strategy and Tactics.* Academic Press, Inc., NY. 410 Pp.

Stier, R.J. and J.H. Crance. 1985. *Habitat Suitability Index Models and Instream Flow Suitability Curves: American Shad.* Fish Wildl. Ser.Biol. Rep. 82(10.88).

Stevenson, R.J. 1997. Scale-dependent determinants and consequences of benthic algal heterogeneity. *J. N. Am. Benthol. Soc.* 16(1): 248-262.

Stewart, B.A. 1992. The effects of invertebrates on leaf decomposition rates in two small woodland streams in Southern Africa. *Arch. Hydrobiol.* 124: 19-33.

Stewart, B.A. and B.R. Davies. 1989. The influence of different litter bag designs on the break-down of leaf material in a small mountain stream. *Hydrobiologia* 202: 135-146.

Strauss, R.E. 1979. Reliability estimates for Ivlev's Electivity Index, the Forage Ratio, and a proposed Linear Index of food selection. *Trans. Am. Fish. Soc.* 108: 344-352.

Svensson, B.W. 1999. Environmental heterogeneity in space and time: patch use, recruitment and dynamics of a rock pool population of gyrinid beetle. *Oikos* 84: 227 -238.

Syms, C. 1995. Multi-scale analysis of habitat association in a guild of blennoid fishes. *Mar. Ecol. Prog. Ser.* 125: 31-43.

Szaro, R.C. 1986. Guild management: an evaluation of avian guilds as a predictive tool. *Envir. Mgmt.* 10: 681-688.

Tennant, D.L. 1976. Instream flow regimes for fish, wildlife, recreation and related environmental resources. *Fisheries.* 1(4): 6-10.

Tilman, D. R. May, C.L. Lehman and M.A. Nowak. 1994. Habitat destruction and the extinction debt. *Nature* 371 (1). 65-66.

Tomasson, T., J.A. Cambray and P.B.N. Jackson. 1984. Reproductive biology of four large riverine fishes (Cyprinidae) in a man-made lake, Orange River, South Africa. *Hydrobiologia* 112(3): 179-195.

Townsend, C.R. 1989. The patch dynamics concept of stream community ecology. *J. N. Am. Benthol. Soc.* 8(1): 36-50.

Townshend, T.J. and R.J. Wootton. 1984. Effects of food supply on the reproduction of the convict cichlid, *Cichlasoma nigrofasciatum. J. Fish. Biol.* 24: 91-104.

Trihey, E.W. and C.B. Stalnaker. 1985. Evolution and application of instream flow methodologies to small hydropower developments: an overview of the issues. Pp. 176-183. *In:* F.W. Olson, R.G. White and R.H. Hamre. Eds. *Proceedings of the Symposium on Small Hydropower and Fisheries.* Colorado. Am. Fish. Soc. Betheseda, MD.

Tsai, C.F. and M.L. Wiley. 1983. *Instream Flow Requirements for Fish and Fisheries in Maryland.* NTIS Report PB83-49672. Water resources Research Centre Completion Report. University of Maryland, MD.

Turner, B.L., W.C. Clark, R.W. Kates, J.F. Richards, J.T. Mathews and W.B. Meyer. 1990. Eds. *The Earth As Transformed by Human Action: Global and Regional Changes in the Biosphere Over the Past 300 Years.* Cambridge University Press, NY.

Turner, M.G. and S. R. Carpenter. 1999. Tips and traps in interdisciplinary research. *Ecosystems* 2: 275 - 276.

Turner, S.J., R.V. O'Neill, W. Conley, M.R. Conley and H.C. Humphries. 1991. Pattern and scale: statistics for landscape ecology. P. 17-49. *In:* M.G.Turner and R.H. Gardner. 1991. Eds. *Quantitative Methods in Landscape Ecology: the Analysis and Interpretation of Landscape Heterogeneity.* Springer-Verlag, NY.

Twomey, K.A., K.L. Williamson and P.C. Nelson. 1984. *Habitat Suitability Index Models and Instream Flow Suitability Curves: White Sucker.* U.S. Fish and Wildlife Service. FWS/OBS-82/10.64.

Tyson, P.D. 1986. *Climatic change and Variability in Southern Africa.* Oxford University Press, Cape Town. 220 Pp.

US Fish & Wildlife Service. 1985. *Guidelines on Developing Suitability Index Curves.* Instream Flow and Aquatic Systems Group. Fort Collins, Colorado. 5 Pp.

Vadas, R.L. and D.J. Orth. 1998. Use of physical variables to discriminate visually determined mesohabitat types in North American streams. *Rivers* 6(3) 143-159.

van Coller, A.L., G.L. Heritage and K.H. Rogers. 1995. Linking riparian vegetation distribution and flow regime of the Sabie River through fluvial geomorphology. *Proc. 7th S. Afr. Nat. Hydr. Symp. Hydrology and Water Resources in South Africa.* Grahamstown.

Van Horn, B. 1983. Density is a misleading indicator of habitat quality. *J. Wildl. Mgmt.* 47: 893-901.

van Niekerk. A.W. and G.L. Heritage. 1993. *Geomorphology of the Sabie River: Overview and Classification.* CWAE, University of the Witwatersrand. Int. Rpt. No. 2/93. 100 Pp.

van Niekerk, A.W., G.L. Heritage and B.P. Moon. 1995. River classification for management: the geomorphology of the Sabie River in the Eastern Transvaal. *S. Afr. Geogr. J.* 77(2): 68-76.

Van Veelen, M., Swart, S.J., 1992. *Kruger National Park: Assessment of the Current Water Quality Status of the Sabie River.* Rep No.NX300/00/REQ0892, Department of Water Affairs and Forestry (Hydrological Services), Pretoria. 36 Pp.

Vannote, R.L., G.W. Minshall, K.W. Cummins J.R. Sedell and C.E. Cushing. 1980. The River Continuum Concept. *Can. J. Fish. Aquat. Sci.* 37: 130-137.

Vannote, R.L. and B.W. Sweeney. 1980. Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *Am. Nat.* 115(5): 667-695.

Verner, J. 1984. The guild concept applied to management of bird populations. *Envir. Mgmt.* 8: 1-14.

Viljoen, P.J. 1989. Habitat selection and preferred food plants of a desert-dwelling elephant population in the northern Namib desert, South West Africa/ Namibia. *Afr. J. Ecol.* 27: 227-240.

Viljoen, P.J. 1989. Habitat selection and preferred food plants of a desert-dwelling elephant population in the northern Namib desert, South West Africa/ Namibia. *Afr. J. Ecol.* 27: 227-240.

Wadeson, R.A. 1994. A geomorphological approach to the identification and classification of instream flow environments. *S. Afr. J. Aq. Sci.* 20 (1/2): 38-61.

Wadeson, R.A. 1996. *The Development of the Hydraulic Biotope Concept Within A Hierarchical Geomorphological Model.* Unpubl. Ph.D. thesis, Rhodes University, Grahamstown, South Africa. 320 Pp.

Wadeson, R. A. and K.M. Rowntree.1994. A hierarchical geomorphological model for the classification of South African River Systems. *In:* M.C. Uys (Compiler). *Classification of Rivers and Environmental Health Indicators. Proc. Joint SA- Australian Workshop,* February 7-14, 1994. Cape Town, South Africa. Water Research Commission Rpt. TT63/94.

Wadeson, R.A. and K.M. Rowntree. 1998. Application of the hydraulic biotope concept to the classification of instream habitats. *Aquat. Syst. Health Mgmt.* 1: 143-157.

Waite, I.R. and R.A. Barnhart. 1992. Habitat criteria for rearing steelhead: A comparison of site-specific and standard curves for use in the Instream Flow Incremental Methodology. *N.Am. J. Fish. Mgmt.* 12(1): 40-46.

Walker,K.F. 1979. Regulated streams in Australia: The Murray-Darling River System. Pp. 143-164. *In:* J.V. Ward and J.A. Stanford. Eds. *The Ecology of Regulated Streams.* Plenum Press, NY.

Walmsley, R.D. and B.R. Davies. 1991. Water for environmental management: an overview. *Water SA* 17: 67-76.

Ward, J.V. 1974. A temperature-stressed ecosystem below a hypolimnial release mountain reservoir. *Arch. Hydrobiol.* 74: 247-275.

Ward, J.A. 1976a. Effects of flow patterns below large dams on stream benthos: A review. *In:* J.F. Osborn and C.H. Allman. Eds. *Instream Flow Needs Symposium.* Amer. Fish. Soc. 2: 235-253.

Ward, J.A. 1976b. Comparative limnology of differentially regulated sections of the Colorado mountain river. *Arch. Hydrobiol.* 78(3): 319-342.

Ward, J.V. 1982. Ecological aspects of stream regulation: Responses in downstream lotic reaches. *Wat. Poll. Mgmt. Rev. (New Delhi)* 2: 1-26.

Ward, J.V. 1986. Altitudinal zonation in a rocky mountain stream. *Archiv. Hydrobiol. Suppl.* 74: 133-199.

Ward, J.V. 1987. Trichoptera of regulated rocky mountain streams. Pp. 375-380. *In:* M. Bournard and H. Tavhet. (Eds). *Proc. 5th Int. Symp. Trichoptera.* Dr. W. Junk Publ. Dordrecht. Netherlands.

Ward, J.V. and J.A. Stanford. 1979. Eds. *The Ecology of Regulated Streams.* Plenum Press, NY. 398 Pp.

Ward, J.V. and J.A. Stanford. 1982. Thermal responses in the evolutionary ecology of aquatic insects. *Ann. Rev. Entomol.* 27: 97-117.

Ward, J.V. and J.A. Stanford. 1983 a. The intermediate-disturbance hypothesis: an explanation for biotic diversity patterns in lotic ecosystems. Pp. 347-356. *In:* T.D. Fontaine III and S.M. Bartell. Eds. *Dynamics of Lotic Ecosystems.* Ann Arbour Science (Butterworths), Massachusetts.

Ward, J.V. and J.A. Stanford. 1983 b. The serial discontinuity concept of lotic ecosystems. Pp. 29-42. *In:* T.D. Fontaine III and S.M. Bartell. Eds. *Dynamics of Lotic Ecosystems.* Ann Arbour Science (Butterworths), Massachusetts.

Ward, J.V. and J.A. Stanford. 1984. The regulated stream as a testing ground for ecological theory. Pp. 23-38. Regulated Rivers. *In:* A. Lillehammer and S.J. Saltveit. Eds. *Regulated Rivers. Proc. 2nd Int. Symp. Reg. Riv.* Oslo University Press, Norway.

Ward, J.V. and J.A. Stanford. 1987. The Ecology of Regulated Streams: Past accomplishments and directions for future research. Pp. 391-410. *In:* J.F. Craig and J.B. Kemper. Eds. *Regulated streams: Advances in Ecology.* Plenum Press, NY.

Ward, J.V. and J.A. Stanford. 1989. Riverine ecosystems: The influence of man on catchment dynamics in fish ecology. Pp. 56-64. *In:* D.P. Dodge. Ed. Proceedings of the International Large River Symposium (LARS). *Spec. Publ. Can. J. Fish. Aquat. Sci.* 106. 629 Pp.

Weeks, D.C., J.H. O'Keeffe, A. Fourie and B.R. Davies. 1996. *A Pre-impoundment Study of the Sabie-Sand River System, Mpumalanga with Special Reference to Predicted Impacts on the Kruger National Park.* Vol.II. Water Research Commission Rpt. 294/1/96

Welcomme, R.L. 1969. The biology and ecology of the fishes of a small tropical stream. *J. Zool. Lond.* 158: 485-529.

Welcomme, R.L. 1979. *Fisheries Ecology of Floodplain Rivers.* Longman, London. 317 Pp.

Welcomme, R.L. 1989. Floodplain fisheries management. Pp. 209-233. *In:* J.A. Gore and G.E. Petts. Eds. *Alternatives in Regulated River Management.* CRC Press Inc., Boca Raton, Fl.

Welcomme, R.L., and B. Merona. 1989. *Fish Communities of Rivers.* Vol. 216, EIFAC, FAO, Rome, Italy.

Wesche, T.A.; C.M. Goertler and W. A. Hubert. 1987. Modified habitat suitability index model for brown trout in Southeastern Wyoming. *N.Am. J. Fish. Mgmt.* 7:232-237.

White, G.C. 1987. *Analysis of Biotelemetry Data- A Primer.* Dept. Fish. Wildl. Biol. Colorado State University, FC. 324 Pp.

Wiens, J.A. 1989. Spatial scaling in ecology. *Functional Ecology* 3: 385-397.

Wiens, J.A. 1995. Landscape mosaics and ecological theory. Pp. 1-26. *In:* L. Hansson, L. Fahrig and G. Merriam. Eds. *Mosaic Landscapes and Ecological Processes.* Chapman and Hall, NY.

Wiens, J.A., C.S. Crawford and J.R. Goss. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. *Oikos* 45: 421-427.

Wiens, J.A., N.C. Stenseth, B. Van Horne and R.A. Ims. 1993. Ecological mechanisms and landscape Ecology. *Oikos* 66: 369-380.

Williams, R.D. and R.N. Winget. 1979. Macroinvertebrate response to flow manipulation in the Strawberry river, Utah (U.S.A.). Pp. 365-376. *In:* J.V. Ward and J.A. Stanford. Eds. *The Ecology of Regulated Streams.* Plenum Press, NY.

Williams, W.D. 1988. Limnological imbalances: an antipodean viewpoint. *Freshw. Biol.* 20: 407-420.

Wilson, E.O. 1988. *Biodiversity.* National Academy, Washington DC.

Winger, P.V. 1981. Physical and chemical characteristics of warmwater streams: A review. Pp. 32-44. *In:* L.A. Krumholz. Ed. *Warmwater Streams Symposium*. Am. Fish. Soc. Bethesda, MD.

Winterbourn, M.J., J.R. Rounik, and B. Cowie. 1981. Are New Zealand stream ecosystems really that different? *N.Z. J. Mar. and Freshw. Res.* 15: 321-328.

Wootton, R.J. 1979. Energy costs of egg production and environmental determinants of fecundity in teleost fish. Symp. *Zool. Soc. Ldn.* 44: 139-159.

Wootton, R.J. 1984. Tactics and strategies in fish reproduction. Pp. 1-12. *In:* G.W. Potts and R.J. Wooton. Eds. *Fish Reproduction, Strategy and Tactics*. Academic Press, Inc., NY. 410 Pp.

Wood, P.J., P.D. Armitage, C.E. Cannan and G.E. Petts. 1999. Instream mesohabitat diversity in three groundwater streams under base-flow conditions. *Aq. Cons. Mar. Freshw. Ecos.* 9: 265-278.

World Bank. 1980. *World Development Report*. Oxford University Press, NY, NY.

APPENDIX A

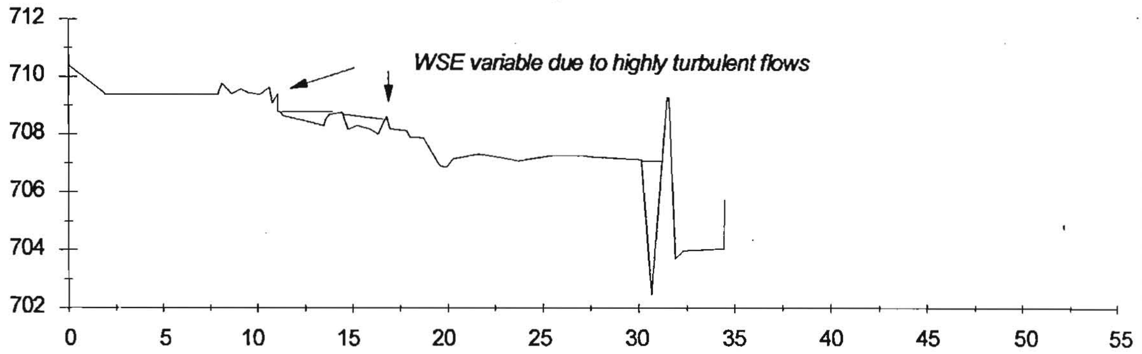
PHABSIM transect profiles and water surface elevations for all transects at three sites on the Marite River, at a discharge of 0.57 $m^3 s^{-1}$

SITE 1

Transect profiles for Site 1 indicating Water Surface Elevations (WSE) in channels

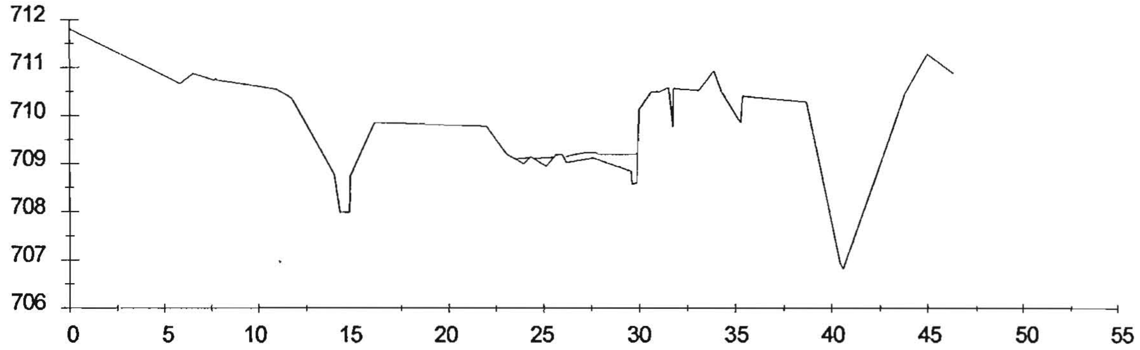
Transect 1

Bedrock chutes, and bedrock island



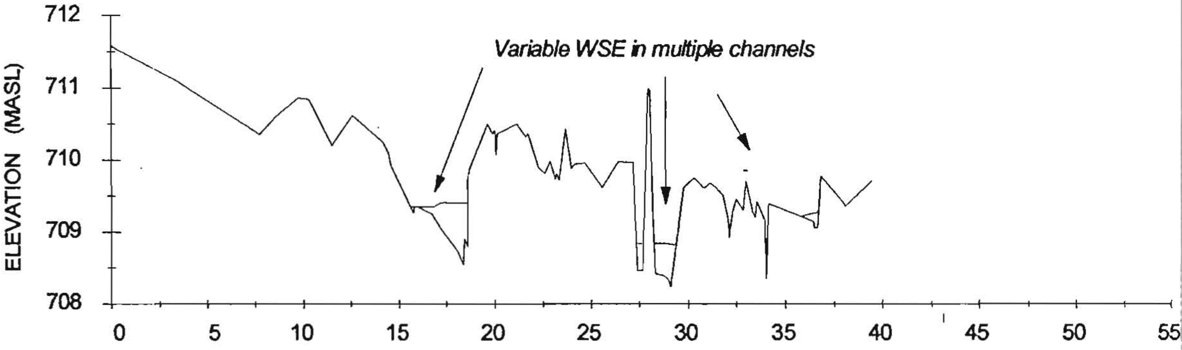
Transect 2

Deep bedrock gulley, and boulder rapid, with bedrock island



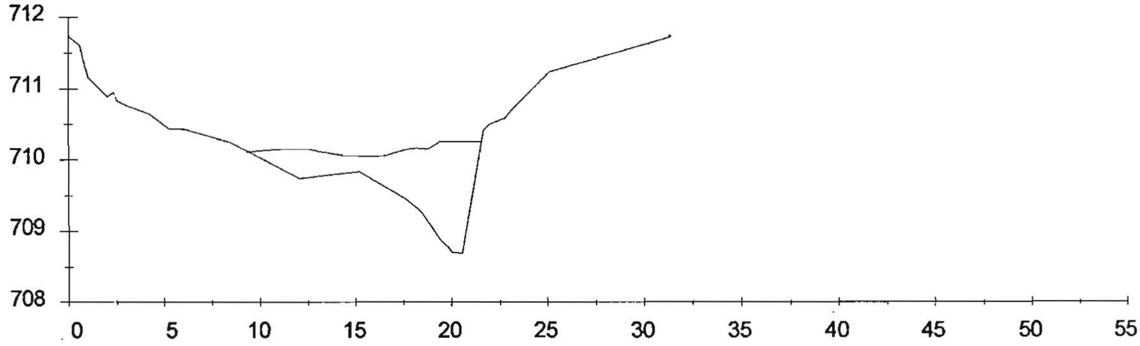
Transect 3

Bedrock gulley, and boulder rapid, with bedrock/ alluvial island



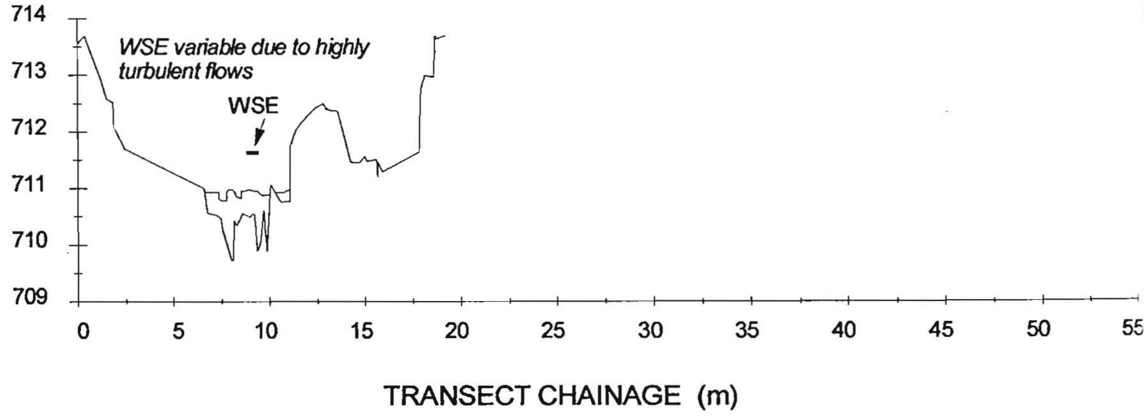
Transect 4

Alluvial/ bedrock pool



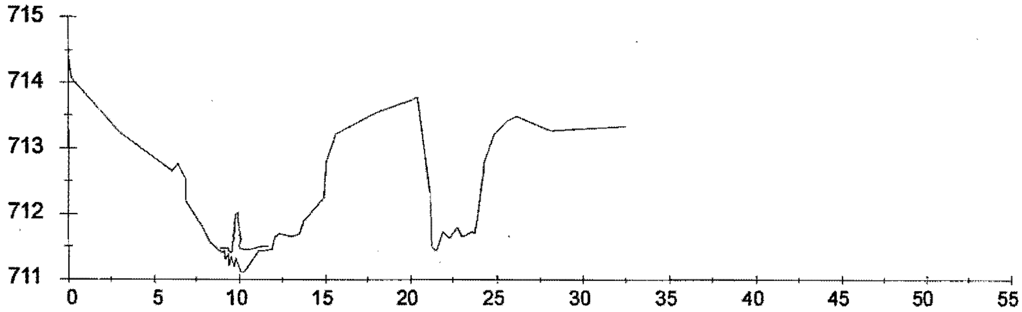
Transect 5

Bedrock and boulder rapid



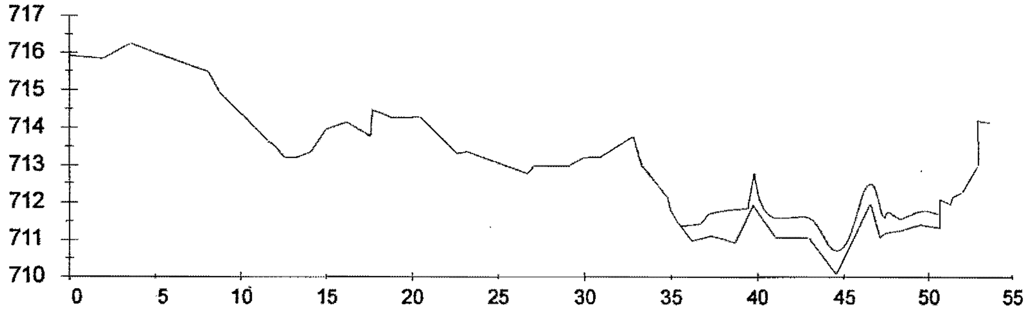
Transect 6

Bedrock run



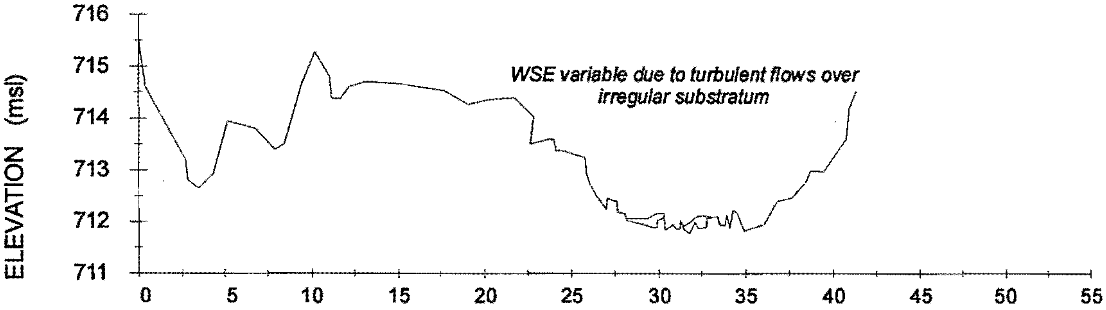
Transect 7

Bedrock and
alluvium pool



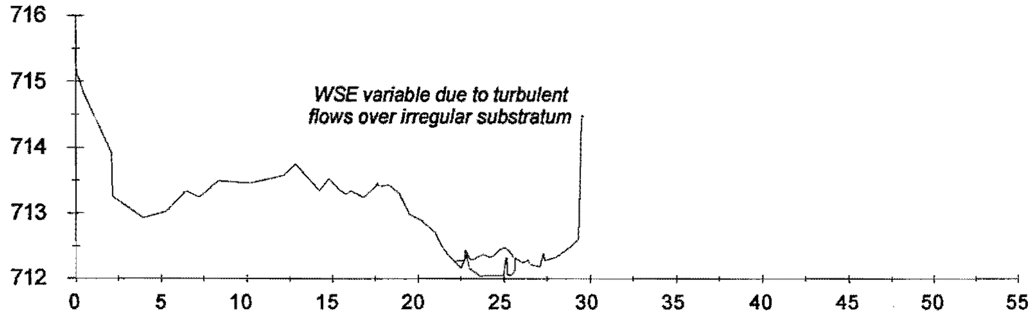
Transect 8

Boulder/
cobble
riffle



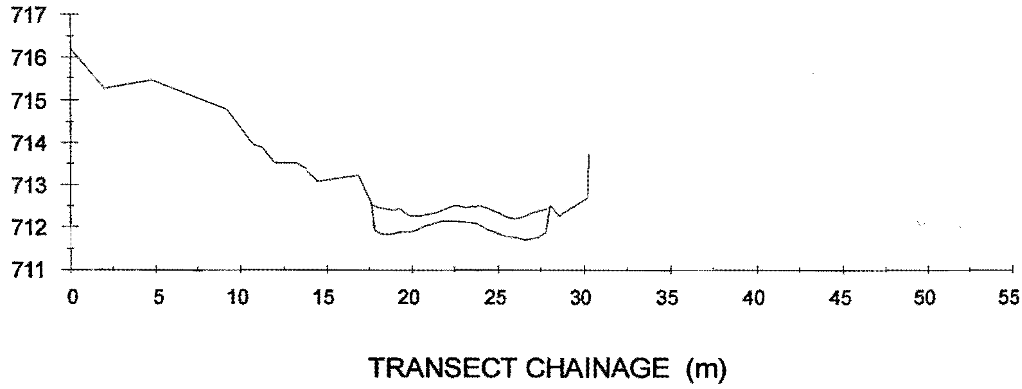
Transect 9

Boulder/
cobble
riffle



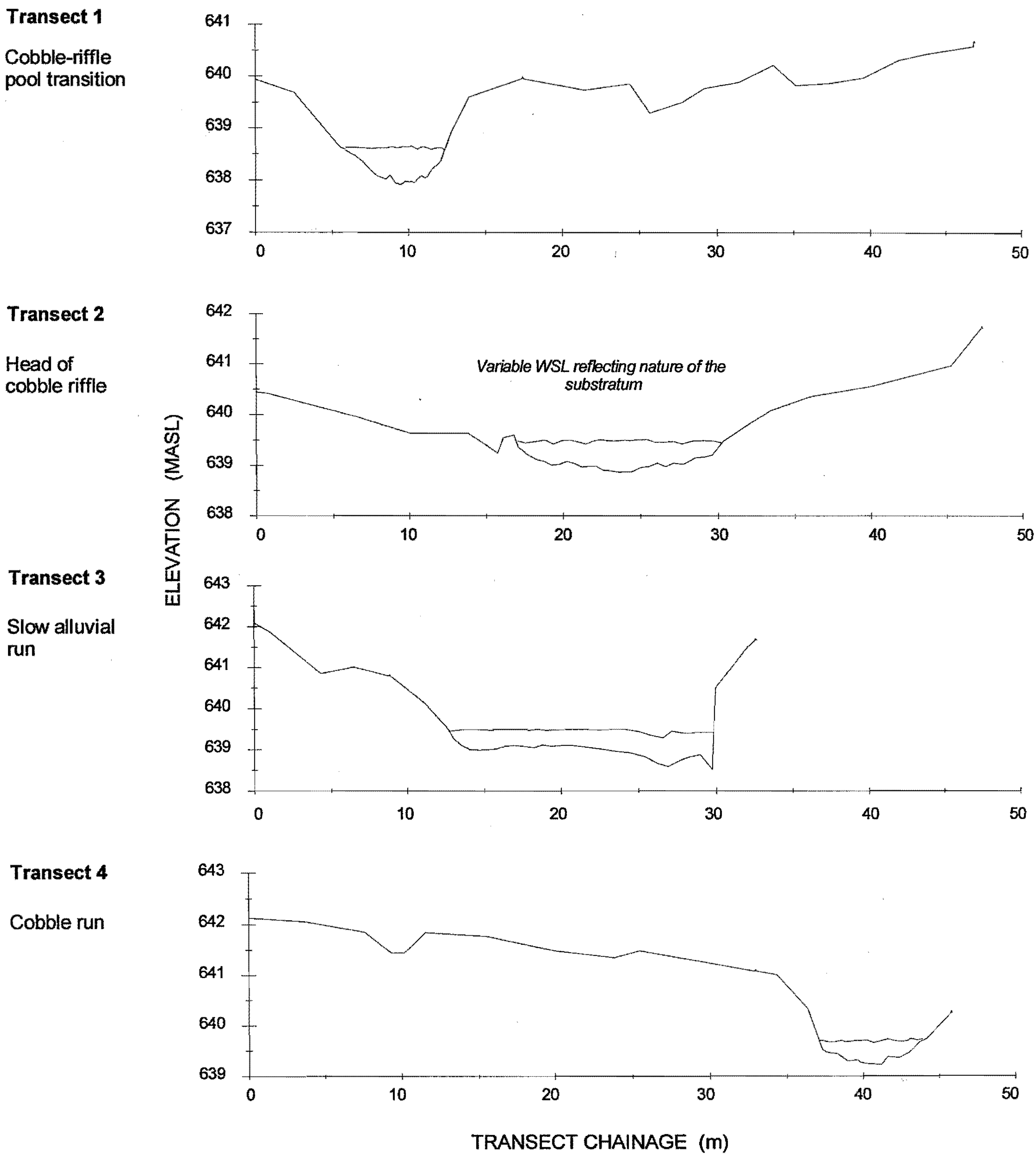
Transect 10

Alluvial run



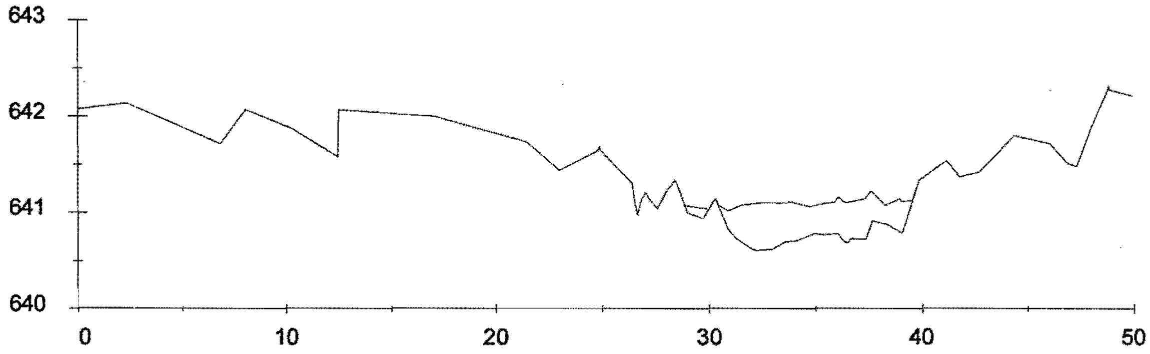
SITE 2

Transect profiles for Site 2 indicating Water Surface Elevations (WSE) in channels



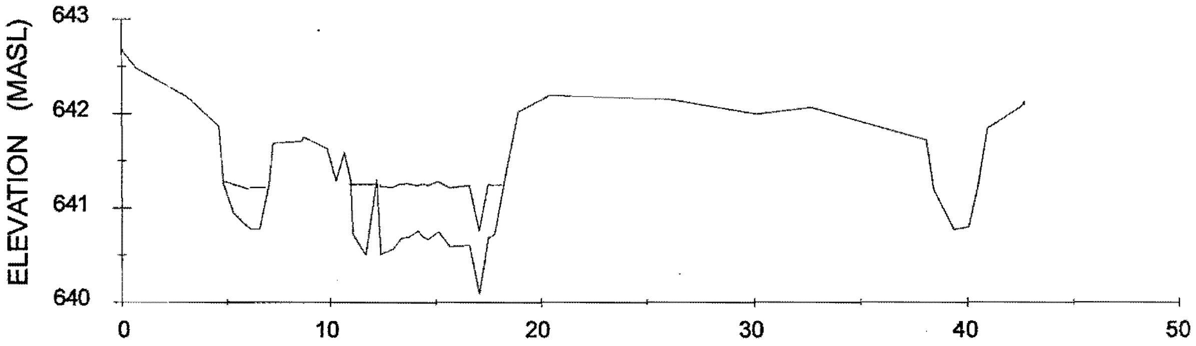
Transect 5

Head of large boulder rapid/ riffle



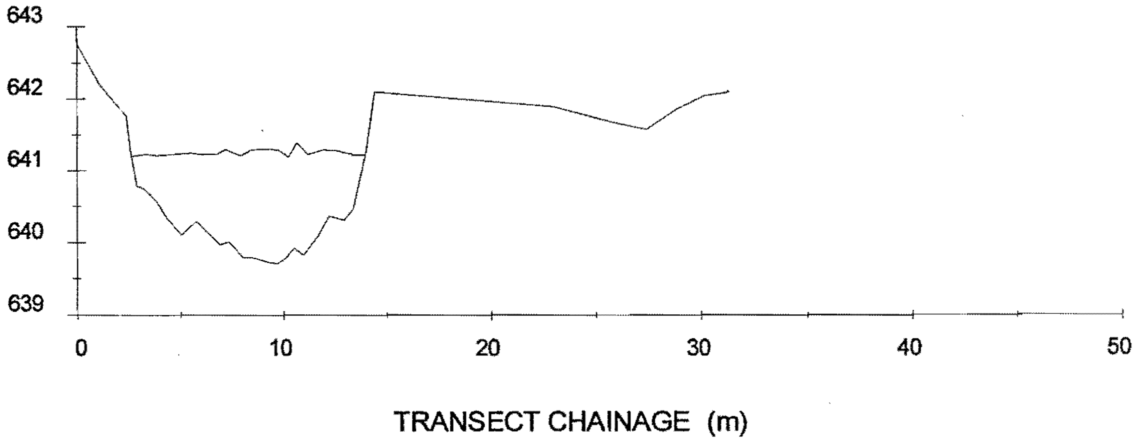
Transect 6

Alluvial/ cobble run

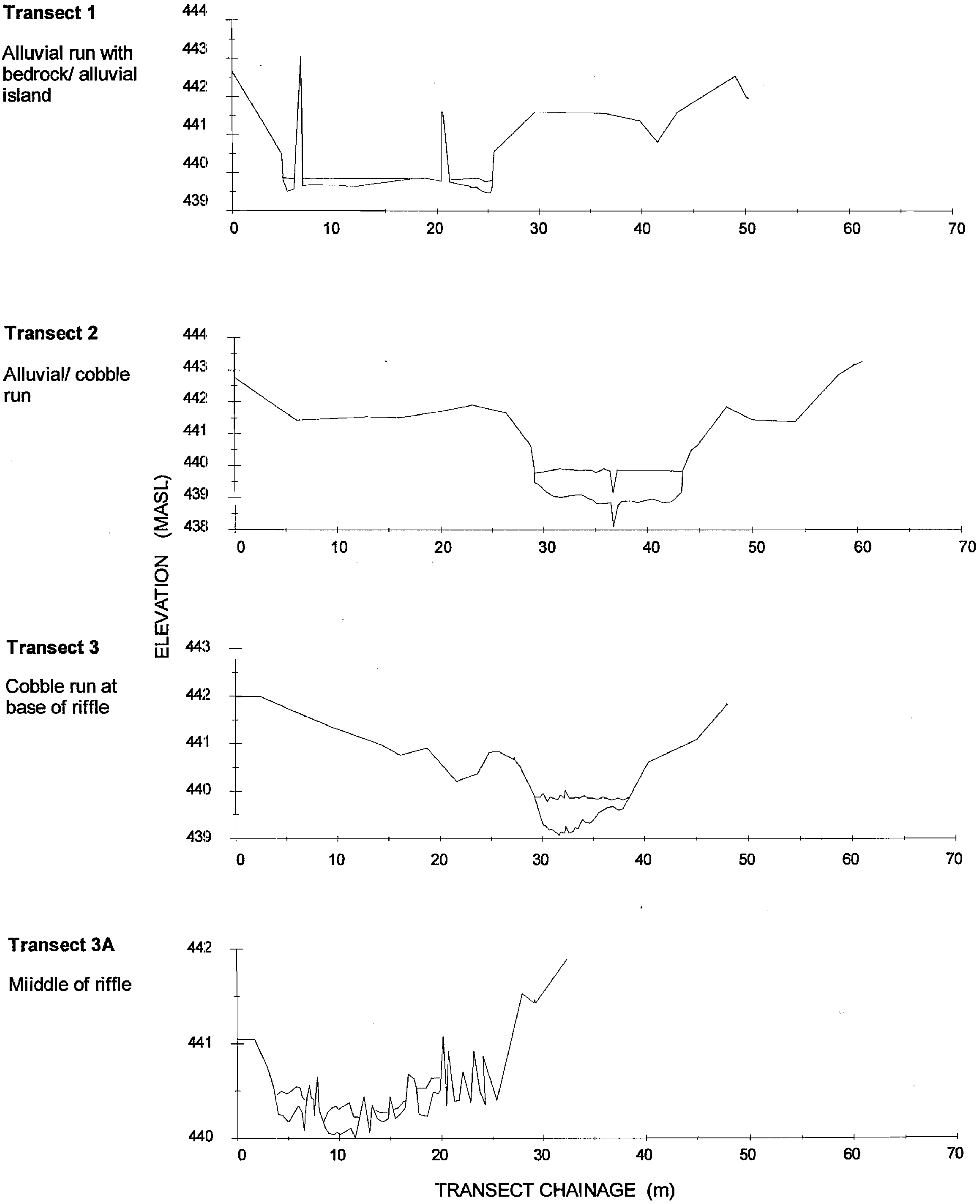


Transect 7

Deep alluvial pool

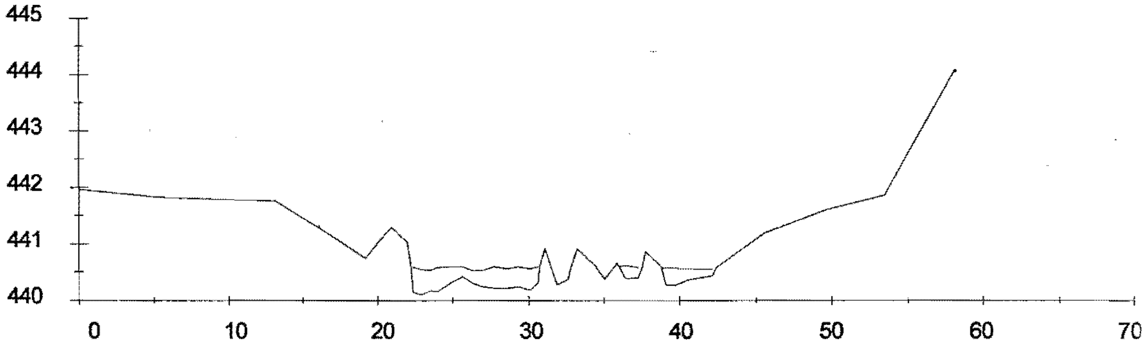


Transect profiles for Site 3 indicating Water Surface Elevations (WSE) in channels



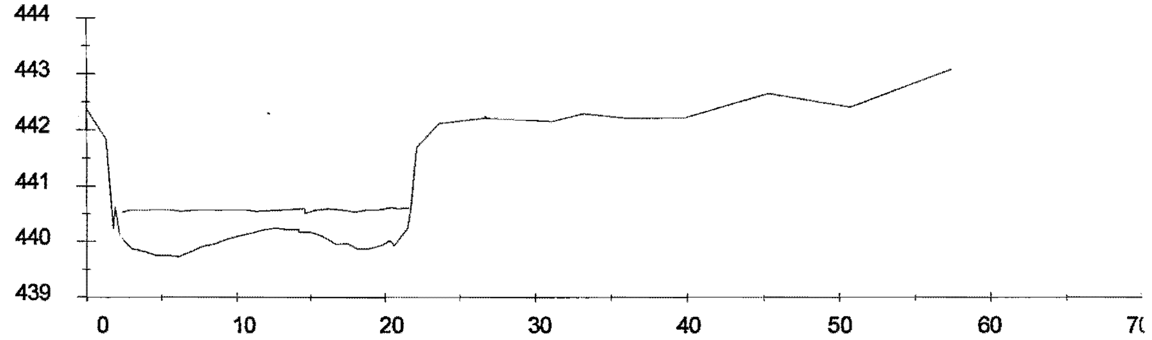
Transect 4

Head of cobble riffle



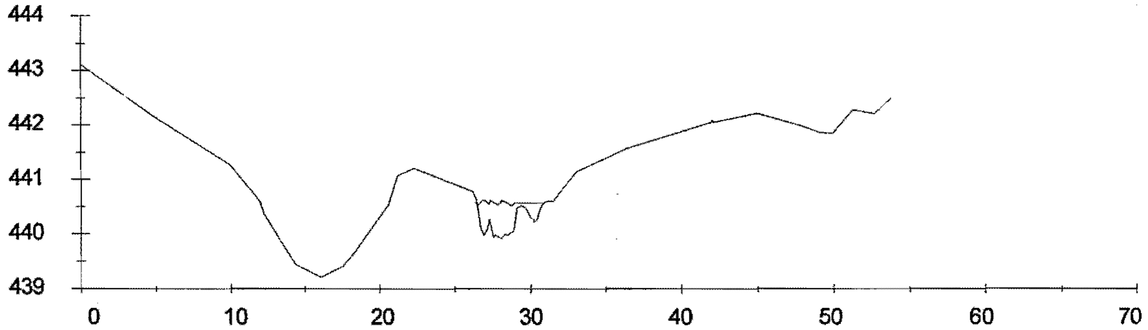
Transect 5

Deep alluvial run



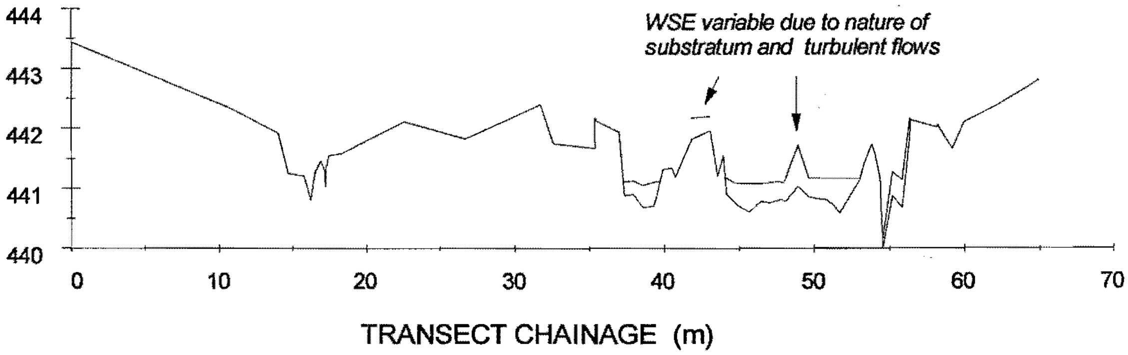
Transect 6

Cobble/ alluvial run and alluvial backwater



Transect 7

Boulder rapid and run downstream of bedrock isalnd



APPENDIX B

Raw cross-section data for the PHABSIM II hydraulic runs for eight transects at Site 3, on the Marite River

MARITE SITE 3 SECTION No: TR. 1: CROSS-SECTION ID: DURR 0.0

				WSE	m	ft	Q (cf/s)
Reach Length	0.0 m	0.0 ft					
Reach weight	0.75			Aug:	439:86	1443.1	24
Slope	0.0005			Nov:	439.77	1442.8	19
Stage of zero flow	439.5 m	1441.8 ft		Sep:	439.53	1442	0.91

Vertical	chainage (m)	chainage (ft)	Elevation (m)	Elevation (ft)	Depth (m)	Depth (ft)	Velocity (m/s)	Velocity (ft/s)	Channel Index
1	0.00	0.00	442.68	1452.35					
2	0.05	0.16	442.64	1452.21					
3	2.89	9.48	441.38	1448.08					82.16
4	4.84	15.88	440.50	1445.19					82.13
5	4.97	16.31	439.81	1442.93					83.29
6	5.44	17.85	439.51	1441.95	0.36	1.18	0.05	0.156	32.19
7	6.06	19.88	439.58	1442.18	0.27	0.89	0.16	0.529	32.19
8	6.75	22.15	443.05	1453.56					
9	6.92	22.70	439.66	1442.44	0.2	0.66	0.21	0.686	32.19
10	7.88	25.85	439.69	1442.54	0.16	0.52	0.20	0.646	32.19
11	8.87	29.10	439.68	1442.50	0.18	0.59	0.17	0.543	32.19
12	9.75	31.99	439.67	1442.47	0.19	0.62	0.16	0.511	32.19
13	10.43	34.22	439.67	1442.47	0.2	0.66	0.15	0.485	32.19
14	11.26	36.94	439.65	1442.41	0.2	0.66	0.14	0.455	32.19
15	12.32	40.42	439.65	1442.41	0.21	0.69	0.14	0.446	32.18
16	13.14	43.11	439.68	1442.50	0.19	0.62	0.14	0.438	32.17
17	14.01	45.96	439.72	1442.63	0.14	0.46	0.12	0.382	32.16
18	15.06	49.41	439.76	1442.77	0.1	0.33	0.07	0.221	32.16
19	16.47	54.03	439.82	1442.96	0.05	0.16	0.06	0.190	32.14
20	17.45	57.25	439.85	1443.06	0.03	0.10	0.06	0.177	32.13
21	18.39	60.33	439.87	1443.13					32.14
22	18.68	61.28	439.88	1443.16					32.15
23	18.95	62.17	439.86	1443.09					32.17
24	20.40	66.93	439.79	1442.86	0.05	0.16	0.17	0.542	32.19
25	20.48	67.19	441.57	1448.70					32.19
26	20.53	67.35	441.61	1448.84					32.19
27	20.58	67.52	441.57	1448.70					32.19
28	21.22	69.62	439.77	1442.80	0.06	0.20	0.20	0.634	32.18
29	21.77	71.42	439.74	1442.70	0.1	0.33	0.32	1.017	32.18
30	22.48	73.75	439.69	1442.54	0.16	0.52	0.44	1.396	32.19
31	23.10	75.79	439.66	1442.44	0.2	0.66	0.48	1.549	32.18
32	23.48	77.03	439.62	1442.31	0.24	0.79	0.50	1.607	32.19
33	23.91	78.44	439.63	1442.34	0.24	0.79	0.51	1.641	32.19
34	24.46	80.25	439.52	1441.98	0.26	0.85	0.48	1.529	2.19
35	24.84	81.49	439.49	1441.88	0.3	0.98	0.39	1.249	2.13
36	25.22	82.74	439.47	1441.81	0.35	1.15	0.25	0.803	2.12
37	25.37	83.23	439.58	1442.18					32.12
38	25.58	83.92	440.56	1445.39					82.17
39	29.70	97.44	441.61	1448.84					82.17
40	36.54	119.88	441.56	1448.67					82.18
41	39.86	130.77	441.38	1448.08					82.18
42	41.51	136.18	440.82	1446.24					82.18
43	43.49	142.68	441.60	1448.80					82.16
44	49.05	160.92	442.55	1451.92					82.15
45	50.23	164.79	441.96	1449.98					
46	50.28	164.96	442.00	1450.11					
47	50.33	165.12	441.96	1449.98					

MARITE SITE 3 SECTION No: TR. 2: CROSS-SECTION ID: DURR 135.3

Reach Length	41.2 m	135.3 ft	**WSE**	m	ft	**Q (cf/s)**
Reach weight	0.9		Aug:	439.88	1443.2	24.00
Slope	0.0005		Nov:	439.78	1442.8	19.00
Stage of zero flow	439.4 m	1441.8 ft	Sep:	439.5	1442	0.91

Vertical	chainage (m)	chainage (ft)	Elevation (m)	Elevation (ft)	Depth (m)	Depth (ft)	Velocity (m/s)	Velocity (ft/s)	Channel Index
1	0.00	0.00	442.79	1452.71					
2	0.05	0.16	442.75	1452.58					
3	0.74	2.43	442.60	1452.08					2.14
4	6.05	19.85	441.42	1448.21					22.12
5	12.80	41.99	441.53	1448.57					22.14
6	16.04	52.62	441.51	1448.51					22.14
7	20.04	65.75	441.71	1449.16					22.14
8	23.16	75.98	441.90	1449.79					82.18
9	26.39	86.58	441.66	1449.00					2.18
10	28.77	94.39	440.64	1445.65					82.18
11	29.09	95.44	439.92	1443.29					82.18
12	29.15	95.63	439.47	1441.81					2.00
13	29.51	96.82	439.40	1441.58	0.38	1.25	0.01	0.020	2.12
14	30.29	99.37	439.19	1440.90	0.62	2.03	0.03	0.107	2.11
15	30.96	101.57	439.04	1440.40	0.82	2.69	0.04	0.121	32.71
16	31.73	104.10	439.01	1440.31	0.88	2.89	0.06	0.205	63.29
17	32.56	106.82	439.06	1440.47	0.82	2.69	0.08	0.254	63.29
18	33.11	108.63	439.08	1440.54	0.79	2.59	0.09	0.304	63.29
19	33.73	110.66	439.08	1440.54	0.76	2.49	0.10	0.308	63.29
20	34.19	112.17	439.00	1440.27	0.87	2.85	0.10	0.324	63.29
21	34.81	114.20	438.93	1440.04	0.92	3.02	0.07	0.221	63.29
22	35.16	115.35	438.81	1439.65	0.98	3.22	0.07	0.226	32.19
23	35.93	117.88	438.81	1439.65	1.09	3.58	0.05	0.169	32.19
24	36.47	119.65	438.84	1439.75	1	3.28	0.03	0.107	32.19
25	36.75	120.57	438.10	1437.32	1.06	3.48	0.03	0.089	32.71
26	37.19	122.01	438.77	1439.52	1.1	3.61	0.03	0.112	32.19
27	37.55	123.19	438.88	1439.88	0.98	3.22	0.04	0.118	32.19
28	37.91	124.37	438.90	1439.94	0.95	3.12	0.04	0.142	32.19
29	38.52	126.37	438.90	1439.94	0.96	3.15	0.07	0.229	32.19
30	39.11	128.31	438.85	1439.78	1	3.28	0.06	0.201	32.18
31	39.76	130.44	438.92	1440.01	0.94	3.08	0.07	0.222	32.19
32	40.50	132.87	438.97	1440.17	0.88	2.89	0.06	0.190	32.19
33	41.52	136.22	438.85	1439.78	1	3.28	0.05	0.175	32.19
34	42.28	138.71	438.87	1439.85	0.97	3.18	0.05	0.165	32.19
35	43.29	142.02	439.17	1440.83	0.64	2.10	0.01	0.020	2.00
36	43.41	142.42	439.85	1443.06					32.09
37	44.20	145.01	440.48	1445.13					82.17
38	44.79	146.95	440.64	1445.65					82.17
39	47.59	156.13	441.83	1449.56					
40	47.64	156.30	441.87	1449.69					
41	47.69	156.46	441.83	1449.56					
42	50.10	164.37	441.44	1448.28					82.16
43	54.17	177.72	441.38	1448.08					82.19
44	58.34	191.40	442.85	1452.90					82.19
45	59.72	195.93	443.15	1453.89					
46	59.77	196.09	443.19	1454.02					
47	59.82	196.26	443.15	1453.89					
48	60.57	198.72	443.27	1454.28					

MARITE SITE 3 **SECTION No: TR. 3: CROSS-SECTION ID: DURR 275.0**

Reach Length	83.82 m	275 ft	**WSE**	m	ft	**Q (cf/s)**
Reach weight	0.5		Aug:	439.90	1443.2	24.00
Slope	0.0131		Nov:	439.81	1442.9	19.00
Stage of zero flow	439.4 m	1441.8 ft	Sep:	439.53	1442	0.91

Vertical	chainage (m)	chainage (ft)	Elevation (m)	Elevation (ft)	Depth (m)	Depth (ft)	Velocity (m/s)	Velocity (ft/s)	Channel Index
1	0.00	0.00	442.02	1450.18					
2	0.05	0.16	441.98	1450.05					
3	2.52	8.27	441.99	1450.08					32.09
4	6.12	20.08	441.65	1448.97					32.08
5	9.72	31.89	441.33	1447.92					32.08
6	14.28	46.85	440.98	1446.77					32.06
7	16.11	52.85	440.75	1446.01					86.29
8	18.75	61.51	440.90	1446.51					86.29
9	21.64	71.00	440.21	1444.24					72.09
10	23.69	77.72	440.37	1444.77					72.03
11	24.88	81.63	440.82	1446.24					32.09
12	25.78	84.58	440.83	1446.28					32.09
13	27.24	89.37	440.67	1445.75					32.09
14	27.29	89.53	440.71	1445.88					32.09
15	27.34	89.70	440.67	1445.75					32.09
16	27.87	91.43	440.52	1445.26					32.09
17	29.24	95.93	439.91	1443.26					32.09
18	29.60	97.11	439.62	1442.31	0.26	0.85	0.13	0.40	82.09
19	30.11	98.78	439.30	1441.26	0.58	1.90	0.13	0.41	32.73
20	30.36	99.60	439.27	1441.16	0.68	2.23	0.12	0.39	32.73
21	30.73	100.82	439.18	1440.86	0.6	1.97	0.27	0.86	65.97
22	30.96	101.57	439.20	1440.93	0.67	2.20	0.25	0.79	65.97
23	31.65	103.84	439.07	1440.50	0.76	2.49	0.16	0.51	65.97
24	31.89	104.62	439.14	1440.73	0.77	2.53	0.27	0.85	65.97
25	32.23	105.74	439.11	1440.63	0.75	2.46	0.32	1.01	65.97
26	32.28	105.90	439.26	1441.13	0.76	2.49	0.25	0.80	65.97
27	32.65	107.12	439.11	1440.63	0.74	2.43	0.12	0.40	54.99
28	33.08	108.53	439.16	1440.80	0.7	2.30	0.32	1.02	54.99
29	33.18	108.86	439.23	1441.03	0.65	2.13	0.32	1.04	54.99
30	33.56	110.10	439.21	1440.96	0.64	2.10	0.23	0.75	54.99
31	33.95	111.38	439.40	1441.58	0.5	1.64	0.16	0.53	54.99
32	34.29	112.50	439.34	1441.39	0.52	1.71	0.07	0.22	54.99
33	34.72	113.91	439.33	1441.36	0.52	1.71	0.03	0.09	54.99
34	35.13	115.25	439.42	1441.65	0.42	1.38	0.04	0.11	57.99
35	35.62	116.86	439.55	1442.08	0.33	1.08	0.05	0.15	57.99
36	36.40	119.42	439.66	1442.44	0.16	0.52	0.01	0.02	52.19
37	36.98	121.32	439.68	1442.50	0.17	0.56	0.01	0.02	52.19
38	37.44	122.83	439.60	1442.24	0.22	0.72	0.12	0.39	52.72
39	37.91	124.37	439.63	1442.34	0.24	0.79	0.05	0.16	52.72
40	38.50	126.31	439.85	1443.06					2.00
41	40.38	132.48	440.61	1445.55					82.09
42	45.02	147.70	441.08	1447.10					82.09
43	47.91	157.18	441.81	1449.49					
44	47.96	157.35	441.85	1449.62					
45	48.01	157.51	441.81	1449.49					

MARITE SITE 3 SECTION No: TR. 3A: CROSS-SECTION ID: DURR 357.7

Reach Length	109.0 m	357.7 m	**WSE**	m	ft	**Q (cf/s)**
Reach weight	0.5		Aug:	440.46	1445.1	24.00
Slope	0.0145		Nov:	440.42	1444.9	19.00
Stage of zero flow	440 m	1443.55 m	Sep:	440.19	1444.2	0.91

Vertical	chainage (m)	chainage (ft)	Elevation (m)	Elevation (ft)	Depth (m)	Depth (ft)	Velocity (m/s)	Velocity (ft/s)	Channel Index
1	0.00	0.00	441.09	1447.13					
2	0.05	0.16	441.05	1447.00					
3	1.71	5.61	441.05	1447.00					82.09
4	3.07	10.07	440.73	1445.95					82.09
5	3.61	11.84	440.52	1445.26	0.00				82.09
6	4.04	13.25	440.25	1444.37	0.21	0.69	0.36	1.140	65.91
7	4.44	14.57	440.24	1444.34	0.26	0.85	0.73	2.348	52.93
8	5.08	16.67	440.17	1444.11	0.30	0.98	0.34	1.092	62.94
9	6.02	19.75	440.34	1444.67	0.21	0.69	0.46	1.462	62.94
10	6.38	20.93	440.28	1444.47	0.25	0.82	0.56	1.800	62.94
11	6.56	21.52	440.08	1443.82	0.35	1.15	0.91	2.912	62.96
12	6.87	22.54	440.42	1444.93					62.96
13	7.10	23.29	440.56	1445.39	0.00	0.00			62.96
14	7.24	23.75	440.43	1444.96					6.00
15	7.54	24.74	440.41	1444.90	0.00	0.00			62.93
16	7.60	24.93	440.24	1444.34	0.17	0.56	1.18	3.797	62.93
17	7.85	25.75	440.65	1445.69					6.00
18	8.08	26.51	440.30	1444.54	0.00	0.00			62.93
19	8.63	28.31	440.11	1443.91	0.06	0.20	0.95	3.056	62.93
20	8.99	29.49	440.05	1443.72	0.23	0.75	0.06	0.190	62.93
21	9.44	30.97	440.04	1443.68	0.28	0.92	1.20	3.846	62.93
22	9.78	32.09	440.06	1443.75	0.28	0.92	1.07	3.443	62.93
23	10.10	33.14	440.04	1443.68	0.27	0.89	1.35	4.329	60.93
24	11.14	36.55	440.11	1443.91	0.27	0.89	0.17	0.560	60.93
25	11.58	37.99	440.00	1443.55	0.23	0.75	0.20	0.641	62.96
26	12.09	39.66	440.26	1444.41	0.00	0.00			62.92
27	12.40	40.68	440.44	1445.00					82.09
28	13.00	42.65	440.06	1443.75	0.19	0.62	0.24	0.770	92.92
29	13.21	43.34	440.35	1444.70					60.94
30	13.70	44.95	440.21	1444.24	0.09	0.30	0.28	0.898	62.95
31	14.26	46.78	440.17	1444.11	0.10	0.33	0.24	0.786	62.95
32	14.81	48.59	440.21	1444.24	0.00	0.00			92.92
33	14.96	49.08	440.44	1445.00					6.00
34	15.49	50.82	440.21	1444.24	0.10	0.33	0.08	0.270	65.96
35	15.92	52.23	440.25	1444.37	0.07	0.23	0.65	2.074	65.94
36	16.47	54.03	440.32	1444.60	0.07	0.23	0.56	1.800	60.94
37	16.75	54.95	440.68	1445.78					60.95
38	17.33	56.86	440.63	1445.62					60.96
39	17.54	57.54	440.54	1445.33	0.00	0.00			62.94
40	17.80	58.40	440.25	1444.37	0.28	0.92	0.29	0.931	62.94
41	18.61	61.05	440.23	1444.31	0.30	0.98	0.24	0.770	62.94
42	19.20	62.99	440.49	1445.16	0.15	0.49	0.13	0.415	52.05
43	19.65	64.47	440.47	1445.10	0.00	0.00			62.02
44	19.86	65.16	440.51	1445.23					
45	20.20	66.27	441.08	1447.10					62.92
46	20.44	67.06	440.50	1445.19	0.00	0.00			60.93
47	20.49	67.22	440.34	1444.67	0.12	0.39	0.65	2.090	60.93
48	20.73	68.01	440.92	1446.57					62.93
49	21.23	69.65	440.39	1444.83					62.93
50	21.74	71.32	440.40	1444.87					62.92
51	22.15	72.67	440.70	1445.85					65.93
52	22.90	75.13	440.38	1444.80					65.93
53	23.20	76.11	440.92	1446.57					65.93
54	23.81	78.11	440.49	1445.16					65.93
55	24.33	79.82	440.35	1444.70					62.92
56	24.08	79.00	440.87	1446.41					62.92
57	25.43	83.43	440.40	1444.87					65.15
58	27.99	91.83	441.53	1448.57					82.12
59	29.17	95.70	441.43	1448.24					
60	29.22	95.86	441.47	1448.38					
61	29.27	96.03	441.43	1448.24					
62	32.40	106.30	441.90	1449.79					2.19

MARITE SITE 3 SECTION No: TR. 4: CROSS-SECTION ID: DURR 407.7

Reach Length	124.3 m	407.7 ft	**WSE**	m	ft	**Q (cf/s)**
Reach weight	0.05		Aug:	440.6	1445.5	24.00
Slope	0.0018		Nov:	440.57	1445.4	19.00
Stage of zero flow	440.1 m	1443.8 ft	Sep:	440.35	1444.7	0.91

Vertical	chainage (m)	chainage (ft)	Elevation (m)	Elevation (ft)	Depth (m)	Depth (ft)	Velocity (m/s)	Velocity (ft/s)	Channel Index
1	0.00	0.00	442.02	1450.18					
2	0.05	0.16	441.97	1450.02					
3	5.33	17.49	441.83	1449.56					
4	13.12	43.04	441.77	1449.36					
5	16.05	52.66	441.29	1447.79					
6	16.10	52.82	441.33	1447.92					
7	16.15	52.98	441.29	1447.79					
8	19.19	62.96	440.75	1446.01					2.15
9	20.33	66.70	441.11	1447.20					82.09
10	20.93	68.67	441.30	1447.82					82.09
11	21.98	72.11	441.04	1446.97					82.09
12	22.22	72.90	440.59	1445.49	0.00	0.00			82.09
13	22.37	73.39	440.15	1444.05	0.44	1.44	0.32	1.03	55.99
14	22.89	75.10	440.10	1443.88	0.45	1.48	0.11	0.37	55.99
15	23.56	77.29	440.17	1444.11	0.37	1.21	0.46	1.46	55.99
16	24.03	78.84	440.16	1444.08	0.42	1.38	0.38	1.20	53.99
17	24.79	81.33	440.29	1444.50	0.30	0.98	0.12	0.38	92.99
18	25.70	84.32	440.42	1444.93	0.17	0.56	0.14	0.45	92.99
19	26.39	86.58	440.30	1444.54	0.23	0.75	0.33	1.06	92.99
20	27.11	88.94	440.24	1444.34	0.30	0.98	0.25	0.80	92.99
21	27.80	91.21	440.22	1444.28	0.37	1.21	0.36	1.14	92.99
22	28.64	93.96	440.22	1444.28	0.34	1.12	0.35	1.12	92.99
23	29.38	96.39	440.24	1444.34	0.36	1.18	0.28	0.88	92.99
24	30.13	98.85	440.18	1444.14	0.38	1.25	0.24	0.77	92.99
25	30.70	100.72	440.32	1444.60	0.27	0.89	0.36	1.16	92.99
26	30.78	100.98	440.59	1445.49	0.00	0.00			60.99
27	31.13	102.13	440.92	1446.57	0.28	0.92	0.16	0.53	60.99
28	31.55	103.51	440.58	1445.46	0.00	0.00			60.99
29	31.93	104.75	440.27	1444.44					65.99
30	32.64	107.08	440.38	1444.80	0.20	0.66	0.12	0.38	65.99
31	32.86	107.81	440.61	1445.55	0.00	0.00			6
32	33.28	109.18	440.92	1446.57					60.99
33	34.47	113.09	440.61	1445.55	0.00	0.00			60.99
34	35.08	115.09	440.38	1444.80	0.21	0.69	0.06	0.21	92.99
35	35.75	117.29	440.61	1445.55	0.00	0.00			60.95
36	35.89	117.75	440.67	1445.75					6
37	36.04	118.24	440.60	1445.52	0.00	0.00			60.95
38	36.49	119.71	440.39	1444.83	0.23	0.75	0.39	1.24	97.99
39	37.30	122.37	440.40	1444.87	0.18	0.59	0.30	0.96	97.99
40	37.54	123.16	440.60	1445.52	0.00	0.00			97.99
41	37.76	123.88	440.87	1446.41					6
42	38.78	127.23	440.60	1445.52	0.00	0.00			6
43	39.09	128.24	440.27	1444.44	0.31	1.02	0.28	0.88	92.99
44	39.75	130.41	440.27	1444.44	0.30	0.98	0.15	0.50	92.99
45	40.58	133.13	440.36	1444.73	0.20	0.66	0.01	0.03	92.99
46	42.15	138.28	440.43	1444.96	0.12	0.39	0.01	0.03	52.08
47	42.50	139.43	440.60	1445.52	0.00	0.00			2.18
48	45.54	149.41	441.19	1447.46					82.02
49	49.79	163.35	441.62	1448.87					2.18
50	53.49	175.49	441.86	1449.66					2.18
51	58.15	190.78	444.09	1456.97					7
52	58.14	190.74	444.04	1456.81					
53	58.19	190.91	444.09	1456.97					
54	58.24	191.07	444.04	1456.81					

MARITE SITE 3 SECTION No: TR. 5: CROSS-SECTION ID: DURR 690.7

Reach Length	210.5 m	690.69 ft	**WSE**	m	ft	**Q (cf/s)**
Reach weight	0.9		Aug:	440.62	1445.6	24.00
Slope	0.0002		Nov:	440.56	1445.4	19.00
Stage of zero flow	440.1 m	1443.88 ft	Sep:	440.39	1444.9	0.91

Vertical	chainage (m)	chainage (ft)	Elevation (m)	Elevation (ft)	Depth (m)	Depth (ft)	Velocity (m/s)	Velocity (ft/s)	Channel Index
1	0.00	0.00	442.42	1451.49					82.15
2	0.05	0.16	442.38	1451.36					
3	1.32	4.33	441.84	1449.59					82.15
4	1.80	5.91	440.23	1444.31					2.16
5	1.94	6.36	440.61	1445.55					2.16
6	2.21	7.25	440.11	1443.91	0.41	1.35	0.01	0.02	2.16
7	3.00	9.84	439.87	1443.13	0.70	2.30	0.01	0.02	2.00
8	3.81	12.50	439.83	1443.00	0.74	2.43	0.04	0.12	32.26
9	4.63	15.19	439.76	1442.77	0.82	2.69	0.03	0.11	32.26
10	5.33	17.49	439.76	1442.77	0.82	2.69	0.05	0.17	32.26
11	6.16	20.21	439.73	1442.67	0.82	2.69	0.07	0.23	53.29
12	7.04	23.10	439.82	1442.96	0.75	2.46	0.10	0.31	33.26
13	7.84	25.72	439.92	1443.29	0.66	2.17	0.11	0.35	32.29
14	8.62	28.28	439.97	1443.45	0.60	1.97	0.11	0.35	32.29
15	9.43	30.94	440.05	1443.72	0.53	1.74	0.10	0.31	32.29
16	10.18	33.40	440.11	1443.91	0.47	1.54	0.10	0.32	32.29
17	11.01	36.12	440.15	1444.05	0.40	1.31	0.12	0.40	32.29
18	11.82	38.78	440.21	1444.24	0.35	1.15	0.12	0.39	32.29
19	12.63	41.44	440.25	1444.37	0.32	1.05	0.10	0.31	32.29
20	13.39	43.93	440.22	1444.28					32.29
21	14.20	46.59	440.22	1444.28	0.37	1.21	0.08	0.25	32.29
22	14.23	46.69	440.18	1444.14	0.33	1.08	0.09	0.29	32.29
23	14.98	49.15	440.18	1444.14	0.39	1.28	0.08	0.27	32.29
24	15.81	51.87	440.11	1443.91	0.48	1.57	0.08	0.27	32.29
25	16.67	54.69	439.95	1443.39	0.62	2.03	0.07	0.23	32.29
26	17.45	57.25	439.96	1443.42	0.57	1.87	0.04	0.12	63.29
27	18.21	59.74	439.87	1443.13	0.70	2.30	0.07	0.22	63.29
28	18.97	62.24	439.88	1443.16	0.69	2.26	0.03	0.08	63.29
29	19.86	65.16	439.94	1443.36	0.68	2.23	0.04	0.12	87.28
30	20.33	66.70	440.02	1443.62	0.57	1.87	0.04	0.12	87.28
31	20.63	67.68	439.93	1443.32	0.67	2.20	0.02	0.08	87.28
32	21.54	70.67	440.24	1444.34	0.32	1.05	0.01	0.02	2.00
33	21.73	71.29	440.60	1445.52					87.23
34	22.17	72.73	441.69	1449.10					82.14
35	23.65	77.59	442.12	1450.51					82.14
36	26.67	87.50	442.22	1450.84					
37	26.72	87.66	442.26	1450.97					82.17
38	26.77	87.83	442.22	1450.84					
39	28.82	94.55	442.20	1450.77					2.16
40	31.12	102.10	442.16	1450.64					2.18
41	33.20	108.92	442.30	1451.10					2.18
42	36.21	118.80	442.21	1450.80					2.18
43	39.86	130.77	442.23	1450.87					82.13
44	45.41	148.98	442.66	1452.28					82.13
45	50.75	166.50	442.41	1451.46					82.12
46	57.44	188.45	443.09	1453.69					82.13

MARITE SITE 3 SECTION No: TR. 6: CROSS-SECTION ID: DURR 879.6

Reach Length	268.09 m	879.56 ft	**WSE**	m	ft	**Q (cf/s)**
Reach weight	0.3		Aug:	440.63	1445.6	24.00
Slope	0.0064		Nov:	440.59	1445.5	19.00
Stage of zero flow	440.1 m	1443.88 ft	Sep:	440.36	1444.7	0.91

Vertical	chainage (m)	chainage (ft)	Elevation (m)	Elevation (ft)	Depth (m)	Depth (ft)	Velocity (m/s)	Velocity (ft/s)	Channel Index
1	0.00	0.00	443.14	1453.86					87.29
2	0.05	0.16	443.10	1453.72					
3	4.66	15.29	442.19	1450.74					82.28
4	9.97	32.71	441.27	1447.72					87.25
5	11.93	39.14	440.61	1445.55					72.09
6	12.24	40.16	440.38	1444.80					82.09
7	14.37	47.14	439.45	1441.75					2
8	16.10	52.82	439.22	1440.99					3
9	17.45	57.25	439.41	1441.62					72.09
10	17.48	57.35	439.41	1441.62					52.29
11	18.39	60.33	439.70	1442.57					2.19
12	20.60	67.58	440.54	1445.33					2
13	21.19	69.52	441.07	1447.06					82.12
14	22.33	73.26	441.21	1447.52					82.12
15	24.78	81.30	440.94	1446.64					82.12
16	26.23	86.05	440.79	1446.15					2
17	26.51	86.97	440.63	1445.62					82.09
18	26.75	87.76	440.15	1444.05	0.48	1.57	0.00	0.00	82.09
19	26.97	88.48	439.98	1443.49	0.58	1.90	0.35	1.11	47.99
20	27.19	89.20	440.08	1443.82	0.59	1.94	0.44	1.41	47.99
21	27.32	89.63	440.28	1444.47	0.39	1.28	0.60	1.92	97.99
22	27.58	90.48	439.93	1443.32	0.65	2.13	0.45	1.46	97.99
23	27.68	90.81	439.99	1443.52	0.68	2.23	0.51	1.64	97.99
24	28.11	92.22	439.92	1443.29	0.64	2.10	0.39	1.24	57.98
25	28.36	93.04	440.01	1443.59	0.66	2.17	0.38	1.22	57.98
26	28.50	93.50	439.98	1443.49	0.66	2.17	0.26	0.85	52.98
27	28.70	94.16	440.03	1443.65	0.59	1.94	0.32	1.04	52.98
28	28.92	94.88	440.06	1443.75	0.48	1.57	0.43	1.38	55.23
29	29.17	95.70	440.48	1445.13	0.15	0.49	0.48	1.52	65.97
30	29.42	96.52	440.53	1445.29	0.08	0.26	0.39	1.26	65.97
31	29.69	97.41	440.50	1445.19	0.12	0.39	0.57	1.82	65.97
32	30.08	98.69	440.30	1444.54	0.31	1.02	0.57	1.83	53.93
33	30.24	99.21	440.27	1444.44	0.34	1.12	0.48	1.55	53.93
34	30.28	99.34	440.23	1444.31					37.98
35	30.48	100.00	440.27	1444.44					37.98
36	30.71	100.75	440.48	1445.13					82.02
37	31.00	101.70	440.60	1445.52	0.01	0.03	0.01	0.02	82.09
38	31.60	103.67	440.61	1445.55					82.09
39	31.62	103.74	440.62	1445.59					82.09
40	33.13	108.69	441.15	1447.33					82.09
41	36.54	119.88	441.59	1448.77					82.17
42	42.01	137.82	442.06	1450.31					
43	42.06	137.99	442.10	1450.44					83.17
44	42.11	138.15	442.06	1450.31					
45	45.01	147.67	442.22	1450.84					2.13
46	47.85	156.98	441.99	1450.08					2.19
47	49.13	161.18	441.86	1449.66					65.18
48	49.96	163.91	441.85	1449.62					65.18
49	51.31	168.34	442.28	1451.03					65.18
50	52.72	172.96	442.20	1450.77					65.18
51	53.85	176.67	442.51	1451.79					2.13

MARITE SITE 3

SECTION No: TR. 7: CROSS-SECTION ID: DURR 1014.1

Reach Length	309.09 m	1014.1 ft	**WSE**	m	ft	**Q (cf/s)**
Reach weight	0.5		Aug:	441.22	1447	24.00
Slope	0.0126		Nov:	441.10	1447	19.00
Stage of zero flow	440.59 m	1445.49 ft	Sep:	440.89	1447	0.91

Vertical	chainage (m)	chainage (ft)	Elevation (m)	Elevation (ft)	Depth (m)	Depth (ft)	Velocity (m/s)	Velocity (ft/s)	Channel Index
1	0.00	0.00	443.48	1454.97					82.18
2	0.05	0.16	443.44	1454.84					82.18
3	10.49	34.42	442.37	1451.33					62.18
4	14.04	46.06	441.92	1449.85					43.75
5	14.71	48.26	441.26	1447.69					43.75
6	15.81	51.87	441.22	1447.56					43.75
7	16.21	53.18	440.81	1446.21					6.00
8	16.55	54.30	441.29	1447.79					63.01
9	16.92	55.51	441.47	1448.38					72.2
10	17.17	56.33	441.28	1447.75					7.0
11	17.20	56.43	441.03	1446.93					87.2
12	17.26	56.63	441.30	1447.82					87.14
13	17.44	57.22	441.55	1448.64					72.21
14	18.33	60.14	441.58	1448.74					7
15	22.60	74.15	442.12	1450.51					43.75
16	26.71	87.63	441.83	1449.56	0.24	0.79	0.29	0.94	43.75
17	31.79	104.30	442.40	1451.43					43.74
18	32.65	107.12	441.75	1449.29					6
19	35.42	116.21	441.67	1449.03					63.01
20	35.39	116.11	442.14	1450.57					63.01
21	35.44	116.27	442.18	1450.71					6
22	35.49	116.43	442.14	1450.57					6
23	37.03	121.49	441.94	1449.92					60.18
24	37.39	122.67	440.88	1446.44	0.24	0.79	0.29	0.94	62.91
25	37.95	124.50	440.91	1446.54	0.22	0.72	0.30	0.96	62.91
26	38.65	126.80	440.68	1445.78	0.38	1.25	0.29	0.94	65.91
27	39.32	129.00	440.71	1445.88	0.40	1.31	0.45	1.46	65.91
28	39.51	129.62	440.85	1446.34	0.28	0.92	0.42	1.33	65.91
29	39.92	130.97	441.32	1447.88					6.00
30	40.54	133.00	441.35	1447.98					6.00
31	40.75	133.69	441.20	1447.49					6.00
34	43.59	143.01	441.21	1447.52					64.92
35	43.96	144.22	441.55	1448.64					6.00
37	44.99	147.60	440.71	1445.88	0.48	1.57	0.13	0.43	62.93
38	45.64	149.73	440.60	1445.52	0.56	1.84	0.18	0.58	64.93
39	46.44	152.36	440.79	1446.15	0.40	1.31	0.20	0.64	62.96
40	46.98	154.13	440.77	1446.08	0.42	1.38	0.35	1.11	62.96
42	47.80	156.82	440.82	1446.24	0.38	1.25	0.42	1.36	63.92
43	48.08	157.74	440.79	1446.15	0.40	1.31	0.43	1.39	63.92
44	48.95	160.59	441.03	1446.93	0.70	2.30	0.03	0.11	63.93
45	49.67	162.96	440.86	1446.37	0.32	1.05	0.27	0.86	92.95
46	50.29	164.99	440.83	1446.28	0.36	1.18	0.13	0.42	63.95
47	50.81	166.70	440.82	1446.24	0.36	1.18	0.38	1.22	62.98
48	51.28	168.24	440.71	1445.88	0.46	1.51	0.06	0.20	62.97
49	51.67	169.52	440.59	1445.49	0.58	1.90	0.12	0.37	62.99
50	53.00	173.88	441.14	1447.29					62.99
51	53.26	174.73	441.38	1448.08					82.09
52	53.77	176.41	441.71	1449.16					82.09
54	53.87	176.73	441.71	1449.16					82.09
55	53.84	176.64	441.75	1449.29					82.09
56	54.07	177.39	441.54	1448.61					82.09
57	54.36	178.34	441.18	1447.42					7.00
58	54.59	179.10	440.00	1443.55	0.16	0.52	0.45	1.46	7.00
59	55.21	181.13	440.88	1446.44	0.40	1.31	0.11	0.35	72.01
60	55.88	183.33	440.68	1445.78	0.48	1.57	0.41	1.32	7.00
61	56.37	184.94	441.88	1449.72	0.30	0.98	0.16	0.53	82.09
62	56.46	185.23	442.15	1450.61					82.09
63	58.16	190.81	442.03	1450.21					82.09
64	58.21	190.97	442.07	1450.34					82.09
65	58.26	191.14	442.03	1450.21					82.09
66	59.19	194.19	441.67	1449.03					82.09
67	59.97	196.75	442.11	1450.48					62.99
68	62.34	204.52	442.41	1451.46					62.99
69	64.87	212.82	442.79	1452.71					62.99
70	64.92	212.99	442.83	1452.84					62.99
71	64.97	213.15	442.79	1452.71					62.99

APPENDIX C

An example of the extrapolation of site-specific biotope information for Rapids to the entire study area.

These data were used to calculate the length of biotope types within the geomorphic unit, Rapids, at four discharges, Q (m^3s^{-1}). See Figure 11.11. The Total length of study area is 30 572.4 m

GEOMORPHIC UNITS = RAPIDS

Category of biotope type	Channel type	Length of Channel type (m)	Q	Rapids: Proportional contribution to site g	Biotope type: Proportional contribution to Rapids b	Biotope type: Proportional contribution to channel type g x b = p	Length of biotope type (m)	TOTAL FOR EACH BIOTOPE TYPE Q	 Length (m)
Biotope type: zero-flow biotopes in rapids									
	MST	10277.7	0.2	0.13	0.32	0.042	427.6	0.2	575.3
	MST	10277.7	0.9	0.13	0.19	0.025	253.9	0.9	341.6
	MST	10277.7	1.5	0.13	0.08	0.010	106.9	1.5	143.8
	MST	10277.7	1.9	0.13	0.11	0.014	147.0	1.9	197.8
	MPR	14047.2	0.2	0.02	0.32	0.006	89.9		
	MPR	14047.2	0.9	0.02	0.19	0.004	53.4		
	MPR	14047.2	1.5	0.02	0.08	0.002	22.5		
	MPR	14047.2	1.9	0.02	0.11	0.002	30.9		
	MAN	4317.7	0.2	0.03	0.32	0.010	41.4		
	MAN	4317.7	0.9	0.03	0.19	0.006	24.6		
	MAN	4317.7	1.5	0.03	0.08	0.002	10.4		
	MAN	4317.7	1.9	0.03	0.11	0.003	14.2		
	BAN	639.4	0.2	0.08	0.32	0.026	16.4		
	BAN	639.4	0.9	0.08	0.19	0.015	9.7		
	BAN	639.4	1.5	0.08	0.08	0.006	4.1		
	BAN	639.4	1.9	0.08	0.11	0.009	5.6		
smooth-boundary flow biotopes									
	MST	10277.7	0.2	0.13	0.08	0.010	106.9	0.2	143.8
	MST	10277.7	0.9	0.13	0.01	0.001	13.4	0.9	18.0
	MST	10277.7	1.5	0.13	0.03	0.004	40.1	1.5	53.9
	MST	10277.7	1.9	0.13	0.03	0.004	40.1	1.9	53.9
	MPR	14047.2	0.2	0.02	0.08	0.002	22.5		
	MPR	14047.2	0.9	0.02	0.01	0.000	2.8		
	MPR	14047.2	1.5	0.02	0.03	0.001	8.4		
	MPR	14047.2	1.9	0.02	0.03	0.001	8.4		
	MAN	4317.7	0.2	0.03	0.08	0.002	10.4		
	MAN	4317.7	0.9	0.03	0.01	0.000	1.3		
	MAN	4317.7	1.5	0.03	0.03	0.001	3.9		
	MAN	4317.7	1.9	0.03	0.03	0.001	3.9		
	BAN	639.4	0.2	0.08	0.08	0.006	4.1		
	BAN	639.4	0.9	0.08	0.01	0.001	0.5		
	BAN	639.4	1.5	0.08	0.03	0.002	1.5		
	BAN	639.4	1.9	0.08	0.03	0.002	1.5		
accelerating-flow biotopes									
	MST	10277.7	0.2	0.13	0.37	0.048	494.4		665.2
	MST	10277.7	0.9	0.13	0.32	0.042	427.6		575.3
	MST	10277.7	1.5	0.13	0.4	0.052	534.4		719.1
	MST	10277.7	1.9	0.13	0.39	0.051	521.1		701.1
	MPR	14047.2	0.2	0.02	0.37	0.007	103.9		
	MPR	14047.2	0.9	0.02	0.32	0.006	89.9		
	MPR	14047.2	1.5	0.02	0.4	0.008	112.4		
	MPR	14047.2	1.9	0.02	0.39	0.008	109.6		
	MAN	4317.7	0.2	0.03	0.37	0.011	47.9		
	MAN	4317.7	0.9	0.03	0.32	0.010	41.4		
	MAN	4317.7	1.5	0.03	0.4	0.012	51.8		
	MAN	4317.7	1.9	0.03	0.39	0.012	50.5		
	BAN	639.4	0.2	0.08	0.37	0.030	18.9		
	BAN	639.4	0.9	0.08	0.32	0.026	16.4		
	BAN	639.4	1.5	0.08	0.4	0.032	20.5		
	BAN	639.4	1.9	0.08	0.39	0.031	19.9		
standing and breaking wave biotopes									
	MST	10277.7	0.2	0.13	0.13	0.017	173.7	0.2	233.7
	MST	10277.7	0.9	0.13	0.3	0.039	400.8	0.9	539.3
	MST	10277.7	1.5	0.13	0.08	0.010	106.9	1.5	143.8
	MST	10277.7	1.9	0.13	0.1	0.013	133.6	1.9	179.8
	MPR	14047.2	0.2	0.02	0.13	0.003	36.5		

Category of biotope type	Channel type	Length of Channel type (m)	Q	Rapids: Proportional contribution to site	Biotope type: Proportional contribution to Rapids	Biotope type: Proportional contribution to channel type	Length of biotope type (m)	TOTAL FOR EACH BIOTOPE TYPE	
				g	b	g x b = p		Q	Length (m)
	MPR	14047.2	0.9	0.02	0.3	0.006	84.3		
	MPR	14047.2	1.5	0.02	0.08	0.002	22.5		
	MPR	14047.2	1.9	0.02	0.1	0.002	28.1		
	MAN	4317.7	0.2	0.03	0.13	0.004	16.8		
	MAN	4317.7	0.9	0.03	0.3	0.009	38.9		
	MAN	4317.7	1.5	0.03	0.08	0.002	10.4		
	MAN	4317.7	1.9	0.03	0.1	0.003	13.0		
	BAN	639.4	0.2	0.08	0.13	0.010	6.6		
	BAN	639.4	0.9	0.08	0.3	0.024	15.3		
	BAN	639.4	1.5	0.08	0.08	0.006	4.1		
	BAN	639.4	1.9	0.08	0.1	0.008	5.1		
Turbulent-flow biotopes									
	MST	10277.7	0.2	0.13	0.08	0.010	106.9	0.2	143.8
	MST	10277.7	0.9	0.13	0.17	0.022	227.1	0.9	305.6
	MST	10277.7	1.5	0.13	0.39	0.051	521.1	1.5	701.1
	MST	10277.7	1.9	0.13	0.34	0.044	454.3	1.9	611.2
	MPR	14047.2	0.2	0.02	0.08	0.002	22.5		
	MPR	14047.2	0.9	0.02	0.17	0.003	47.8		
	MPR	14047.2	1.5	0.02	0.39	0.008	109.6		
	MPR	14047.2	1.9	0.02	0.34	0.007	95.5		
	MAN	4317.7	0.2	0.03	0.08	0.002	10.4		
	MAN	4317.7	0.9	0.03	0.17	0.005	22.0		
	MAN	4317.7	1.5	0.03	0.39	0.012	50.5		
	MAN	4317.7	1.9	0.03	0.34	0.010	44.0		
	BAN	639.4	0.2	0.08	0.08	0.006	4.1		
	BAN	639.4	0.9	0.08	0.17	0.014	8.7		
	BAN	639.4	1.5	0.08	0.39	0.031	19.9		
	BAN	639.4	1.9	0.08	0.34	0.027	17.4		
freefall biotopes									
	MST	10277.7	0.2	0.13	0.02	0.003	26.7	0.2	63.7
	MST	10277.7	0.9	0.13	0.01	0.001	13.4	0.9	91.8
	MST	10277.7	1.5	0.13	0.01	0.001	13.4	1.5	193.4
	MST	10277.7	1.9	0.13	0.12	0.016	160.3	1.9	317.3
	MPR	14047.2	0.2	0.02	0.08	0.002	22.5		
	MPR	14047.2	0.9	0.02	0.17	0.003	47.8		
	MPR	14047.2	1.5	0.02	0.39	0.008	109.6		
	MPR	14047.2	1.9	0.02	0.34	0.007	95.5		
	MAN	4317.7	0.2	0.03	0.08	0.002	10.4		
	MAN	4317.7	0.9	0.03	0.17	0.005	22.0		
	MAN	4317.7	1.5	0.03	0.39	0.012	50.5		
	MAN	4317.7	1.9	0.03	0.34	0.010	44.0		
	BAN	639.4	0.2	0.08	0.08	0.006	4.1		
	BAN	639.4	0.9	0.08	0.17	0.014	8.7		
	BAN	639.4	1.5	0.08	0.39	0.031	19.9		
	BAN	639.4	1.9	0.08	0.34	0.027	17.4		