WATER TEMPERATURE AND FISH DISTRIBUTION IN THE SABIE RIVER SYSTEM: TOWARDS THE DEVELOPMENT OF AN ADAPTIVE MANAGEMENT TOOL

by.

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ABSTRACT

Water temperatures are a fundamental water quality component, and a key abiotic determinant of fish distribution patterns in rivers. A river's thermal regime is the product of a multitude of thermal drivers and buffers interacting at different temporal and spatial scales, including, *inter alia*, air temperatures, flow volumes (including groundwater flows and lateral inputs from tributaries), channel geomorphology and riparian vegetation.

"Healthy" river systems are self-sustaining, with adequate thermal variability to maintain biotic diversity. Temporal variability of flow volumes and water temperatures, and how these change along the longitudinal axis of a river, contribute towards a rivers "signature". Rivers that have had their signatures altered through anthropogenic impacts may no longer be sustainable, and require varying levels of management. Successful river management should include a quantification of these signatures, a definition of the "desired" state which management aims to achieve, associated "thresholds" of change or concern, and monitoring programmes. Such an approach requires flexibility and adaptability, as well as appropriate tools being available to natural resource managers. Indices, the utility of which are enhanced when included in predicative modelling systems, are a common means of assessing system variability and change. The degree of confidence placed in such tools depends on the level of fundamental science, and the degree of system understanding, underpinning them.

This research contributes to the understanding of the ecological significance of water temperatures in variable semi-arid river systems, using the Sabie River (Mpumalanga, South Africa) as a case study, and indices derived from biological indicators (*Chiloglanis*, Pisces: Mochokidae) to quantify the effects of cumulative changes in heat units against a hypothesised critical water temperature threshold. Hourly water temperatures for 2000-2002 collected at nine sites in the main rivers of the Sabie catchment, together with biannual surveys of relative abundances and community patterns of fish collected using standard electrofishing techniques, were used to provide the basis for a modelling system which aims to provide river managers with a tool for quantifying changes to the thermal regime of the Sabie River. This modelling system consisted of a suite of pragmatic models, including multiple linear regression models for simulating daily maximum water temperatures, and simple cause-and-effect relationships between biological indices (change

in condition factor and change in the ratio of relative abundances of two species of *Chiloglanis*) and annual metrics of time-of-exposure to heat stress.

It was concluded that changes in the thermal regimes of the rivers in the Sabie catchment are likely to lead to changes in fish distribution patterns, and a decline in river health. Inherent system variability suggests that management decisions will be made in the face considerable uncertainty. Indirect management of water temperatures may be possible through maintenance of flow volumes and flow variability. However, the most appropriate management approach for maintaining fish diversity within these rivers is to ensure that obstacles to fish migration are minimized, to maximise the ability of river biota to respond to thermal changes, by accessing suitable alternative habitats or refugia. Future research should focus on extending the time series of water temperatures from such river systems, and further understanding the drivers and buffers contributing to the thermal regimes of variable semi-arid river systems in South Africa. Additional testing of the validity of the hypothesized relationships between abiotic processes underpinning biotic patterns should be undertaken.

PREFACE

The research described in this thesis was carried out in the School of Bioresources Engineering and Environmental Hydrology, University of Natal, Pietermaritzburg, under the supervision of Doctor Graham P. W. Jewitt (School of Bioresources Engineering and Environmental Hydrology) and Professor Charles Breen (Institute of Natural Resources).

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others it is duly acknowledged in the text.

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"REMEMBER THE LORD IN EVERYTHING YOU DO, AND HE WILL SHOW YOU THE RIGHT WAY." (PROVERBS 3:6)

1 INTRODUCTION

1.1 Background

River systems are primarily defined by the quantity and quality of their water, and how these change along their longitudinal axes. Symptoms of river "ill health" become apparent when flow volumes and water quality signatures change. River managers are faced not only with the challenge of measuring these variable signatures, but also in deciding when a river has changed too much due to anthropogenic influences, as distinct from natural change. Various indices to "measure" changes in these signatures (for example, Richter et al. 1996) exist, although these judgements are generally based on human values and the scientific level of understanding of river system patterns and processes.

Natural resource management approaches, including those applied to river systems, often advocate the development of support tools to aid decision-making when attempting to sustain societal benefits. This is an ongoing imperative that drives much water related research, and is a key component of many river research and management initiatives, such as the erstwhile Kruger National Park Rivers Research Programme (KNPRRP). The KNPRRP was described as "an interdisciplinary and co-operative endeavor aimed at contributing to the conservation of the natural environment of rivers, through developing skills and methodologies required to predict responses of the systems to natural and anthropogenic influences, and to improve the quality of the advice to resource managers, researchers and stakeholders" (Breen *et al.* 1997). Breen *et al.* (2000) provide a comprehensive review of this work, together with lessons learned about the nature of such trans-disciplinary research.

Of particular importance to the ongoing development of management approaches applicable to river systems in South Africa that emerged from the Kruger National Park Rivers Research Programme are:

 The pre-impoundment study of fish diversity in the Sabie catchment (Weeks et al. 1996). This was a three-year survey of the aquatic macro arthropods and fish of the Sabie River catchment, which is an important perennial river flowing through the Kruger National Park. Emphasis was placed on understanding the abiotic determinants of fish distribution, as well as detailed microhabitat studies of the main Sabie River fish species. This study proposed that water temperature was a key determinant in fish distributions; with a clear distinction in ichthyofauna of the Sabie catchment emerging between the cooler headwaters (the foothill zone) and the warmer middle waters (the lowveld zone);

- A detailed configuration of the Sabie catchment for simulation of streamflow with a hydrological model (Jewitt et al. 1998) to provide hydrological inputs for the BLINKS¹ models for fish, riparian vegetation and geomorphology (James et al. 1996; Jewitt et al. 1998). The BLINKS models are unique in many ways because they successfully bring together abiotic (flow, geomorphology) and biotic (fish, riparian vegetation) components into qualitative models. These models simulate changes in fish numbers (as qualitative values), river geomorphology and riparian vegetation, in response to changes in hydrology, using simple "If...Then...Else" rules. This is despite the fact that the processes within the different model components are occurring at different spatial and temporal scales, and that historically, the various model components have been dealt with under separate academic disciplines. The pre-impoundment research provided some of the ecological inputs when the BLINKS models were developed (Jewitt et al. 1998);
- A rule-based simulation model for management of riparian systems in the Kruger National Park (Mackenzie et al. 2000). This model provides river managers in the Kruger National Park with a decision-support tool aimed at detecting changes in annual flow dynamics in the Sabie River, by linking an abiotic agent of change ("loss of bedrock influence in the Sabie River"; i.e. sedimentation) to a biotic pattern (change in population structure of the bedrock-associated riparian tree Breonadia salicina). In the model, site-specific predicted changes in the population structure of B. salicina are compared against threshold values of perceived or hypothesised limits of acceptable change in population structure, within a variable river system, under different flow scenarios. Associated

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¹ Abiotic-Biotic Links project

guidelines have been formulated to guide management actions regarding loss of bedrock influence in the event of perceived anthropogenic change.

Much of the abovementioned research in the KNPRRP focussed on the flow requirements of aquatic ecosystems, in particular for fish and riparian vegetation, the effect that changing hydrology and geomorphology have on these, and the development of simulation models to predict their responses to altered hydrological flow patterns. The later projects (e.g. Mackenzie et al., 2000) focused on the development of simulation models to serve the adaptive management (AM) process now adopted by the Kruger National Park as a fundamental approach to the management of its natural resources. Such models simulate biotic responses to abiotic drivers under different environmental scenarios, and "measure" system change against hypothesized acceptable upper and lower limits of "natural" variability.

Following a Water Research Commission funded assessment of the ability of the aforementioned BLINK models to serve the KNPRRP AM process (Breen et al. 2000), it was recommended that a research project which was designed more specifically to address management issues which considered the links between changes in fish diversity in response to water quantity and quality aspects, be developed. In particular, it was noted that the BLINK models were developed before the Kruger National Park's adaptive management process had been defined, and that a need existed to refine the models further to make them more useful as management tools. Furthermore, Breen et al. (2000) identified a need to address water quality issues.

A key component of the AM approach adopted in the Kruger National Park is the definition of "thresholds of probable concern" (TPCs) that set upper and lower limits of acceptable change for the environmental systems within the Park (Rogers and Bestbier 1997). According to Mackenzie et al. (2000), TPCs define a range of flux of acceptable change for chosen environmental drivers, and thus account for variability and heterogeneity exhibited by the system. Thus, TPCs are not fixed, but are modified if found to be invalid or inappropriate, and as such, can be considered as testable hypotheses on the limits of acceptable system change, based on the current level of scientific understanding. Rogers and Bestbier (1997) suggest the use of biological indicators, which act as surrogates of measurable criteria that can be related to specific agents of change (such as

water temperatures or sedimentation) identified by conservation managers. TPCs are defined for a variety of management issues in the Kruger National Park, such as numbers and distributions of elephants, as well as river "health".

The existing BLINK fish models do not relate directly to particular TPCs, and consequently do not have an explicit management component. Further development of the fish models, and relating these outputs, as biological indicators, to suitable TPCs, would add value to the existing suite of tools available to resource managers. Fundamental to defining a TPC is to establish baseline conditions (Noss 1990). However, as Schindler (1987) asks, "How do we identify when critical, measurable variables begin to vary outside the normal range, thereby indicating that the ecosystem is perturbed or stressed?" The concept of TPCs, and how they relate to the research reported in this document, is discussed in greater detail in Chapter 6.

The research reported in this document arises from the issues raised in above, and builds on outcomes from the KNPRRP, continuing with the use of the Sabie River, one of six important rivers flowing through the Kruger National Park (KNP), as the pilot study area. The Sabie catchment is approximately 709 600 ha in size, and is the most fish species-rich river system in the country, with forty-nine species of fish (four of which are aliens) having been recorded from it (Weeks *et al.* 1996). Weeks *et al.* (1996) divided the fish species assemblage of the Sabie catchment into two distinct groups based on multivariate community classification techniques, viz. a foothill group, characterized by cool water fish species, and a lowveld group, characterized by warm water species. A transition in fish community assemblage occurs in the Sabie River in the vicinity of the town of Hazyview (Figure 1.1).

Despite this rich species diversity, water quality and quantity issues, and how they impact on aquatic species diversity, are poorly understood within the catchment. This is in spite of the fact that the Sabie catchment is under increasing threat from developments such as afforestation, rural population growth, urban development and the construction of impoundments. Impoundments, while safeguarding water supply, have the effect of stabilizing river flows and water temperatures. Flow regulation is recognized as the "most disruptive factor for fish assemblages" (Ponton et al. 2000). Natural variation in river

flows and quality, in particular water temperatures, is a key factor in maintaining habitat integrity and species diversity.

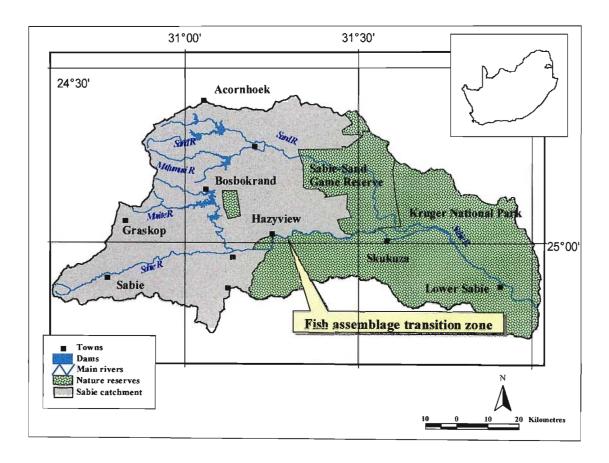


Figure 1.1 The Sabie catchment, showing main rivers, towns and nature reserves. The zone where the transition between cold-water and warm-water fish assemblages on the Sabie River occurs, as identified by Weeks *et al.* (1996), is also shown.

1.2 Aims and objectives

Aquatic scientists recognise water temperatures are a key water quality variable, which affects species diversity and distribution patterns within river systems. Water temperature was identified as a key driver of fish distribution within the Sabie River by Weeks et al. (1996). Thus, a central component of this study is an investigation of the biotic significance of a river's thermal regime, with particular reference to the Sabie system. Weeks et al. (1999) proposed that two species of Chiloglanis (Pisces: Mochokidae) would be suitable biological indicators of thermal change in the Sabie River. The ratio of relative abundances of a cool water species (C. anoterus) to a warmwater species (C. paratus) was proposed as a readily obtainable biological index which could relate to a proposed TPC for annual water temperatures, in a similar manner to the population structure index of the tree B. salicina was used by Mackenzie et al. (2000) to address the TPC for loss of bedrock influence.

This study contributes to aquatic ecosystem management, using the Sabie River as a case study, and simulation modelling of relative abundances and condition factors of Chiloglanids as a tool, to anticipate the consequences of changes to annual water temperatures under different flow or climate scenarios. The research contributes to the understanding of the significance of variable water temperatures to fish species diversity within the main rivers of the Sabie catchment, and relates this to adaptive management policies. The following broad questions are posed:

- To what degree is it possible to manage a river for desired levels of variability in its thermal regime?
- Is the definition and use of TPCs, particularly with respect to water temperatures, a practical management option for river systems that are inherently variable?

To this end, the four main objectives for this research were to:

- Describe intra-annual water temperature variation in the Sabie River at the catchment scale;
- Develop a prototype model of water temperature for the Sabie River, which may have broader applications in other South African rivers;

- Develop a model for simulating the responses of two species of the suckermouth catlets *Chiloglanis* (Mochokidae) to changes in annual water temperatures, in order to test the recommendation of Weeks *et al.* (1996) that the spatio-temporal change in ratio of relative abundances of these species provides an index for a proposed TPC for water temperature over the past season;
- Assess how the findings of this model add to the tools available to natural resource managers in the Kruger National Park.

Two hypotheses are proposed:

- H_{o1}: Water temperature is an important determinant of the spatial distribution of fish species in the Sabie River system;
- H_{02} : The ratio of relative abundances of *Chiloglanis anoterus* to *C. paratus* is a good indicator of inter-annual thermal change in the Sabie River.

1.3 Wider context to this research project

This research was undertaken within the framework of a Water Research Commission (WRC) funded project, which began in July 1999. This was a co-operative project, led by the Institute for Water Research (IWR) at Rhodes University, and in association with the School of Bioresources Engineering and Environmental Hydrology, University of Natal. The WRC project was concerned principally with evaluating the aforementioned BLINKS fish model, and the development of additional fish models, both of which were to be developed to add to the tools available to river managers within the Kruger National Park. These models, together with those of, for example Mackenzie *et al.* (2000), are intended to add to the decision-making process within the adaptive management framework adopted by the Kruger National Park.

These objectives dictated that the outcomes of this research serve the major WRC objectives detailed above, and this guided and constrained the research reported herein. The general approach, as reported in Chapters 2 and 3, has been to collect water temperature data at several points along the longitudinal profile of the Sabie River, and to relate these data to those collected from twice-annual fishing surveys undertaken by the IWR. These latter surveys formed the basis of the aforementioned Pre-impoundment (Weeks *et al.* 1996) and BLINKS (Jewitt *et al.* 1998) projects and were to continue in the

current WRC project. The WRC project was already underway by the beginning of 2000. when the research reported in this document began, and the first electrofishing survey occurred in May 2000. A literature review, and a necessary planning period to decide on appropriate approaches and technology for the collection of water temperatures, delayed the installation of temperature data monitoring equipment until February 2001. Thus, a lag exists between water temperature data collection, and the collection of the fish data. This necessitated the use of averaged water temperature data derived from the 2001 - 2002 water temperature time series for use with the 2000 fish survey data, and is recognised as a weakness of this research, as discussed more fully in Chapter 4. Furthermore, the placement and spatial resolution of the water temperature loggers was determined as a trade-off between serving the research needs of this component of the project, and being applicable to the sites chosen for the fish surveys (cf. Chapters 4 and 6). The number of temperature loggers available for placement was further constrained by available financial resources, since the temperature component was not explicitly budgeted for in the original WRC proposal, and limited funding was obtained from the University of Natal's Research Fund (URF). A consequence of this was that fish survey sites could not always coincide with water temperature collection sites. This too is recognized as less than ideal, as the spatio-temporal resolution of the water temperature time series is not the same as that the fish data, an issue which is discussed more fully in Chapter 4.

It is recognised that the realities of research within an applied project constrained by financial resources and time available may result in gaps in the research process. However, it is also recognised that these are the realities of applied research. Where such gaps do occur, they have been clearly identified and ways to address them have been suggested.

1.4 Thesis structure

A broad outline of the thesis components is provided in Figure 1.2. The study has been divided into two parts, with Part I concentrating on water temperature issues, and Part II concerned primarily with biotic responses to these, and what these mean in practical terms to river managers working within the Sabie catchment.

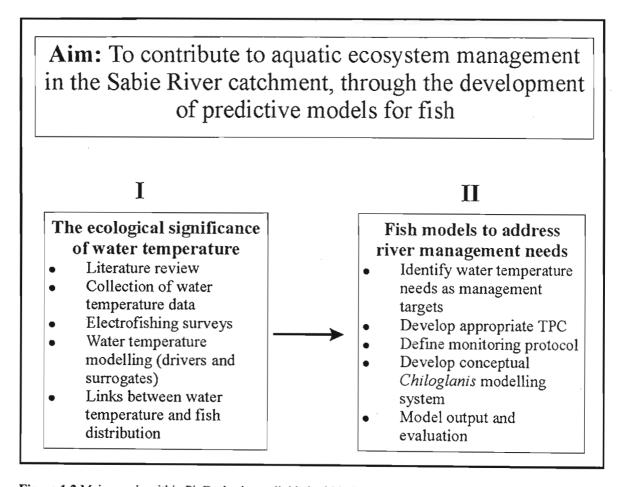


Figure 1.2 Major goals within Ph.D. thesis, as divided within Part I and II.

In Part I, the first two objectives listed in Section 1.2 are addressed through a consideration of the ecological importance of water temperature in the rivers of the Sabie catchment. Chapter Two provides a description of the thermal regime of the Sabie River at different scales of ecological importance. The ecological importance of water temperature, the importance of scale, and the potential impacts of altering a natural temperature regime are considered. Different modelling approaches for simulating daily maximum water temperatures are evaluated in Chapter Three, and a pragmatic statistical model, with

potentially broader applications in other rivers, is proposed for simulating water temperatures within the main rivers of the Sabie catchment. The link between water temperature (an abiotic process), and fish distributions (a biotic pattern), is made in Chapter Four. Multivariate ordination techniques have been used to establish possible correlations between sites, species, and key environmental variables.

In Part II, the third and fourth objectives are addressed through the development of the so-called "Chiloglanis modelling system". Chapter Five provides an objective basis for the choice of Chiloglanis anoterus as a suitable indicator species for seasonal change in water temperatures. Different measures of change (viz. change in relative abundances and condition) as indices for a candidate TPC for water temperature change are explored in Chapter Six, and a monitoring programme suitable for measuring TPC exceedance is suggested. Chiloglanids are the subjects of a simple model, which could be developed further within a more generic object-oriented modelling framework (Chapter Seven). Model output, based on three broad scenarios of maximum daily water temperatures, incorporating reductions in daily flow volumes and increases in daily mean air temperatures, is described in Chapter Eight, as well as the model's potential as an adaptive management tool for the Kruger National Park. Conclusions and the potential for future research are discussed in Chapter Nine.

2 INTRA-ANNUAL THERMAL PATTERNS IN THE MAIN RIVERS OF THE SABIE CATCHMENT

2.1 Introduction

Water temperatures play an important role in structuring fish distribution patterns (Sullivan et al. 2000; Caissie et al. 2001; Dunham et al. 2003). This link between abiotic process and biotic pattern is an important river management consideration, if biodiversity is to be maintained with the rivers of the Sabie catchment. A fundamental step in this process is characterizing and understanding water temperatures, particularly as an environmental gradient in the Sabie River. It is also important to understand the drivers of, and patterns in water temperatures at different spatial and temporal scales within this catchment.

2.1.1 Components of water temperature

According to the Second Law of Thermodynamics, the entropy of a system increases with time (Hawking 1988); to create and maintain an ordered system requires continuous inputs of energy. Energy is one of the currencies of any ecological system, including all freshwater systems (Reynolds 1998). Constant renewal and release of energy down a river system aids in balancing the energy budget, which may be broken down according to Equation 2.1 (Webb 1996):

$$Q_n = \pm Q_r \pm Q_e \pm Q_h \pm Q_{hb} \pm Q_{fc} \pm Q_a$$
 [2.1]

where Q_n = total net heat exchange; Q_r = heat flux due to net radiation; Q_e = heat flux due to evaporation and condensation; Q_h = heat flux due to sensible transfer between air and water; Q_{hb} = heat flux due to bed conduction; Q_{fc} = heat flux due to friction; Q_a = heat flux due to advective transfer in precipitation, groundwater, tributary inflows, streamflow and effluent discharges.

Water temperature may be considered as a surrogate measure of the energy fluxes in a river, which indirectly reflects the energy exchanges with the catchment. A river's annual thermal regime is one of its most important water quality parameters, being a key component in determining the distribution of aquatic communities (Nikolsky 1963; Smith 1979, 1981; Ward 1985; Weeks *et al.* 1996). Furthermore, most of the chemical, physical

and biological properties of water are temperature-dependent (Smith 1981). The physical or environmental variables within a river present a gradient of physical conditions from the headwaters downstream (Vannote et al. 1980). This in turn determines the resources available to biotic communities, which shapes community patterns over time and space (Frissel et al. 1986). Despite numerous papers on the relationships between temperature and aquatic organisms, as well as a large body of research on the physical mechanisms controlling natural water temperature variations, a limited understanding exists of the temperature conditions of natural rivers (Smith 1979), especially in the southern hemisphere (Ward 1985). This is certainly true of the rivers of the Sabie catchment, where a limited understanding exists of the intra-annual water temperature dynamics (Jewitt et al. 1998), and even less on the inter-annual cycles.

Water temperatures themselves are a function of many variables, and serve as an index of catchment condition (Poole and Berman 2001). The thermal inputs, or drivers, of a river (solar radiation and surface friction) are in dynamic equilibrium with thermal losses through heat transfer processes, such as evaporation (Bartholow 1989). Thermal gains or losses to a river are in turn "buffered" by factors such as the degree of riparian shading, and the extent of the hyporheic zone (i.e. the stream or rivers alluvium and associated groundwater from the alluvial aquifer) (Poole and Berman 2001). A consequence of this dynamism is that water temperature varies along the longitudinal axis of a river, on a seasonal and daily basis (Webb and Walling 1985; Allan 1995), with diel fluctuations superimposed on seasonal and annual cycles (Webb and Walling 1985). The magnitude and speed of these changes over space and time are a function of many variables, which operate at different spatial and temporal scales (Figure 2.1). The components of a river's thermal regime (annual range, diurnal range, thermal periodicity, winter minimum and summer maximum) may be altered because of smoothed hydrographs (Boon and Shires 1976; Smith 1979; Ward 1985), which ultimately detracts from a river's health, as defined and discussed in Chapter 5.

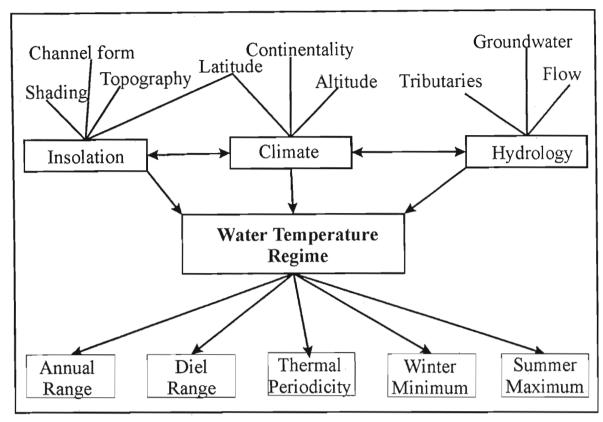


Figure 2.1 Key scale-dependant determinants of a river's water temperature regime, and biologically important components of this regime (after Ward 1985)

Gunderson *et al.* (1995) define three broad spatio-temporal scales, which are appropriate for categorizing abiotic process cycles, including water temperatures, and the system components they affect. At the micro-scale (< 10m²; hours), insolation (exposure to the sun's rays) impacts directly on water temperatures. Factors such as topography (which includes aspect and slope), channel form, bedrock and substratum, and the degree of shading determine the degree to which a river is exposed to direct solar radiation (Essig 1998). For example, the degree of sinuosity of a river is significant because it determines the residency time of a body of water within a given reach, and consequently the amount of solar radiation a body of water is exposed to (Bartholow 1989). In addition, these different factors affecting water temperature vary in importance with the size of a river. In small streams, shading can be a major factor in determining water temperatures (Gray and Edington 1969). The effects of tree shading are modified as the river becomes larger, due to thermal inertia (increasing water volumes and a widening channel) (Gray and Edington 1969). This fine-scale variation results in horizontal and vertical stratification of the water body, which in turn is a habitat parameter for resident aquatic biota.

At the meso-scale (10m² to 10km²; days), the flow regime of a river plays a central role in determining water temperature patterns, with water temperature inversely related to discharge (Webb 2000). As flow drops, water velocity decreases, allowing more time for water to approach thermal equilibrium with the air (Essig 1998). Differences in volume between headwaters and lower reaches mean that the thermal lag (i.e. the time difference between water temperature response to air temperatures) becomes of increasing significance downstream (Smith 1972). Two additional hydrological variables at this scale are the thermal inputs from tributary flows, together with the buffering effects of the hyporheic zone (Poole and Berman 2001). In the latter case, hyporheic groundwater is defined as water that infiltrates into the alluvial aquifer from the stream, travels along localized flow pathways, and re-emerges from the stream channel downstream (Poole and Berman 2001). Hyporheic flow is considered by Poole and Berman (2001) to be the most important stream temperature buffer. For example, Fowler and Scarsbrook (2002) found that the water temperature in areas of down-welling was equal to the temperature in the stream channel, while the water temperature in areas of up-welling was cooler, due to river water mixing with cooler groundwater. Thus, water temperatures cannot be fully understood without due consideration of a river's hydrograph, although Smith (1972) regarded the volume of overall discharge as the most important single hydrological factor influencing water temperature in a river.

At the macro-scale (> 10 km²; years), the overriding natural influences on water temperature are latitude, altitude and continentality. These variables define the climate of a region, and are responsible for the broad thermal regime of a river.

While water temperatures of a river are not equally sensitive to the different variables mentioned above, it has been shown that the variable to which they are on average most sensitive is air temperature (Bartholow 1989). This is especially true when air temperatures are considered in combination with stream flow, and the width to depth ratio of a river channel (Bartholow 1989). In combination, all these driving variables interact to produce a thermal regime within a river. Additionally, using this thermal regime, a river may be divided into "thermal reaches". This concept is similar to that of a "hydrological reach", which is a length of river with relatively uniform flow and geomorphology (Weeks et al., 1996). A thermal reach has similar riparian and channel conditions for a sufficient distance to allow the stream temperature to reach equilibrium with those conditions. Deep,

slow moving streams have longer thermal reaches than those that are shallow and fast moving (Lewis 1999).

In spite of many thermal characteristics of rivers being regarded as universal, South Africa's rivers have their own distinct characteristics. One immediate difference is that snowmelt is a major influence on water temperature in more temperate rivers (Webb and Nobilis, 1997). Ward (1985, p. 43), in comparing the thermal characteristics of northern hemisphere versus southern hemisphere rivers, concluded that what makes southern hemisphere rivers distinct from northern hemisphere rivers is "a matter of degree rather than of kind", i.e. South African rivers may have parallels in the northern hemisphere, but a greater proportion of these will be more variable than in the northern hemisphere. These differences of degree can be explained by the latitudinal differences in landmasses between northern and southern hemispheres. This has important implications for aquatic biota. Life histories of biota in variable systems are more flexible than in systems that are less variable. Consequently life histories of species found in less variable systems are more predictable (Webb 2000), and biotic communities are predictably structured along a river's profile because of the relative uniformity of the abiotic conditions (Vannote et al. 1980).

2.1.2 Water temperature and aquatic biota

Any natural system is the product of "fast" processes, such as daily temperature variation, occurring within the confines of "slow" processes. Fast processes tend to be associated with small spatial scales and short time periods; conversely, slow processes occur over large spatial and temporal scales. These physical patterns, including those of water temperatures, shape the biological communities within a river (Frissel *et al.* 1986), and form a continuous gradient of conditions along a river's longitudinal axis. This is the essence of the River Continuum Concept (Vannote *et al.* 1980), according to which biological communities form a spatial and temporal continuum, and species dynamics are in equilibrium with the dynamic physical conditions of the channel. In the case of fish, their morphology and life histories are adapted to the prevailing conditions in the river. Fish in the headwaters of a river generally have different temperature/oxygen tolerances to those species further down the river (Wootton 1992). Fish in highly variable environments tend to produce large numbers of eggs over short time periods, whereas fish living in more stable environments tend to produce fewer, larger eggs less often (Wootton 1992). This

continuous replacement of species over time and space leads to a distribution of energy within river reaches, and along the longitudinal axis of a river (Vannote et al. 1980), which aids in balancing a river's energy budget.

Aquatic systems are subject to great variability (Reynolds 1998), and water temperatures are an integral component of this variability. The importance of variability in maintaining ecosystem health and integrity is now well recognized (Richter et al. 1997), through its role in the constant revision of the thermodynamic base (Reynolds 1998). This is central to the intermediate disturbance hypothesis (Connel 1978) that states that species diversity is maximized at levels of intermediate disturbance. Highly diverse systems have more pathways for energy flow (Reynolds 1998) and greater resilience to disturbance. Less diverse systems tend to be less resilient (where resilience is defined as the rate at which a system returns to "normal" conditions) (Holling 1973; Hashimoto et al. 1982), since they are unable to accommodate such variability. In addition, variability is crucial in maintaining species diversity. For example, streams with a wide diel temperature range tend to have a correspondingly large diversity of fish (Vannote et al. 1980). Two of the explanations for this phenomenon are that more variability results in more habitat niches (sensu Hutchinson, 1957), and that competitive exclusions (where one species outcompetes another species to the point when one species is lost from the system) are less likely (Reynolds 1998). Vannote and Sweeney (1980) proposed that variable seasonal river temperature patterns appeared to be the critical factor in maintaining temporal segregation in aquatic invertebrate communities, thus allowing for resource partitioning, and preventing competitive exclusions. Temperature patterns influenced both the stability and number of species in a given community complex (Vannote and Sweeney 1980).

There is currently renewed interest, particularly in the United States and Great Britain, in understanding the thermal regime of rivers and streams, due to anticipated alterations to the natural thermal regimes of many rivers (Johnson 2003). This may be a consequence of impoundments (Brown 1969), changes in land use, and climate change (Mohseni *et al.* 1999). Changing the thermal regime of a river significantly alters a component of the environment for which river organisms are adapted (tolerances and life cycle cues) (Appleton 1976; Ward 1985). The primary concern regarding impoundments is usually their potential impact upon the natural seasonal variability that would be present in an unimpounded river, and to which biota have adapted over evolutionary timescales (Pielou

1998). For example, Walters *et al.* (2000) developed a multi-component model to explain the links between variability and ecosystem functioning in the Grand Canyon in the Colorado River. This ecosystem has been described as "violently seasonal" (Walters *et al.* 2000), but has been regulated to meet hydroelectric power demands. Altered flow regimes typically lead to a reduction in the range of temperature variation, even though mean temperatures may be unchanged (Gray and Edington 1969; Smith 1972; Wootton 1992). Therefore, a detailed knowledge of the complexity of the natural thermal regime is important as "biologically significant alterations of the thermal regime may result without appreciable changes in mean annual temperature" (Ward 1982). Water temperature variability has been positively correlated with diversity (Vannote *et al.* 1980). Thus, when variability is lost, there may be a consequent impoverishment of biological communities (Smith 1972) due to the loss of hypervolume area (*cf.* Chapter 5).

This chapter highlights general trends in intra-annual water temperature variability in the Sabie River, at the micro- and meso-scales. A basic understanding of this is central to understanding the links between water temperatures and ichthyological zonation patterns. A management priority is to develop a greater understanding of the life-histories of keystone aquatic species, and how these relate to water temperatures. In Chapter six, the links between water temperatures and fish abundances are explored further, using seasonal temperature indices and how they relate to the probability of occurrence of certain fish species. In the absence of adequate life-history data, this was the most appropriate approach to making links between water temperature (an abiotic process) and fish distribution (a biotic pattern).

2.2 Methods to quantify the thermal regime of the Sabie River

The main river of the Sabie catchment is the Sabie River, with the Sand and Marite Rivers as major tributaries (Figure 2.2a). Daily flow volumes within the rivers of the Sabie catchment are highly variable, as shown by the coefficient of variation (%) for the 56 subcatchments of the Sabie catchment, as defined by Pike and Schule (2000) (Figure 2.2a). It is anticipated that the thermal regimes of these rivers are equally variable, given the links between daily water temperatures and daily flow volumes.

Water temperature data were collected along the longitudinal axis of the Sabie River for different temporal periods between 8 February 2001 and 28 February 2003. Hourly water temperatures were collected at nine sites within the Sabie catchment ranging from 1190m.asl (top site) to 157m.asl (lowest site) (Figure 2.2b) throughout the study period, in order to provide data on intra-annual changes in water temperature along the longitudinal axis of the Sabie River, and to allow for comparison between the major rivers of the Sabie catchment. Site descriptions are provided in Table 2.1. In addition, water temperature data were also collected over short time periods (hours) at different depths (vertical profiles) and over a small (<100m²) surface area (horizontal profiles) to provide data for the consideration of the significance of water temperature variability at the micro-scale (Figure 2.2b).

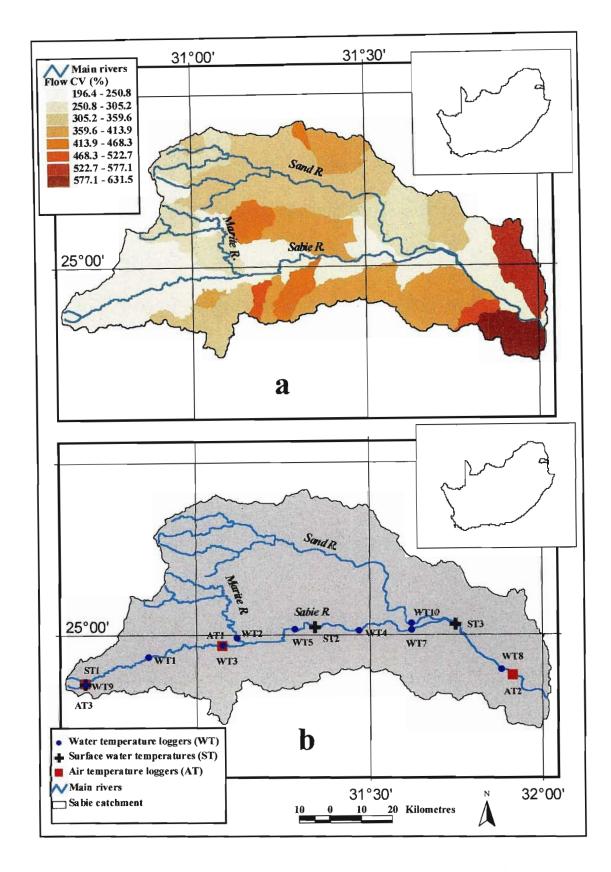


Figure 2.2 (a) Flow variability (coefficient of variation) within 56 subcatchments, as defined by Pike and Schulze (2000), of the Sabie catchment. This was based on simulated mean daily flows (m³.s⁻¹) for the period 1950 to 2000 using Acocks (1988) veld types for land use; (b) water and air temperature monitoring sites within the Sabie catchment.

Table 2.1 Site information for nine water temperature monitoring sites within the Sabie catchment.							
Downstrream distance is calculated from the source of the Sabie River; consequently this parameter does not							
apply to the sites on either the Sand or the Marite River sites (N/A).							

Site	River	Logger depth (m)	Channel width (m)	Altitude (m.asl)	Latitude (decimal °S)	Longitude (decimal °E)	Downstream distance (km)
WT9 ¹	Sabie	0.35	4.80	1193	25.14	30.68	5.87
WT1 ²	Sabie	0.50	13.00	870	25.06	30.86	30.09
WT3 ³	Sabie	0.60	13.30	523	25.04	31.07	57.29
WT5 ⁴	Sabie	3.00	25.00	357	24.98	31.31	83.85
WT4 ⁵	Sabie	0.50	5.00	287	24.99	31.47	106.94
WT7 ⁶	Sabie	0.50	28.00	242	24.99	31.62	125.17
WT8 ⁷	Sabie	1.00	6.00	157	25.10	31.89	160.90
WT10 ⁸	Sand	0.30	3.00	237	24.97	31.63	N/A
WT2 ⁹	Marite	0.35	20.00	443	25.02	31.13	N/A

- . 1 WT9 installed 16 May 2001. Uppermost site, situated on private property (Trout hatchery) in main channel against a slightly undercut stream bank. Air temperature logger at same site.
- WT1 installed 1 February 2001. Site 10 kilometres north east of the town of Sabie. Logger attached to in-stream boulder within a rocky, shaded reach of river.
- ³ WT3 installed 31 January 2001. Located on a citrus farm, in a shaded riffle section of the Sabie River. Logger hidden under submerged roots of a fig tree (*Ficus* sp.)
- 4 WT5 installed on 5 February 2001 within the Kruger National Park. Logger placed in a deep backwater of the main channel using steel cable.
- The WT4 installed on 2 February 2001 within the Kruger National Park. Logger attached to an in-stream rock in a riffle side-channel.
- 6 WT7 installed on 5 February 2001 within the Kruger National Park. Situated on the periphery of the main channel and secured to bedrock using steel cable.
- TWT8 installed on 6 February 2001, at the confluence of the Lubyelubye and Sabie Rivers within the Kruger National Park. Logger attached to bedrock and located within a side-channel. Missing data from 23 September 2001 to 10 October 2001 due to logger malfunction.
- WT2 installed on 1 February 2001 on a citrus farm on the Marite River.
 Logger secured onto roots of *Breonadia salicina* within a sandy reach of the river. Occasional shallow submergence by sediment.
- ⁹ WT10 installed on 16 May 2001, after original logger (installed 5 February 2001) lost. Attached to roots of *Breonadia salicina* in main channel of Sand River. Unreliable water temperature records from this site due to the logger being repeatedly submerged under > 0.5m of sediment.

2.2.1 Data collection

Vertical water temperature profiles were measured over short (< 3 days) time periods using eight temperature sensors (thermistors) attached to a submersible aluminium keel on a vertical axis. This was in turn attached to a polystyrene and fibreglass float (Figure 2.3), which compensated for possible short-term (sub-daily) changes in river depth. Thermistors change resistance with a change in their temperature, and are accurate to 0.1°C (Baker et al. 1975). They are stable and accurate, and are small and inexpensive (Schooley 1986). Temperatures were recorded 0.2m above the water surface (air temperature), and 0.0 to 1.0 m water depth, with thermistors placed at 0.2m intervals. A final thermistor recorded river bed temperature. The thermistors were attached to a data logger (MCSystems, 1997). Temperatures were recorded every ten minutes on four different occasions at two sites (Figure 2.2b; Table 2.2). By necessity, the equipment was placed in relatively slowmoving, deep sections of the river. The thermistors were calibrated in a laboratory situation by placing them in water baths of 0°C and 50°C. The recorded temperatures were compared to the water bath temperatures, so that for each thermistor, a straight line was plotted of known water temperature (x-axis) versus recorded water temperature (y axis). A correction factor was calculated from the straight-line equation derived from the plots (y = $mx + c)^{1}$.

Table 2.2 Logging dates, durations and sample sizes for collection of vertical water temperature profiles (refer to Figure 2.2b for locations).

Site	Date	Duration (Hours:minutes)	Sample size
WT5a	12-15 October 2001	71:20	429
WT5b	23-25 October 2001	52:40	317
WT5c	21-22 February 2002	28:20	171
WT8	19 October 2001	3:30	28

¹ In the case of a completely accurate logger, c = 0 and m = 1.

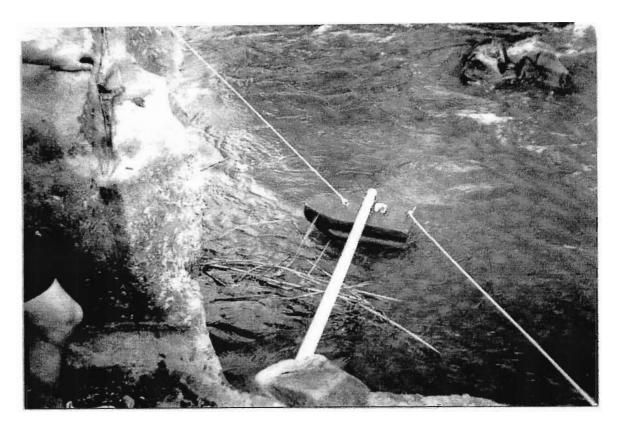


Figure 2.3 Fibreglass float with attached thermistors for collection of vertical water temperature profile

In addition, surface water temperatures were recorded at three sites (Figure 2.2) on the following dates: 8 July 2001 (ST1), 9 July 2001 (ST2) and 12 October 2001 (ST3). Surface temperatures were recorded as either spot temperatures (ST1), or every thirty (ST2) to sixty (ST3) minutes for three to four hours using an infra-red thermometer (Calex 2001) with a wavelength of 650nm. Fixed points were established in the river at each site by using corks attached to sinkers. The position of each point was captured using a GPS.

For the meso-scale analyses, twenty-five months of hourly air and water temperature were collected in the Sabie catchment. However, a subset of these data (1 June 2001 to 31 May 2002) was used in these analyses. This subset was chosen for two reasons:

- To provide the same starting date at all nine sites monitored. Two additional loggers were installed in mid-May 2001 (Table 2.1), so that a logical period for analyses would begin on 1 June 2001.
- A single year was chosen, to coincide with the final May electrofishing survey undertaken in May 2002 (see Chapter 4).

Water temperatures were recorded using Hobo (H8 series) single-channel data loggers (Onset 1999) and measured with internal temperature sensors (thermisters) sealed within

waterproof polycarbon submersible cases (Figure 2.4a) mounted inside steel pipes (Figure 2.4b). These units were immersed in flowing sections of river at a depth of at least 0.5 m, and attached to anchor points (rocks or trees) using 3mm steel cable (Figures 2.4a, b). Sites were chosen based on proximity to anchor points, stability of channel bottom, and cryptic value. The temperature data were calibrated using a linear calibration curve, in the same way as the sensors used to collect vertical temperature profiles. The Hobo loggers were accurate to approximately 0.5°C². Higher accuracy could have been achieved, but at higher data collection costs; these needed to be offset against the risks of losing loggers due to high flows or vandalism. This equipment has been used successfully elsewhere for recording water temperatures (see for example Lewis 1999; Robison et al. 1999). The loggers were powered by batteries that last for one year, and are able to store a total of 7944 data points, which translated into 331 days of hourly water temperatures. Logged data were downloaded every 2-3 months. Laboratory studies showed that a time lag of 10-15 minutes existed between temperature change and logger response due to the loggers being located within submersible cases. A logging interval of 60 minutes compensated for (Anon. 1998) found that a logging interval of one hour was adequate for this lag. measuring biologically meaningful water temperatures, and numerous ecological studies (for example Anon. (1998); Sullivan et al. (2000); Caissie et al. (2001)) have used the same logging interval. Using this scale of data collection makes it possible to obtain daily descriptive water temperature statistics (maximum, minimum, mean and median).



Figure 2.4a Water temperature logger inside polycarbon case

² The Hobo loggers are 8-bit loggers, with a 256-point resolution (2^8). Thus, the wider the temperature range the sensors are able to record temperatures at, the less accurate the readings will be, and vice versa. The sensors operate from -20° to $+70^{\circ}$ C, so that their resolution is 0.35° C. In practice it was found that the loggers "toggled" every 0.44° C, which suggests that the sensors record over a range of 110° C.

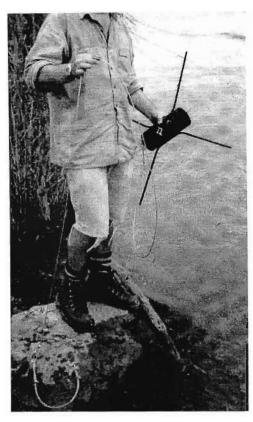


Figure 2.4b Steel casing containing data logger, showing steel cables securing equipment to bedrock.

In addition to these data loggers, three temperature/relative humidity Hobo loggers (Hobo H8 pro-Series Temp/RH) (Onset 1999), mounted inside radiation shields (Davis 2000) attached to steel poles at a height of one metre from the ground, recorded hourly air temperature and humidity (absolute and relative). The loggers were placed to ensure a suitable spread along the Sabie River, being located within one kilometre from the river (Figure 2.2), and offset from buildings.

2.2.2 Data analysis techniques

For the micro-scale analyses, mean water temperatures were calculated for the periods indicated in Table 2.2, for each of the four sites where vertical water temperature data were collected. These were plotted as horizontal bar graphs. Differences between datasets of water temperatures from different depths were tested for using a one-way ANOVA (no blocking) (Genstat 2000). The least significant difference test was used in order to establish which means from the ANOVA were significantly different from each other (Steel and Torrie 1981).

Spot surface water temperatures were averaged over three to four hour periods, and differences between the sites were tested using one-way ANOVAs (no blocking) (Genstat 2000). One-metre grids of surface water temperatures were generated by interpolation techniques (inverse distance weighting; power = 2) using the point coverages of mean water temperatures, in Arcview Spatial Analyst (ESRI 2001).

For the macro-scale (catchment-level) study, a subset of loggers was chosen to summarize catchment trends. Sites WT9 and WT8 were selected based on their location at the upper and lower extremes of the catchment respectively, while site WT3 was selected as the "middle" site since this area was highlighted as being transitional, with respect to fish community structure, between the foothill and lowveld zones of the Sabie catchment by Weeks et al. (1996). The time lag between hourly air and water temperatures was estimated using simple linear regression, and taking the highest correlation (R²) between water temperatures and air temperatures lagged from zero to four hours. Hourly proportion curves of water temperatures were calculated for sites at the upper (WT9), "middle" (WT3) and lower (WT8) reaches of the Sabie River. Mean daily ranges for each site were obtained by calculating the annual average of the daily range (maximum - minimum) of water temperatures. Hourly water temperatures for each logger were analysed in order to provide data on daily means, minimums and maximums of water temperatures. Box-and-Whisker plots of water temperature as a function of downstream distance were used to illustrate water temperature changes with downstream distance (which is used in this document as a generic term, inherent within which are the effects of flow volume, altitude and geomorphology). Daily duration and cumulative degree-day curves for temperatures greater than 15°C were used to provide information on the sequence in which the Sabie River was heated on an annual basis. This threshold was chosen as it corresponded with the median water temperature at the upper catchment site (WT9) (cf. Figure 2.9).

2.3 Results of Sabie River temperature monitoring

2.3.1 Thermal variation at the micro-scale

For the eight loggers recording vertical temperatures (Figure 2.5), mean air temperatures were warmer than mean water temperatures. On all four sampling occasions (refer to Table 2.2 for dates), water temperatures were lowest at 0.2 m below the water surface and on the river bed. Water temperatures were highest at a river depth of 0.8m. Based on the ANOVAs of the four data sets, mean temperatures for each of the eight loggers were significantly different (F < 0.001). In general, air temperatures were significantly warmer than the water temperatures, and temperatures at a depth of 0.8m were consistently significantly warmer than on the river bed, and for those at depths 0.2 and 0.4m (Tables 2.3a-d).

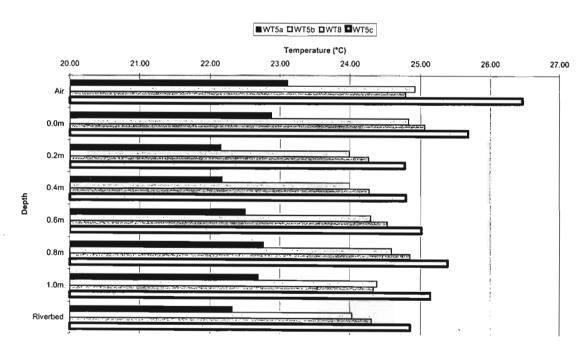


Figure 2.5 Mean water temperatures for different river depths on the Sabie River at sites WT5 (a-c) and WT8 (see Table 2.2 for sampling dates).

Table 2.3a Least significant difference test statistics of water temperature means for WT5a (shaded areas are logger depths), based on temperatures collected at ten-minute intervals for the period 12-15 October 2001. Logging intervals and sample sizes are provided in Table 2.2.

	River-	1.0	0.8	0.6	0.4	0.2	River surface
Air Temp.	0.79*	0.43*	0.35	0.61*	0.94*	0.96*	0.23
River surface	0.56*	0.19	0.12	0.37	0.71	0.72*	
0.2	0.17	0.53*	0.61*	0.35	0.02		
0.4	0.15	0.52*	0.59*	0.34			
0.6	0.18	0.18	0.25				
0.8	0.44*	0.07					
1.0	0.36						

* Significant differences between depths (p < 0.05)

Table 2.3b Least significant difference test statistics of water temperature means for WT5b (shaded areas are logger depths), based on temperatures collected at ten-minute intervals for the period 23-25 October 2001. Logging intervals and sample sizes are provided in Table 2.2.

	River- bed	1.0	0.8	0.6	0.4	0.2	River surface
Air Temp.	0.89*	0.54*	0.33	0.63*	0.92*	0.93*	0.09
River surface	0.80*	0.45*	0.24	0.54*	0.83*	0.84*	
0.2	0.04	0.39*	0.60*	0.30	0.01	_	
0.4	0.03	0.38*	0.59*	0.29			_
0.6	0.26	0.09	0.30				
0.8	0.56*	0.21					
1.0	0.35*						

* Significant differences between depths (p < 0.05)

Table 2.3c Least significant difference test statistics of water temperature means for WT8 (shaded areas are logger depths), based on temperatures collected at ten-minute intervals on 19 October 2001. Logging

intervals and sample sizes are provided in Table 2.2.

intervals and sam	River-		分加 对常是			计学 注题	River
Application of the state of the	bed	1.0	0.8	0.6	0.4	0.2	surface
Air Temp.	0.48*	0.46*	0.07	0.26	0.52*	0.53*	0.27
River surface	0.75 [*]	0.73*	0.20	0.53*	0.79 [*]	0.80*	
0.2	0.05	0.07	0.60*	0.27	0.01		
0.4	0.04	0.06	0.59*	0.26			
0.6	0.22	0.20	0.33				
0.8	0.55*	0.52*					
1.0	0.03						

Significant differences between depths (p < 0.05)

Table 2.3d Least significant difference test statistics of water temperature means for WT5c (shaded areas are logger depths), based on temperatures collected at ten-minute intervals for the period 21-22 February 2002.

Logging intervals and sample sizes are provided in Table 2.2.

	River- bed	1.0	0.8	0.6	0.4	0.2	River surface
Air Temp.	1.60*	1.31*	1.07*	1.45*	1.66*	1.68*	0.78*
River surface	0.82*	0.54*	0.29	0.67*	0.88*	0.90*	
0.2	0.08	0.37	0.61*	0.23	0.02		
0.4	0.06	0.35	0.59*	0.22	_		
0.6	0.16	0.13	0.38				
0.8	0.53*	0.25					
1.0	0.29					_	

* Significant differences between depths (p < 0.05)

Mean surface water temperatures showed no significant differences between sampling points (one-way ANOVA with no blocking; F > 0.05). A limited amount of "patchiness" of surface water temperatures was apparent from the interpolated surfaces (Figures 2.6a-c).

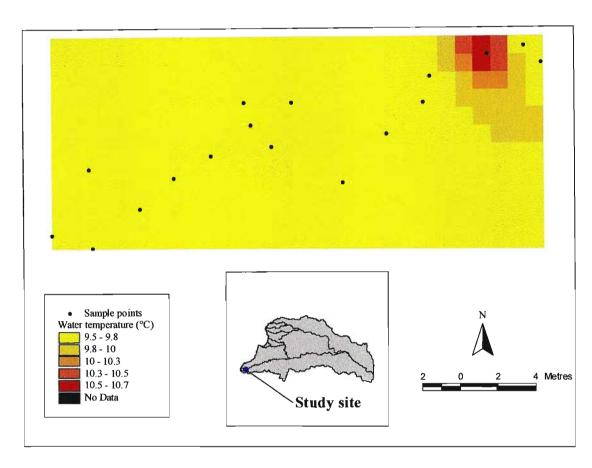


Figure 2.6a Spot surface water temperature variation in the upper Sabie River (ST1) at 11h00 - 11h10 on 8 July 2001, for 17 sample points that were interpolated to generate a one-metre resolution grid. The position of the sample site within the catchment is shown in the thumbnail map.

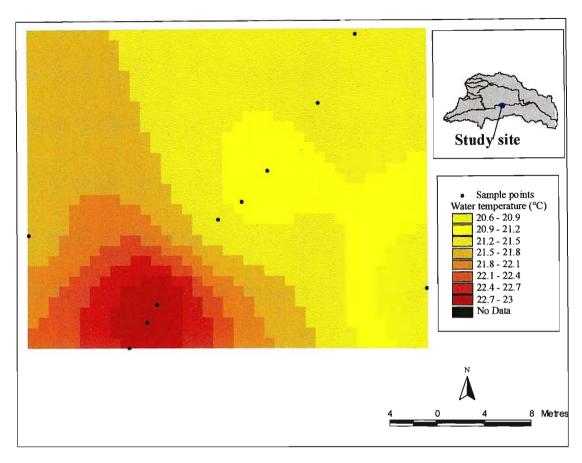


Figure 2.6b Mean surface water temperature variation based on 30-minute intervals from 11h00 - 13h00 on 12 October 2001 in the middle Sabie River (ST2), for 10 sample points that were interpolated to generate a one-metre resolution grid. The position of the sample site within the catchment is shown in the thumbnail map.

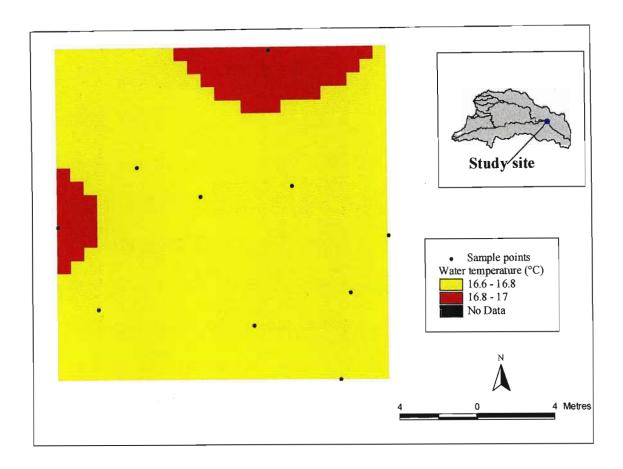


Figure 2.6c Mean surface water temperature variation based on 60-minute intervals from 11h00 – 14h00 on 9 July 2001 in the lower Sabie River (ST3), for 10 sample points that were interpolated to generate a one-metre resolution grid. The position of the sample site within the catchment is shown in the thumbnail map.

2.3.2 Thermal variation at the catchment scale

Calibrations of the loggers used to measure hourly water temperatures in the rivers of the Sabie catchment showed that the hourly temperature data needed to be corrected by an amount not exceeding 0.5°C. This was within the measurement resolution of the loggers.

Sample plots of hourly air and water temperatures plotted for June 2001 for the upper and lower catchment sites on the Sabie River (Figures 2.7a-b) are typical of trends for the entire record length, with daily range and variability of water temperatures increasing along the longitudinal axis of the Sabie River. The data also showed clear diurnal trends. The time lag between air and water temperatures was shown to increase from one to three hours with downstream distance (Table 2.4).

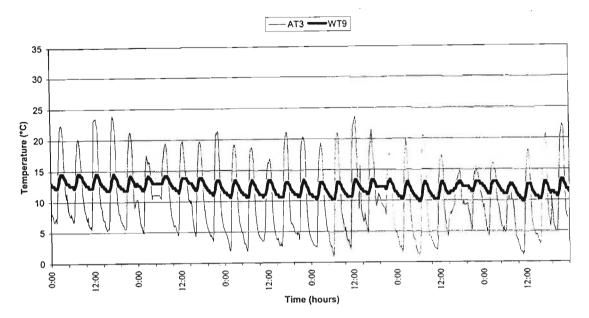


Figure 2.7a Hourly air and water temperatures from 1 to 30 June 2001 for the upper Sabie River

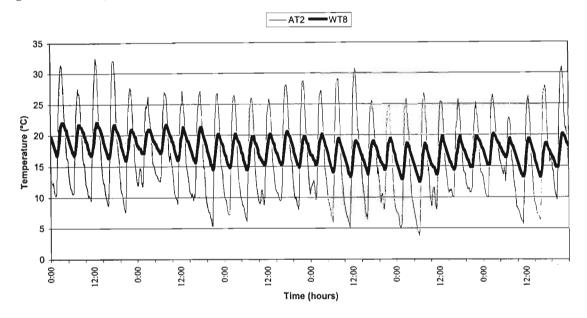


Figure 2.7b Hourly air and water temperatures from 1-30 June 2001 for the lower Sabie River

Table 2.4 R^2 values for simple linear regression of air versus water temperature at 0-4 hour time lags of water temperatures. R^2 values of highest significance are shaded.

River position	Time lag (hours) and R ² value								
	0	1	2	3	4				
Upper Sabie	0.657	0.705	0.701	0.649	N/A				
Middle Sabie	0.542	0.604	0.635	0.630	0.594				
Lower Sabie	0.467	0.510	0.534	0.538	0.521				

Based on the data for the sites for the upper, middle and lower sections of the Sabie River, it was clear that the intra-annual thermal regime became more complex with downstream distance. This was further substantiated in the plot of water temperature versus percentage time within different temperature classes (Figure 2.8). These curves changed from unimodal (WT9) to multimodal (WT8) along the longitudinal axis of the Sabie River. Water temperatures became progressively warmer for longer periods of time with downstream distance.

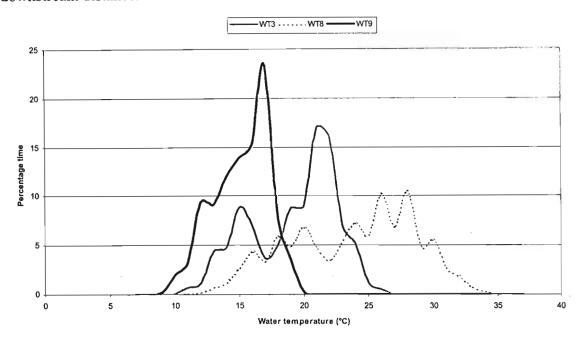


Figure 2.8 Hourly proportion curves for sites on the upper, middle and lower reaches of the Sabie River

When hourly water temperatures were summarized to provide (mean) daily water temperature statistics, patterns at the catchment level became more evident. A box-and-whisker plot of seven water temperature sites for the period 1 June 2001 to 31 May 2002 (Figure 2.9) showed that median water temperatures increased with downstream distance, as did the range of the middle 50% of the data. Minimum values remained relatively constant, while mean maximum water temperatures increased with downstream distance.

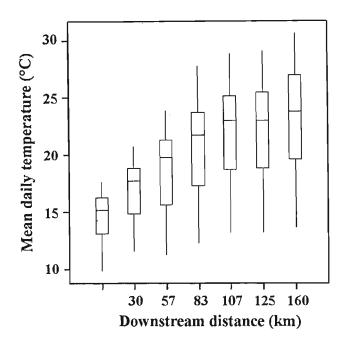


Figure 2.9 Box-and-whisker plot of daily water temperatures as a function of downstream distance. Maximum and minimum water temperatures are shown as "whiskers", while the middle 50% of the data for each site is shown by each box. The median is shown as a line within the box.

Absolute daily minima and maxima did not show a clear downstream trend (Figure 2.10), although minima were more consistent than maxima. Observed water temperatures within the Marite (WT2) and Sand (WT10) Rivers displayed higher maxima and lower minima than those recorded from adjacent sites in the Sabie River – WT3 and WT7, respectively. The average annual daily water temperature range (Figure 2.11) could be divided into two clusters viz. the sites from 0 to 57 kilometres downstream, and sites from 57 to 160 kilometres downstream, with sites downstream of 57 kilometres showing a greater daily range. This split coincided with the transition between the foothill and lowveld zones of the Sabie River catchment, as defined by Weeks *et al.* (1996).

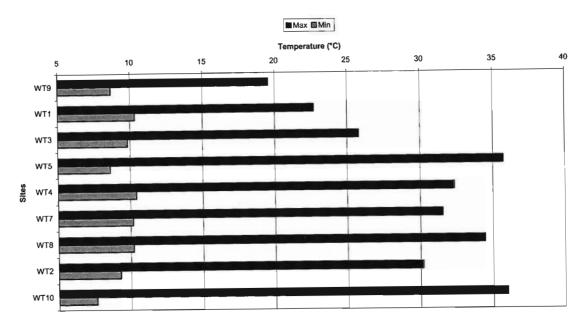


Figure 2.10 Absolute daily minima and maxima of water temperatures from the nine water temperature sites within the Sabie catchment

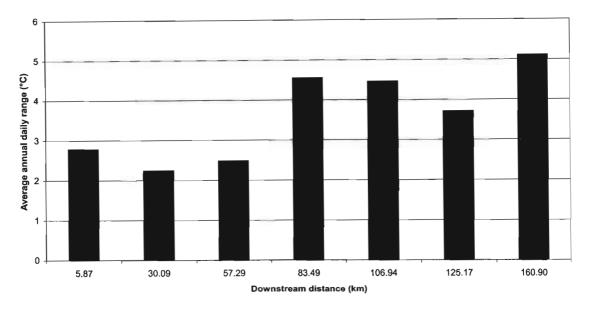


Figure 2.11 Average annual daily range in water temperatures as a function of downstream distance on the Sabie River. Daily ranges increased between 57 and 83 kilometres downstream of the headwaters.

The upper, middle and lower sections of the Sabie River showed different patterns of water heating sequences, as represented by the cumulative degree day and duration curves (Figures 2.12-13). Thermal energy was progressively added with downstream distance, as shown by the increase in cumulative degree days greater than 15°C. The percentage time spent at different temperatures (Figure 2.13) varied for each section of the Sabie River

examined. Based on these duration curves, a warming of 5-8°C occurred between upper and lower sites.

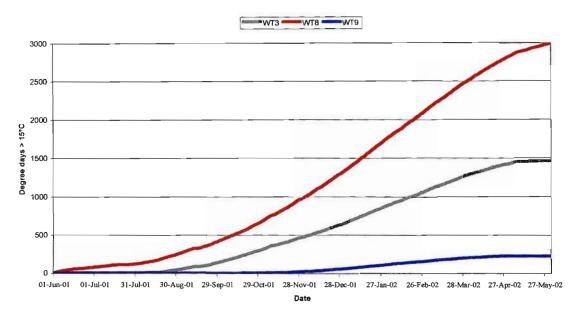


Figure 2.12 Cumulative degree days greater than 15°C for the upper, middle and lower reaches of the Sabie River

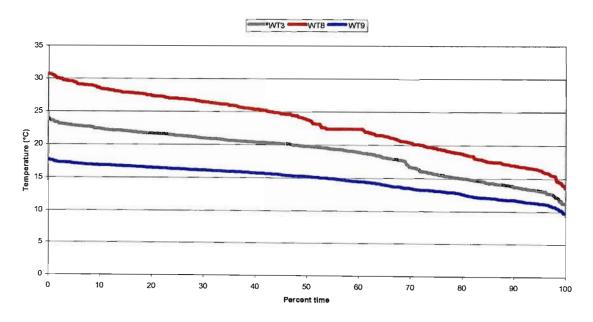


Figure 2.13 Duration curves of water temperature for the upper, middle and lower reaches of the Sabie River

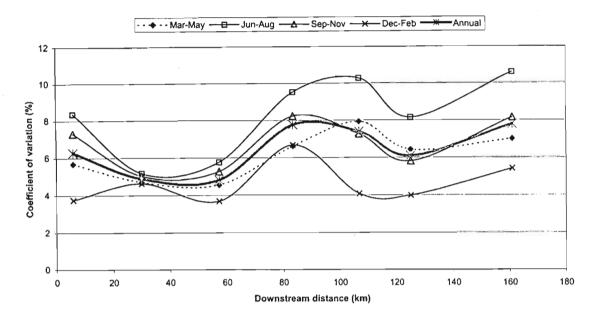


Figure 2.14 Annual seasonal coefficient of variation (%) of mean daily water temperatures in the Sabie River as a function of downstream distance

Variability increased with downstream distance, as shown by the percentage coefficient of variation (an expression of the sample standard deviation expressed as a percentage of the sample mean), which was calculated from mean daily water temperatures expressed as a seasonal mean with an associated standard deviation (Figure 2.14). Sites between 20 and 60 km downstream from the headwaters showed a decrease in variability. The underlying reasons for this may be due to a combination of factors such as groundwater inputs, residency times of water and more stable air temperatures at higher altitudes. There was a marked difference in variability between the seasons, with the greatest variability being recorded for the winter months (June to August). This same seasonal pattern was also evident in the mean annual water temperatures along the longitudinal axis of the Sabie River (Figure 2.15). The warmest temperatures were in summer (December to February), while the coolest water temperatures were during winter (June to August). In general, water temperature progressively increased downstream.

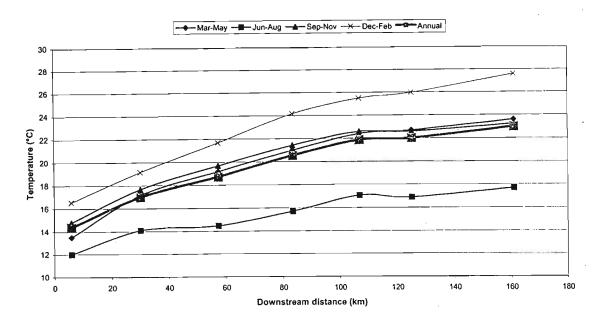


Figure 2.15 Mean daily seasonal and annual water temperatures along the longitudinal axis of the Sabie River for the period 1 June 2001 to 31 May 2002

2.4 Discussion and conclusions

A small, non-significant level of thermal heterogeneity was apparent within the Sabie River at the micro-scale, both vertically and horizontally, based on the limited scope of this study. However, the Sabie River is geomorphologically complex (Weeks *et al.* 1996), and it would be unwise to assume that thermal heterogeneity at the micro-scale habitat level does not play a role in creating thermal refuges for aquatic organisms.

The descriptive techniques of proportion, duration and degree day curves highlighted broad catchment-scale thermal trends, which are a function of large-scale processes (Frissel *et al.* 1986). However, the interpretation of the results can only be as accurate as the equipment used to measure these processes, and is based on the assumption that the scale of observation is compatible with the scale of the process. This is important because while aquatic organisms respond to a mosaic of water temperatures within a river reach, their response is often hidden by the scale at which temperature data are measured and observed (Essig 1998).

The quality of the data is also a function of the accuracy of the temperature loggers themselves, as well as in the choice of appropriate locations within the river channel. Essig (1998) defines three water temperatures of concern, viz:

- True water temperature;
- The water temperature near the temperature sensor. Sensors are often near banks, where the water tends to be more sluggish, and thus warmer;
- Recorded water temperatures, which is a function of the accuracy and calibration of the logger.

The data from this study will at best approximate true water temperatures occurring on the river bed, due to the 0.5°C resolution of the Hobo loggers (Section 2.2.1). The difference between true water temperatures and the water temperatures near the loggers is not quantifiable, although it is accepted that such differences might be found owing to the loggers (Table 2.1).

An additional variable not considered in this study was the role of hyporheic flow in buffering water temperatures. Within the middle and lower portions of the Sabie River, the role of this buffer was considered negligible, due to the large degree of bedrock control within the macro-channel (Heritage et al. 1997). The Sabie River is confined to a narrow deep valley within existing host rock, and active channel evolution and sedimentation is restricted to within this "macro-channel" zone (van Niekerk and Heritage 1993). However, the role of hyporheic flow may nevertheless play a limited role within the macro-channel, which does display some alluvial characteristics (Heritage et al. 1997). Such flows may also play a more significant role in the upper reaches of the Sabie River, together with the more alluvial Sand River. These variable inputs of ground and surface water have important ecological implications, not only in terms of nutrient supply and water temperatures, but also in terms of the hypogean invertebrate communities (Fowler and Scarsbrook 2002) and fish survival (Malcolm et al. 2003). The extent of influence of the hyporheic zone within different reaches of the Sabie-Sand River systems could be quantified using piezometer nests (i.e. a cluster of bank-side boreholes at different depths) positioned at areas of down-welling and up-welling, such as the head and tail of riffles (Gordon et al. 1993; Fowler and Scarsbrook 2002; Malcolm et al. 2003). Additionally, residence times of hyporheic flows could be determined using hydrochemical tracing techniques (Malcolm et al. 2003).

For this study, the derivation of seasonal trends was considered more important than a high level of accuracy at an hourly time step, owing to the scale of the research. Lewis *et al.* (2000) provide a comprehensive monitoring protocol for river managers in the United

States, which is also applicable to river temperature monitoring programmes in South Africa. Of particular relevance, the choice of location is critical in ensuring that water temperatures recorded are representative of the reach of the river being considered. Thus, loggers should be placed in well-mixed areas, such as riffles, and not in contact with the river bottom, to avoid issues of cold or warm pockets, and thermal stratification (Lewis *et al.* 2000). However, these considerations need to be balanced against threats from vandalism and animal damage, as was the case in this study.

In general, mean and maximum temperatures, as well as thermal variability, increased with downstream distance in the Sabie River. This trend is consistent with those proposed by (Vannote et al. 1980) as part of the River Continuum Concept. These trends are the result of complex interactions between, inter alia, river geomorphology, flow volume (and how this varies seasonally), lateral inputs from tributaries, altitude, and solar radiation (Poole and Berman 2001). For example, lateral flow inputs from tributaries (Marite and Sand Rivers) may affect water temperatures in the Sabie River by adding warmer water at the point of confluence, and contributing to thermal variability, due to the observed higher maxima and lower minima within these two tributaries (cf. Figure 2.10). A combination of such factors may explain the apparent anomaly of the coefficient of variation being highest during the winter months, since this coincides with the low flow period, and water temperatures have been shown to be inversely proportional to flow volume (Webb 2000). An additional factor that may explain this phenomenon is that during the winter months, cloud cover is generally less, such that the diurnal radiation flux (and air temperature) has a wider diurnal range than experienced during the summer months. Within each reach, a sinusoidal pattern with a 24 hour periodicity was visible for both air and water temperatures, although the oscillations of the water temperatures were dampened.

Based on the data from this study, the Sabie River can be divided into two distinct thermal zones. These zones coincide with the zones suggested by Weeks *et al.* (1996), who grouped the fish species assemblage of the Sabie River into two groups; a cool water group (foothill zone) and a warm water group (lowveld zone). Stuckenberg (1969) highlighted the links between thermal zones and species distributions. Within the Sabie River system, it was suggested by Weeks *et al.* (1996) that the ichthylogical patterns observed were largely explained by thermal patterns. The Sabie River system is one of the most species-

rich systems in South Africa (Weeks et al. 1996), with the fish having evolved to be in equilibrium with the prevailing thermal regime.

Thus, in terms of overall management issues for the Sabie catchment, and in particular the management goal of the Kruger National Park of maintaining diversity, it is important to understand the following more fully:

- Impacts of climate change, and activities which may result in flow reductions, on water temperatures, which necessitates modelling water temperatures at the appropriate scale (Chapter 3);
- Links between cumulative seasonal water temperatures and fish response (Chapters 6-8);
- Drivers of fish community patterns, and the role of water temperature (Chapter 4).

* * * * *

This chapter illustrated the complex nature of water temperature in the main rivers of the Sabie catchment. Understanding these water temperatures requires a multi-scale approach. Generalizations that can be made, based on the data collected for this research, are that heat units and variability both increase with downstream distance. It is important that river managers be aware of this variability. One approach to understanding this is through simulation modelling, which is discussed in Chapter 3.

3 SIMULATING MAXIMUM DAILY WATER TEMPERATURES IN THE SABIE RIVER

3.1 Introduction

Water temperature is a fundamental index used to determine the nature of an aquatic environment (Jewitt and Görgens 2000b; Poole and Berman 2001), because of its role in the life histories of aquatic organisms. Furthermore, "temperature prediction may be used as a first step in predicting the effect of man's activity on the aquatic ecosystem of a body of water" (Brown 1969). There is renewed interest, particularly in the United States and Great Britain, in simulating the thermal regime of rivers and streams, in response to anticipated alterations to the natural thermal regime of many rivers as a result of impoundments (Walters et al., 2000), changes in land use, and climate change (Mohseni et al. 1999). Predicting water temperatures, and changes to water temperature regimes, is important for anticipating the potential impacts of temperature changes on the provision of ecosystem goods, such as fisheries (for example Morse 1970; Hostetler 1991; Eaton and Scheller 1996; Graham et al. 1996). However, the general paucity of water temperature data, compared to river flow data, is a global problem, reflecting the later interest in water quality issues compared with water quantity issues. Data for Africa are particularly scarce (Ward 1985; Webb 1996), and river temperature data, where it exists, may have been collected incidentally during other aquatic studies (Appleton 1976). The advent of costeffective, continuous temperature sensor technology has made it possible to collect fine resolution water temperature data with relative ease (Lewis 1999).

Water temperature simulation models are able to provide data for use in constructing thermographs for a river. The most common ecological use of these models is that the output can be used as inputs into plots of cumulative heat units, such as duration curves and degree curves. Temperature duration curves (percentage time versus temperature) are useful in comparing sites (Webb and Walling 1985), while cumulative degree curves (hours, days) are useful in showing the sequence in which water is heated over time (Webb and Walling 1985), thereby quantifying the cumulative warmth in a season at a particular location (Essig 1998). Cumulative degree curves are useful for evaluating the potential of a stream to achieve or maintain a temperature below a given threshold (Webb and Walling

1985; Essig 1998), and are a measure of average temperature reached and the time for which it is maintained (Appleton 1976). Furthermore, degree units (days or hours) are a useful criterion for comparing temperature regimes between sites, and for relating field results to experimental data (Appleton 1976). These curves take into account magnitude and duration of departure from a chosen threshold temperature (Essig 1998). Degree hour curves can be used for establishing threshold levels for population distributions (Appleton 1976; Vannote and Sweeney 1980), and have often been used to predict year-class strength of certain species of fish (Nunn *et al.* 2003). Growing degree days have been used extensively in crop yield modelling (Kiker 2001) because they link a plant's growth stage to environmental cues rather than calendar days (Schulze 1995).

Thermal factors, such as increased rates of cooling after sunset in shallow water during autumn and winter (which affects the survival of fish, particularly juveniles), increased turbidity loads during summer (which modify rates of water heating), and seasonal differences in penetration of specific wavelengths of light (low sun zenith angles in winter cause greater reflectance) are recognised as drivers and buffers of river water temperatures (cf. Section 2.11). While such considerations are worthy of further research, cumulative daily maximum water temperatures have been shown to have the greatest effect on the distribution of aquatic species (Armour 1991; Essig 1998; Hines and Ambrose 1998; Robison et al. 1999; Sullivan et al. 2000; Caissie et al. 2001). For example, Dunham et al. (2003) found that daily maximum water temperatures play a dominant role in determining fish occurrence. Biologically, daily maximum water temperatures are significant to fish, and in particular cold-water species, which show signs of acute stress at warm (> 22°C) water temperatures (Dunham et al. 2003). Thus, while many water temperature models predict mean weekly or mean daily water temperatures (Caissie et al. 2001), water temperature models appropriate to river ecologists should predict ecologically significant water temperature characteristics, such as daily maxima (Dunham et al. 2003; Johnson 2003). The aim of this chapter is to evaluate different approaches to water temperature modelling (cf. Section 3.2), before selecting the most appropriate approach for simulating maximum daily water temperatures for the Sabie River. The aim in developing a water temperature model was to provide a basis for river managers for predicting the consequences of environmental change within the Sabie catchment, such as reduced flows resulting from impoundments, or increased air temperatures due to potential climate

change, to seasonal water temperatures (Chapter 8). The requirements of the model were that it should simulate daily maximum water temperatures:

- Using readily available surrogates for predicting water temperature, namely flow and air temperature;
- On a site-by-site basis on an annual basis (temporally explicit);
- Incorporate dynamism ($\Delta T^{\circ}/\Delta downstream\ distance$) by being spatially explicit.

3.2 Review of water temperature modelling approaches

Water temperature models are generally either process-based (heat exchange and energy budget) or statistical (regression and sine curves). Statistical methods, while usually deterministic, often include a stochastic element (Webb 2000), and frequently operate at medium to coarse time scales. The process-based approaches are deterministic, and attempt to model fundamental physical processes (Webb 2000), usually at relatively small spatial and temporal scales. Additionally, water temperature models may either be point-based, predicting water temperatures over time for a specific spatial location (a particular river reach), or spatial (dynamic), predicting change in water temperatures over time and space. These usually take the form of differential equations, and are usually based on heat gain or loss as water moves downstream.

3.2.1 Statistical methods

According to Dahmen and Hall (1990), time series data being used for water management studies should be stationary, consistent, and homogenous when used in system simulations. A time series is stationary if its statistical properties (e.g. its mean, variance, and higher-order moments) are unaffected by the choice of time origin. The stationarity criterion is met when the mean and variance of the data are stable, so that there is no systematic change in the mean (i.e. no trend). For stationarity, the probability distribution at times t_1 , t_2 , t_m must be the same at times t_{1+k} , t_{2+k} , t_{m+k} , where k is an arbitrary shift along the time axis (Makridakis *et al.* 1983). The recommended procedure for screening data is to test the seasonal time series for absence of trend, and for stability of variance and mean. If the time series does have a trend, the data cannot be used reliably for frequency analyses or simulations. When this is found to be the case, subsets of the data could be selected for

analysis after checking for break-points in the trend, using techniques such as double-mass analysis.

3.2.1.1 Linear regression analysis

The development of a linear relationship between air and water temperatures is based on the assumption that the rate of change in heat storage in a river can be related to air temperature change (Stefan and Preud'homme 1993). This approach relies on the (generally) linear relationship between air and water temperatures. Inherent in this approach is that the data conform to the basic assumptions of linear regression (McConway et al. 1999), viz. that the:

- Mean of the response variate (y_i) is linear; or in other words that the mean is stable;
- Variation about the mean (ε_i) has a normal distribution;
- Variance (ε_i) is the same for all values of the explanatory variable (i.e. constant variance);
- ε_i are independent of each other.

Air temperature is widely measured, which makes it convenient to use as a basis for predicting water temperatures (Webb and Nobilis 1997). Typically, such studies are undertaken using large (1-100km) areas and coarse time scales (5 days to months). Stefan and Preud'homme (1993) used weather stations which were an average of 70 kilometres from the rivers; correlations decreased when the distance exceeded 160 kilometres. Smith (1981) found significant simple linear relationships between monthly air and water temperatures for rivers in Great Britain. Crisp and Howson (1982) found a simple linear relationship between air and water temperatures to be adequate to predict 5- or 7-day mean water temperatures for streams in the north Pennines and English Lake District. Webb and Nobilis (1997) examined the relationship between monthly mean air and water temperatures for a small catchment in Austria that had data for 90 years, and found a significant relationship between monthly air and water temperatures.

However, a simple linear relationship between air and water temperatures may not always be adequate in describing water temperatures completely. Relationships may vary between catchments because of factors such as slope and aspect (Webb and Nobilis 1997), which

makes generally applicable models elusive. Furthermore, Webb and Nobilis (1997) found between-month differences in regression slopes, suggesting that the relationship between air and water temperatures is influenced by other seasonally-dependant variables, such as flow volume and flow rate. As flow volumes drop, so do water velocities, giving more time for a body of water to approach thermal equilibrium with the air above it (Essig, 1998). The instability of the relationship between air and water temperatures during the year implies that it is not one of true cause and effect. Water temperature depends on a number of meteorological and hydrological parameters, such as relative humidity, water depth, flow and sediment load (Stefan and Preud'homme 1993). Other factors, such as adjusting temperatures for flow, need to be considered (Webb 1996), and these can be included into more complex water temperature models using multiple linear regressions, with the basic form of the model shown in Equation 3.1. However, "multiple regression analysis has suggested that the effects of rainfall and river flow on water temperature are small compared with those of air temperature" (Webb and Nobilis 1997).

$$y = \sum_{i=0}^{n} \beta_i x_i + \gamma \tag{3.1}$$

where y is the response variable, x_i is the i^{th} explanatory variable, β_i is the i^{th} coefficient, and y is a random error term.

Crisp and Howson (1982) found that a simple linear relationship was not adequate for predicting water temperatures below 0°C. According to Mohseni and Stefan (1999), interpolations of water temperatures outside the range 0-20°C are less accurate because the essentially linear relationship becomes logistic. High air temperatures often coincide with low flow periods, and in the northern hemisphere at low temperatures, snowmelt complicates water temperature prediction (Mohseni and Stefan 1999). An S-shaped logistic function derived from daily air temperatures plus two stream temperature variables (Equation 3.2) was developed by Mohseni *et al.* (1998) to compensate for these non-linearities, which also captured the stochastic nature of stream temperature.

$$Ts = \mu + \frac{\alpha - \mu}{1 + e^{\gamma(\beta - Ta)}}$$
 [3.2]

where Ts is the estimated stream temperature; Ta is the air temperature measured at or near the stream gauging site; α is the estimated maximum stream temperature; μ is the estimated minimum stream temperature; γ is a measure of the steepest slope of the logistic function; and β represents the air temperature at the inflection point (or curve midpoint).

3.2.1.2 Time series analysis

A set of observations collected sequentially over time, and represented graphically, constitutes a time series. Due to the earth's annual revolution around the sun, and the twenty-four hour rotation on its axis, meteorological data exhibit seasonal patterns, ranging upwards from cycles with a 24-hour periodicity (Abraham and Ledolter 1983). A river's thermal regime is subject to the same series of periodicity that other meteorological data are. The traditional approach to modelling seasonal data is to decompose it into the following components (Chatfield 1980; Abraham and Ledolter 1983):

- Seasonal effect;
- Other cyclic changes, such as daily variation;
- Trend, for example long term climatic trends;
- Random/stochastic fluctuations (residuals).

These components are agglomerated into what is known as an "additive" model (Equation 3.3). Both the trend and seasonal components can be fitted using least-squares methods, with the trend component being modeled using low-order polynomials (such as linear regression), while seasonal components are modeled using trigonometric functions (such as in spectral analysis) (Abraham and Ledolter 1983). Time series analyses involve the decomposition of a time series into these various components. (Stochastic) time series models are concerned with modelling the errors (ε_t) or residuals, once the seasonal and trend components are removed. The errors, and therefore the observations, are assumed to be uncorrelated, described by a normal distribution probability curve, free of trend (stationary; i.e. constant mean and variance), and free of seasonal influences (cf. Section 3.2.1). In practice, the residuals are rarely uncorrelated, and there is usually some degree of serial correlation, especially if the data are collected in sequence (Abraham and Ledolter

1983). Time series models should thus incorporate the correlation structure of the residuals.

Data exploration typically begins with determining the correlation between data points at time t and time t+1 (the autocorrelation coefficient at lag k), using the raw data. Plotting the autocorrelation coefficient (r_k) against time lag k in a correlogram provides an indication of the degree of seasonality of the time series, as well as trend. If the time series contains seasonal oscillations, the correlogram will also exhibit seasonal fluctuations, which show as a sine wave on the correlogram. Trend (non-stationarity) is apparent where values of r_k are significantly different from zero for more than three lag periods, or in other words r_k remains significantly large until k gets big enough so that random error components dominate (Makridakis et al. 1983). Stationarity (removal of trend) can be achieved through nth order differencing techniques. Usually, first-order differencing is adequate to remove trend $(z'_t = z_{t+1} - z_t)$. Variances may be smoothed using appropriate data transformations, such as logarithmic transformations. The effects of seasonality may be removed using data smoothing techniques, such as moving averages. For data that are stationary and free of seasonal effects, the autocorrelation coefficients should be nonsignificantly different from zero, if the pattern is completely random. In cases where the correlation coefficients are significantly different to zero, this may be attributed to shortterm correlations, such as when a cold day is followed by one or two successive cold days. A time series model will be able to be developed if the data are stationary and nonseasonal, and if the autocorrelations drop to values not significantly different to zero within two to three time lags.

Simple time series models may be developed using deseasonalized data that has been "smoothed" by calculating moving averages. Autoregressive techniques provide a more sophisticated method for modelling time series. Such models (Equation 3.4) are similar to multiple linear regression models, although in this case the water temperature, x, at time t, is regressed on past values, to yield models of order p. A more sophisticated approach involves the use of ARIMA (Autoregressive Integrated Moving Average) models, which integrate autoregressive and moving averages models. ARIMA models may be used for seasonal and non-seasonal data. Non-seasonal ARIMA models are of the form ARIMA (p,d,q) where p, d, and q refer to the order of autoregressive, differencing and moving average components respectively. Seasonal ARIMA models are of the form ARIMA

 $(p,d,q)(P,D,Q)^n$, where *n* refers to the seasonal periodicity of the seasonal component of the model, and *P*, *D* and *Q* refer to the autoregressive, differencing and moving average components of the seasonal model respectively (Makridakis *et al.* 1983).

$$z_t = T_t + S_t + \varepsilon_t \tag{3.3}$$

where z_t is the time series, T_t is the trend component for time t; S_t is the seasonal component, and ε_t is the stochastic process.

$$x_{t} = \sum_{i=1}^{p} \alpha_{i} x_{t-i} + z_{t}$$
 [3.4]

where x_t is water temperature at time t, x_{t-i} is water temperature at time interval i preceding t, α_i is a coefficient, and z_t is a random term.

There may be a chance that a river's temperature changes over time as a result of anthropogenic influences such as impoundments and pollution. Time series analyses make use of historical records to predict future temperatures (Webb 2000). For example, Hostetler (1991) used time series analysis to examine the impacts of timber logging on stream temperatures. The study examined twenty years of data; it was known when logging began. By fitting a time-series model to the data, it was possible to separate the temperature time series into various components. Effects accounted for by climate and flow could be excluded, and any remaining trend components could be attributed to logging. However, trends in water temperatures are generally difficult to show because of a general lack of long-term water temperature records (Webb 2000).

3.2.1.3 Spectral analysis

Spectral analysis, which is also called Fourier or Harmonic analysis (Makradakis *et al.* 1983) decomposes a time series with a seasonal component, into a set of sine waves, and is fitted using least-squares methods, i.e. a derivative of a regression model. Such analyses involve the discovery of hidden periodicities in a given time series (Chatfield 1980). In the case of water temperatures, spectral analysis makes use of harmonic curves to approximate the annual cycle of water temperature (Webb 2000). Harmonic functions will produce

smooth water temperature curves that account for the seasonal component of a time series, and therefore trend and variability are not inherently included in such models. Stefan and Preud'homme (1993) broke water temperature down into a deterministic component (a sinusoidal function of the time of year) and a stochastic component (a function of air temperature on the same day). The inclusion of a random term brings a stochastic element into the harmonic curves (Webb 2000). First-order harmonic curves, which take the general form of Equation 3.5, have been found to approximate the seasonal variability of water temperatures, when the variability is symmetric over seasons (Smith 1981; Ward 1985; Hostetler 1991; Stefan and Preud'homme 1993; Caissie *et al.* 2001). Such models are appropriate for time series with seasonal patterns where the amplitude and phases are fixed (Abraham and Ledolter 1983). Seasonality adds an asymmetric element, which can be simulated using higher order harmonic curves (Long 1976; Ward 1985; Webb 2000), where the amplitude and phase shift are able to change dynamically, based on previous values (Abraham and Ledolter 1983).

$$T_i = \overline{T} + A\sin\left(2\pi \frac{ft_i}{N} + \theta\right) + \gamma$$
 [3.5]

where T_i is daily water temperature; \overline{T} is the mean annual air temperature; A is the amplitude of the sine curve; N is the number of observations within a cycle; t_i is the i^{th} observation within the cycle N, γ is a random term. Two optional additional terms may be included in the sine function, θ (phase angle) and f (frequency). If the phase angle (i.e. the horizontal displacement of the wave from the origin) is 90°, the vertical axis of the graph goes through the first maximum amplitude) of the wave of the curve, expressed as radians (for example if the phase angle is 45°, this converts to $\pi/4$ radians). The frequency, f, changes the number of waves over 360° over N observations of the sine wave. The wavelength (λ) is the number of periods within a cycle, and is calculated by dividing N by f. The fraction ft_i/N , for different values of t, converts the discrete time scale of the time series into a proportion of 2π (or 360°) (Makridakis et al. 1983).

3.2.2 Process-based approaches

Process-based water temperature models relate functions to system physics, and operate by attempting to solve the energy budget of a river, which is a function of the amount of net solar radiation a water body absorbs through the atmosphere. The total solar radiation reaching the water surface will be absorbed (by the water), reflected (onto riparian vegetation) and transmitted (to the river bed) in different proportions which should add up to one (Fishenden and Saunders 1965). The relative values of these processes will be a function of, *inter alia*, the presence of aquatic vegetation, and the turbidity and turbulence of the water within the channel, so that accurate physically-based models will require multiple input variables. Calculations make use of surface area and cross-sectional depths, as well as the specific heat and density of water, and heat exchange coefficients between air and water (Webb 2000). The energy budget techniques gained popularity in the 1970s, as more accurate methods were sought to predict stream temperatures, which was probably in response to concerns over impacts of impoundments on fisheries (Brown 1969; Morse 1970). Physically based models begin by examining heat exchange rates in water, using an energy balance equation (Equation 3.6) (Keijman 1974):

$$\Delta S = R - LE_B - C - G \tag{3.6}$$

where ΔS is the change in energy stored in water; R is net radiation (Watts/m²); L is latent heat of evaporation (Joules/kg); E_B is evaporation; C is the flux of sensible heat from water to atmosphere; G is the heat flux into the ground. Net radiation (R) is measured using a radiometer; heat flux (C) may be measured using heat flux plates, and the change in energy stored in water (ΔS) using thermocouples. The final terms (C and E_B) can be estimated using the Bowen ratio (B) (Equation 3.7):

$$\beta = \frac{C}{LE_B} = \gamma \frac{T_0 - T_2}{e_s(T_0) - e_2}$$
 [3.7]

where γ is the psychrometric constant (psychrometer = wet and dry bulb thermometer for measurement of atmospheric humidity); T_0 and T_2 are the potential temperatures (°C) at the surface and at a height of 2m above the water, $e_s(T_0)$ is the saturation vapour pressure at temperature T_0 , and e_2 is the vapour pressure at a height of 2m (Keijman 1974).

The energy value for a known volume of water can then be converted into a temperature change (Brown 1969). These methods of estimating the various energy balance terms rely on highly accurate measurement of parameters such as net radiation, water temperature, relative humidity (dry and wet bulb temperatures), subsurface heat flows, precipitation, and wind speed and direction (Morse 1970; Keijman 1974; DeWalle 1976; Stewart and Rouse 1976; Everson 1999). However, heat budget models may not be appropriate for all situations, and it is rare that such data are readily available in South Africa (Jewitt and Görgens 2000b).

The energy balance approach is useful when relating water temperatures of reservoirs or slow-moving bodies of water, to water quantity issues, since rates and quantities of evaporation can be calculated. This becomes important when calculating water budgets. Keijman (1974) and Stewart and Rouse (1976) used the energy balance approach to estimate evaporation from lakes, while Everson (1999) used an energy balance approach to estimate evaporation losses from the Orange River.

3.2.3 Dynamic water temperature models

With the current renewed interest in water temperature modelling, more dynamic heat transfer models which incorporate flow dynamics are being used (Sinokrat and Stefan 1993). These are better able to provide information on the effect of man's activities on river ecosystems than the traditional "balance" analysis of heat budgets, which tend to be deterministic, site-specific, and applicable to static water bodies. Dynamic water temperature models are complex physical models that simulate how water temperature changes as it moves along the river profile (Webb 2000), or in other words deterministic equations are used in a dynamic way using equations of the form $\Delta T^{\circ}/\Delta distance$ (Morse 1970). Such models incorporate the rate of heat gain and heat loss over time, using a spatial component. The use of differential equations to predict temperature change over a river reach has been used by, for example, Morse (1970), DeWalle (1976), Sinokrat and Stefan (1993), and Walters et al. (2000), in various northern Hemisphere studies. Southern Hemisphere studies are still rare. The following are typical of the heat transfer modelling approach:

i) DeWalle (1976) used a one-dimensional energy budget equation (Equation 3.8) to predict water temperature along a reach for five hour periods with initial temperature known, downstream temperatures could be calculated, provided the heat exchange rate was assumed constant (DeWalle 1976).

$$\frac{\Delta T}{\Delta x} = \frac{Q_n}{\rho C_n(Q/w)} \tag{3.8}$$

where T is water temperature, x is longitudinal stream distance, Q_n is the net heat exchange rate at the air-water interface, ρ is water density, C_p is specific heat of water, Q is stream discharge, and w is stream surface width (DeWalle 1976). De Walle (1976) noted that wind velocity had a significant effect on evaporation, and needed to be considered when predicting water temperatures.

ii) Sinokrat and Stefan (1993) used a dynamic deterministic model to successfully predict daily water temperatures for streams. This equation can be used to predict water temperatures in steady flow streams that are well mixed, with no significant transverse temperature gradients (Sinokrat and Stefan 1993). Forty-six variables relating to geographic, weather and stream data were needed to run the model. The basic form of the heat transport equation (Equation 3.9) was:

$$\frac{\Delta T}{\Delta t} = -U \frac{\Delta T}{\Delta x} + D_L \frac{\Delta^2 T}{\Delta x^2} + \frac{S}{\rho c_n d}$$
 [3.9]

where T is water temperature; x is streamwise distance; t is time; D_L is a dispersion coefficient in the direction of flow; S is a source or sink term which includes heat transfer with the surrounding environment; d is the mean channel depth; U is the mean channel velocity; ρ is the density of water; C_P is the specific heat of water.

iii) Walters et al. (2000) simulated monthly water temperature for the Colorado River, as part of a larger modelling exercise to understand the effects of flow regulation on this river system. Water temperature change along the downstream axis of the Colorado River was calculated as input – ouput of temperature for different river reaches. Downstream water

temperatures (C_{i+L}) were simulated by multiplying the upstream water temperature entering the reach (C_i) by a coefficient that is a function of the residency time of the water within a reach (which in turn is a function of reach length and water velocity), and a heat exchange coefficient (Equation 3.10).

$$C_{i+L} = C_{eq} + (C_i - C_{eq}) \exp(-\nu W_i L_i / Q_i)$$
 (3.10)

where C_{i+L} is downstream temperature; C_{eq} is equilibrium temperature; C_i is the input temperature; and exp() is a modifier term with v being a heat exchange coefficient; W_i is wetted width; L_i is reach length and Q_i is mean monthly water discharge.

Each of the above three models operates at a different time step (hourly to monthly), which would have been chosen to suit the particular study objectives. For example, in the case of Walters *et al.* (2000), one of the modelling objectives was to support river management goals, which in general tend to operate on relatively course spatial and temporal scales. The monthly time step for the temperature model is therefore appropriate to the objectives of the research. Each model was developed for different rivers, with different characteristics. This highlights the difficulties in finding a generic model that can be applied to different river systems for different time steps. What is common to all three approaches is that use is made of numerous quantitative variables, such as discharge and channel width, which could be measured with relative ease, in addition to a heat exchange coefficient, which is a dimensionless variable for calibrating the models.

3.3 Methods for simulating water temperatures in the Sabie catchment

Hourly water temperatures collected over a 25-month period, from 8 February 2001 to 28 February 2003, at nine sites within the Sabie catchment (cf. Section 2.2), were used as the basis for the analyses and models in this chapter. Hourly water temperature data were calibrated (cf. Section 2.2.1), and used to calculate daily maximum water temperatures. The data were checked for absence of trend, and stability of mean and variance (cf. Section 3.3.1) prior to their use in the water temperature models. This was a fundamental step, since both linear regression and time series models assume absence of trend and stability of mean and variance for validity.

Based on the review of the different water temperature models, and the objectives of this study, five different modelling approaches for simulating water temperatures for any particular point on the Sabie River (cf. Section 3.3.2) were assessed, based on maximum daily water temperatures for the period 1 June 2001 to 28 August 2002. These five static approaches were:

- i) Simple linear regression (daily time scale; statistical);
- ii) Multiple linear regression (daily time scale; statistical);
- iii) Time series analysis (daily time scale; statistical);
- iv) First order harmonic analysis (daily time scale; statistical);
- v) Air temperature dispersion (hourly time scale; mixed process-based/statistical)

In addition to these modelling approaches, a dynamic water temperature model that predicted change in water temperature over space (10¹ km) and time (sub-daily) was developed using a similar approach to Walters *et al.* (2000) (*cf.* Section 3.3.3).

3.3.1 Tests for trend and stability of mean and variance

Model data (daily maximum water temperatures for the period 8 February 2001 to 28 August 2002, with the exception of WT9 which used data from 18 May 2001 to 28 August 2002, on account of this logger being installed three months after the other loggers) were tested for absence or presence of trend using the Spearman's Rank-Correlation method (Dahmen and Hall 1990, p. 17). The Spearman's Rank-Correlation coefficient was tested against a Student's t-distribution with n-2 degrees of freedom (p < 0.05, two-tailed). Stability of variance and mean were tested using the F-test and t-test for stability of variance and mean respectively (Dahmen and Hall 1990 pp. 20-23). Both test statistics were compared to table values (F-distribution and t-distributions respectively) for a five percent significance level (two-tailed). For both tests, each data set was equally divided into two groups, and the mean and variance calculated for each set.

3.3.2 Static water temperature models

Daily maximum water temperatures were simulated using five different modelling approaches at all water temperature monitoring sites (cf Table 2.1). Water temperature site WT10 was excluded from the analyses, since this site was repeatedly buried under sand, so

that recorded water temperatures were not a true reflection of actual hourly water temperatures (cf. Table 2.1). The models were evaluated using simple linear regressions of observed versus predicted water temperatures, and comparing these regression lines against a fitted line for an R² of 1, using a six-month dataset of water temperatures from 4 September 2002 to 28 February 2003.

- (i) Simple linear regressions, using mean maximum and minimum daily air temperatures as the explanatory variables. For these models, datasets for eight of the monitoring sites were combined. Simple linear regressions using no interaction between sites, and incorporating interaction (a dummy variable with eight factors corresponding to each logging site) were modelled. In addition, a "broken-stick" model was developed since the relationship between mean daily air temperatures and maximum daily water temperatures was non-linear for the lower (< 15°C) water temperatures. This method uses iterative loops to calculate the two lines of best fit around the point of non-linearity or inflection of the data.
- (ii) **Multiple linear regressions** using the statistical software Genstat (Genstat 2000). Daily maximum water temperatures were simulated using the following explanatory variables:
 - Daily mean, maximum and minimum air temperatures;
 - Inverse daily flows (m³.s⁻¹), and natural logarithm thereof;
 - Mean daily absolute humidity (g.m⁻³);
 - Dummy variable (a factor of 7 levels correlating to each logger site) for each of the seven data sets used.

Daily air temperature statistics were derived from hourly air temperatures collected at three sites along the Sabie catchment (Chapter 2). Daily flows for the weirs listed in Table 3.1 were obtained from the Department of Water Affairs and Forestry (DWAF 2002a) for gauging weirs in close proximity to water temperature sites (cf. Figure 4.1). The dummy variable was used to determine whether the slopes and/or intercepts of the regression equation at each monitoring site were significantly different, which could be a function of factors such as altitude, shading, and aspect. Two groups of multiple linear regression models were developed using these explanatory variables. The first group was based on a one-to-many relationship between air temperature recording sites and water temperature

sites (i.e. data from AT1 was used for the water temperature sites WT2, WT3 and WT5; AT2 was used for the sites WT4, WT7, WT8 and WT10; and AT3 was used for the sites WT1 and WT9). The second group of models simulated water temperatures using air temperatures unique to each water temperature site. In this case, air temperatures at water temperature monitoring sites lacking an air temperature logger were calculated using interpolations, assuming a linear relationship between altitude and air temperature. Output from both series of models was compared. In addition, the effect of seasonality at the upper, middle and lower sites (WT9, WT3 and WT8) was evaluated by using four dummy variables, for spring (September to November), summer (December to February), autumn (March to May) and winter (June to August).

Table 3.1 Water temperature loggers and gauging weirs used in flow-dependant multiple linear regression model.

River	Water	temperature	Gauging weir	Record length		
	logger			·		
Sabie	WT1		X3H002	16 May 2001 –		
				30 August 2001		
Marite	WT2		X3H011	8 February 2001		
				- 30 August 2001		

(iii) Time series models.

Autocorrelations on daily maximum water temperatures were performed using the time series analysis routines in Genstat (Genstat 2000). Raw data of daily maximum water temperatures for sites WT9, WT3 and WT8 were checked for seasonality and trend, using correlograms, and subsequent analyses performed based on the shape of the correlograms (Section 3.2.1).

(iv) First-order harmonic analysis with a random term included (Equation 3.11).

$$Tw_{\text{max}} = \overline{T} + A\sin\left(\frac{2\pi t}{365} - \theta\right) + \gamma$$
 [3.11]

where Tw_{max} is maximum daily water temperature, \overline{T} is mean air temperature, A is the amplitude, t is the observation number, θ is the phase shift in degrees, and γ is a random term.

(v) A dispersion model, based on a convolution integral (Equation 3.12), which is used in a similar form in the unit hydrograph (Chow 1964), was used to model hourly water temperatures. These were summarized to daily maximum water temperatures to ensure that the output from this model was compatible with the previous four models. Water temperatures were shown to be responding to air temperatures from the previous two hours (Chapter 2), in a similar way to the response of a body to a heat pulse (Lorentz 2003). Hourly water temperatures were simulated using Equations 3.13a, which was based on a dispersion model used by Kreft and Zuber (1978), and Equation 3.13b. Water temperatures at time t_0 were predicted as a function of air temperatures over the past twenty-four, thirty-six and forty eight hours (Lorentz 2003). The air temperatures with the greatest influence on hourly water temperature were from two hours previously, at time t_{-2} , according to the dispersion curve shown in Figure 3.1. The dispersion curves for the 36-and 48-hour periods used the same lag for peak leverage; the additional 12-and 24-hour periods of these curves provided longer "memory" periods between air and water temperatures.

$$\int_{0}^{t \le t_0} u(t - \gamma)I(\gamma)d\gamma \tag{3.12}$$

$$g(t) = \left(16\pi D_p\right)^{-\frac{1}{2}} * \left[(t/\tau)^{\frac{1}{2}} + (\tau/t)^{\frac{1}{2}} \right]^{-1} * \exp\left[-((1-t/\tau)^2 (\tau/4D_p)) \right]$$
 [3.13a]

where g(t) is the dispersion curve, D_p is a dispersion coefficient (affecting the amplitude of the curve), t is the time step of the curve, and τ is the mean residence time of each pulse (determines the position of the peak with respect to time).

$$T_{w} = \left[\sum_{i=1}^{24} (g(t) * \beta) * Ta_{i}\right] + c$$
 [3.13b]

where T_w is hourly water temperature, β is a multiplier, Ta_i is hourly air temperature at time i, and c is a fitted constant.

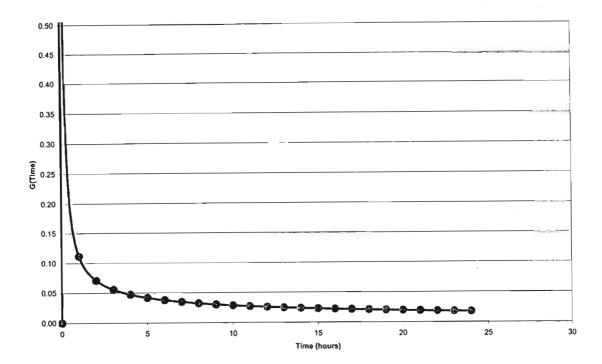


Figure 3.1 Dispersion curve generated for a twenty-four hour time period and a two-hour time lag, using Equation 3.12b. This curve was used to calculate hourly water temperatures, where each calculated value was a function of the preceding 24 hours of air temperatures. The air temperature with the highest leverage was from two hours prior to the calculated water temperature.

3.3.3 Dynamic water temperature model

The Sabie River was divided into 7 reaches, based on the location of water temperature collection sites (cf. Chapter 2); reach lengths are provided in Table 3.2. The additive effects of tributary water temperatures on reach water temperatures were not included in the model at this stage, although the position of tributaries within reaches is noted. Hourly water temperatures for each reach were simulated using hourly air temperatures. Since hourly air temperatures were available for the upper, middle and lower reaches only (cf. Section 2.2.1), additional air temperatures were calculated by interpolating between the three air temperature stations. A linear relationship between altitude and air temperature was assumed, and interpolated air temperatures were calculated using Equation 3.14.

$$Ta_i = Ta_1 + \left((Ta_2 - Ta_1) * \frac{A_1 - A_i}{A_1 - A_2} \right)$$
 [3.14]

where Ta is hourly air temperature (°C), A is altitude (m.asl), and the subscripts 1, 2, and i refer to upper, lower and interpolated station points respectively.

Table 3.2 Reach lengths and physical data used for calculating hourly water temperatures using the dynamic water temperature model

Reach no.	Logger	Length (km)	Width (m)	Depth (m)	Altitude (m.asl)
1	WT9	18	4.8	0.35	1193
2	WT1	26	12.0	0.50	870
3	WT3	27	13.3	0.60	480
4*	WT5	25	25.0	3.00	357
5	WT4	21	15.0	2.00	287
6	WT7	27	28.0	1.50	242
7*	WT8	18	20.0	1.00	157

Denotes tributary entering this reach.

Water temperatures for the initial reach were calculated using the dispersion model presented by Equation 3.13b, with the first twenty-four hours of data taken from the observed data for that reach. Hourly water temperatures in subsequent downstream reaches were calculated using Equation 3.15, with an initial water temperature for each reach being obtained from the observed data. This equation is based on concepts of dynamic water temperature models, where reach water temperature is a function of heat exchange between air and water, and the "concentration" of heat energy (temperature) within a reach. It is assumed that there is complete mixing of incoming and existing water within each reach within the hourly time step. This assumption negates the necessity of using residency time of water within a reach, which is determined by water velocity. A modified version of Equation 3.10 was used to predict hourly water temperatures in downstream reaches. Water temperatures (T_{final}) were a function of the temperature of water entering a reach and mixing with the existing water in the reach (T_{mix}) , and the amount of heat gained or lost over time (t) due to heat exchange with air (T_{diff}) in that reach. In turn, T_{mix} was calculated by adding a "concentration" of water temperature (water temperature in a given volume of river water) to the temperature in the reach at the previous time step, t_{-1} (Equation 3.16). Observed daily flow volumes (m³.s⁻¹) were not available from the Department of Water Affairs and Forestry (DWAF 2002a) for the required weirs for the period simulated. Consequently, simulated daily flow volumes for the period 1995 to 2000 based on output from the agro-hydrological model ACRU (Schulze 1995; Smithers and Schulze 1995) were used. Output from this model has been

verified for the Sabie catchment (Pike and Schulze 2000), and is based on daily rainfall data (mm), which was available to the period ending in May 2002, and other relevant catchment data, such as soils and land use. For the purposes of this model, flow volumes were based on averaged values for the preceding five years. This was due to a lack of daily rainfall data for the period 2001-2002 in the Sabie catchment, which precluded the simulation of average daily flows for this same period. The heat gain or loss (T_{diff}) was calculated using a fitted heat exchange coefficient and the air temperature for that reach (Equation 3.17). Flow volumes ($m^3.s^{-1}$) were adjusted for the hourly period of this model.

$$T_{final} = T_{mix} + \Delta T_{diff}$$
 [3.15]

$$T_{mix} = T_{t-1} + \frac{(Q_{i,t-1} * T_{i,t-1}) + (Q_{o,t-1} * T_{o,t-1})}{V} * \Delta t$$
 [3.16]

where T_{t-1} is water temperature for the previous hour, $Q_{i, t-1}$ and $Q_{o, t-1}$ are the water discharge (m³s⁻¹) entering and leaving the reach respectively for the previous hour, $T_{i, t-1}$ and $T_{o, t-1}$ are water temperatures entering and leaving the current reach for the previous hour, and V is the volume of water within the current reach.

$$\Delta T_{diff} = \gamma (T_a - T_{mix}) \tag{3.17}$$

where γ is a heat exchange coefficient, and T_a is hourly air temperature.

3.4 Results

3.4.1 Quality of water temperature data

Significant (p < 0.05) trends were found to exist in all of the water temperature time series considered. Additionally, all data sets had significant non-stable means and variances (p < 0.05), with the exception of WT9 where the variance was stable. Thus, these data do not meet the requirements recommended by Dahmen and Hall (1990) for use in statistical modelling of time series data (cf. Section 3.2.1), and additionally violate the fundamental assumptions of both linear regression and time series models (cf. Section 3.2.1).

However, since twelve months of daily water temperatures were used in the analyses, these trends may be a function of seasonality rather than of actual trend. Longer water temperature time series would be needed to make this distinction. Given the limited temporal length of these data, and on the large body of past research that has made use of these modelling approaches, these statistical models were nevertheless applied to the water temperature time series collected within the main rivers of the Sabie catchment. This decision was made as a trade-off between using significantly shorter water temperature time series, versus using a longer, more representative time series of annual water temperatures in the Sabie River. The accuracy of the models presented below should be regarded within this context.

3.4.2 Statistical approaches for simulating daily water temperatures

(i) Simple linear regression models

Mean ($R^2 = 0.84$), maximum ($R^2 = 0.58$) and minimum ($R^2 = 0.64$) daily air temperatures were regressed against maximum water temperatures. Mean daily air temperature was the best predictor of daily maximum water temperatures, using simple linear regression (Equation 3.18; n = 4 112; $R^2 = 0.84$). When a dummy variable was included as part of the simple linear regression model, with interaction between variables, the fit of the model improved (Equations 3.19a-h); $R^2 = 0.92$). In both cases however, the relationship appeared to be non-linear for maximum daily water temperatures less than 15°C (Figure 3.2), and the error variance was not constant. Using the broken stick modelling approach, it was found that the point of inflection was at a daily mean air temperature of 16.04°C. Two models (Equations 3.20a-b) were derived ($R^2 = 0.86$), the choice of which is

determined by the value of explanatory variable (air temperature) i.e. Equation 3.20b should be used for air temperature less than 16.04°C.

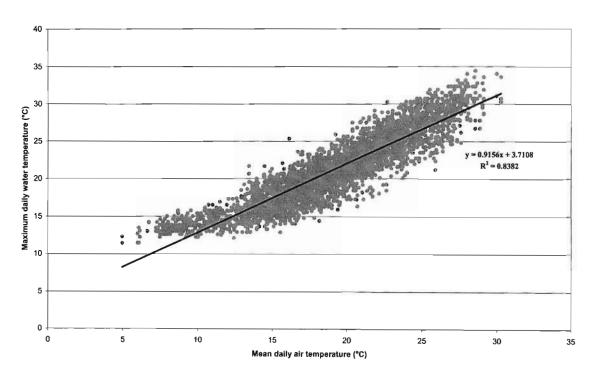


Figure 3.2 Simple linear regression between mean daily air temperature and maximum daily water temperatures for the period 8 February 2001 to 31 August 2002 for eight sites within the Sabie River catchment.

$$Tw_{max} = 3.710 + 0.916*Ta_{mean}$$
 [3.18]

WT1 -
$$Tw_{max} = 8.671 + 0.617*Ta_{mean}$$
 [3.19a]

WT2 -
$$Tw_{max} = 0.421 + 1.081 * Ta_{mean}$$
 [3.19b]

WT3 -
$$Tw_{max} = 2.074 + 0.894 * Ta_{mean}$$
 [3.19c]

WT4 -
$$Tw_{max} = 5.401 + 0.855 * Ta_{mean}$$
 [3.19d]

WT5 -
$$Tw_{max} = 2.393 + 1.014*Ta_{mean}$$
 [3.19e]

WT7 -
$$Tw_{max} = 3.021 + 0.947 * Ta_{mean}$$
 [3.19f]

WT8 -
$$Tw_{max} = 3.560 + 1.006 * Ta_{mean}$$
 [3.19g]

WT9 -
$$Tw_{max} = 8.671 + 0.453 * Ta_{mean}$$
 [3.19h]

$$Tw_{max} = 8.705 + 0.552*Ta_{mean} ag{3.20a}$$

$$Tw_{max} = 0.588 + 1.058*Ta_{mean}$$
 [3.20b]

where Tw_{max} is maximum daily water temperature and Ta_{mean} is mean daily air temperature.

(ii) Multiple linear regression models

The best predictors of maximum daily water temperatures in a flow-dependant model were mean daily air temperature and the inverse of daily flow (Equation 3.21, p<0.001; $R^2 = 0.83$), using daily data at sites WT1 and WT2 only. Daily flow data were available for site WT10, but since this logger was repeatedly buried under sediment, it was felt that the hourly water temperature data were unreliable (cf. Section 2.2, Table 2.1). A similar model, but derived by transforming the inverse of daily flow using natural logarithms accounted for slightly less variation than that using the inverse of daily flows.

In the absence of daily flow data, maximum daily water temperatures could be predicted by the explanatory variables mean daily air temperature, minimum daily air temperature and absolute humidity. Seven different significant regression equations ($R^2 = 0.927$) were obtained through the incorporation of a dummy variable with seven levels, corresponding to the seven data sets used (Equations 3.22a-g). The use of interpolated daily mean air temperatures did not improve the model ($R^2 = 0.926$). Thus, using one air temperature site for multiple water temperature sites, without linear interpolation of air temperatures, is considered a more pragmatic approach than either using interpolated air temperatures for each water temperature site or matching each water temperature site with an air temperature site. Furthermore, in simulating water temperatures along the downstream axis of the Sabie River, no single generic model was adequate.

Multiple linear regression models in which seasonality was considered for the upper, middle and lower reaches of the Sabie River, did not generally show significantly different slopes or intercepts for each season, with the exception of the middle reach (WT3). For the middle reach, spring and summer (factor levels 4 and 1 respectively) water temperatures

could be explained by one model (Equation 3.23a), while autumn (factor level 2) and winter (factor level 3) water temperatures were explained by alternative models (Equations 3.23b-c).

$$Tw_{max} = 6.121 + 0.793 * Ta_{mean} - 0.175 * 1/flow$$
 [3.21]

WT1 -
$$Tw_{max} = 8.583 + 0.476*Ta_{mean} + 0.200*AbsH$$
 [3.22a]

WT3 -
$$Tw_{max} = 2.678 + 0.732 * Ta_{mean} + 0.200 * AbsH$$
 [3.22b]

$$WT4 - Tw_{max} = 5.442 + 0.845 * Ta_{mean} + 0.013 * AbsH$$
 [3.22c]

WT5 -
$$Tw_{max} = 3.241 + 0.948 * Ta_{mean} + 0.050 * AbsH$$
 [3.22d]

WT7 -
$$Tw_{max} = 3.535 + 0.818*Ta_{mean} + 0.200*AbsH$$
 [3.22e]

WT8 -
$$Tw_{max} = 3.854 + 0.936*Ta_{mean} + 0.200*AbsH$$
 [3.22f]

WT9 -
$$Tw_{max} = 8.583 + 0.476 * Ta_{mean} - 0.056 * AbsH$$
 [3.22g]

$$Tw_{max} = 8.52 + 0.623*Ta_{mean}$$
 [3.23a]

$$Tw_{max} = 2.65 + 0.876*Ta_{mean}$$
 [3.23b]

$$Tw_{max} = 4.68 + 0.623 * Ta_{mean}$$
 [3.23c]

(iii) Time series model

Time series plots of daily maximum water temperatures for sites WT9 (Figure 3.3a), WT3 and WT8 suggest the presence of trend, and a seasonal component. The patterns of the autocorrelations for sites WT9 (Figure 3.3b), WT3 and WT8 were all similar, with an exponential decay of correlation coefficients. This suggested that all three time series were non-stationary, although there was no indication of seasonality. Data were differenced using first-order differencing (Figure 3.4a), and the autocorrelations plotted (Figure 3.4b). Based on the correlograms, which were similar for all three sites, first-order differencing was sufficient to make the time series stationary, with the stability in the mean visible, although the variances were not stabilized (Figure 3.4a). The autocorrelation plot confirmed that first-order differencing removed trend from the data (Figure 3.4b). Logarithmic transformations of the data failed to stabilize the variance for all three sites. Based on this preliminary data exploration, the following generalizations could be made:

- The record lengths for the data series are not long enough to detect seasonal patterns;
- It was not possible to stabilize the variances, even by transforming the data.
 This condition violates a basic assumption of time series analysis (Section 3.2.1.2). The stochastic component of these data showed no significant correlation between residuals, but exhibited non-constant variance. It is possible to model the variance, but such models are beyond the scope of this study;
- Based on the abovementioned points, these data, with their current record lengths, are unsuited to ARIMA modelling (Haines 2003). Based on the current data set, a low-order polynomial which predicts trend (i.e. linear regression models) would be the most appropriate and pragmatic solution.

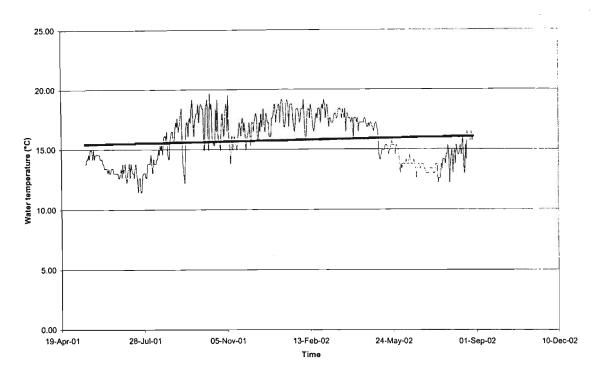


Figure 3.3a Daily maximum water temperatures at site WT9 for the period 18 May 2001 to 18 August 2002.

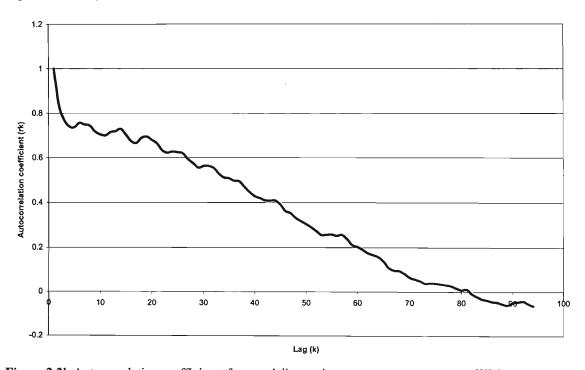


Figure 3.3b Autocorrelation coefficients for raw daily maximum water temperatures at WT9

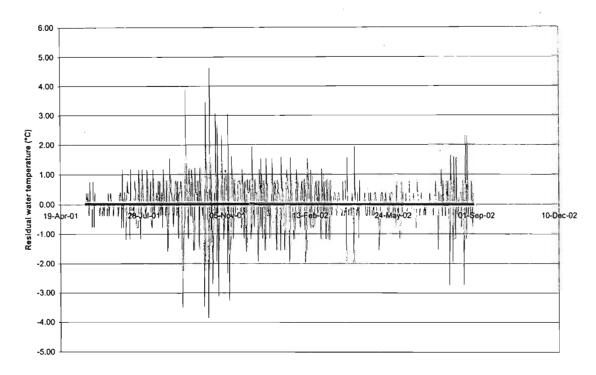


Figure 3.4a Time series of daily maximum water temperatures for site WT9 for the period 18 May 2001 to 18 August 2002, with trend removed using first-order differencing.

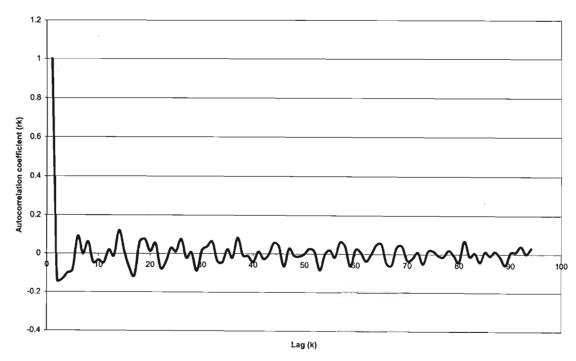


Figure 3.4b Autocorrelation coefficients for daily maximum water temperatures at WT9, using first-order differencing.

(iv) First order Harmonic analysis

Daily maximum water temperatures were approximated with Equation 3.10 (cf. Section 3.2.1.3) using the values provided in Table 3.3, for the particular water temperature station used. The stochastic function of the model was generated by a random number (γ) between 0 and 1, and multiplied by a constant (Figure 3.5).

Table 3.3 Values	used for Fourier	analysis of water temperatures	3
------------------	------------------	--------------------------------	---

Variable WT9		WT3	WT8		
T (°C) 15		19	22		
A (°C)	5	5	5		
γ	γ 6		5		
θ (degrees/radians)	344° (6 rad)	344° (6 rad)	344° (6 rad)		

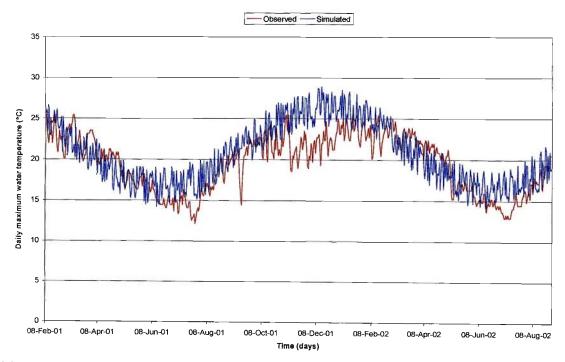


Figure 3.5 Time series plot of daily maximum water temperatures for site WT3, using observed data and Fourier analysis model.

(v) Heat dispersion model

Fitted parameters that best approximated hourly water temperatures in Equations 3.13a-b were 1000 for D_p , 0.25 for τ , with multipliers (β) and fitted constants (c) listed in Table 3.4.

Table 3.4 Fitted constants (c) and multipliers for the sites WT9, WT3 and WT8 using 24, 36 and 48-hour dispersion curves

Site	24 hour	24 hour response time		sponse time	48 hour response time		
	β	С	β	c	β	<i>c</i> .	
WT9	8	5	6	6	6	5	
WT3	12	0	10	0	8	0	
WT8	12	2	9	3	9	1	

The timing, duration and magnitude of simulated and observed hourly water temperatures were of similar magnitudes and periodicities (Figure 3.6). Correlation coefficients for the different lag times showed that for the water temperatures at sites WT9 and WT8, a 24 hour lag time was most appropriate for predicting hourly water temperatures, while for WT3, a 48 hour lag time gave the best correlation (Table 3.5). While the correlation coefficients for 24 and 48 hours were comparable at site WT9, a lag of 24 hours was chosen based on this site being near the source where residency times of water will be less than further downstream.

Table 3.5 Correlation coefficients (R²) between hourly observed and simulated water temperatures for sites WT9, WT3 and WT8 using 24, 36 and 48 hour lag periods in air temperatures. Shaded cells indicate lag time used.

Site	24 hour lag	36 hour lag	48 hour lag
WT9	0.826	0.806	0.827
WT3	0.879	0.879	0.913
WT8	0.729	0.711	0.686

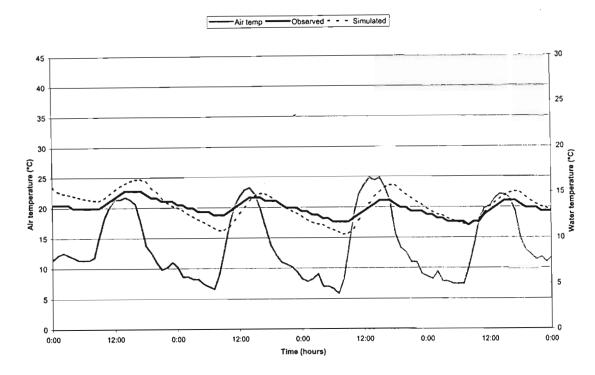


Figure 3.6 Sample plot showing hourly air temperatures, and water temperatures from observed and simulated data, using the heat dispersion model.

3.4.3 Synthesis

R² values for all five modelling approaches are given in Table 3.6. The multiple linear regression models incorporating a flow-dependant term could not be validated owing to a lack of flow data. The highest correlations with observed data was given by the multiple linear regression models without a flow-dependant term. An issue common to all models was that a single observed value correlated with many predicted values (the "striping" in Figures 3.7-8), which may be a function of the non-constant variance of the observed values. Correlations between observed and simulated water temperatures using Fourier analysis were weak, and might have been improved using a Fourier analysis model which incorporated amplitude and frequency terms that changed dynamically based on past values. An additional compounding issue is that the time series was based on one year's data, where the effect of inter-annual seasonality could not be assessed. This same issue prevented a more comprehensive time series model being developed. The simple and multiple linear regression models, together with the dispersion model, all under-predicted maximum daily water temperatures for the period used to validate the models. However, based on the correlation coefficients, the use of linear regression techniques to model daily

maximum water temperatures would be the most appropriate and pragmatic approach at the spatial and temporal scales needed for this study.

Table 3.6 Correlations (R² values) between observed maximum water temperatures and simulated maximum water temperatures using five different modelling techniques.

Western terror eventures model	Correlation coefficients (R ²)					
Water temperature model	WT9	WT3	WT8			
Simple linear regression	0.556	0.797	0.729			
Multiple linear regression	0.583	0.805	0.749			
Fourier analysis	0.033	0.212	0.067			
Heat dispersion model	0.564	0.781	0.612			
Time series	N/A	N/A	N/A			

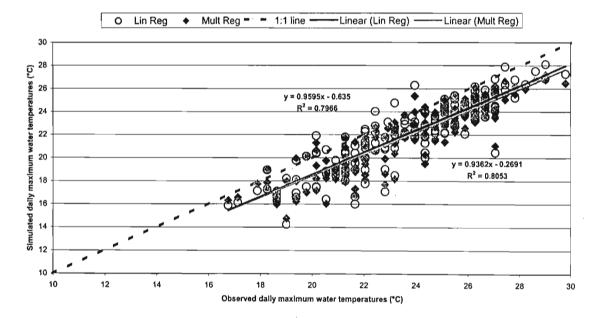


Figure 3.7 Observed versus predicted daily maximum water temperatures at site WT3, using simple and multiple linear regression models.

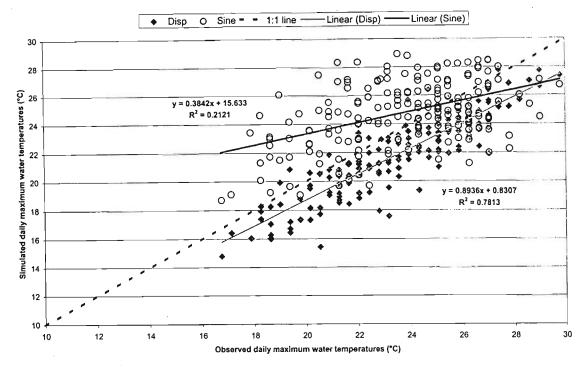


Figure 3.8 Observed versus predicted daily maximum water temperatures at site WT3, using Fourier analysis and heat dispersion models.

3.4.4 Dynamic water temperature model

The diffusion constant influenced the degree to which air temperatures influenced water temperatures. A diffusion constant of 0.03-0.04 was found to be most effective in the model. Diffusion constants of magnitude 0.001 dampened the effect of air temperatures too much, while those greater than 0.1 brought about daily variations similar to those of water temperatures. The model fit changed with the average reach width and depth parameters. Errors in model predictions became additive with downstream distance, due to the use of upstream water temperatures in downstream predictions. Water temperatures in reach one were simulated using the dispersion model for WT 9 (cf. Section 3.4.2v). Water temperatures in subsequent reaches were simulated using the dynamic water temperature model. However, since errors were additive, only reach 2 was considered in analyses of model performance. Based on water temperatures from this reach, the dynamic water temperature model did not simulate hourly water temperatures meaningfully, neither following seasonal patterns (Figure 3.9) nor providing a good correlation between observed and simulated data ($R^2 = 0.04$) (Figure 3.10). At this stage, it is apparent that a process-based dynamic water temperature model is more complex than envisioned. This model currently assumes that water moves between reaches after one hour. residency times are not explicitly factored in to this model. For further model calibration

and verification, additional data on groundwater inputs, residency times and more accurate river profile data (widths and depths) would be basic data requirements.

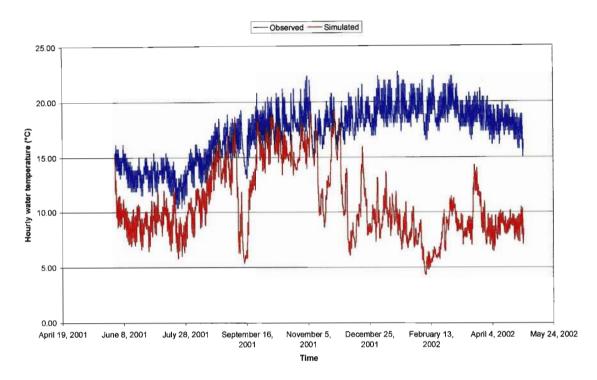


Figure 3.9 Simulated and observed hourly water temperatures for the period 1 June 2001 to 31 May 2002 at site WT1 (reach 2)

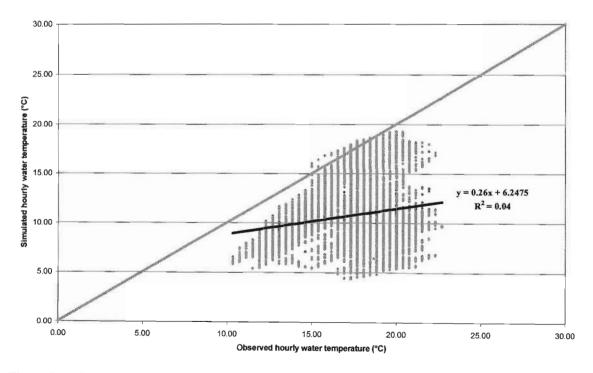


Figure 3.10 Correlation between observed and simulated hourly water temperatures using the dynamic water temperature model for site WT1 for the period 1 June 2001 to 31 May 2002.

3.5 Discussion and conclusions

3.5.1 Physical versus statistical spproaches

Water temperature modelling has been the focus of much controversy (Johnson 2003), at least over the last three decades. The ecological modeller is faced with a wide choice of temperature models, of varying complexity. Should existing models be used, or new problem-specific models be developed? If an existing model is to be used, which one? The decision as to which modelling approach to adopt should be tempered with considerations of accuracy versus general predictability, and the resolution of related data. For example, information such as thermal tolerances of fish (Eaton and Scheller 1996) may only be available at a weekly time step, such that a water temperature model at a weekly scale would suffice. The quality and availability of data desired needs to be balanced against the costs in collecting it.

Ultimately, the approach adopted is dictated by the objectives of the research, and the temporal/spatial scale chosen. While ecosystems are recognized as complex, natural resource managers tend to consider broad scenarios (good, no change or bad) in their decision-making. Thus, although river temperature variations are most accurately determined using heat transfer processes and energy budget analysis (Smith 1979; Sinokrat and Stefan 1993; Webb and Nobilis 1997), surrogates for water temperature may be more appropriate in the absence of energy balance data (Smith, 1979). It is, however, also important to note that in the case of statistical models, correlation does not necessarily imply causation (Johnson 2003). Process-based models are expensive to develop (Webb 1996), require a lot of meteorological and hydraulic data in order to run and calibrate (Jeppesen and Iversen, 1987; Stefan and Preud'homme, 1993; Webb, 2000), and the approach is complex (Smith 1972; Jeppesen and Iversen 1987). Conversely, the temporal and spatial scales of thermal modelling using the linear approach (one to 100 kilometres; five days to months) is well suited to ecological processes; the predictive power of this "less" rigorous approach is often higher than the heat-balance approach (Jewitt and Görgens 2000b). The overriding management issue is the ability to predict the consequences of alterations to the river environment (Jeppesen and Iversen 1987), and the use of simple, pragmatic models that require relatively fewer parameters are useful in ecological studies in rivers (Jeppesen and Iversen 1987). A final consideration is the growing concern regarding the impact of global climate change on freshwater ecosystems

(Mohseni and Stefan 1999). General Circulation Models are able to predict air temperatures better than other climatic variables (Mohseni and Stefan 1999), so that water temperature models that make use of air temperatures could be used to predict the effects of climate change on water temperature.

In natural resource management, a common trend is the development and use of many parsimonious, single-purpose models, (Jewitt and Görgens 2000b; Wagener *et al.* 2000), which is a pragmatic approach under situations of data scarcity (as is the case in many South African rivers). The use of coarse-resolution models has distinct advantages: the rapid development of prototype models; ease of understanding by non-specialists; and relative ease in developing model code (Jewitt and Görgens 2000b).

3.5.2 Choice of modelling approach and model scale

Despite an element of non-causality between air and water temperatures, their statistical relationship remains a useful way of predicting water temperatures. The greater the variability that needs to be accounted for in the model, the greater the complexity needed, in terms of both the number of variables and their mathematical relationships. At a subdaily time step, the fit of regression models may be improved by using increasingly lagged values of water in relation to air temperature for rivers of increasing depth (Webb and Nobilis 1997), and a good understanding of the thermal lags in water temperatures is important for accurately simulating water temperatures when using air temperatures (Smith 1972). For example, Stefan and Preud'homme (1993) found that water temperatures followed air temperatures closely, but with a time lag of two to three days. From the analyses, a significant time lag of one to three hours was found (Table 2.3, Chapter 2), although water temperatures in the Sabie River have a "memory" of up to 48 hours, based on the dispersion model (Table 3.5). The implication of this is that the time lag between air and water temperatures becomes a critical factor depending on the temporal scale of modelling; at the scale of a month or a week the time lag does not necessarily need to be modelled, but a daily or hourly model will need to incorporate this lag.

The most pragmatic approach at this stage for calculating ecologically significant water temperatures for rivers in southern Africa would be to model daily water temperatures using daily air temperatures. Slightly more complex models that incorporate flowdependency can be developed using multiple linear regression techniques, which can also include dummy variables to incorporate the effects of site location and seasonality. Thus, factors such as altitude or aspect suggest that generally applicable models along the longitudinal axis of the Sabie River are elusive, although the non-significance of seasonality implies that these models are adequate in describing water temperatures on an annual basis. In South Africa, the use of daily air temperatures as a surrogate for water temperatures, especially in rivers for which water temperature data are not available, is a useful tool for aquatic scientists who need to consider the links between the distributions of aquatic biota and water temperatures. Maximum and minimum daily air temperatures are available for over 700 stations (Schulze 2001), so that such models could be developed for most South African rivers. However, this should not lead to complacency with respect to the current status of simulating water temperatures. According to Johnson (2003), river temperatures, due to their flowing nature, are controlled not only by the immediate surroundings, but also by upstream conditions. This implies not only an understanding of complex surface and subsurface flow paths, but also of the drivers and buffers of water temperatures described in Section 2.1.1 (Poole and Berman 2001). These complexities may explain the relatively poor correlations between observed and simulated water temperatures for the upper reaches of the Sabie catchment (Table 3.6). Future research should focus on the role of tributaries and the hyporheic zone in determining the thermal regime of the Sabie River

While most efforts have been aimed at understanding the drivers of maximum water temperatures, due to the effects of thermal stress on the distribution of aquatic species (cf. Section 3.1), the study of the drivers of minimum water temperatures could also bring valuable insights into understanding the magnitude and direction of energy fluxes influencing water temperatures (Johnson 2003). Certainly these points reinforce the comments of Poole and Berman (cf. Section 2.1) and Jewitt and Görgens (2000b) (Section 3.1), that water temperatures serve not only as a fundamental index in determining the nature of an aquatic environment, but that they also reflect the energy fluxes within a catchment as a whole. Thus, a holistic understanding of water temperature drivers, the ability to accurately simulate them, and objective ways of linking these to biotic response, significantly adds to the "toolbox" available to a catchment-scale adaptive management programme.

The objectives of adaptive management are to evaluate management options under different environmental scenarios, particularly at an annual, catchment scale. While the simple linear regression model is the most pragmatic approach for simulating daily maximum water temperatures, this model did under-predict, and water temperatures would need to be adjusted accordingly. Furthermore, the relationship between air and water temperatures was not completely linear, necessitating the use of alternative approaches, such as broken-stick models.

Since the seasonal accumulation of maximum daily water temperatures is of significance to aquatic organisms, the precision of a daily temperature model is unnecessary. In spite of under-predicting daily maximum water temperatures, the multiple linear regression and heat dispersion models developed in this chapter are suitable tools for simulating water temperatures for use in eco-hydrological research. A more complex heat balance model might predict water temperatures more consistently, although the added expense in collecting data to fit the additional model parameters might not justify the accuracy gained. The heat dispersion model is more complex than the multiple regression model, although this needs to be balanced against the advantages of being able to generate daily water temperature statistics (daily means, maximums and minimums) using the predicted hourly water temperatures.

Based on the available literature, a northern hemisphere bias exists in the arena of water temperature research and modelling, although the issue of non-constant variance in observed data has not been reported. Either this problem does occur in certain cases but has been ignored, or the rivers studied do not have thermal regimes exhibiting the degree of variability found in the Sabie River. This "difference in degree" was highlighted by Ward (1985), who pointed out that southern hemisphere rivers are generally more variable than northern hemisphere rivers (cf. Section 2.1.1). Chiew et al. (1995) have demonstrated that southern African rivers, like Australian rivers, have very extreme flow regimes, displaying twice the world average of flow variability. In the case of the Sabie River, elevated and more variable flows are linked to the rains between October and March (Heritage et al. 1997). The February 2000 floods within the Sabie catchment are a case in point, where rainfall depths with return periods exceeding 200 years fell over the middle and upper portion of the catchment, resulting in runoff periods exceeding 200 years in the middle portion of the catchment (Jewitt and Smithers 2002). The highly variable

hydrological nature of the rivers in the Sabie catchment is reflected in the fact that eight years prior to this flood, in September 1992, runoff in the Sabie River was reduced to drought conditions, particularly in the lower reaches, where base flows were at their lowest in recorded history (Weeks *et al.* 1996).

Similar modelling problems related to levels of variability in daily flow volumes in southern hemisphere rivers, as distinct from northern hemisphere rivers, were also reported by Basson et al. (1994) (cf. Section 8.4.1). In spite of violating the basic assumptions of linear regression models (cf. Section 3.2.1.1), simulation of maximum daily water temperatures using multiple linear regressions is nevertheless considered the most pragmatic and appropriate approach for the objectives of this study. Additionally, these water temperature models are a means to an end, viz. simulating water temperature time series under different environmental scenarios as inputs for the ecological model developed in Chapters 7 and 8. However, a need does exist for further research that aims to understand the nature of variability, particularly with respect to water temperatures, in southern African river systems, as this could be a critical factor influencing distribution patterns of aquatic organisms. Links between water temperatures and fish distribution patterns are discussed further in Chapter 4.

* * * * *

In order to understand the consequences of changes in river flows or climate, simulation models at appropriate management scales become important. Additionally, time series of water temperatures are useful as inputs into models that simulate biotic responses to abiotic drivers, which provide river managers with tools to assess system response under different scenarios. This chapter focused on the two main approaches to simulating water temperatures (process-based versus statistical). Simple correlative statistical models were shown to be the most pragmatic approach for simulating maximum daily water temperatures. However, all approaches were unable to account for the non-constant variance in the observed water temperature data.

4 WATER TEMPERATURE AND DISTRIBUTION PATTERNS OF FISH IN THE RIVERS OF THE SABIE CATCHMENT

4.1 Introduction

Historically, rivers have often been managed merely as open conduits of water (Breen et al. 2000), but are now increasingly recognized as complex natural systems. Furthermore, aquatic scientists accept that understanding issues relating to both water quantity and quality are of equal importance for effective river management (Reynolds 1998). A river may be thought of, in part, as a collection of physical components that flow in a linear direction downstream, with the physical, chemical and biological properties of the river changing along a downstream gradient. These gradients form a continuum, which has been termed the "River Continuum Concept" (Section 2.1.2, Chapter 2) (Vannote et al. 1980). At each point along the river, the system is in an apparently steady state, which on closer analysis is a state of dynamic equilibrium which tends towards some mean state, with the observed species patterns reflecting the abiotic components of the system (Vannote et al. 1980). Different species respond in different ways to these variables, so that their abundance curves, as a function of any environmental gradient, are typically unimodal. No two species are the same in their distributions, since each species will respond in a specific way to these environmental gradients, according to physiological and life-history mechanisms (Mueller-Dombois and Ellenborg 1974).

4.1.1 Water temperature and river species patterns

The aim of this chapter is to examine the role of different environmental variables, and principally water temperatures and flow volumes, in structuring fish community patterns in the Sabie-Sand River system. Weeks *et al.* (1996) suggested that water temperature best explains observed ichthyological zonation patterns in the rivers of the Sabie catchment. This pattern concurs with a substantial body of literature highlighting the importance of water temperatures in determining species distribution patterns (for example Stuckenberg 1969; Skelton 1993).

Webb and Nobilis (1997) remark that "water temperature has long been recognized as an important influence on the quality and ecology of streams and rivers". The importance of water temperatures as an abiotic process structuring biotic patterns in rivers is emphasized

by Smith (1972), who comments that "although water quality embraces a broad technical field, the thermal condition of a river is one of the most important single criteria since temperature influences most of the physical, chemical and biological properties of water [bodies]". Water temperatures affect the physical nature of water by, inter alia, changing its density, viscosity, and surface tension (Gordon et al. 1994). Temperature also affects the chemical reactions of solutes in water, both by changing the rate of chemical reactions, as well as the types of reactions (Nikolsky 1963; Allan 1995; Webb 1996). Webb (1996) provides a comprehensive review of the effects of water temperature on the physical and chemical characteristics of water. A strong link exists between water temperatures and the physiology of aquatic organisms, since most are poikilothermic (Webb 2000), being either stenothermal (species occupying a narrow temperature range), or eurythermal (species occupying a wide temperature range) (Allan 1995). Metabolic rates, survival rates, growth rates, and fecundity are temperature dependent (Nikolsky 1963; Crisp and Howson 1982; Hostetler 1991; Allan 1995; Claska and Gilbert 1998). The timing and magnitude of heating and cooling periods act as cues for different life history stages of fish and invertebrates, which tend to correspond with critical flows volumes, and availability of food, sexual partners and habitats (Nikolsky 1963; Vannote and Sweeney 1980; Allan 1995; Webb 2000). Temperatures outside an organism's optimal range lead to thermal stress (Webb 2000), and in such situations biota will attempt to move to more favourable refugia habitats (Essig 1998). Distributional patterns are the final manifestation of how individuals have been responding to environmental pressures.

4.1.2 Quantification of species patterns

Collective species distribution patterns may be defined as species diversity, which Whittaker (1972) breaks down further into:

- Alpha (α) diversity, or within-habitat diversity; and
- Beta (β) diversity, or between-habitat diversity. This is measured as species turnover along environmental gradients, and is concerned with the change in diversity from habitat to habitat (Southwood 1978).

Species and environmental data are typically recorded as data matrices, where each row represents species or environmental data, and each column corresponds to a sampling unit. These large multidimensional data sets can best be interpreted by using techniques that reduce the matrices to one or two-dimensions.

Measures of species richness and evenness are useful techniques for objectively quantifying α -diversities, and indicate the number of species in a community (species richness), and how the relative abundances of different species are distributed within each sampling unit or community (species evenness). Diversity indices combine the number of species with their relative abundances, making it possible to quantify sites by species, although the resulting reduction in the number of variables is also one of the criticisms of diversity indices.

Similarity coefficients, such as Sørrenson's similarity coefficients, which were used, for example, by Zalewski (1985) for comparing fish diversity between sites, and multivariate ordination techniques, which simplify and condense multidimensional data sets so that eological relationships can be postulated (Ludwig and Reynolds 1988), are best suited for understanding β -diversity. Different ordination techniques are typically used in such analyses, depending on the type of data being analysed. A commonly used technique for exploring relationships between sites and environmental variables is Principal Components Analysis (PCA), which is a linear model. For example, Graham et al. (1998) used principal components analyses to highlight the key environmental drivers of algal blooms in dams in KwaZulu-Natal, South Africa. However, because the relationships between species and their environments are generally non-linear, with species tending to have single-peaked response functions (bell-shaped) to environmental variables (ter Braak 1987), PCA is not an appropriate ordination technique for analyzing species-environment In this regard, canonical correspondence analyses (CCA) are more relationships. appropriate for exploring species-environment relationships (ter Braak 1987), and consequently this technique was selected for the fish-environment relationships in the main rivers of the Sabie catchment in this study (cf. Section 4.2.2). Such analyses have been previously used in a number of studies. For example, ter Braak (1983) used canonical correspondence analysis to study algal diversities in a lake from 1920 and 1978, where sites were compared over time to determine whether their diversities had changed; Koel and Sparks (2002) used CCA to explore the links between fish abundances and different flow parameters. CCA is a technique that can be used to relate species data to environmental variables, so that it is possible to identify which species are responding to what environmental variables, and also which sites are being structured by certain environmental variables. According to this technique, weighted averages (scores) are calculated for each species and for each environmental variable¹. Linear combinations of these variables are found in CCA, in order to identify the combination of variables that maximizes the dispersion of species scores. Direct gradient analysis is a useful technique for elucidating the underlying causes of community distribution, by examining the joint effects of environmental conditions on a species (ter Braak 1987). However, other cause and effect relationships, such as inter and intra-specific competition, also contribute to these patterns, which can only be evaluated through experimentation (Mueller-Dombois and Ellenborg 1974).

4.2 Data collection and analysis methods

In order to assess the extent to which fish distributions in the Sabie catchment are dependant on water temperatures, as hypothesised by Weeks *et al.* (1996), surveys using standard electrofishing techniques were undertaken at ten sites in May 2000, May 2001 and May 2002 (Figure 4.1). Three of the nine water temperature sites coincided with the May electrofishing sites. Although this is accepted and recognized as a weakness in directly relating fish community patterns to water temperatures, this is due to the fact that the water temperature sites were chosen subsequent to the May, and October *Chiloglanis*-focus (*cf.* Section 6.2, Chapter 6) electrofishing survey sites, and a trade-off between budgetary constraints and an optimal placement of water temperature loggers along the longitudinal axis of the Sabie River, was necessary (*cf.* Section 1.4, Chapter 1).

Pertinent site information is listed in Table 4.1, with a more detailed site description provided by Weeks et al. (1996). In general, upstream sites were generally rocky, while sites further downstream were shallower and sandier. A 220V electroshocker attached to a generator was used to provide data on fish species compositions and relative abundances at each survey site. Electrofishing is appropriate at shallow (<1.5m) sites with good clarity and lacking dense cover (Horne & Goldman 1994; Harris & Silveira 1999). Each site was surveyed by sampling all shallow habitats within a 30-50m reach of river, moving upstream. Fish were identified to species level, and lengths and weights recorded for specific species, notably *Chiloglanis anoterus* and *C. paratus* (see Chapters 5 and 6). May was chosen as an appropriate sampling time since it preceded winter flows and reflected

 $u_k = \sum_{i=1}^n y_{ik} - x_i / y_{+k}$, where u_k is the weighted average of the k^{th} species, x_i is the environmental value of the *i*th (out of *n*) site, and y_{ik} is the abundance of species *k* at site *i*, y_{+k} is the total abundance of species *k*.

the relative abundances succeeding the summer breeding season. This is consistent with the methods of analysis used in previous Sabie River ichthyological studies, as well as coinciding with the survey period of Weeks *et al.* (1996) for the pre-impoundment surveys in the Sabie catchment, as described in Chapter 1.

Spot water quality variables (Table 4.2) were recorded for each site; substratum types were classified qualitatively (Table 4.3). Data matrices of fish species relative abundances and water quality are provided in Appendices A1-2 respectively.

Table 4.1 Site information relating to May electrofishing surveys

Site	Name*	River	Altitude (m.asl)	Zone#	Predominant habitat type§
3	Rocky Boulder	Sabie	867	FHZ	Rocks and riffles
5	Hazyview	Sabie	488	LZ	Rocks and riffles
7	Lisbon	Sabie	320	LZ	Bedrock and sand
9	Confluence	Sabie	220	LZ	Sandy and shallow
20	Molondozi	Sabie	140	LZ	Bedrock and shallow
11	Rooiboklaagte	Sand	538	FHZ	Bedrock and sand
19	New Forest	Mutlumuvi	499	FHZ	Sandy and shallow
14	Londolozi	Sand	315	LZ	Bedrock and sand
26	Meat Factory	Sand	260	LZ	Bedrock and shallow
21	The Gums	Marite	620	LZ	Rocks and riffles

^{*} Relates to original site names used by Weeks et al. (1996);

^{*} Foothill (FHZ) and lowveld zones (LZ) used by Weeks et al. (1996) (Section 1.4.1, Chapter 1);

[§] See Table 4.3.

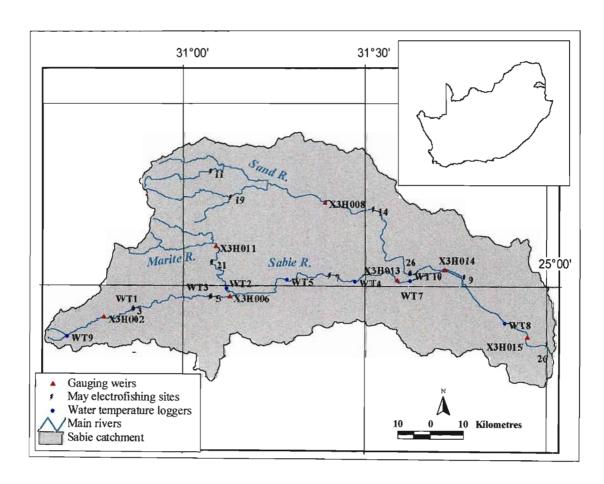


Figure 4.1 May electrofishing sites in relation to gauging weirs and water temperature field sites in the Sabie catchment.

Table 4.2 List of spot water quality variables collected for May fish survey sites

Abbreviation	Variable	Sampling Method				
		Turbidity meter (Orbeco-Hellige				
NTUs	Turbidity units	portable turbidimeter)				
DO	Dissolved Oxygen (%)	Dissolved oxygen meter				
		Digital pH meter (Hanna HI 8424				
рН	pH	microcomputer pH meter)				
N	Nitrate + Nitrite as N (mg.l ⁻¹)	Laboratory analyses				
P	Orthophosphate as P (µg.l ⁻¹)	Laboratory analyses				
SO ₄	Sulphate as SO ₄ (mg.l ⁻¹)	Laboratory analyses				
	Electrical Conductivity	Conductivity meter (Hanna HI				
Cond	(25°C, mS.m ⁻¹)	8733)				
TDS	Total dissolved solids (mg.l ⁻¹)	Laboratory analyses				

Table 4.3 Qualitative values for substratum classification

Substratum type	Value
Rocks and riffles	1
Sandy	2
Bedrock and sand	3
Bedrock	4

4.2.1 Diversity indices in explaining species patterns

Diversity measures for the Sabie River were calculated on the basis of Ludwig and Reynolds (1988), who recommend using Hill's diversity indices (Hill 1973). These indices are a measure of the degree to which proportional relative abundances are distributed among the species at each site, and are composed of three numbers:

- N_0 a measure of all the species (Equation 4.1);
- N_1 a measure of the effectively abundant species (Equations 4.2a-b);
- N_2 a measure of the effectively very abundant species (Equation 4.3a-b).

In the case of N_1 and N_2 , the rare species are not emphasized. N_1 is based on the Shannon and Weaver Index (H') (Ludwig and Reynolds 1988), and is "a measure of the average degree of 'uncertainty' in predicting to what species an individual chosen at random from a

collection of S species and N individuals will belong" (Ludwig and Reynolds 1988, p. 92). Therefore, uncertainty increases as the number of species increases, and as their abundances become more even, so that H' = 0 when there is only one species in the sample, and H' is at a maximum when all possible species are represented by the same number of individuals. Thus when this index is used to calculate N_1 , the closer the number is to one, the lower the site's diversity. N_2 is based on Simpson's index, which is a number from zero to one, and gives the probability that two individuals drawn at random from a population belong to the same species (Ludwig and Reynolds 1988). The closer this number is to one, the more the community is dominated by few, abundant species, and the site's diversity is concomitantly low. When the inverse of λ (N_2) is calculated, the larger this number is, the more diverse a site is.

$$N_0 = S \tag{4.1}$$

where S is the number of species at a site. This does not take account of the relative abundances.

$$N_1 = e^{H'} ag{4.2a}$$

where H' is the Shannon Index, based on the work of (Shannon and Weaver 1949), and

$$H' = \sum_{i=1}^{S} (p_i \ln p_i)$$
 [4.2b]

$$N_2 = \frac{1}{\lambda}$$
 [4.3a]

where λ is Simpson's index (Simpson 1949), and

$$\lambda = \sum_{i=1}^{S} p_i^2 \tag{4.3b}$$

Note that $p_i = \frac{n_i}{N}$, and is the proportional abundance of the i^{th} species, where n_i is the number of individuals of the i^{th} species, and N is the total number of species at each site.

Evenness values for each site were calculated using modified Hill's ratio (Equation 4.4), which Ludwig and Reynolds (1988) recommend as a measure of how relative abundances are distributed between species collected at a site. The evenness value, *E*, approaches one

when the abundances are evenly distributed between species, and zero as a single species becomes more dominant.

$$E = \frac{N_2 - 1}{N_1 - 1} \tag{4.4}$$

Sørrenson's similarity coefficients (Equation 4.5), which provide a ratio of similarity between pairs of sites, were calculated for the ten sites on the Sabie River surveyed during May 2002, using a matrix for common species between sites (Table 4.4). The denominator is independent of the numerator, because theoretically each species has an equal chance of being present in both areas; the index thus measures the actual measured coinciding species occurrences against those that are theoretically possible (Mueller-Dombois and Ellenborg 1974).

$$C_s = \frac{2j}{a+b} \tag{4.5}$$

where j is the number of species common to both samples, and a and b are the total number of species in each sample.

Results from these analyses are presented in Section 4.3.1.

Table 4.4 Matrix of species common to pairs of sites for the May 2002 electrofishing survey. Species common to pairs of sites form the basis for calculating of Sørrenson's similarity coefficients.

Sites	3	5	21	7	9	20	11	19	14	26
3	2							avi.	1 min 1	1.01
5	1	4								*
21	2	2	3							4
7	1	3	1	15						
9	1	2 ·	1	8	9					
20	0	1	0	7	6	10	1			
11	1	3	1	6	4	3	8	4		
19	1	2	1	8	6	5	3	9		
14	0	2	0	10	6	8	5	5	13	
26	0	0	0	5	3	4	3	4	6	10

4.2.2 Ordination techniques in explaining species patterns

Correlation matrices were calculated for the May 2000, May 2001 and May 2002 environmental data, since these variables are often highly correlated (ter Braak 1987). The list of environmental variables considered should preferably be refined prior to performing ordinations that aim to explore species-environment analyses, since too many variables that are highly correlated are likely to complicate the ordination analyses unnecessarily. The list of environmental variables was further refined through principal components analyses using the May 2000, May 2001 and May 2002 environmental data. Standardized PCAs were used since the data units for the various indices were different. Flow and water temperature indices were added to the existing list of variables (Table 4.5). parameters were obtained by using the gauging weir and water temperature logger data closest to the fishing sites, respectively (Figure 4.1). Available flow data were "patchy", having many missing records; and the flow record lengths did not completely coincide with the electrofishing dates. Consequently, daily flow volumes derived from the daily flow data recorded at the gauging weirs listed in Table 4.6, were applied to all three May data sets. Flow statistics were calculated based on the entire record length for each gauging weir. Records for water temperature data were longer than for flow data, and coincided more completely with the fish survey dates viz. data were available for 2001 and 2002. However, since the water temperature data loggers were installed in February 2001 (Chapter 2), water temperature data were not available for 2000. Values calculated from the average of the 2001 and 2002 data were used for the temperature statistics for 2000. Hourly water temperatures collected for the period 8 February 2001 to 28 February 2003 were used to calculated mean daily water temperatures, which were used as the basis for the water temperature parameters listed in Table 4.5. Water temperature monitoring sites were matched with fish survey sites based on²:

- Proximity to fish survey site;
- Similarity in altitudes.

² The exception to these criteria was site WT9, which was assigned WT4, based on Sørrensen's similarity coefficients. This is because the fish community at site 19 was most similar to site 7, which was closest to WT4 – see Section 4.3.1, Table 4.8.

Table 4.5 List of environmental variables considered for the PCA

Abbreviation	Variables
NTUs	Turbidity units
DO	Dissolved Oxygen (%)
pН	рН
N	Nitrate + Nitrite as N (mg.l ⁻¹)
P	Orthophosphate as P (µg.l ⁻¹)
SO ₄	Sulphate as SO ₄ (mg.1 ⁻¹)
Cond	Electrical Conductivity (25°C, mS.m ⁻¹)
Tmin	Minimum annual daily water temperature (°C)
Tmax	Maximum annual daily water temperature (°C)
Tmmin	Mean minimum daily water temperature (°C)
Tmmax	Mean maximum daily water temperature (°C)
Tmean3	Mean daily water temperature (3 month) (°C)
Tmean	Mean daily water temperature (12 month) (°C)
Tsd	Standard deviation of daily water temperature (°C)
Tcv	Coefficient of variation of daily water temperature (°C)
Tdd	Degree days > 25°C for preceding four months*
Fmin	Minimum daily annual flow (m ³ .s ⁻¹)
Fmax	Maximum daily annual flow (m ³ .s ⁻¹)
Fmean	Mean daily flow (m ³ .s ⁻¹)
Fsd	Standard deviation of daily flow (m ³ .s ⁻¹)
Fcv	Coefficient of variation of daily flow (m ³ .s ⁻¹)
Substratum	Substratum type by site (qualitative)

* February to May

Table 4.6 Derivation of mean daily flow (m³.s⁻¹) and water temperature (°C) data for ordinations

Fish survey site	Altitude (m.asl)	Gauging weir	Weir record length (months)#	Water temperature logger	Temperature record length (months)*	Altitude of water temperature logger (m.asl)
3	868	X3H002	23	WTI	16	870
5	480	X3H006	16	WT3	16	523
7	318	X3H015	16	WT4	16	287
9	198	X3H015	16	WT7	16	242
20	135	X3H015	16	WT8	16	157
21	615	X3H011	23§	WT2	16	443
11	531	X3H011	23 [§]	WT3	16	523
19	490	X3H011	23 [§]	WT4	16	287
14	308	X3H008	30 [§]	WT4	16	287
26	249	X3H008	30 [§]	WT10	12	287

^{*}Records lengths of weirs X3H002 and X3H011 was from 1 October 1999 to 30 August 2001; weir X3H015 was from 1 October 1999 to 19 January 2000; weir X3H008 was from 1 October 1999 to 3 April 2002.

A direct gradient canonical correspondence analysis was performed using the statistical software package Canoco (ter Braak 1992) for the electrofishing sites, and the associated environmental variables, for May 2000, May 2001 and May 2002. Data inputs were species, environmental and covariance (survey date) matrices. Species response curves were assumed to be unimodal. The data were not transformed, and symmetric scaling was used for the analyses (i.e. data were plotted for axes with an origin at zero). Selection of environmental variables was automatic, and based on unrestricted permutations (i.e. samples were not restricted to locations) for the Monte Carlo tests of significance. These were used to test for the effects of specific environmental variables after the influences of other variables had been removed. Results are presented in Section 4.3.2.

[§] Missing data (X3H008: 8-23 February 2000 and 31 August – 12 September 2000; X3H011: 21 January – 22 February 2000).

^{*} Record length for 16 months was 8 February 2001 – 15 May 2002; for 12 months was 16 May 2001 – 15 May 2002.

4.3 Results

4.3.1 Species patterns in the Sabie River using diversity indices

Values for diversity indices (Tables 4.7a-c) were plotted as a function of downstream distance for the subset of sites on the Sabie River (Figure 4.2a). Species numbers (N_0) increased with downstream distance for May 2000, although during May 2001 and May 2002 diversity decreased at site 9 and also site 20. Site 20, which was the site furthest downstream, may have acted as a "sink" for fish washed downstream after the major floods that occurred in February 2000. Site 7 was the most diverse site from May 2000 to May 2002, which may reflect a new post-flood equilibrium. The highest diversity on the Sabie River was recorded for the middle reaches (100 kilometres downstream), which is consistent with the River Continuum Concept (Vannote et al. 1980) which predicts highest species diversities in the middle reaches of a river due to its productivity and habitat diversity. Sites upstream tended to be characterized by a low diversity, although the evenness indices (E) (Figure 4.2b), being close to one, suggest that these species were evenly distributed. Evenness values were generally greater than 0.5; no single site appeared to be dominated by a single species. However, evenness numbers did not remain stable from year to year, suggesting that population numbers of different species were dynamic between years. Site 7 was the most diverse on the Sabie River, although the trend over the past three years was a decrease in species evenness, suggesting an increasing dominance at this site by a few species, notably Labeobarbus marequensis. Site 21, on the Marite River, exhibited low fish species diversity for the period surveyed, while site 26, on the Sand River, showed a high level of species diversity for all three diversity indices, as well as showing a high level of evenness, suggesting that no single species is dominant at this site (Appendix A1).

Table 4.7a Diversity (N) and evenness (E) indices for May 2000 electrofishing survey. The diversity indices N_0 , N_1 and N_2 are measures of the total, abundant and very abundant species respectively, at each site.

Index	3	5	21	7	9	20	11	19	14	26
N_0	2	6	3	10		13	9	10	12	13
$N_{\rm i}$	2.00	2.28	2.18	8.13		6.91	5.77	6.12	5.54	7.33
N_2	1.99	1.62	1.86	7.07		4.94	4.32	3.91	3.90	5.94
Е	1.00	0.48	0.73	0.85		0.67	0.70	0.57	0.64	0.78

Table 4.7b Diversity (N) and evenness (E) indices for May 2001 electrofishing survey. The diversity indices N_0 , N_1 and N_2 are measures of the total, abundant and very abundant species respectively, at each site.

Index	3	5	21	7	9	20	11	19	14	26
N_0	2	7	5	12	9	13	5	15	12	
N_1	1.89	3.69	1.83	6.24	5.47	7.87	3.06	9.73	7.42	
N_2	1.80	2.87	1.40	4.40	3.63	6.01	2.40	7.38	6.38	
Е	0.90	0.70	0.48	0.65	0.59	0.73	0.68	0.73	0.84	+

Table 4.7c Diversity (N) and evenness (E) indices for May 2002 electrofishing survey. The diversity indices N_0 , N_1 and N_2 are measures of the total, abundant and very abundant species respectively, at each site.

Index	3	5	21	7	9	20	11	19	14	26
N_0	2	4	3	15	9	10	8	9	13	10
N_1	1.92	1.80	1.81	6.47	5.24	5.36	3.93	6.96	8.08	7.11
N_2	1.84	1.37	1.49	4.19	4.42	3.76	2.84	6.04	6.13	5.62
E	0.92	0.46	0.60	0.58	0.81	0.63	0.63	0.85	0.72	0.76

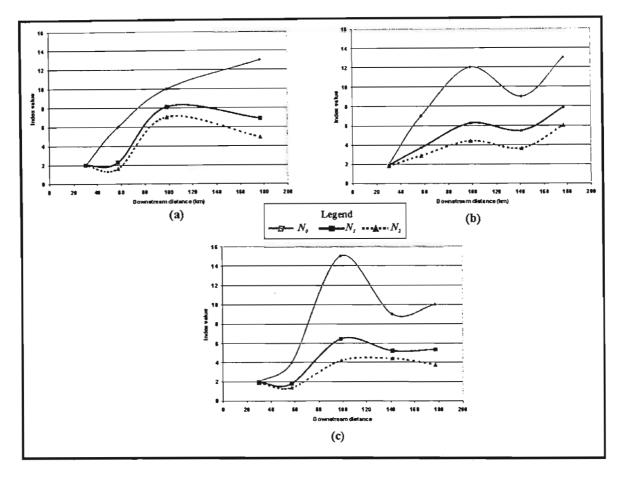


Figure 4.2a Diversity indices for May 2000 (a), 2001 (b) and 2002 (c) electrofishing surveys, for sites along the Sabie River. Diversity indices N_0 , N_1 and N_2 (Section 4.2.1), as indicated in the legend, refer to the total number of species at each site, the number of abundant species, and the number of very abundant species, respectively.

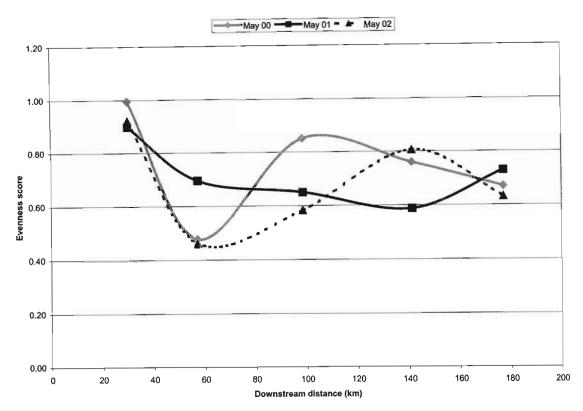


Figure 4.2b Evenness values for May 2000, 2001 and 2002 electrofishing surveys, for sites along the Sabie River.

Sørrenson's similarity coefficients exceeding 0.70 (Table 4.8) were considered to show a high degree of similarity, or conversely, a low β -diversity. Sites showing low β -diversity (> 0.70) were site 20 with site 14; site 7 with site 14; and site 3 with site 21. Site 20 was similar to site 14 in spite of being on the Sabie and Sand Rivers respectively. This may be a result of both sites being lowveld sites where the river substratum was similar: flat and sandy with large rocks. This may also explain the similarities between sites 7 and 14. The similarity coefficient between sites 21 and 3 was high, due to a shared cold-water fish species assemblage. The high β -diversity (low Sørrenson coefficient) between sites 5 and 7 coincides with a thermal breakpoint on the Sabie River, which was shown to occur between 57 and 80 kilometres downstream, as discussed in Chapter 2 (Section 2.3.2). This may be due to a species "turnover", with cold-water species being replaced by warm water species, which coincides with the foothill/lowveld transition zone described by Weeks et al. (1996). Typically cold-water fish species of the Sabie catchment, such as Amphilius uranoscopus and Chiloglanis anoterus, are replaced by fish species which were shown to be typical warm water lowveld fish species by Weeks et al. (1996) through the use of cluster analyses, viz. C. paratus; C. swierstrai; Labeo molybdinus; Labeobarbus

marequensis; Barbus viviparous; B. trimaculatus; Tilapia rendalli and Opsaridium perengii (Appendix A2). A low similarity index between site 26 and the remaining May sites, in the context of the diversity indices, suggests that this site has a high β -diversity, with a unique fish community within the rivers surveyed in the Sabie catchment.

Table 4.8 Sørrenson's Similarity coefficients between sites based on May 2002 electrofishing survey. "High similarity" values (i.e. low β diversity) are shaded.

Sites	3	5	21	7	9	20	11	19	14	26
3	1.00									
5	0.33	1.00					City;			5 (8)
21	0.80	0.57	1.00					A.	2.0	
7	0.12	0.32	0.11	1.00						
9	0.18	0.31	0.17	0.67	1.00		7			
20	0.00	0.14	0.00	0.56	0.63	1.00		4.52	i.	
11	0.20	0.50	0.18	0.52	0.47	0.33	1.00			
19	0.18	0.31	0.17	0.67	0.67	0.53	0.35	1.00		
14	0.00	0.24	0.00	0.71	0.55	0.70	0.48	0.45	1.00	
26	0.00	0.00	0.00	0.40	0.32	0.40	0.33	0.42	0.52	1.00

4.3.2 Species patterns in the Sabie River using ordination techniques

Correlation matrices for the May 2000, May 2001 and May 2002 surveys (Appendix A3) showed that Fcv was highly correlated with Fmax, and the temperature variables Tdd, Tmax, Tmean, Tmean3, Tmmax and Tmmin were all highly correlated³. The PCAs for the same water quality and quantity data showed that for each year, the greatest contributions to PCA Axis 1 were the temperature variables Tdd, Tmax, Tmean, Tmean3, Tmmax and Tmmin (Figures 4.3-4.5). Eigenvalues for each year are given in Table 4.9, together with the percentage variation accounted for by each axis. Total percentage variations for May 2000, May 2001 and May 2002, calculated as the sum of percentage variation accounted for by PCA Axes one and two (cf. Table 4.9), were 65.24, 64.85 and 70.31 respectively. Since the temperature variables were all highly correlated, PC Axis 1 was defined as a "temperature" axis. The most important variables for PC Axis 2 varied from year to year:

- 2000 = Fev, Fmax, Tev, Tmin, P and SO₄;
- 2001 = Fev, Fmax, N (and SO₄, Fmin and DO);
- 2002 = Fmin, NTUs, SO₄ and Tmin.

For and Fmax were highly correlated, and could be described as "flow", while DO and SO₄ contributed to "water quality". Thus, the combined interactions of flow and water quality variables contributed most to explaining the variation for Axis 2. However, their interactions were not consistent from year to year, which suggests that temperature is the overriding driver of fish community patterns observed at the sites surveyed, followed by a more complicated and dynamic interaction between flow and water quality. Substratum type did not contribute significantly to the site groupings. The sites 26 and 20 were consistent outliers, while sites 7 with 9, and 3, 5, 11 and 21, could be grouped together. However, the clusters were dynamic on an inter-annual basis.

³ See Table 4.5 for explanation of codes.

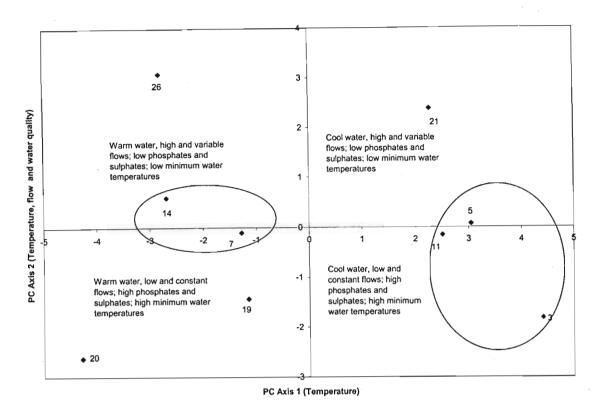


Figure 4.3 PCA of May 2000 electrofishing survey sites within the Sabie catchment, based on environmental variables listed in Table 4.5. Environmental variables contributing most to Axes one and two, and which characterize each site, are described for each quadrant.

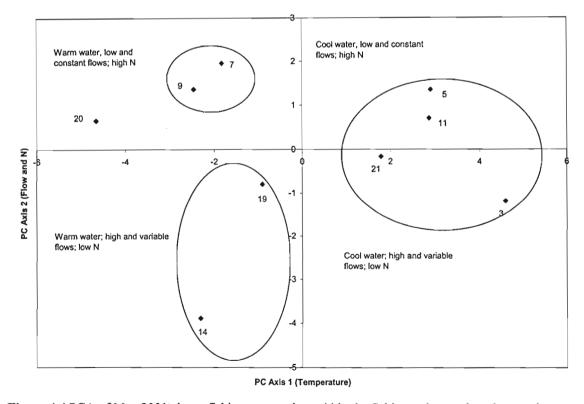


Figure 4.4 PCA of May 2001 electrofishing survey sites within the Sabie catchment, based on environmental variables listed in Table 4.5. Environmental variables contributing most to Axes one and two, and which characterize each site, are described for each quadrant.

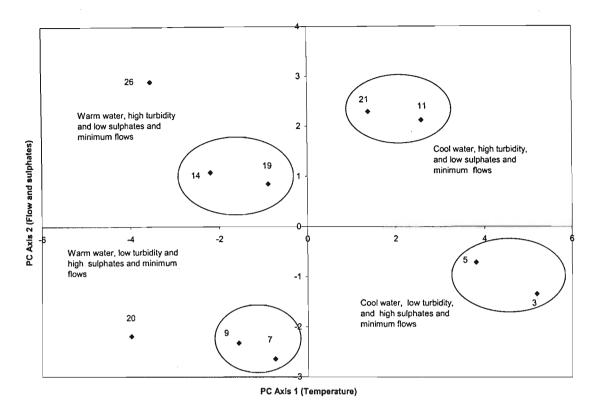


Figure 4.5 PCA of May 2002 electrofishing survey sites within the Sabie catchment, based on environmental variables listed in Table 4.5. Environmental variables contributing most to Axes one and two, and which characterize each site, are described for each quadrant.

Table 4.9 Eigenvalues and latent vectors for PCAs of sites by environmental variables for May 2000, May

2001 and May 2	May 2000		May 2001		May 2002	
	PC Axis 1	PC Axis 2	PC Axis 1	PC Axis 2	PC Axis 1	PC Axis 2
Eigenvalue	9.57	3.48	9.77	3.20	9.67	4.39
% variation	47.86	17.38	48.83	16.02	48.36	21.95
Cond	-0.24	-0.27	-0.22	-0.03	-0.25	-0.15
DO	-0.23	0.01	0.07	0.37	0.18	-0.17
Fcv	-0.15	0.32	-0.07	-0.43	-0.14	0.26
Fmax	-0.17	0.31	-0.10	-0.44	-0.16	0.24
Fmean	-0.26	-0.01	-0.27	0.17	-0.24	-0.25
Fmin	-0.13	-0.21	-0.20	0.37	-0.11	-0.40
N	0.02	-0.10	0.15	0.43	0.24	-0.23
NTUs	-0.13	-0.07	-0.09	-0.12	-0.12	0.38
P	-0.05	-0.30	-0.03	-0.01	0.03	0.04
pН	-0.19	-0.27	-0.17	-0.12	0.17	-0.01
SO ₄	-0.10	-0.31	-0.20	0.32	0.06	-0.40
Subs	-0.24	-0.18	-0.23	0.00	-0.21	-0.10
Tev	-0.23	0.31	-0.22	0.10	-0.25	0.20
Tdd	-0.32	-0.02	-0.31	-0.03	-0.30	-0.14
Tmax	-0.30	0.14	-0.30	-0.02	-0.31	0.04
Tmean	-0.31	0.02	-0.31	0.01	-0.31	-0.08
Tmean3	-0.31	0.06	-0.31	0.02	-0.31	-0.07
Tmin	-0.07	-0.48	-0.19	-0.02	-0.05	-0.39
Tmmax	-0.31	0.13	-0.31	-0.01	-0.31	0.02
Tmmin	-0.31	0.00	-0.31	0.02	-0.30	-0.10

A subset of environmental variables used for the CCA (Table 4.10) was based on the correlation coefficients (Appendix A3), and the PCA analyses (Figures 4.3-5). Based on the CCA, the main source of variation could be explained by water temperatures (Axis 1), while a combination of conductivity, substrate type and flow accounted for the main source of variation in Axis 2 (Table 4.11). The ordination diagram (Figure 4.6) shows sites and species as points, and environmental variables as vectors, on the same plot. The direction

of each vector represents the gradient, while vector length represents the relative importance, of each environmental variable. An imaginary perpendicular line between a species point (a weighted average) and an associated vector indicates the optimum position of a species distribution along an environmental gradient. The ordination diagram also shows which species are likely to be present at a particular site. The species points approximate the optima of these surfaces; hence the abundance or probability of occurrence of a species at a site decreases with distance from its location in the diagram. The ordination suggests that the fish community patterns at the cold water sites were influenced most by a gradient of mean annual water temperatures and maximum annual daily flows, while the communities from the warmer sites were structured by a combination of abiotic variables, the most important being mean annual minimum water temperature, conductivity and substrate type. Mean annual water temperature was the longest vector, which suggests that of the variables considered in the analyses, this parameter is the most influential abiotic driver of fish species distribution patterns within the main rivers of the Sabie catchment.

Table 4.10 List of environmental variables used for the CCA analyses

Variables			
Turbidity units			
Dissolved Oxygen (%)			
рН			
Nitrate + Nitrite as N (mg.l ⁻¹)			
Orthophosphate as P (µg.l ⁻¹)			
Sulphate as SO ₄ (mg.l ⁻¹)			
Electrical Conductivity (25°C, mS.m ⁻¹)			
Mean daily minimum water temperature (°C)			
Mean daily water temperature (12 month) (°C)			
Coefficient of variation of daily water temperature (°C)			
Minimum annual daily flow (m ³ .s ⁻¹)			
Maximum daily annual flow (m ³ .s ⁻¹)			
Mean daily flow (m ³ .s ⁻¹)			
Substrate type by site (qualitative)			

Table 4.11 Conditional effects of environmental variables determined by automatic selection for Axes 1 (CC1) and 2 (CC2) of CCA

Variable	P*	F#	CC1	CC2
Percent v	ariation		(35.1)	(15.4)
Cond	0.050	1.88	-0.4624	1.1237
DO	0.260	1.33	0.0810	0.3994
Fmax	0.005	2.89	0.0861	0.2457
Fmean	0.115	1.58	-0.3856	-0.6909
Fmin	0.085	1.75	0.5898	1.0196
N	0.120	1.67	-0.0572	-0.6777
NTUs	0.055	1.71	0.0233	0.0922
P	0.770	0.56	-0.1043	0.5755
pН	0.125	1.53	-0.1228	0.1623
SO ₄	0.390	1.07	0.1606	0.2290
Subs	0.005	2.81	-0.2949	-0.8421
Tcv	0.080	1.86	-0.2033	-0.041
Tmean	0.005	2.50	3.6010	0.2828
Tmmin	0.005	5.83	-3.9886	-0.0318

Significance level

[#] F-statistic

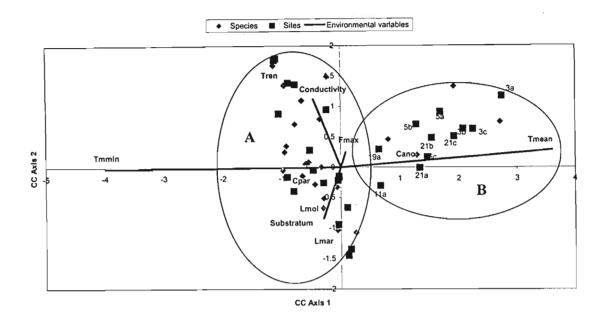


Figure 4.6 CCA plot for May electrofishing surveys from 2000 – 2002 within the Sabie catchment, showing the relationships between sites, species and main environmental gradients determining species distributions. Sites and species are grouped into warm water (A) and cool water (B) groups, which correspond to the lowveld and foothill zones of Weeks et al. (1996) respectively.

4.4 Discussion and conclusions

4.4.1 Reliability of fish diversity data using relative abundances

Electrofishing is a relative sampling technique (Southwood 1978), providing data on species diversity and relative abundances of species sampled at each site surveyed. This technique is not without its limitations, with electrofishing efficiency being affected by fish body size, water temperature⁴ (Zalewski 1985), river width (Kennedy and Strenge 1981), and water conductivity (Alabaster and Hartley 1962). Absolute estimates of fish species and abundances can be obtained through repeated electrofishing surveys at the same site to establish a relationship curve between sample size and actual population size or species diversity (Zalewski 1985), or alternatively through the use of piscicides with counts regressed against relative abundance samples (Larimore 1961; Zalewski 1985). Inconsistencies may also be corrected for using measures of catch per unit effort (CPUE), which are typically expressed as fish per stream surface area, reach length or time (Paller 1995). Such methods have been widely used in fish surveys (see for example (Zalewski 1985; Zalewski et al. 1990; Paller 1995; Weeks et al. 1996).

The techniques used to measure α - and β -diversities are equally well suited to absolute and relative abundances, and the objectives of this study did not require absolute values.

⁴ Metabolism is faster at higher temperatures and fish are able to escape the electric current.

Southwood (1978) is of the opinion that because electrofishing efficiency differs between habitats, fixed-time collecting is not satisfactory for the comparison of faunas of different habitats, and that searching a fixed area efficiently provides a reliable estimate. Consequently, it was not considered necessary to adjust the relative abundances for CPUE. In spite of the potential pitfalls of electrofishing techniques, it was felt that the relative abundances from each reach, uncorrected for CPUE, were representative of what was in the river at that time, and are directly comparable between sites.

4.4.2 Fish species patterns in the Sabie catchment

For the sites sampled along the gradient of the Sabie River, it was hypothesized that N_0 , the measure of all species at a site (Equation 4.1, Section 4.2.1), would increase downstream as the number of species increases through addition of species, a consequence of increasing habitat diversity as conceptualized by Vannote *et al.* (1980) in the River Continuum Concept. Similarly, N_1 , N_2 and evenness should increase with downstream distance. This would be in agreement with studies such as that of Zalewski (1985), who reported a downstream increase in fish species diversity. For three consecutive years, similar trends were found in the downstream gradient of the Sabie River. The peak in species numbers was at the interface of the lowveld and foothill zones (Figure 4.2). However, it must also be noted that the communities are composed of a few very abundant, generalist species, a few rare species that are occasionally present at different sites, and the majority of species of intermediate abundances.

Site groupings based on the similarity coefficients (Section 4.3.1) did not generally show similar patterns to the site groupings from the PCAs (Section 4.3.2). The fish community at site 26 was unique within the Sabie-Sand River system, based on the similarity and principal components analyses. The observed biotic compositions are a function of species additions and turnovers along a river gradient. However, a species absence may not necessarily be due to an unsuitable habitat. The species observed at a site are present because the habitat is suitable, and also because of the opportunity to migrate to the site. Furthermore, different fish species are likely to respond to cumulative abiotic effects in different ways. Biologically, it has been suggested that cumulative seasonal water temperatures are more important in determining species patterns than single temperature values (Armour 1991; Hines and Ambrose 1998). Therefore, even though gradients of "average" conditions accounts for species community patterns, as shown by the canonical

correspondence analyses, modeling of any single species will need to focus on cumulative effects of extreme events. This is discussed further in Chapter 6.

It has been shown in this chapter that water temperature, *per se*, is the principle abiotic driver of fish species distribution patterns within the rivers of the Sabie catchment, with secondary effects from flow volume gradients. The longest, and thus most influential environmental vectors of those considered, were both measures of annual water temperatures within the Sabie River (*cf.* Figure 4.6). Electrofishing sites were divided into two distinct groups ("warm" versus "cold") based on these criteria, with additional environmental drivers (flow, substratum and conductivity) being of secondary importance. Thus, river management should focus on water temperature issues if the objective is the maintenance of aquatic diversity. However, the following limitations are recognized:

- Analyses were based on data from three replicates of the same season (May);
- Site characterizations by water quality parameters were based on spot readings. Time series of water quality parameters, and associated seasonal indices characterizing sites, would be desirable for more reliable multivariate analyses of species-site patterns;
- Imperfect flow and water temperature data, which lack complete synchronicity with fish survey data.

Based on the analyses within this chapter, it is clear that river management policies within the Sabie catchment should take cognizance of the uniqueness and dynamism of each river reach. Furthermore, since it has been shown that water temperatures are the primary abiotic drivers of fish community patterns within the rivers of the Sabie catchment, it is likely that any changes in the thermal regimes of these rivers are likely to result in a change in species distribution patterns and consequently in community functioning. These changes fall under the collective term of "river health", which is discussed in the next chapter. Inherent in this link between abiotic processes and biotic patterns is the potential to utilize an appropriate fish species, or group of species, as in-stream indicators of abiotic conditions, such as changes in cumulative annual heat units, within the water. A suitable indicator species should be chosen only after the following broad considerations have been answered:

- Is the target species sensitive enough to reflect system changes? The process of objectively choosing a suitable indicator species for the Sabie River is discussed in more detail in Chapter 5.
- Which indices for an indicator species, such as "condition" or relative abundances, could be most effectively used, as a measure of species performance within a river system? This process is described in Chapter 6.
- What are acceptable upper and lower thresholds of thermal change? And within highly variable systems, is it a practical management approach to set thresholds of environmental change, when the distinction between natural versus anthropogenic effects may not always be clear? Answering these questions imply a management approach to the river system of interest, which should include the use of scenario modeling to assist river managers in the choice of the most appropriate management strategies, given the current level of system understanding. The choice of appropriate upper and lower thresholds of water temperature change, and the use of appropriate fish indicators of this changes, is discussed in Section 6.4. Scenario modeling for change in water temperatures in the Sabie River is discussed further in Chapters 7-8.

* * * * *

Fish diversities have been shown to increase with downstream distance, peaking at approximately 100 kilometres from the source of the Sabie River. This coincides with high variability in water temperatures (cf. Figure 2.14), and approximately with the reach of river exhibiting a thermal disjunction (cf. Figure 2.11). Principal components analyses additionally divided the electrofishing sites on a thermal basis ("cool" versus "warm"). A CCA analysis highlighted the significance of water temperature as a determinant of fish community patterns and relative abundances, for those sites surveyed within the Sabie catchment. A pragmatic management approach for maintaining fish diversity within the rivers of the Sabie catchment would be to make use of fish as biological indicators of annual thermal changes, which is discussed in the subsequent Chapter.

5 CHILOGLANIS ANOTERUS AS AN INDICATOR SPECIES OF CHANGING WATER TEMPERATURES IN THE SABIE RIVER

5.1 Introduction

Defining a river's "health" is subject to much debate (Norris and Thoms 1999), complicated by the nebulous nature of this term when used in an ecological context (Karr 1999). However, in spite of this apparent confusion, "health" is a generic and intuitively appealing concept that people are able to relate to, and which Karr (1999) suggests is shorthand for "good condition".

River management which aims to preserve species diversity and "health" can be facilitated through an objective choice of a group or an individual species which represent(s) the broader fish community of the area of interest. Such "indicator" species should be chosen based on their sensitivity to the abiotic process of concern. Their degree of sensitivity to such change is assumed to be a function of their niche dimensions, which can be measured using a range of statistical techniques. The choice of suitable indicators of changes in annual water temperatures in the Sabie River is discussed in this chapter, through analyses of the niche dimensions of five species of fish occurring in the lowveld zone of the Sabie River.

5.1.1 Aims and objectives for choosing suitable indicator species for annual water temperature in the Sabie River

Weeks et al. (1996) proposed that species of the genus Chiloglanis are good indicators of changes in cumulative heat units in the Sabie River. Thus, the aim of this component of the research was to "measure" the niche dimensions for two species of Chiloglanis fish and three additional generalist species of shallow-water fish found in the lowveld region of the Sabie River. This was done in order to determine whether there was any objective ecological basis for using C. anoterus (Figure 5.1a) and/ or C. paratus (Figure 5.1b) as suitable indicators of river temperatures in the Sabie River. The five co-occurring species considered in this research, and the abbreviations used in the text, are:

- Chiloglanis anoterus (Mochokidae; pennant-tailed suckermouth, Cano);
- C. paratus (Mochokidae; sawfin suckermouth, Cpar);

- Labeobarbus marequensis¹ (Cyprinidae; largescale yellowfish, Lmar);
- Labeo molybdinus (Cyprinidae; leaden labeo, Lmol);
- Tilapia rendalli (Cichlidae; redbreast tilapia, Tren).

The genus Chiloglanis (Mochokidae; suckermouth catlets) includes 34 species, eight of which are from southern Africa and most of these are endemic to the region. Chiloglanids are small, dorso-ventrally flattened fish, and are usually found in fast-flowing rocky streams and rocky stretches of large rivers (Skelton 1993). Adult fish have complex discshaped mouths and strong spines in the dorsal and pectoral fins. The small size and habitat specificity of C. anoterus and C. paratus suggests that these fish are sensitive to changes in abiotic river conditions, and thus potential indicators of changes to annual flow and water temperatures. While the former species is cold warm-tolerant (prefers "cool" rivers, but is able to survive in warmer water), and the latter is warm cold-tolerant (occurs in "warm" rivers, but is able to survive in cooler water) (Weeks et al. 1996), both species obtain their nutrients by grazing algae growing on riffle rocks. Very little ecological data exist for either C. anoterus or C. paratus (Weeks 2001), although the research by Weeks et al. (1996) on the microhabitat requirements of these species does provide ecological information on their requirements of flow velocities, water depths, and substrate and cover preferences. According to Weeks (2001), C. anoterus is sensitive to low flows and high temperatures, and shows signs of stress in warm water. Populations showed slow recovery to unfavorable flow conditions, based on the sampling undertaken in the early 1990s in the rivers of the Sabie catchment (Weeks et al. 1996). Conversely, Weeks (2001) considers C. paratus to be less sensitive to low flows, having been observed to persist in pools under conditions of low flow. Their life-histories appear to be adapted to a more uncertain flow environment than C. anoterus.

The Cyprinid and Cichlid species are flow-dependant spawners, which in previous studies in the Sabie River were grouped together in cluster analyses based on broadly shared life-history traits (Jewitt *et al.* 1998). These two groups were included in the analyses as potentially useful bio-indicators of critical flow periods. Additionally, these three species are ubiquitous lowveld fish, and co-occurred with the Chiloglanids (see Appendix A1), suggesting that there may be a degree of overlap for habitat resources. Based on the

¹ Previously Barbus marequensis

correspondence analyses in Chapter 4, C. paratus, L. molybdinus and L. marequensis were classified with the warm-water fish assemblage, and had similar abiotic habitat requirements. C. anoterus was expected to occupy a different hypervolume space, primarily due to the effects of water temperatures (Figure 4.6). T. rendalli, while associated with the warm water fish assemblage identified using canonical correspondence analysis (cf. Section 4.3.2), was expected to occupy a different hypervolume space, being furthest away (Euclidean distance) from the other four fish species considered in this chapter. L. molybdinus was specifically chosen due to its wide distribution within the rivers of Sabie lowveld, to represent a generalist species with an assumed large niche hypervolume.

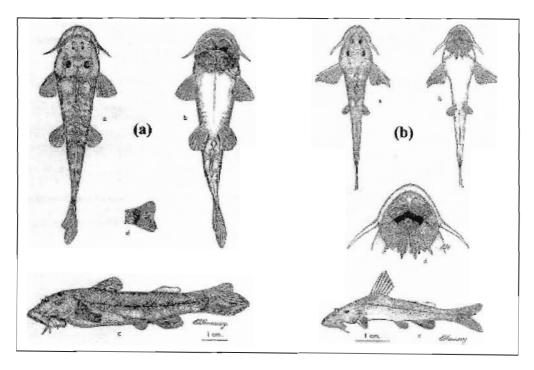


Figure 5.1 Lateral, ventral and dorsal views of Chiloglanis anoterus (a) and C. paratus (b) (from Crass 1960)

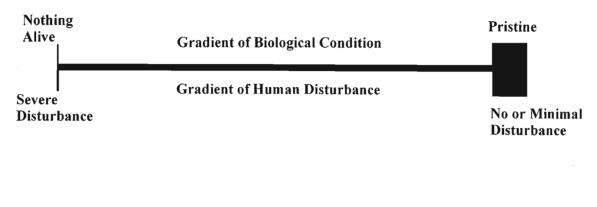
5.1.2 Indicator species and river health

One of many definitions of river health is provided by Karr (1999): the degree to which the main physical and chemical attributes of a river (its energy sources, water quality and flow), plus its biota and their habitats match the natural condition at all scales. However, Norris and Thoms (1999) disagreed with the use of so-called "natural" conditions and comparisons with sites that are thought to be similar in the absence of degradation, and suggest rather the use of "reference" conditions as controls. Implicit in the use of reference conditions, which are intended to establish a yardstick against which to measure system

change, is the recognition of the uniqueness of different systems, in addition to an acceptance that it is difficult to define the natural condition within an anthropogenic landscape.

The concept of reference conditions implies the use of tools to "measure" river health (i.e. indicators) by integrating and assessing the condition of each of the above five components relative to a known condition. Consequently, the level of disturbance or biological integrity can, in theory, be assessed and measured against thresholds defined according to the current level of understanding of system functioning, as illustrated in Figure 5.2. This process must be relevant at management scales. Harris and Silveira (1999) emphasize that measuring river health should be ecologically based, efficient, rapid and consistently applicable in different ecological regions. Rapport (1989) highlights three aspects to consider when measuring river health:

- The absence of distress defined by measured characteristics or indicators;
- A system's resilience to stress;
- The identification of risk factors, for example industrial effluents.



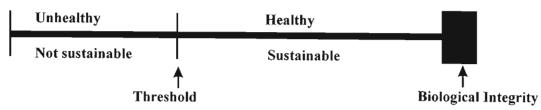


Figure 5.2 Continuum of human influence on biological condition (top), and the resultant biological integrity and river health (bottom) (from Karr 1999).

The first aspect has received the most attention (Norris and Thoms 1999), and according to Karr (1999), biological monitoring provides the most integrated view of river health. Biological effects typically used for ecosystem health assessments are changes in:

- Species composition;
- The dominant species group;
- Mortality rates;
- Physiological metabolisms (Chapman 1992).

The River Health Programme (DWAF 2002b) in South Africa uses indices of instream and riparian biological communities, including fish, to characterize the response of an aquatic environment to disturbance. Central to this initiative are comprehensive monitoring programmes, which make use of different ecological indices. Various indices are in use in South Africa and internationally for assessing river health, both for invertebrates (Chutter 1998), and fish (Karr 1987, 1999; Kleynhans 1999). The rationale behind using these indices is that aquatic organisms provide a direct and integrated measure of the health of a river (Chapman 1992), since they integrate the effects of the environment on themselves. Short-lived organisms, such as protozoans, reflect water quality changes over short time periods (days), while longer-lived organisms, such as fish, reflect the water quality at larger temporal and spatial scales (months and river reaches).

In many cases, it may not be practical to consider all the species within a system, but rather to use a single species that represents the biotic community i.e. indicator species (Matsinos *et al.* 1994). A species has potential value as an indicator if its presence is indicative of the existence of certain environmental conditions, whereas its absence is indicative of the absence of those conditions (Majer 1993). Furthermore, a good indicator species should be easily identified and sampled. However, as Harris (1995) points out, change in population numbers is one of the most variable components of biology, in time and space, and distinguishing between natural and anthropogenic change is difficult. This uncertainty in susceptibility to natural changes in the aquatic environment is regarded as the main weakness in the use of indicator species. Despite this pitfall, fish are considered as useful bio-indicators of river health over large temporal and spatial scales (Karr 1981; Harris 1995) for the following main reasons:

• Fish are readily sampled;

- Identification is relatively straightforward, since fish taxonomy is well established;
- Due to their size, relative longevity and mobility, fish assimilate food chain effects (Chapman 1992) and macro-environmental influences over a seasonal time scale (Karr 1987).

In the context of this study, the most significant abiotic determinant of fish community patterns within the rivers of the Sabie catchment was water temperature. Thus, it stands to reason that river managers should focus on fish species which are sensitive to thermal change in these rivers, if detrimental thermal changes, with their resultant impacts on aquatic biotia, are to be detected. Such biological indicators would be appropriate for detecting thermal change at a seasonal to annual time scale, and a macro (> 10 km²) spatial scale.

5.1.3 Indicator species and the niche hypervolume concept

In natural systems, different resources commonly exist as gradients, with each species responding to different resource levels, such as food or spawning ground availability, in different ways. Gaussian curves are typically used to represent species' responses to the combined effects of abiotic variables along a gradient, such as the longitudinal axis of a river. Attempting to define an organism's "niche" is an important ecological consideration that aids in understanding how coexisting species utilize common resources. organism's niche at any point in space and time may be represented by an n-dimensional hypervolume² (Hutchinson, 1957), which defines the set of conditions constraining individuals of different species to where they are to be found geographically, and how productive they are within that system. The hypervolume is defined by the upper and lower tolerance thresholds for a species for each variable being plotted in that multidimensional space. This optimal space defines the fundamental niche of any species, which is determined by the prevailing abiotic factors of the natural system (Vannote et al. 1980; Frissel et al. 1986). However, interactions with natural enemies (parasites, predators, competitors) restrict each species to a sub-set of the fundamental niche - the realized niche (Wootton 1992). System variability is important in defining the axes of this hypervolume.

² A theoretical, multidimensional volume.

Different approaches are useful in understanding the dimensions of a species niche. One approach is to consider each resource separately, and how different species respond to this. When each axis is considered individually, an index that gives an indication of the degree of niche overlap provides evidence as to how different species may be competing for common resources. Niche overlap indices are useful in quantifying the relative usages of different resources by different species; a drawback of such indices is that they do not reflect the relative abundances of the resource, as these are often difficult to quantify (Ludwig and Reynolds 1988). Each species utilizes a specific resource to a certain extent, which can be plotted as a curve. For each species there is a breadth of use, and a degree of overlap between its utilization curve and that of another species. Niche breadths and overlaps are useful parameters in identifying suitable indicator species. Species with a wide niche breadth (eurytopic species) are less useful as biological indicators, being such generalists that they are able to tolerate a wide range of conditions. Species with a narrow niche breadth (stenotopic species) are likely to be so rare in a system that their absence may be more a function of sampling efficiency than the system's health. Thus, a useful indicator species should have sufficient niche overlap with coexisting species, so as to be representative of a system, and a niche breadth which is wide enough not to imply rarity, but narrow enough for the species to be sensitive to system changes. This is in agreement with Noss (1990), who points out that a good indicator species should be sufficiently sensitive to provide an early warning of change, yet widely distributed over a geographical range. Noss (1990) also points out that a good indicator should be easy to sample and relevant to perceived ecologically significant phenomena, such as water temperatures.

When considering multiple resource axes together, the niche hypervolume concept (Figure 5.3) is useful in selecting an indicator species for a particular system. A good indicator species should not have a niche hypervolume that is so large that the species is able to survive and reproduce under a wide range of environmental conditions. Conversely, a species should not be chosen when it has a small niche hypervolume, since this species will be so rare that its absence may not be linked to system change. A good indicator species should be habitat-specific with a relatively small niche hypervolume. Since this niche hypervolume is made up of n variables, it becomes difficult to measure overlap and to visualize the niche dimensions. The use of multivariate statistics to reduce the

dimensionality of the hypervolume to a two- or three-dimensional plot is appropriate in visualizing and understanding a species' niche hypervolume (see Section 5.2.1).

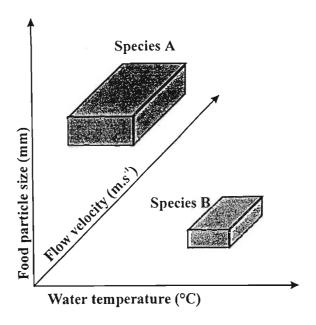


Figure 5.3 Illustrative, hypothetical niche hypervolume in three dimensions, for the resources food particle size, flow velocity and water temperature, for the hypothetical species A and B.

5.1.4 Significance of water temperature to fish

As was discussed in Chapters 2 and 3, it is useful to monitor and measure water temperatures, as they not only affect the chemical reactions occurring in a river, but also indirectly reflect daily flow volumes. At a larger scale, water temperatures reflect the overall condition of a catchment, being a measure of the energy fluxes within a river, and illustrate the interplay of numerous environmental drivers and buffers at different spatial and temporal scales within a catchment. It was further shown in Chapter 4 that water temperatures were the primary abiotic mechanism influencing ichthyological distribution patterns within the rivers of the Sabie catchment. This is in agreement with the existing body of literature on the links between water temperatures and species distribution patterns. Based on these factors, it is suggested that water temperatures can be considered a measure of a catchment's signature and river health. The "health" of a river could thus be measured indirectly though the use of a suitable indicator species that reflects changes in water temperatures.

Fish are obligate poikilotherms: heat is exchanged between their bodies and water through gills via a countercurrent exchange mechanism. Metabolic rate increases exponentially with temperature (Beitinger and Fitzpatrick 1979). Swimming speed and maintaining instream position are temperature dependant, since movement increases oxygen consumption and metabolism (see for example Graham et al. 1996). Furthermore, growth increases with temperature, although other biotic (food availability, population density) and abiotic (season and water quality) factors modify this relationship (Beitinger and Fitzpatrick 1979). When food is limited, fish can reduce their metabolic costs by seeking lower water temperatures (Beitinger and Fitzpatrick 1979). Egg incubation and hatching success are also temperature dependant (Beitinger and Fitzpatrick 1979). "Because of interactions among temperature, activity, metabolic rates and oxygen tension in water, fish generally are more labile to environmental temperature changes than terrestrial ectotherms" (Beitinger and Fitzpatrick 1979). Most fish control body temperatures via behavioural thermoregulation, by seeking appropriate water temperatures (i.e. gradient responses) (Beitinger and Fitzpatrick 1979). Temperatures selected by fish very likely represent temperatures at which they have evolved to carry out physiological functions with maximal efficiency (Crawshaw 1977). Furthermore, fish will tend to seek localities where their species-specific thermal preferences are available, when other factors, such as food, are not of overriding importance. This final thermal preference coincides with temperatures at which key physiological, biochemical and life history processes are optimized. However, "since fish are not always found at their final [preference] in nature, even when it is available, it is obvious that thermoselection can be overridden or masked by other factors" (Beitinger and Fitzpatrick 1979), such as food availability. Following a rapid temperature change fish experience thermal stress due to altered respiratory demand and respond accordingly through physiological feedback mechanisms (Crawshaw 1977).

Because of changes induced by thermal acclimatization, fish exhibit altered thermal optima for various physiological optima and tend to select temperatures accordingly (Crawshaw 1977). Thus, an animal will be inclined to follow a gradient of conditions to maximize its reproductive fitness (Railsback 2001). Fish have the ability to discriminate small (0.03°C) changes in temperature (Bardach and Bjorkling 1957). A time lag that increases with fish size and mass will exist before thermal equilibrium is reached between a fish and its environment (Beitinger and Fitzpatrick 1979). Thus, small fish are vulnerable to small and rapid fluctuations in water temperature, while large fish are buffered against these rapid temperature changes (Elliott 1994).

Magnuson *et al.* (1979) suggested viewing temperature as a resource that is competed for. As with any other resource, temperature can be viewed as spatially linked, where the range of suitable temperatures for any species changes over space (i.e. as a gradient). Dominant individuals may exclude subordinates from the optimal resource by occupying a temperature space to maximize their growth and fitness. They can also use temperature space to the exclusion of other species. Hence there may be competition and aggression within and between species for optimal temperature zones.

The thermal axis forming part of the niche hypervolume for any particular fish species may be defined in a number of ways - lethal limits; physiological or metabolic optima, behavioural performance optima, or by behavioural preferences (Magnuson et al. 1979). Lethal temperatures set bounds, but are only loosely associated with an animals' resource utilization. The niche breadth for the resource temperature is obtained from an animal's thermal preferences, typically established through laboratory experiments of thermal preferences and percentage of time spent at different temperatures. Magnuson et al. (1979) proposed using the median of this utilization curve as the midpoint an organism's thermal preferences, since the thermal distribution is often skewed, plus or minus 33% of the laboratory-determined distribution. However, there is some disagreement in the available literature as to whether field and laboratory distributions correspond (Magnuson et al. 1979; Sullivan et al. 2000). This apparent conflict may be a function of the fundamental versus the realized niche of a species. For purposes of river management, field ecologists are ultimately concerned with the realized niche. Such a thermal niche breadth for many species of fish is similar, and has been found to be about 4.04°C on average. Furthermore, adults and juveniles of the same species may have different thermal ranges, so that there may be a partitioning of thermal resources between size or age classes of a single species Magnuson et al. (1979).

5.2 Methods of quantifying niche dimensions of fish species in the Sabie River

Niche characteristics of five species of fish were compared using the environmental variables for water temperature (°C), water depth (cm), water velocity (m.s⁻¹) and cover (visual and velocity, or a combination of these). These comparisons were based on microhabitat data, collected by Weeks *et al.* (1996) during 1990-1993 as part of a pre-impoundment study in the Sabie catchment (*cf.* Chapter 1), and in May 2001 as part of a

broader electrofishing survey (Section 4.2, Chapter 4), to record which species were associated with what range of environmental variables. Standard electrofishing techniques (Section 4.2, Chapter 4) were used to sample fish at points in the river marked by floats attached to sinkers, so that the presence of a species could be associated with specific depths, velocities, substrates and cover classes. Niche breadths for cover and depth were calculated for five species of co-occurring fish. The cover classification used in this analysis (Table 5.1) was that of Weeks *et al.* (1996); water depth and flow velocity values were also reclassified into class intervals (Table 5.1). The frequencies of each fish species occurring in each class interval for each resource were calculated. In cases where a zero occurred for a resource class, a value of one was substituted, since the niche overlap calculations make use of natural logarithms.

Table 5.1 Resource classes used to calculate specific overlaps

Resource class	Cover type	Water depth (cm)	Flow velocity (m.s ⁻¹)
1	No cover	0-10	0.05-0.10
2	Offstream overhead (indirect visual cover)	10-20	0.11-0.25
3	Instream object (velocity shelter)	20-40	0.26-0.50
4	Instream overhead (direct visual cover)	40-80	0.51-1.00
5	Combination (velocity and visual cover)	80-160	1.10-3.80

Two approaches, both making use of the same microhabitat data, were used to quantify the niche dimensions of these fish. The first approach (Section 5.2.1) considered the use of four resources by five Sabie River fish species as a group. The "niches" of these fish was considered in multidimensional space, making use of the niche hypervolume concept. The second approach (Section 5.2.2) considered the use of different resources individually, by making use of niche breadth and niche overlap measures.

5.2.1 Quantification of niche dimensions using the niche hypervolume concept

The first approach was based on the niche hypervolume concept. These were represented as 1x2, 2x4, and 3x8 matrices that contain the co-ordinates of niche hypervolumes in one, two and three dimensions respectively. Niche breadths were calculated from mean ± standard deviation for each resource type (Section 5.1) (Magnuson et al. 1979). In such matrices, each column represents the co-ordinates for a point of the hypervolume, and each row represents a different resource. Such matrices are appropriate for n-dimensional hypervolumes represented by an $n \times 2^n$ matrix, which are manipulated using suitable matrix algebra. Because multidimensional hypervolumes are difficult to visualize, the niche hypervolumes were reduced to two dimensions by using Principal Components Analyses, that grouped the five fish species identified in Section 5.1.1, based on cover, depth and velocity; and cover, depth, velocity and water temperature were performed (Genstat 2000). Using this approach, which was discussed in more detail in Chapter 4 (Section 4.2.2), species with similar niche requirements are closer, in terms of Euclidian distance on the PCA plot, than species with more different habitat requirements. Mean values for each resource for n species were calculated, and represented in a species (rows) by resource type (column) matrix (Table 5.2). Mean annual water temperatures, calculated from the hourly water temperatures collected during 2001-2002 on the Sabie River (Chapter 2), were obtained from the point on the Sabie River where maximum abundances of each species (Figure 5.4) occurred. Since different resources were measured in different units, a correlation matrix was used to standardize the data (Pielou 1984).

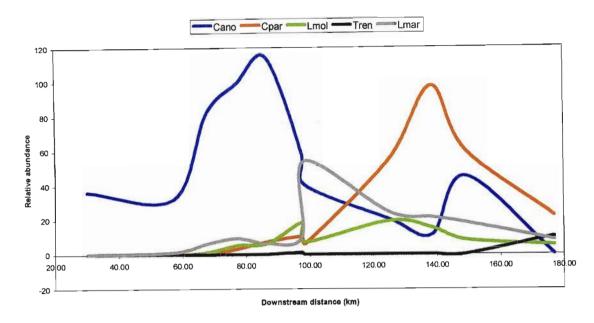


Figure 5.4 Relative abundance curves of five Sabie River lowveld fish species, as a function of downstream distance on the Sabie River

Table 5.2 Species by resource use (mean value) matrix for five Sabie River fish species.

	Depth (cm)	Velocity (m.s ⁻¹)	Cover class	Water temperature (°C)
C. anoterus	32.41	0.73	5	20.56
C. paratus	38.15	0.72	5	22.01
L. marequensis	37.8	0.31	5	21.87
L. molybdinus	37.76	0.44	5	21.87
T. rendalli	28.24	0.10	4	22.98

5.2.2 Quantification of niche dimensions using niche breadths and niche overlaps

A second technique for exploring the niche dimensions of the different fish species was the calculation and comparison of niche breadths, and niche overlaps. Niche breadths (B) for the i^{th} species and the j^{th} resource, using r resource classes, were calculated using Equations 5.1a-b (Ludwig and Reynolds 1988).

$$B_i = \frac{1}{\sum_{i}'(p_{ii}^2)}$$
 [5.1a]

where
$$p_{ij} = \frac{n_{ij}}{N_i}$$
 [5.1b]

and n_{ij} is the frequency value (n) of the i^{th} species for the j^{th} resource class, and N_i is the row and column total.

The amount of specific overlap by species i onto species k is the probability that the utilization curve of species i could have been drawn from species k's utilization curve (Petraitis 1979). Specific overlaps were calculated for the five species, using Equations 5.2 - 5.5. In particular, C anoterus and C paratus were chosen since these species were candidate indicator species, while L marequensis was chosen because of its ubiquitous distribution (cf. Section 5.1.1).

Niche overlap of species 1 with species 2:

$$SO_{1,2} = e^{E_{1,2}}$$
 [5.2]

where
$$E_{1,2} = \sum_{j}^{r} (p_{ij} \ln p_{2j}) - \sum_{j}^{r} (p_{1j} \ln p_{1j})$$
 [5.3]

Niche overlap of species 2 with species 1:

$$SO_{1,2} = e^{E_{2,1}}$$
 [5.4]

where
$$E_{2,1} = \sum_{j=1}^{r} (p_{2j} \ln p_{1j}) - \sum_{j=1}^{r} (p_{2j} \ln p_{2j})$$
 [5.5]

Based on the above, the following hypotheses could be tested:

 H_{n1a} : The specific overlap of *C. anoterus* with *C. paratus* is complete (i.e. complete overlap of resource utilization curves);

 \mathbf{H}_{n1b} : The specific overlap of C. paratus with C. anoterus is complete;

 \mathbf{H}_{n2} : The specific overlap of C. anoterus (m) with C. paratus (i) is greater than that of C. anoterus with Labeobarbus marequensis (k).

 H_{nl} was tested using Equation 5.6, where $U_{i,k}$ is a chi-square distribution with r-1 degrees of freedom.

$$U_{i'k} = -2N_i \ln(SO_{i,k})$$
 [5.6]

 H_{n2} was tested by calculating the log-likelihood ratio W (Equation 5.7).

$$W = N_i \ln(SO_{i,k} / SO_{i,m}) \tag{5.7}$$

and if W > 2, then specific overlap by species i onto species k is greater than the overlap of species i onto species m.

General overlaps were calculated for the five different species for cover and depth (Equations 5.8 a, b). Petraitis (1979) defined "general overlap" (GO) as the probability that the utilization curves of all species was drawn from a common utilization curve, and where *n* species can be compared. GO was calculated as a weighted average of species utilization curves using Equation 5.8, and the null hypothesis was that there was complete overlap of the species. The closer GO is to 1, the higher the probability that the utilization curves for the five species were drawn from the same common utilization curve. This was tested for complete versus incomplete overlap.

$$GO = e^{E} ag{5.8a}$$

where
$$E = \frac{\sum_{j=1}^{r} \sum_{j=1}^{r} [n_{ij} (\ln c_{j} - \ln p_{ij})]}{T}$$
 [5.8b]

The test statistic V has a chi-square distribution with (S-1)(r-1) degrees of freedom, and is calculated using Equation 5.9. If V exceeds the critical value for chi-square, the null hypothesis of complete overlap is rejected.

$$V = -2T \ln GO ag{5.9}$$

5.3 Results

Results of the analyses of niche dimensions of the five species of fish considered from the Sabie River are discussed below. Section 5.2.1 provides results using the niche hypervolume concept, while comparisons of niche overlaps and niche breadths are provided in Section 5.2.2.

5.3.1 Quantification of niche dimensions using the niche hypervolume concept

The matrices of co-ordinates for hypervolumes in one (Table 5.3), two (Table 5.4) and three (Table 5.5) dimensions are tabulated below. Since these matrices contain co-ordinate values, the niches of these species could be plotted in one-, two- and three-dimensional space. Plotting the values in Table 5.4 would result in a straight-line graph. The values in Table 5.4 were plotted in two-dimensional space, to provide areas for water depth and water velocity (Figure 5.5). Similar matrices to that of Table 5.5 could be constructed for the remaining four species, so that five 3x8 matrices could be used to plot the niche volumes in three dimensions. *Chiloglanis anoterus* had the widest niche breadth for water velocity use, with considerable overlap with *C. paratus*. Conversely, *C. anoterus* had the narrowest niche breadth for depth, while *L. marequensis* had the widest niche breadth for this resource.

Table 5.3 One by two vector matrices for water depth (cm) use by five species of fish in the Sabie River. These are the co-ordinate points for a one-dimensional niche hypervolume plot.

Species	Lower niche value	Upper niche value
C. anoterus	17.42	47.40
C. paratus	23.59	52.71
L. marequensis	19.48	56.12
L. molybdinus	18.80	56.57
T. rendalli	14.63	41.85

Table 5.4 Grouping of five two-dimensional 2x4 matrices for water depth (cm) and water velocity (m.s⁻¹) use by five species of fish in the Sabie River. These are the co-ordinate points for a two-dimensional niche hypervolume plot (see Figure 5.5).

C. anoterus	Velocity	0.33	1.13	1.13	0.33
	Depth	17.42	17.42	47.40	47.40
C. paratus	Velocity	0.47	0.97	0.97	0.47
	Depth	23.59	23.59	52.71	52.71
L. marequensis	Velocity	0.05	0.57	0.57	0.05
	Depth	19.48	19.48	56.12	56.12
L. molybdinus	Velocity	0.09	0.79	0.79	0.09
	Depth	18.80	18.80	56.76	56.76
T. rendalli	Velocity	0.00	0.20	0.20	0.00
	Depth	14.63	14.63	41.85	41.85

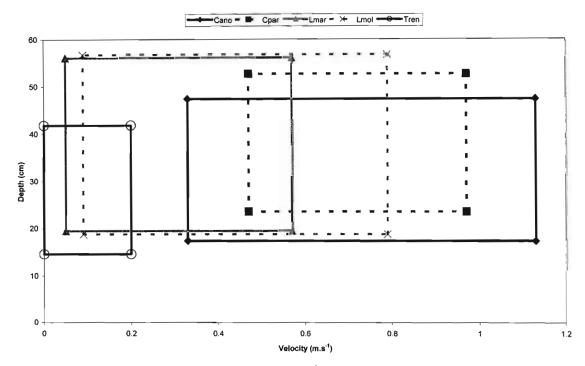


Figure 5.5 Niche dimensions for water velocity (m.s⁻¹) and water depth (cm) for five species of fish occurring in the Sabie River, represented in two-dimensional space, plotted using the co-ordinate values contained in Table 5.5.

Table 5.5 Three by eight matrix for *Chiloglanis anoterus* for water depth (cm), water velocity (m.s⁻¹) and cover usage. These are the co-ordinate points for a three-dimensional niche hypervolume plot for one species.

Velocity	0.33	1.13	1.13	0.33	0.33	1.13	1.13	0.33
Depth	17.42	17.42	47.40	47.40	17.42	17.42	47.40	47.40
Cover	4	4	4	4	5	5	5	5

An alternative approach to the use of $nx2^n$ matrices was to calculate the mean values for water depth, water velocity and cover for each of the five species. The dimensionality of this plot was reduced to two using PCA. Weighted co-ordinate points, which are a linear combination of the input matrix, were calculated and plotted in two dimensions. Axis one of the PCA accounted for 78.68% of the variation, while Axis two accounted for 18.97% of the variation; both axes accounted for 97.65% of the variation (Table 5.6). A linear combination of cover, depth and velocity contributed to Axis one, with the greatest leverage being exerted by cover. A combination of depth and velocity contributed most to Axis two. A PCA plot of these environmental resources (Figure 5.6) showed that *C. anoterus* and *C. paratus* group together, preferring habitats with relatively high velocities, in shallow water that offer a combination of visual and velocity cover, although *C. anoterus* was shown to prefer shallower habitat than *C. paratus*. Similarly, *L. marequensis* and *L. molybdinus* had similar preferences for the velocity, depth and cover habitat requirements, while *T. rendalli* was separated in co-ordinate space.

Table 5.6 Principal components analysis statistics for five species of fish by the habitat parameters water depth (cm), water velocity (m.s⁻¹) and cover

	Principal component 1	Principal component 2
Eigenvalues	2.360	0.569
Percentage variation	78.68	18.97
Cover (latent vector)	-0.636	0.206
Depth (latent vector)	-0.562	0.641
Velocity (latent vector)	-0.528	-0.764

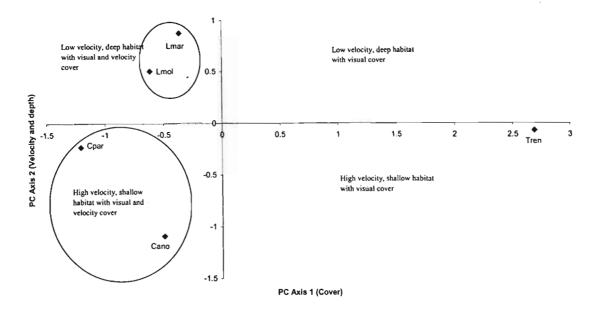


Figure 5.6 PCA of five fish species in habitat variable space, based on microhabitat data from electrofishing surveys in the Sabie River.

When mean water temperatures were incorporated, Axis one of the resulting PCA accounted for 72.75% of the variation, while axis 2 accounted for 21.51% of the variation; both axes accounted for 94.26% of the variation (Table 5.7). With water temperatures incorporated into the analyses, *C. anoterus* was shown to be a more "unique" species, while *C. paratus* was more closely grouped with *L. molybdinus* and *L. marequensis* (Figure 5.7).

Table 5.7 Principal components analysis statistics for five species of fish by the habitat parameters water depth (cm), water velocity (m.s⁻¹), cover and mean water temperature (°C)

	Principal component 1	Principal component 2
Eigenvalues	2.910	0.860
Percentage variation	72.75	21.51
Cover (latent vector)	0.570	0.206
Depth (latent vector)	0.429	0.736
Velocity (latent vector)	0.512	-0.326
Temperature (latent vector)	-0.478	0.557

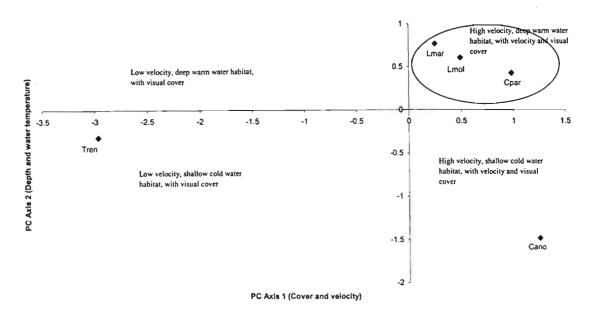


Figure 5.7 PCA incorporating water temperatures, based on microhabitat data from electrofishing surveys in the Sabie River.

5.3.2 Quantification of niche dimensions use niche breadths and niche overlaps

Using an alternative approach for calculating niche breadths, as discussed in Section 5.2.2, *Chiloglanis paratus* exhibited the narrowest niche breadths, while *L. molybdinus* exhibited the broadest niche breadths (Table 5.8). *C. anoterus* had the narrowest requirements for both depth and cover, although the niche breadth for flow velocity was intermediate within the group of species examined.

Table 5.8 Niche breadths for water depth (cm), cover type and flow velocity (m.s⁻¹) for five species of fish in the Sabie River.

Resource	C. anoterus	C. paratus	L.	L. L.	
			marequensis	molybdinus	
Depth	2.72	2.73	2.93	3.09	2.81
Cover	1.41	1.67	2.56	2.56	2.77
Velocity	3.11	1.78	3.88	4.64	2.50

Specific overlaps for water depth usage were relatively high for all five fish species (Table 5.9). However, *T. rendalli* had relatively low overlap with *C. anoterus* and *C. paratus* for use of cover, and vice versa (Table 5.10). The results of the tests of significance for hypotheses one and two (Section 5.2.2) provided in Table 5.11 show that both these hypotheses can be rejected.

Table 5.9 Specific overlaps of five species of lowveld fish for water depth (cm) use. Note that specific overlap of species 1 with species 2 will not necessarily be the same as species 2 with species 1, based on Equations 5.2-3 and 5.4-5 respectively.

	C. anoterus	C. paratus	L. marequensis	L. molybdinus	T. rendalli
C. anoterus	1.00	0.86*	0.96	0.94	0.80
C. paratus	0.88*	1.00	0.94	0.94	0.81
L. marequensis	0.96*	0.92	1.00	1.00	0.78
L. molybdinus	0.93	0.90	1.00	1.00	0.77
T. rendalli	0.79	0.80	0.76	0.77	1.00

^{*} Tests of significance for specific overlap

Table 5.10 Specific overlaps of five species of lowveld fish for cover use. Note that specific overlap of species 1 with species 2 will not necessarily be the same as species 2 with species 1, based on Equations 5.2-3 and 5.4-5 respectively.

	C. anoterus	C. paratus	L. marequensis	L. molybdinus	T. rendalli
C. anoterus	1.00	0.97*	0.80	0.84	0.65
C. paratus	0.96*	1.00	0.89	0.88	0.64
L. marequensis	0.69*	0.85	1.00	0.81	0.72
L. molybdinus	0.79	0.84	0.87	1.00	0.72
T. rendalli	0.45	0.51	0.75	0.67	1.00

^{*} Tests of significance for specific overlap

Table 5.11 Acceptance or rejection of hypotheses 1a-b and 2 for specific niche overlaps in use of water depth and cover habitat by C. anoterus, C. paratus and L. marequensis.

Resource	Hypothesis 1a	Hypothesis 1b	Hypothesis 2
Depth	Reject*	Reject*	Reject** $(W = -63.05)$
Cover	Reject*	Reject*	Accept** $(W = 113.82)$

p < 0.05

Rejection of hypotheses 1a and 1b (H_{n1a} and H_{n1b}) (Section 5.2.2) suggests that specific overlap is incomplete: each species is utilizing different components of the same resource curve. Rejection of hypothesis 2 suggests that *C. anoterus* and *C. paratus* are using more similar parts of the resource curve than *C. anoterus* with *L. marequensis*. The specific overlap by *C. anoterus* onto *C. paratus* based on cover use was greater than the overlap of species *C. anoterus* onto *L. marequensis*. Conversely, for depth, the specific overlap by *C. anoterus* onto *C. paratus* was less than the overlap of *C. anoterus* onto *L. marequensis*. Thus, *C. anoterus* is using different resources in different ways – for cover *C. anoterus* and *C. paratus* are competing more directly with each other than with *L. marequensis*, while the competition is less for depth, and there is possibly more competition with *L. marequensis*.

The general overlaps for the five species for depth and cover were 0.95 and 0.91 respectively, i.e. the species considered are utilizing a common resource curve. However, in both cases the test value (V, Equation 5.9) exceeded the critical value of 7.96 (16 degrees of freedom, p < 0.05), and the null hypothesis was rejected. Thus, while each species is making use of a common resource, there was not significant overlap in terms of use, suggesting that for this subset of species, there was not a high degree of interspecific competition for cover or depth. However, this may not necessarily be the case for other resources such as temperature.

[&]quot;W is greater than, or less than 2 (see Equation 5.7).

5.4 Discussion and conclusions

According to the River Continuum Concept (Vannote et al. 1980), system variability increases with downstream distance along a river's longitudinal axis. Thus, species found in the lower reaches of a river are adapted to greater environmental variability than species occurring higher upstream. This implies that species whose abundance curves peak higher up a catchment will tend to have narrower niche breadths than species further downstream. The relative abundance curve of C. anoterus peaked higher upstream than the other four species considered, and it was expected that niche breadths would be correspondingly narrow. The niche breadths for depth and cover calculated using the niche breadth equation (Equation 5.1) showed that C. anoterus had the narrowest niche breadths of the five species considered. In apparent contradiction of this, niche breadths, which were calculated using the approach of Magnuson et al. (1979) using mean values and standard deviations, and plotted in the two-dimensional niche hypervolume, revealed that T. rendalli had the smallest niche volume for water depth and flow velocity, while C. anoterus had an intermediate niche hypervolume. This effect was due to a broad niche breadth for flow velocity, offset by a relatively small niche breadth for water depth. In mitigation of the conflicting niche breadths for flow velocity use, niche breadths calculated using mean values plus one standard deviation focus on the range or variation in velocities used, while those using the niche breadth calculation (Equation 5.1a) emphasize modal values. This latter approach is more likely to be a more accurate reflection of resource selection. Using this approach, C. anoterus did not exhibit the broadest niche breadth for flow velocities. Additionally, while the physiognomy of these two Chiloglanid species, with marked dorsoventral flattening, suggests that these fish are adapted for living in higher velocity environments than the other species considered, the direct use of these flow velocities in niche breadth and niche overlap calculations is uncertain. This is due to the roosting behaviour of these fish, viz. attachment to in-stream rocks in riffles, where a boundary layer exists with water velocities approximating 0 m.s⁻¹ (Gordon et al. 1994). Based on this argument, and the subset of abiotic habitat resources considered in this chapter, there is indeed agreement with the concepts of Vannote et al. (1980), that niche breadths of C. anoterus appeared to be narrower than for species whose abundance curves peaked further downstream.

A comparison of niche dimensions, based on the abiotic variables considered in this chapter, using both the niche hypervolume concept (Section 5.2.1), and niche overlaps and niche breadths (Section 5.2.2), showed that *C. anoterus* and *C. paratus* approximated the criteria for suitable indicator species (Section 5.1.2). Furthermore, both these species met these criteria more closely than the remaining three species considered. Analyses using the niche hypervolume concepts were in agreement with those of niche breadths and overlaps. These two fish species are likely to respond in similar ways to abiotic changes within a river reach. From the niche overlap comparisons, *C. anoterus* and *C. paratus* may be using significantly different components of the resource curves relating to both depth and cover.

A limitation to these findings is that the species considered were compared using a narrow range of abiotic factors. Since both Chiloglanid species prefer habitats with higher overhead velocities than the other three species considered, a drop in flow volumes, and a consequent increase in water temperatures, will affect these two species first. Both fish species, by virtue of their small size, should exhibit sensitivity to thermal changes. Their preference for riffle habitat has the additional benefit in that riffles are considered the most sensitive part of a river (Gordon et al. 1994). Furthermore, C. anoterus prefers shallower habitats to C. paratus, which makes C. anoterus a more sensitive indicator of flow volumes and water temperatures than C. paratus within the Sabie River. There appears to be sufficient overlap between all five species considered, with all species considered appearing to be making use of common resource curves, to suggest that changes in the distribution of C. anoterus are also likely to be reflected in changes in the distributions of the other species. The niche dimensions of C. anoterus and C. paratus are narrow enough to make these fish sensitive to environmental changes, yet broad enough for these fish not to be so rare as to make them inappropriate as indicators of river health.

Water temperature is the resource that separates *C. anoterus* from *C. paratus*, with *C. anoterus* preferring cooler water temperatures to *C. paratus*. It follows from this that *C. anoterus* could be used as a sensitive indicator species of a progressive warming of river water temperatures. The use of *C. anoterus* and *C. paratus* as indicators of changes river water temperatures, with emphasis on the former species, implies that a suitable measure of success within a habitat (abundance values or the average condition of fish populations along the downstream length of the river) can be linked to abiotic conditions. A measure of the average condition of *C. anoterus* populations with downstream distance, such as a

length to weight ratio, is one approach that could be used to reflect changing water temperatures. This is based on the assumption that thermal stress will result in a diminished condition of fish populations. An alternative approach is the relative shift in space of the relative abundance curves of *C. anoterus* and *C. paratus*, which could be expressed as a ratio. Such an approach assumes a significant negative association between these two fish species. Both these indices are developed further and evaluated in Chapter 6.

This research could be extended by quantifying additional microhabitat parameters, such as dissolved oxygen content and food effects, and for additional fish species, within the multivariate analyses. Similar analyses using other species of Chiloglanis and additional control species could be performed using Chiloglanids as indicators of changing water temperatures in other river systems. Dose response curves for, in particular water temperatures, should be established under laboratory conditions for C. anoterus and C. paratus, which would contribute towards defining the thermal niche dimensions of these two species. However, it is recognized that what may be true in the laboratory, under controlled conditions, may not necessarily hold true for a natural system, where the interchange between abiotic and biotic conditions force different species of fish to make trade-offs between the myriad of variables that effect them, so as to maximize their fitness. In terms of optimal foraging theory, animals should feed in areas that maximize their breeding fitness (Railsback et al. 1999; Railsback and Harvey 2000). Thus, when an animal is not found within its optimal temperature range, it may be making trade-offs between food and temperature in maximizing its breeding fitness. Additional ecophysiology research could be undertaken in order to understand the differences between the fundamental and realized niches of these fish. How are trade-offs made between water temperature when additional constraints, such as predation, competition and food scarcity, prevent Chiloglanids from seeking their thermal preferences? Furthermore, it is possible that there is a degree of competition for thermal resources, which compounds the effects of different tolerances to particular temperatures that bound the region of niche space. However, as discussed in Chapter 1, the resources and time available for this study do not allow this level of investigation.

Chiloglanis anoterus and C. paratus, in comparison with three eurytopic lowveld fish species, were shown to fulfill broad characteristics desirable in biological indicators reflecting system change. While both species exhibited similar niche requirements for three environmental variables (cover, depth and velocity), their small size and habitat specificity suggests the suitability of these fish as indicators of annual thermal stress. C. anoterus is more sensitive to warming of river water than C. paratus, and appears to be the more sensitive indicator of thermal change of the two Chiloglanis species considered. The usefulness of these species as indicators of water temperature change is enhanced through the use of suitable biological indices, which is discussed further in Chapter 6.

6 A TPC FOR CUMULATIVE ANNUAL WATER TEMPERATURE IN THE SABIE RIVER, AND ITS ASSESSMENT USING BIOLOGICAL INDICATORS (CHILOGLANIS SPP., MOCHOKIDAE)

6.1 Introduction

The importance of water temperatures in structuring fish community patterns in the rivers of the Sabie catchment, and the concept of river health, together with the practicalities of using biological indicators of this health, were discussed in Chapters 4 and 5 respectively. The fish species *Chiloglanis anoterus* and *C. paratus* (Mochokidae) were further shown to be sensitive to annual changes in heat units in the Sabie River, by virtue of their small size and niche dimensions. In this chapter, these issues are related to each other by providing statistical links between biotic responses and annual changes in water temperatures, although it is recognised that to validate these links requires long-term (10 to 15 years of annual records as a minimum) ecological research. A spatially explicit "threshold of probable concern" (TPC) for changes in annual water temperatures is proposed, and two biological indices (ratio of relative abundances of *C. anoterus* to *C. paratus*, and a mean population condition factor of *C. anoterus* on a reach-specific basis) are evaluated as indicators of exceedance of this TPC. This TPC has value as an additional management tool for river managers aiming to maintain system "health" in the Sabie River.

6.1.1 Natural systems and sustainability

Ecosystems exist within matrices of human landscapes. It is increasingly recognised that "natural dynamics are composed of numerous interwoven processes involving different resources at different spatial and temporal scales" (Lynman et al. 2002). Additionally, "the goal of conservation management is shifting from managing species for their intrinsic value, to managing them for their interactive roles in ecosystem functioning..." (Rogers and Bestbier 1997). This interactive role of environmental system components provides, amongst other things, societal benefits, such that ecosystems are now accepted as having economic value (Costanza et al. 1997). From a narrow economic sense, the ongoing provision of societal benefits by ecosystems requires their sustainable management. The demise of various civilizations in the past few thousand years, such as those in the Indus

and Mesopotamia valleys, is suspected to be the result of overexploitation and mismanagement of the environment (Diamond 1991).

While these demises represent site-specific incidents of unsustainable use of the environment, the core problem is that the scales at which human activities are currently occurring is approaching the scale at which global ecosystem dynamics occur (O'Neill et al. 1998), such that ecology and economics become part of the same dynamic system. Additionally, the spatial and temporal scales of environmental use are not balanced i.e. humans have wide spatial impact over relatively short temporal scales (Jewitt 2003). Consequently, ecosystems become less resilient to exploitation and the appropriate management of these systems becomes increasingly important.

Sustainability cannot be achieved by adopting a rigid management policy (Carpenter *et al.* 1999), and management needs to be able to "admit uncertainty, encourage risk, and accept 'failures', which can be the most productive form of learning" (Gray 2000). However, there is not the time for different sectors of society to operate at cross-purposes in managing natural systems. Society must be bold enough to confront the "Pandora's box" that may be opened through the marriage of science, management and economics, as the only means of achieving long-term environmental sustainability. As O'Neill *et al.* (1998) contend, "economic theory predicts how [people] (sic) respond to the resource environment, and ecological theory predicts how the system reacts". Interdisciplinary collaboration is the key to resolving natural resource problems of the 21st century (O'Neill *et al.* 1998; Holling 1999), within which greater sharing and collaboration between scientists is implicit as a way of achieving "bigger" science (Houlahan 1998) to better manage ecosystems. This does not necessarily mean "large-scale science" (Walters 1997), nor does it mean that results from small-scale experiments can be scaled up without a clear understanding of scaling rules (Rastetter *et al.* 1992).

Inevitably, management occurs under situations of imperfect data, but invariably takes the form of "what happens if...?" questions, such as "What will happen to this system if we have a dry season?"; "What happens if a severe flood occurs?", and "What happens if I do nothing?". Thus natural resource managers operate within a spectrum that ranges from "do nothing", to micro-management, which focuses on particular land units, to macro-management, where a blanket management policy is applied to an entire area of interest,

such as a catchment. Gray (2000) summarises the management approaches towards determining desired ecosystem conditions into three schools viz. "species-based reserves", "range of natural variation" and "structure-based management". The first approach might be applied to choosing new reserves, where the needs of keystone species are met, and appropriate habitat is allocated for these. This is essentially an umbrella approach, with the belief being that if the key species are protected, all other species will also be included In the second approach, management aims to perpetuate the under this umbrella. understood pattern of natural variation. The final approach, that of structure-based management, involves defining a "desired future state" (sensu Rogers and Bestbier 1997), and managing the ecosystem accordingly. However, inherent in this approach is recognition of the role of system flux and variability (cf. Section 1.1, Chapter 1) such that management approaches remain flexible enough to adapt as new insights emerge. Adaptive management, and how it relates to system change (Section 6.1.2) is discussed with respect to the importance of water temperatures in the Sabie River, and the use of biological indicators (cf. Chapter 5) in alerting river managers to change Section 6.1.3).

6.1.2 Adaptive management and thresholds of probable concern (TPCs)

While management of natural resources occurs under uncertainty, their use and need for management will continue (Johnson 1999a). The management challenge is to gain insight into change in complex natural systems, and to manage to maintain this flux within so-called natural limits. One approach to meeting this challenge is "adaptive" management, and is based on managing natural systems through a process of careful testing of hypotheses rather than a reactive trial and error process (Walters 1997). Gray (2000) defines adaptive management as "a structured process designed to improve understanding and management by helping managers and scientists learn from the implementation and consequences of natural resource policies".

The implementation of a successful adaptive management programme is largely dependant upon visions (Rogers et al. 2000), institutional adaptation (Anon. 1999, 2000), and defined endpoints (Rogers 1998). Problems of institutional buy-in are overcome through "carefully nurtured partnerships of science and management", and by focusing on long-term goals, management moves away from reacting to crises, to a strategic approach (Rogers 1998) (cf. Section 9.2.2). Rogers and Bestbier (1997) provide a protocol for an

adaptive management programme that is being implemented in the Kruger National Park, which provides the framework for translating visions into reality through the implementation of hierarchically arranged goals and objectives. This "objectives hierarchy" may be represented as a pyramid, which scales the management process from a vision (the apex of the pyramid) down to a broad base of management goals that relate to specific management objectives. A "desired future state" for a system, such as a river, is defined, with incumbent goals, models and monitoring programmes (Rogers and Bestbier 1997).

Managing towards this "desired future state" is facilitated through an iterative cycle wherein system change or flux is monitored and compared against perceived thresholds of unacceptable change (TPCs or thresholds of probable concern) (Figure 6.1). This process functions as a decision support system to facilitate interactions between managers, stakeholders and researchers. Within this cycle, research identifies "agents of change" within the system, and identifies suitable indicators of such change. According to Biggs (2002), the indicator is a particular physical reality around which the particular TPC is built. The response of such indicators towards the agents of change is measured against the relevant TPC, which is aimed at providing natural resource managers with a decisionmaking tool to distinguish when natural variability is superseded by anthropogenic change. Change outside the limits of this acceptable flux is deemed "TPC exceedance". Should change be found to exceed the TPC, appropriate action may be taken, which may be to mitigate the problem. Alternatively, the action may be a reappraisal of the TPC, which is viewed as a hypothesis of the limits of acceptable change in ecosystem structure, function and composition (Rogers and Biggs 1999). This TPC may be refined or discarded, as the mechanisms underlying its behaviour become better understood, and it is recognized that the TPC represents the current level of understanding of the system it is "indicating". Central to the successful use of a TPC is an appropriate monitoring programme (Rogers and Biggs 1999), which should be designed to be pragmatic - i.e. simple and robust for ease of data collection by field staff, yet complex enough to provide the information necessary to use the TPC.

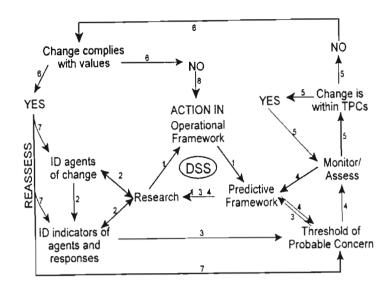


Figure 6.1 The adaptive management process for the Kruger National Park. Arrow numbers define the sequence in which steps are taken (Rogers and Biggs 1999).

6.1.3 Adaptive management for water temperatures in the Sabie River

According to Rogers and Bestbier (1997), "the primary problem facing scientists and managers in the Kruger National Park has been to develop the potential to predict and monitor the response of biodiversity in specific river sections (i.e. within the park) to modifications in hydrology, sediment supply and water quality originating at the catchment scale". Managing river "health" (cf. Section 5.1.1) is distinct from measuring it (Rogers and Biggs 1999), and part of the management process is to gain an understanding of the physical processes that govern the hydrologic condition of water, viz. quality, and flow magnitude, direction, timing and rate of change (McCammon et al. 1998). Previous research on the characterization of ecological flows (for example Richter et al. 1996; Harris and Silveira 1999) and water temperatures (for example Eaton and Scheller 1996; Essig 1998; Poole and Berman 2001) can be used as the basis for detecting system change. Most important in characterizing temperature or flow regimes is to establish reference levels, which are those that would be expected if the system were operating without significant human influence; they are not necessarily desired conditions (McCammon et al. 1998).

The importance of water temperatures to aquatic biota has been well documented (for example (Elliott 1994; Eaton and Scheller 1996; Claska and Gilbert 1998; Sullivan *et al.* 2000). Stuckenberg (1969) reports that it is the warm months that are the most important

biologically, since it is during the summer months that the important life-history processes, such as breeding and growth, occur. However, mean daily water temperature is considered a poor ecological measure, and it is rather the accumulation of daily maximum temperatures above a critical threshold that affects fish condition and distribution (Stuckenberg 1969; Armour 1991; Essig 1998; Caissie *et al.* 2001). Hines and Ambrose (1998) found that the best predictor for presence or absence of trout (*Oncorhynchus kisutch*) was the number of days a site exceeded a critical temperature threshold, and that single temperature values correlated poorly with fish presence and absence.

It has been shown that water temperature is one of the primary variables explaining the distribution of fish in the Sabie River (cf. Chapter 4), and consequently an important agent of change. Furthermore, it is clear from the available literature that no single temperature value is considered generally detrimental to fish, but rather it is the cumulative duration and frequency of exceedance of a threshold water temperature that is most critical in determining the presence or absence of particular fish species, although there may be other variables contributing to this. For example, Nunn et al. (2003) found a combination of flow and temperatures determined annual fish numbers. However, when choosing a suitable water temperature metric, it is important to note that water temperature criteria must compare with biological reality (Essig 1998).

In this chapter, a spatially explicit TPC is proposed for change in the annual water temperature range in the Sabie River (cf. Section 6.4.3), where exceedance is measured using biological indices (cf. Sections 6.1.3.1-2). These biological indices are based on the response of two species of Chiloglanid fish to annual changes in water temperatures, and can be used to indicate a significant change in the thermal regime of the Sabie River, by measuring species response to annual water temperatures over time at a particular spatial point. Chiloglanis sp. are an appropriate group of indicators of annual thermal change in the Sabie River system because of their small size (individuals are susceptible to small changes in water temperatures), and habitat specificity to riffles (riffles are the first habitat type to be degraded within a river system) (cf. Chapter 5). Electrofishing surveys showed that the abundant upstream species, C. anoterus, is characterized by much reduced numbers in the lowveld zone. In comparison, the upstream distributional limit of C. paratus, is abrupt (Weeks et al. 1996). Although adults of both species are pre-adapted and capable of maintaining their position at the highest of flows, there is strong evidence

that *C. anoterus* adults do not migrate. In contrast, *C. paratus*, like most lowveld species subjected to drought, has been known to colonize seasonal streams (Skelton 1993). Juveniles of both species are probably swept downstream involuntarily during high flows (Weeks 2001).

It is assumed that changes in the indices of the chosen indicator species will be a precursor to a change in the fish community patterns as a whole, since fish communities of the Sabie catchment were generally shown to be sensitive to water temperature gradients (cf. Chapter 4), and the Chiloglanids were shown to be suitable indicator species of these communities. Depending on how the "desired future state" may have been defined within the adaptive management process, such changes will assist in meeting the specific management goal of the Kruger National Park of maintaining biodiversity (Braack 1997). The proposed water temperature TPC has been defined using a similar approach to that of Mackenzie et al. (2000), who defined a TPC (loss of bedrock influence), and were able to link a biotic index (change in populations structure of the bedrock-associated riparian species Breonadia salicina) to an abiotic agent of change (sedimentation). The specific objectives of this chapter are to define:

- Relationships of how a chosen group of fish indicator species (Chiloglanids)
 are responding to annual water temperature indices (i.e. establish biological
 indices);
- A spatially-linked ecological baseline using these indices;
- An appropriate monitoring approach to detect changes in the annual thermal regime of the Sabie River.

6.1.3.1 The Chiloglanis anoterus: C. paratus ratio of relative abundance index

As shown in Section 5.3.1, *C. anoterus* and *C. paratus* have similar habitat requirements in terms of the abiotic variables considered – water depth, flow velocity and cover (cf. Chapter 5), with water temperature tolerances appearing to be a key factor, based on the abiotic variables considered, in separating these species in niche hypervolume space. Relative abundance curves of fish peak at that point in the river where the thermal optimum is found (Beitinger and Fitzpatrick 1979). An index that is based on the ratio of relative abundances of *C. anoterus* to *C. paratus*, and assumes that a reference ratio can be defined at a specific point in space, and measured over time, is proposed as a measurable

indicator of TPC exceedance. The ratio of abundances of these two species can be determined equally efficiently using relative or absolute abundances of fish (cf. Section 4.4.1). Inherent in the ratio index is the assumption that a negative association exists between C. anoterus and C. paratus. Both distributional and abundance criteria are combined into a single measurable index.

6.1.3.2 The C. anoterus condition factor index

Water temperature has been linked to the metabolic rate of fish (Nikolsky 1963; Beitinger and Fitzpatrick 1979; Crisp and Howson1982). Under assumptions of unlimited food resources and no competition, the fish closest to their thermal optimum will be in good condition; condition declines with prolonged exposure to non-optimal thermal conditions. While condition cannot be measured directly, various indirect measures are available, such as changes in metabolic rate. This is measured as a change in respiration in response to changes in environmental conditions, under laboratory conditions (Magnuson *et al.* 1979). An alternative, more practical field approach to determining condition is to calculate the average length to mass ratio of a sample of fish at different survey sites, to provide a condition factor. Such condition factors are commonly used in biological studies to investigate seasonal and habitat differences in "condition" or general "well-being", and was used, for example, by Taylor (1996) in research on rodents in plantations in the KwaZulu-Natal Midlands. However, such condition factors are recognised as contentious, being potentially confounded by additional sources of variability such as nutrition, season, maturity of individuals, and the life stage (or stanza) sampled (Ricker 1968).

Hines and Ambrose (1998) proposed that a condition factor could be linked to the number of days a threshold water temperature was exceeded. In spite of sudden and extreme changes in abiotic conditions potentially resulting in death, repeated and lasting exposure to sub-optimal thermal conditions leads to a deterioration in condition. Fish in good condition are assumed to have lower length to mass ratios than fish in poor condition. This index assumes that the average condition of *C. anoterus* adults declines with downstream distance, due to prolonged thermal stress because of the water temperature gradient shown to exist in the Sabie River (Chapter 2).

6.2 Methods for evaluating Chiloglanid biological indices

Standard electrofishing techniques (Chapter 4) were used to sample riffle habitats within the Sabie River during October 2000 and 2001, and May 2000, 2001 and 2002 (Figure 6.2). Site descriptions are provided in Table 6.1. Lengths (mm) and masses (g) for *C. anoterus* adult individuals were recorded. Unadjusted abundance numbers were used to plot abundance curves of *C. anoterus* and *C. paratus*.

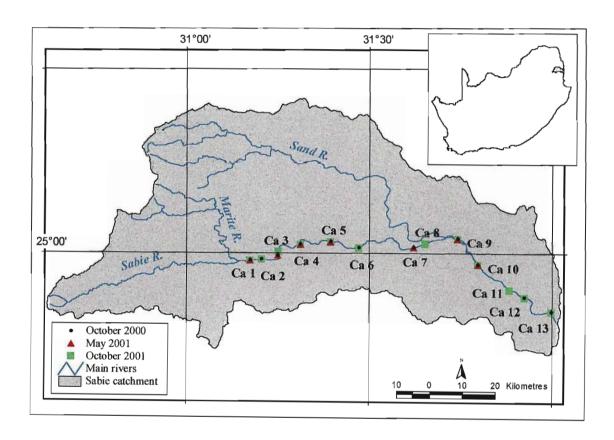


Figure 6.2 May and October electrofishing survey sites for Chiloglanis sampling within the Sabie catchment.

Table 6.1 Chiloglanis electrofishing site names and co-ordinate information

	ntiogiants electronishing sit	Altitude	Longitude	
Site no.	Site name	(m.asl)	(°E)	(°S)
Ca 1	Madras	421.15	31.173	25.022
Ca 2	Hoxani	401.69	31.205	25.019
Ca 3	Mkuhlu	395.3	31.250	24.998
Ca 4	Cork	342.04	31.312	24.978
Ca 5	Lisbon	309.98	31.394	24.971
Ca 6	Sabie Park	285.25	31.471	24.987
Ca 7	Visvang 1	234.84	31.621	24.985
Ca 8	Visvang 2	252.83	31.653	24.976
Ca 9	Post confluence Sabie	216.87	31.742	24.963
Ca 10	Nkuhlu	187.97	31.798	25.032
Ca 11	Lubyelubye	157.26	31.886	25.099
Ca 12	Lower Sabie weir	165.91	31.925	25.121
Ca 13	Molondosi	131.67	31.999	25.160

Stuckenberg (1969) recognised the biological relevance of a cumulative heating parameter (effective temperature – analogous to cumulative degree days above some threshold value). A temperature threshold used extensively in studies between water temperature and trout is a measure known as the **maximum weekly allowable temperature** (MWAT) (Armour 1991). This upper temperature threshold can be related to maximum daily water temperatures using Equation 6.1.

$$MWAT = OT + (UUILT - OT)/3$$
 [6.1]

where OT is the optimal temperature for that species, and UUILT is the upper temperature tolerance for the species of fish being considered. OT was calculated as the midpoint in the temperature range of C. anoterus, which was estimated using the absolute minimum and maximum water temperatures recorded at the upper and lower sites that C. anoterus was recorded from during May 2001, respectively. While it is recognised that cool season water temperature values are not necessarily an ideal measure of optimal temperatures, May temperatures were chosen since these values could be directly applied to the relative

abundance curves obtained from the May 2001 electrofishing survey. *UUILT* was estimated by adding two degrees to the upper limit temperature.

This approach was used to calculate a critical upper threshold temperature for *C. anoterus*. The duration (number of hours) that this temperature was exceeded annually was calculated using hourly temperature data from eight water temperature sites for the period 1 June 2001 to 31 May 2002 (Chapter 2). In addition, the frequency that this threshold was exceeded during the same time period was calculated, based on a seven-day moving average of daily maximum water temperatures. This is a similar approach to that used by Robison *et al.* (1999), who characterized water temperatures using a seven-day moving average of maximum water temperatures, as a measure representing prolonged exposure by aquatic life to high temperatures. Logistic regressions were calculated using the presence (1) or absence (0) of *C. anoterus* at 16 sites, to calculate the probability of occurrence of *C. anoterus* as a function of MWAT.

6.2.1 Chiloglanis ratio of relative abundances index

Two approaches were followed to determine the degree of species affinity that may exist between C anoterus and C paratus. For the first approach, a 2x2 contingency table was constructed, based on presence (1) and absence data (0) for all sample sites surveyed throughout the study period, to test for species association, i.e. did both species of Chiloglanis tend to occur together more often than expected? Expected values for each cell within the contingency table were calculated by dividing the product of row and column totals by the grand total. The null hypothesis was that both species were independent (no association). A chi-square (χ^2) test statistic was calculated to test for significance of this association (Ludwig and Reynolds 1988).

A second qualitative approach was used to test for the degree of significance of species covariation, and in particular to determine whether there was a significant negative association between *C. anoterus* and *C. paratus*. The Spearman's Rank correlation is a robust non-parametric measure of species association (Ludwig and Reynolds 1988). The relative abundances of *Chiloglanis anoterus* and *C. paratus* were ranked from largest to smallest according to sites arranged on a downstream gradient. This exercise was performed using the abundance values obtained from the May 2000, October 2000, May 2001, October 2001 and May 2002 electrofishing surveys. These data were kept separate since the October sites were sampled at riffle sites only, while the May sites were chosen as representative sites along the longitudinal axis of the Sabie River, and did not necessarily include riffle habitat. Spearman's Rank Correlations were also performed using each of the survey dates individually. The null hypothesis was that the species ranked abundances were uncorrelated. The Spearman's Rank Correlation coefficient was calculated using Equation 6.2 (Ludwig and Reynolds 1988).

$$r(i,k) = \frac{\sum y_i y_k}{\sqrt{\sum y_i^2 \sum y_k^2}}$$
 [6.2]

where y is the relative abundance (a ranked vector) for species i and k.

These values range from +1 to -1. In all cases, sample size (N) was less than 10, and the coefficient (r) was compared against significance values in Ludwig and Reynolds (1988) (p. 149) for p < 0.05 (degrees of freedom = N-2). For a small sample (N < 10) the assumption of normality is not valid (Ludwig and Reynolds 1988).

Relative abundances for each species were used to calculate ratios of *C. anoterus* and *C. paratus*. Ratios were calculated using two different approaches (Equations 6.3a-b). Point values for October 2000, October 2001 and May 2001 were plotted against downstream distance (chainage), and simple linear regressions fitted to each dataset.

$$R = \left(\frac{A}{A+B}\right) * 100 \tag{6.3a}$$

$$R = \log_{10}\left(\frac{A}{B}\right) \tag{6.3b}$$

where R is the calculated ratio, and A and B are two different species. It was necessary to log-transform the calculated ratio in Equation 6.3b to adjust for cases of extreme low values (abundances of 1).

Results from these analyses are presented in Section 6.3.1.

6.2.2 C. anoterus condition factor index

Determining a condition factor involved defining the relationship between the lengths (mm) and masses (g) of *C. anoterus*. This relationship is used for calculating condition factors in fish (Ricker (1968), due to allometric scaling between body mass and body length in fish (Equation 6.4a) (Ricker 1968; Peters 1983; McEwan and Hecht 1984; Schmidt-Nielsen 1984). Condition factors were calculated by dividing mass by length, according to Equation 6.4b. A subsequent step in using the condition factor as an index of thermal change was to determine whether a trend existed between the condition factor, and downstream distance (km) along the longitudinal axis of the Sabie River. Box-and-whisker plots were used to illustrate the relationship between condition factor variability and downstream distance.

$$M = aL^b ag{6.4a}$$

$$CF = \frac{M}{L^b}$$
 [6.4b]

where M is body mass (g), L is body length (mm), a is the proportionality coefficient or intercept; b is the exponent or slope; and CF is the condition factor.

The influences of sampling date and sex, on the condition factor were tested for using one-way analyses of variance (no blocking). ANOVAs of length, mass and condition versus sampling dates (May 2000, October 2000, May 2001 and May 2002); and length, mass and condition versus sex (male and female), were performed, with the hypothesis (p < 0.01) that sampling dates and sex had no effect on body length, mass or condition. Results from these analyses are presented in Section 6.3.2.

6.3 Results

The relative abundance curves of *C. anoterus* and *C. paratus* were generally unstable between surveys (Figures 6.3a, b). Abundance peaks for *C. anoterus* exhibited a general downstream movement with successive sample periods, peaking at 71.20, 86.69 and 97.60 kilometres downstream from the source of the Sabie River, based on the October 2000,

May 2001 and October 2001 surveys respectively. Conversely, the abundance peaks for *C. paratus* displayed an upstream movement, which appeared to stabilize in October 2001, viz. 149.10, 138.48 and 138.48 kilometres for the same sample dates, respectively.

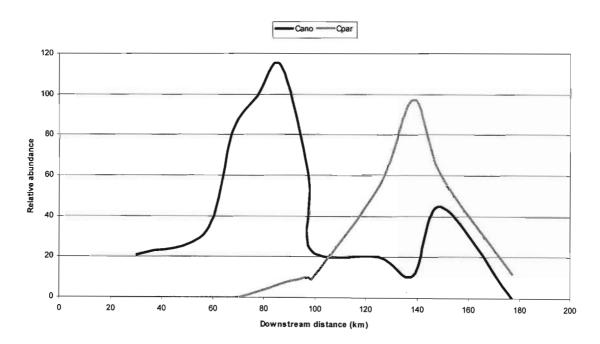


Figure 6.3a Relative abundance curves of C. anoterus and C. paratus for May 2001 electrofishing survey

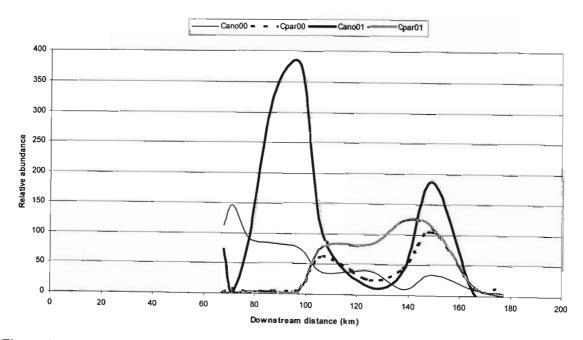


Figure 6.3b Relative abundance curves of C. anoterus and C. paratus for October 2000 and October 2001 electrofishing surveys

The MWAT for C. anoterus was estimated to be 25°C. The annual frequency of exceedance of MWAT was plotted as a function of downstream distance (Figure 6.4); this relationship could be approximated by a fitted logistic equation (Equation 6.5).

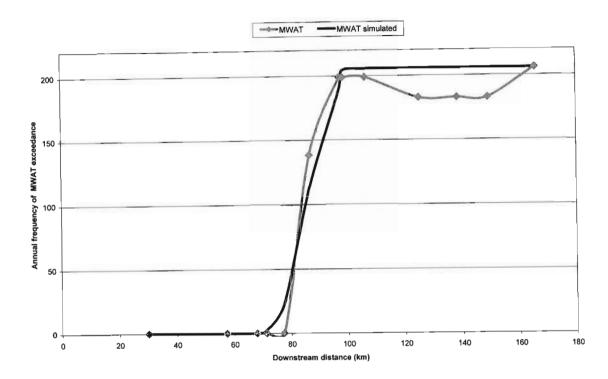


Figure 6.4 Observed and simulated annual frequency of exceedance of a MWAT of 25°C for C. anoterus, as a function of downstream distance

$$MWAT_{D+1} = \frac{MWAT_{D} * r}{1 + \frac{(r-1)*MWAT_{D}}{K}}$$
 [6.5]

where MWAT $_{D+1}$ is the MWAT at x kilometres downstream from MWAT $_D$, r is the rate of increase of MWAT with downstream distance (10^{1}), and K is the upper limit of the 25°C MWAT for C. anoterus in the Sabie River (2062 days per annum exceeding this MWAT).

Annual frequency and duration of exceedance of MWAT are shown in Table 6.2. Frequencies and durations of MWAT exceedances were highly correlated ($R^2 = 0.95$), so that two separate alternative logistic regression equations (Equations 6.6.a-b) were developed to calculate the probabilities of occurrence based on water temperatures metrics, rather than a single combined logistic regression. Both logistic regression models were

² Derived from Table 6.2 for downstream distance of 177 kilometres

significant (p < 0.05). The annual probability of occurrence (p) of C. anoterus was calculated for the annual frequency (Equation 6.6a) and cumulative annual hourly duration (Equation 6.6b) of exceedance of MWAT (x) in the range 0-206 days (Figure 6.5a) and 0-3600 hours (Figure 6.5b) respectively. The duration and frequency of exceedance of MWAT at which the probability of not finding C. anoterus versus finding C. anoterus at a site was greater than 0.5 were 2796 hours (or 32% of the annual time) and 198 days respectively.

Table 6.2 Frequency and duration of exceedance of MWAT for *C. anoterus*, based on seven-day moving average of maximum daily water temperatures from 31 May 2001 to 30 June 2002.

T	MWAT exceedances					
Downstream	Fraguency	Duration				
distance/River	Frequency	(hours)				
30.09	0	0				
57.29	0	49				
67.88	0	49				
77.34	0	49				
86.69	138	1116				
97.60	138	1116				
98.62	199	2269				
106.58	199	2269				
125.17	183	2717				
138.48	183	2717				
141.40	183	2717				
149.14	183	2717				
165.66	206	3535				
177.05	206	3535				
Sand River	205	2419				
Marite River	107	982				

$$p = \frac{e^{23.0 - 0.0117(x)}}{1 + e^{23.0 - 0.0117(x)}}$$
 [6.6a]

$$p = \frac{e^{10.02 - 0.0036(x)}}{1 + e^{10.02 - 0.0036(x)}}$$
 [6.6b]

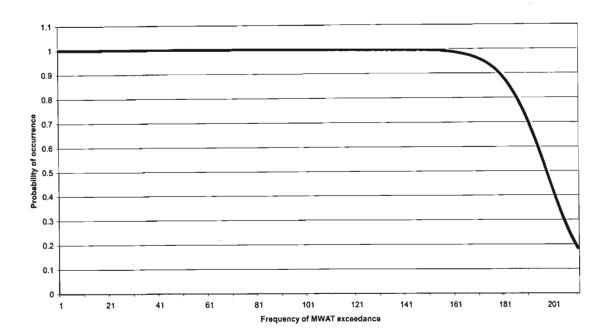


Figure 6.5a Probability of occurrence of C. anoterus with annual cumulative frequency of exceedance of MWAT

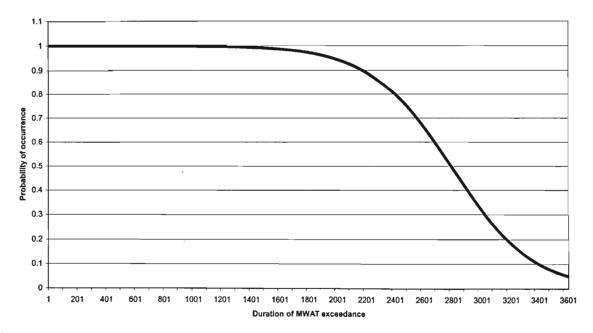


Figure 6.5b Probability of occurrence of C. anoterus with cumulative annual hourly duration of exceedance of MWAT

6.3.1 Chiloglanis ratio of relative abundances index

While both Chiloglanid species tended to occur together more often than expected (13 observed versus 12.75 expected), there was no significant association between C anoterus and C paratus, and the null hypothesis of no association between these species was accepted (Table 6.3, $\chi^2 = 0.13$; 1 df, p < 0.05).

Table 6.3 2x2 Species association table for *C. anoterus* and *C. paratus*, based on combined presence/absence data for all sites surveyed between May 2000 and May 2002

of the second		C. pa	Totals	
		Present	Absent	Totals
C. anoterus	Present	13	4	17
C. unoterus	Absent	2	1	3
Total	s .	15	. 5	20

According to the Spearman's Rank correlations (Tables 6.4-5), most sites showed a non-significant (p < 0.05) negative association between *C. anoterus* and *C. paratus*. The exceptions to this generalization were: October 2001 (non-significant positive association), October 2000 (significant negative association), and the combined May data sets (significant negative association). A weak negative association appeared to exist between *C. anoterus* and *C. paratus*, which changed on an intra- and inter-annual basis. The strength of this association may be a function of different population dynamics for the two species, as they respond to different abiotic drivers in different ways, but may also be a function of electrofishing efficiency at the different sites (cf. Section 4.4.1).

Simple linear regressions of ratio versus downstream distance using both methods for calculating ratios of C. anoterus to C. paratus (Equations 6.3a-b) were significant for each of the sampling periods. However, while the correlations tended to be weaker using Equation 6.3a (Figure 6.6a – correlations (R^2) for October 2000 = 0.77; October 2001: = 0.72; and May 2001: = 0.81) than those based on Equation 6.3b (Figure 6.6b – correlations (R^2) for October 2000 = 0.91; October 2001 = 0.67; and May 2001 = 0.90), ratios were calculated using Equation 6.3a for the following reasons:

- The slope of the regression lines using Equation 6.3a were more similar (greater constancy) (Figure 6.6b) than the regression slopes derived using the alternative ratio calculations;
- Correlations were more consistent between years using equation 6.3a than those produced using Equation 6.3b;
- Ratios based on Equation 6.3a are intuitively easier to work with than those values using Equation 6.3b.

Consequently, Equations 6.7a-c derived from the ratios calculated using Equation 6.3a were used to calculate expected ratios for the TPC (Table 6.7). However, in spite of the significance of these regressions, data did show a marked degree of scatter, which reinforces the results of the Spearman's Rank correlations of a weak negative association between these two species.

October 2000: Ratio =
$$-0.821$$
(downstream distance) + 153.12 [6.7a]

October 2001: Ratio =
$$-0.724$$
(downstream distance) + 151.06 [6.7b]

May 2001: Ratio =
$$-0.813$$
 (downstream distance) + 142.28 [6.7c]

Table 6.4 Relative abundances and Spearmans Rank values for *Chiloglanis*-focus electrofishing surveys. Sites shaded in gray are those not sampled during the respective electrofishing survey.

Date	Species		Site numbers#						_	Correlation			
Date	Species	Ca 1	Ca 2	Ca 3	Ca 4	Ca 5	Ca 6	Ca 8	Ca 9	Ca 10	Ca 12	Ca 13	
October 2000	C. anoterus	112	146	92		75	36	40	9	35	11	0	-0.648*
	C. paratus	1	8	3		9	64	25	46	105	13	16	0.010
October 2001	C. anoterus	73	1	86	326	378	98	13	. 43	188	5	0	0.187
October 2001	C. paratus	1	0	3	4	7	79	83	123	111	16	4	
May 2001	C. anoterus	82		99	114	59		20	11	45			-0.821*
	C. paratus	0		3	7	10		55	97	60			
Combined	C. anoterus	93	74	89	326	227	67	27	26	112	8	0	-0.351
October	C. paratus	1	4	3	4	8	72	54	85	108	15	10	

^{*} Significant negative association (p < 0.05)

[#] Refer to Figure 6.2

Table 6.5 Relative abundances and Spearmans Rank values for May electrofishing surveys. Sites shaded in gray are those not sampled during the respective electrofishing survey.

Date	Species		Site numbers#							Correlation		
Date	Species	3	5	21 ^s	7	9	20	11 [§]	19 [§]	14 [§]	26 [§]	
May 2000	C. anoterus	7	31	11	4		0	29	14	0	11	-0.566
141ay 2000	C. paratus	0	0	0	11		13	0	1	5	61	0.500
May 2001	C. anoterus	36	32	47	40	0	0	15	34	0		-0 371
171ay 2001	C. paratus	0	0	0	6	0	22	0	8	29		
May 2002	C. anoterus	20	34	61	25	1	0	31	10	0	0	-0.452
	C. paratus	0	0	0	11	3	2	0	6	32	0	-0.732
Combined May	C. anoterus	21	32	40	23	1	0	25	19	0	6	-0.759*
Combined Ma	C. paratus	0	0	0	9	2	12	0	5	22	31	

Significant negative association (p < 0.05)

[#] Refer to Figure 4.1

[§] Marite River

[§] Sand River

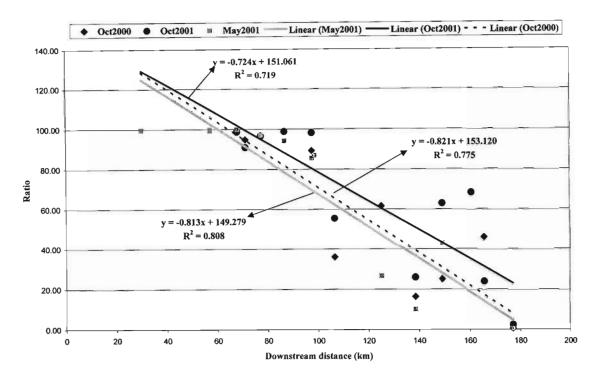


Figure 6.6a Ratio of relative abundances of *C. anoterus* to *C. paratus*, determined using Equation 6.3a, as a function of downstream distance on the Sabie River. Trend lines and their significances are shown.

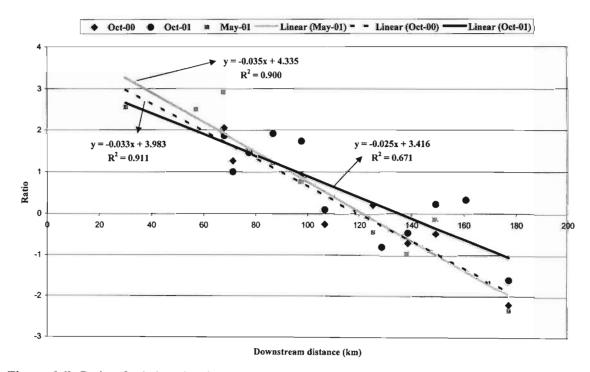


Figure 6.6b Ratio of relative abundances of *C. anoterus* to *C. paratus*, determined using Equation 6.3b, as a function of downstream distance on the Sabie River. Trend lines and their significances are shown.

6.3.2 C. anoterus condition factor index

As the initial step in calculating a condition factor index (cf. Section 6.2.2), the relationship between mass and length for C. anoterus was shown to be significant (n = 360; $R^2 = 0.85$) (Figure 6.7), and could be predicted by Equation 6.8.

$$M = 0.1121e^{0.0582L} ag{6.8}$$

where M is mass (g), and L is length (mm).

Furthermore, length and mass showed a significant negative trend with downstream distance, with mass decreasing at a faster rate (six times) than length (Figure 6.8).

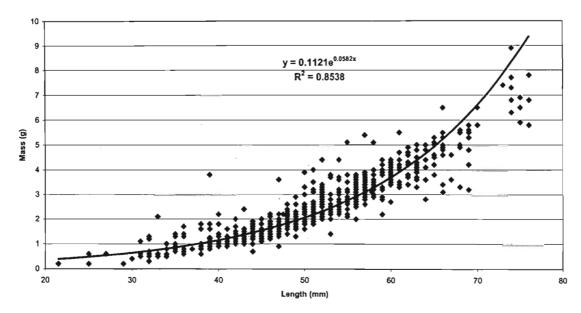


Figure 6.7 Relationship between mass (g) and length (mm) for C. anoterus

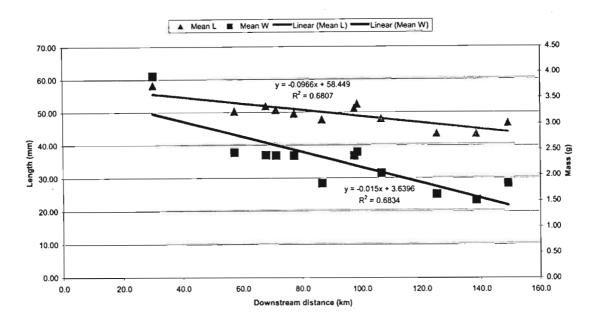


Figure 6.8 Change in mean length and mass with downstream distance

Based on the analyses of variance to test for the effects of sampling date and sex on the lengths, masses and conditions of C. anoterus adults, it was shown that lengths did not vary between sampling dates, but that mass and condition did vary significantly (p < 0.01) between sampling dates (Table 6.6a). Conversely, males tended to be significantly longer than females (p < 0.01), although there were no significant differences in mass or condition between male and female C. anoterus adults (Table 6.6b). The implication of these results in calculating a condition index is that data for lengths and masses of males and females for C. anoterus need not be separated in calculating a condition index. Due to the inter-annual variation in condition, conditions calculated based on data from all four electrofishing surveys were combined, although it is recognized that a more reliable relationship between condition and downstream distance should be based on data collected at the same time each year, for a number of years.

Table 6.6a Summary of analysis of variance output to test for differences between length, mass and

condition based on sampling date

Sample	Sample size	Mean \pm s.d.	Mean ± s.d.	Mean ± s.d.
date	(n)	length (mm)	mass (g)	condition
May 2000	61	48.12 ± 11.30	1.98 ± 1.42	1.57 ± 1.10
October	159	52.05 ± 9.12	2.83 ± 1.31	2.24 ± 1.02
2000				
May 2001	430	50.42 ± 8.27	2.31 ± 1.18	1.84 ± 0.92
May 2002	117	50.33 ± 10.65	2.70 ± 1.54	2.14 ± 1.20
F-value		0.033	< 0.001*	< 0.001*

Significant difference between sample dates (p < 0.01)

Table 6.6b Summary of analysis of variance output to test for differences between length, mass and condition based on sex

Condition based on	Sample size	Mean ± s.d.	Mean ± s.d.	Mean ± s.d.
Sex	(n)	length (mm)	mass (g)	condition
Female	355	50.51 ± 8.75	2.46 ± 1.23	1.95 ± 0.98
Male	304	52.43 ± 8.56	2.68 ± 1.35	2.12 ± 1.04
F-value		0.005*	0.034	0.035

Significant difference between sexes (p < 0.01)

A Box-and-whisker plot (Figure 6.9) of condition factor (as a combined data set from all four electrofishing surveys; n = 629) versus downstream distance along the longitudinal axis of the Sabie River, showed that while the range in condition was greatest at the upstream sites, median condition followed a downward trend, where condition was highest at the top of the catchment, and decreased with downstream distance. Based on the trend in lengths and masses with downstream distance (Figure 6.8), this is more likely to be a function of a change in mass than a change in length. Mean, median and modal condition factor values, calculated using combined data from all sampling occasions, were each regressed against downstream distance to determine which statistic provided the best prediction (or correlation) of the condition factor index (Figure 6.10). The mean condition factor was found to provide the best correlation with downstream distance, and was consequently chosen as the statistic by which to calculate average *C. anoterus* condition factors on the Sabie River.

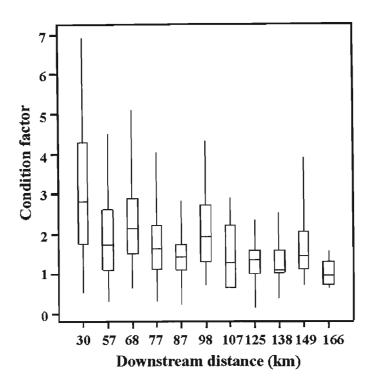


Figure 6.9 Box-and-whisker plot of condition (mass to length ratio) of *C. anoterus* adults versus site. Whiskers show maximum and minimum values, while the box shows the middle 50% of the data, with the median shown as a line within the box.

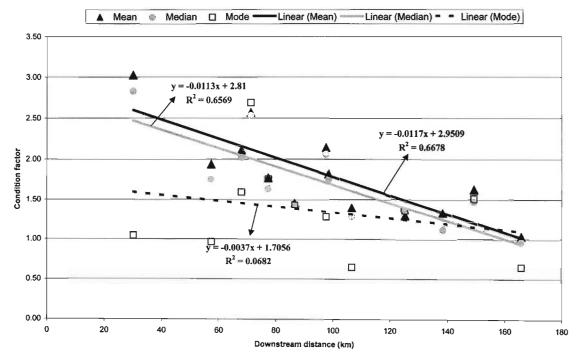


Figure 6.10 Linear regressions of condition versus downstream distance using mean, median and modal values of *C. anoterus* condition.

In calculating the linear relationship between the mean condition factors of *C. anoterus* and downstream distance along the Sabie River, the May 2001 data were

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used as these gave the most comprehensive distribution of sites along the longitudinal axis of the Sabie River. The October 2001 survey data were excluded from the relationship to standardize the data by time of year; additional motivating factors in choosing the May 2001 survey period were that mean conditions were available for two and three sites for the May 2000 and May 2002 survey sites respectively. Based on these data, the condition factor (CF) showed a decrease with downstream distance (Figure 6.11) ($R^2 = 0.71$). Mean condition factors of *C. anoterus* remained within a ten percent envelope of the regression line between condition and downstream distance (Equation 6.9), with the exception of the site 86 kilometres downstream from the top of the Sabie River.

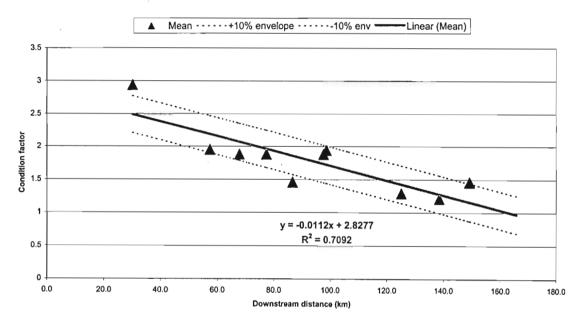


Figure 6.11 Condition index for *C. anoterus* with downstream distance along the longitudinal axis of the Sabie River.

May 2001:
$$CF = -0.0112(downstream distance) + 2.8277$$
 [6.9]

The relationship between relative abundance and mean condition for the May 2001 data was approximated by a third order polynomial (Figure 6.12), although this relationship was not significant, which suggests that condition and abundance are not correlated.

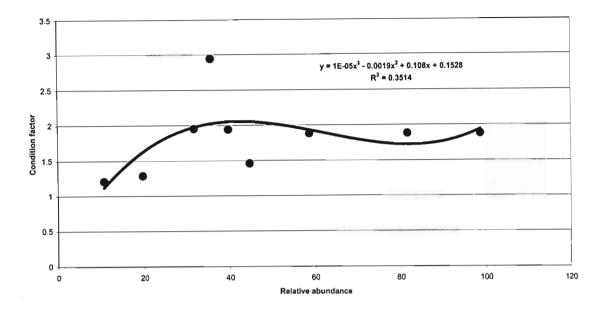


Figure 6.12 Relationship between mean condition factor of *C. anoterus* adults, and relative abundances based on the May 2001 electrofishing survey in the Sabie River.

6.4 Discussion and conclusions

6.4.1 General considerations

The species relative abundance curves were dynamic and unstable during the study period, with no equilibrium apparent in the three years when data were collected. The February 2000 floods may have skewed the relative abundance curves of both species, due to fish having been washed downstream, while experiencing a concomitant reduction in condition. Additionally, not enough is known about the migration strategies of either species to understand how these fish respond to disturbance or unfavourable water temperature conditions. The reasons for the second, smaller abundance peak of *C. anoterus* further downstream of the first peak are not known, but may be due to the presence of ideal riffle habitat, where a population of *C. anoterus* exists by making trade-offs between habitat, food availability and water temperatures.

The use of the ratio and condition indices, as opposed to the use of abundances, is significant since population size in fish has been shown to be highly variable both temporally and spatially (Harris, 1995, Jobling 1995), and discerning the importance of natural versus anthropogenic changes is difficult (Harris 1995). However, while the relationship between the ratios of *C. anoterus* to *C. paratus* and downstream

distance was significant, the degree of scatter was high for all three years of data. Furthermore, C. anoterus and C. paratus did not exhibit a significant negative association within the study period. Based on these findings, the ratio index is not strong enough to be used on its own as an indicator of changes in annual water temperatures. A significant negative trend between the average condition of C. anoterus and downstream distance of the Sabie River was calculated, which was independent of assumptions of inter-specific associations. Fish condition has the potential to be used as a suitable index to reflect annual changes in water temperatures. However, the use of a condition index is a contentious issue, due to differences between sex and age classes, and seasonal effects (Kleynhans, 2003), which are additionally compounded by issues such as intra- and inter-specific competition, and the gravid state of females. Adult C. anoterus fish may lose condition in the downstream reaches of the Sabie River due to factors external to water temperatures, such as increased predation and inter-specific competition associated with the increase in community diversity and number of species (cf. Section 4.3.1, Chapter 4).

6.4.2 Choice of water temperature TPC for the Sabie River

It has been shown that the probability of occurrence of *C. anoterus* could be significantly linked to an annual index of heating within the Sabie River using logistic regression curves (*cf.* Section 6.3). The presence or absence of *C. anoterus* will ultimately be due to the cumulative effects of thermal (and/or additional abiotic and biotic) stress. However, according to Hines and Ambrose (1998), fish presence is only one measure of success. While fish may persist, temperature conditions may be contributing to their decline, which will be manifested as a change in condition and/or relative abundances. Both measures were shown to be mutually exclusive, and relevant in reflecting responses to environmental stress. Setting a threshold value based on the average condition of a population present at a site provides a method of determining "unacceptable" water temperature conditions.

Relative abundances of *C. anoterus* decreased sharply as the annual duration and frequency of MWAT exceedance rose above zero (Point A on Figure 6.13). The relationship between the frequency of exceedance of MWAT and condition (Figure

6.14) is generally linear, with condition decreasing as the duration of MWAT exceedance increased. MWAT exceedance reached an asymptote at 106 kilometres downstream from the top of the catchment, with condition continuing to decline with prolonged exposure to water temperatures exceeding 25°C. Fish condition and relative abundance could therefore be used as surrogate measures of the degree of heating within different sections of the Sabie River. However, it is important to point out that the relationship between relative abundance and MWAT is only valid from approximately 80 kilometres downstream from the source of the Sabie River, corresponding to point A on Figure 6.13. Additional drivers, either abiotic or biotic, would seem to be defining the relative abundances further upstream from this point. A TPC for water temperatures within the Sabie River could be chosen using correlations of MWAT versus condition, and MWAT versus relative abundance, as measures of exceedance of this TPC. The logistic regression models (Equations 6.6a, b) have been shown to be useful in choosing a threshold MWAT corresponding to a chosen probability of finding adults of *C. anoterus* within certain river reaches.

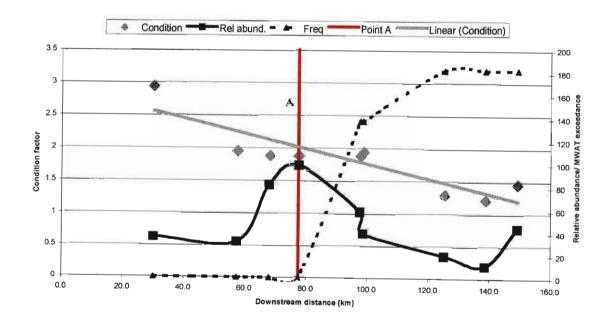


Figure 6.13 Relationships between relative abundance, condition factor of *C. anoterus* and annual frequency of exceedance of MWAT, based on the May 2001 electrofishing survey.

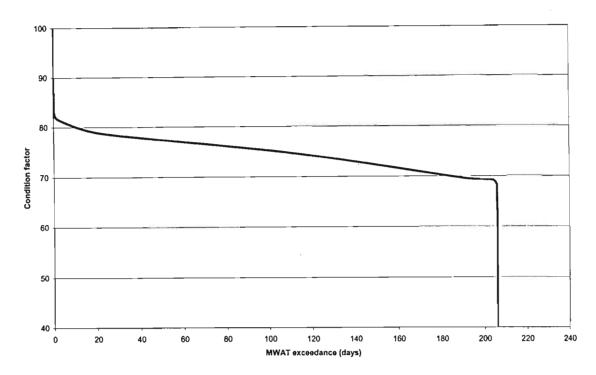


Figure 6.14 Correlative relationship between average condition of *C. anoterus* and annual simulated frequency of exceedance of a MWAT of 25°C for *C. anoterus*

Since duration and frequency of annual MWAT for C. anoterus were highly correlated, either parameter could be used to determine the probability of occurrence of C. anoterus adults. The cumulative water temperature threshold at which the probability of finding C. anoterus was less than 0.5 was chosen as the threshold value for the TPC. Should conditions on the Sabie River become warmer, C. anoterus is likely to retreat upstream. An appropriate TPC could thus be chosen, and linked to a defined river reach. MWAT exceedance of 25°C by 200 days coincided with site WT4 (Chapter 2), which was located 106 kilometres downstream from the top of the Sabie catchment. The relative abundance of *C. anoterus* was greatest at 86 kilometres downstream from the top of the catchment (site Ca 4). Downstream from this point, relative abundance declined abruptly, and it was also within this reach of the Sabie River that MWAT exceedance of 25°C rose from 138 to 199 days. The thermal regime does not change significantly between 106 kilometres (WT4) and 125 kilometres (WT7) downstream, and beyond this the water temperatures are warmer (WT8) (Figure 6.15a, b). Highest water temperatures occurred from December to March (Figure 6.15a), which is likely to correspond with the period when populations of C. anoterus experience the greatest amounts of thermal stress.

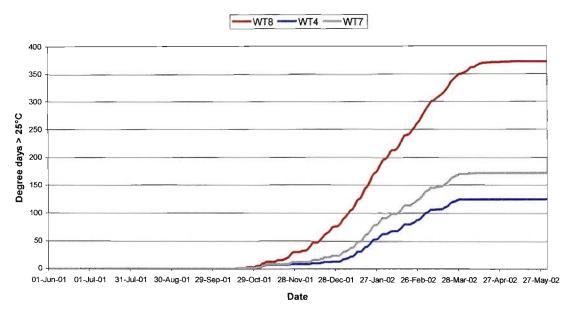


Figure 6.15a Cumulative degree days >25°C for the period 1 June 2001 to 31 May 2002 for three Sabie River sites.

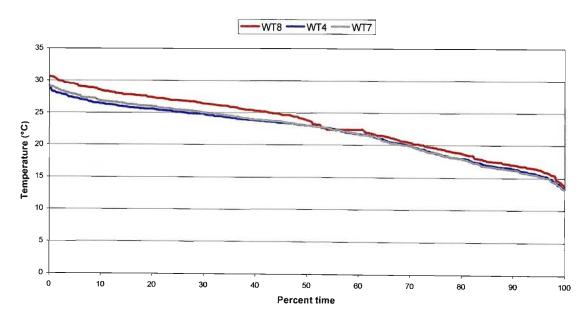


Figure 6.15b Water temperature duration curves for three lowveld sites on the Sabie River.

6.4.3 TPC definition

The proposed TPC is exceedance of the *C. anoterus* MWAT of 25°C by 200 days according to a seven day moving average of maximum daily water temperatures of the Sabie River for the annual period 1 June to 31 May, within the thermal reach extending from 98 kilometres from the top of the catchment (WT4) to 125 kilometres downstream, (WT7).

The indicators of the TPC will be the presence of *C. anoterus*, the average condition of these fish during May of each year, and the ratio of relative abundances of *C. anoterus* to *C. paratus*. The predicted average fish condition at 106 kilometres downstream from the source of the Sabie River for an MWAT exceedance of 200 days is 1.64 (66%), which was calculated from the relationship between condition factor and downstream distance (Equation 6.9). Predicted average conditions are 1.73 (69%) and 1.43 (57%) for downstream distances of 98 and 125 kilometres respectively. Fish condition should be within 10% of the value at 106 kilometres, giving upper and lower values of 1.80 (72%) and 1.48 (59%) respectively. As an additional measure, the ratio of relative abundances of *C. anoterus* to *C. paratus* should approximate the means provided in Table 6.7, which were calculated from Equations 6.7a-c. The change in dominance (equal ratios of relative abundances of *C. anoterus* and *C. paratus*) also occurs within the reach occurring around 125 kilometres downstream.

Table 6.7 Ratios (relative abundances) of *C. anoterus* to *C. paratus* for October 2000, October 2001 and May 2001, together with mean ratios

Date	Downstream distance (kms)		
	98	106	125
October 2000	72.64	66.07	50.47
October 2001	80.11	74.32	60.56
May 2001	62.59	56.08	40.63
Mean	71.78	65.49	50.55

Monitoring programmes, to be successful, must be inexpensive (to survive budget cuts); simple and verifiable (independent of staff changes); and include measurements

which are sensitive to changes in ecosystems (Schindler 1987). A monitoring programme should include sampling annually, during May, to coincide with the winter low-flows, for these threshold values to be comparable between years and with the threshold values suggested in this chapter. Electrofishing surveys should target riffle habitat within the reach extending from 98 to 125 kilometres downstream from the top of the Sabie catchment. The average condition factor should be based on a sample size of 20 adult individuals, although the confidence in the condition estimate will increase with greater sample sizes (Siegel and Castellan 1988). Predicted condition factors should be tested against measured condition factors using a student's t-test for comparing the mean values of predicted and observed condition. monitoring programme should not be an end in itself, but should be a means of continually testing and evaluating any hypotheses of environmental change and system functioning with the adaptive management programme. The monitoring programme should test the efficacy of management practices; furthermore, the management goals should define the monitoring programme (Rogers and Biggs 1999). Management strategies need to be adapted as new data and insights emerge (Dawe et al. 2000), which can only be achieved with long-term monitoring programmes. Ideally, monitoring programmes should be in place before any pre- and post-treatment operations, such as the construction of impoundments, are implemented (Walters et al. 2000).

The following limitations are recognized:

• The optimum and upper incipient levels of temperatures for *C. anoterus* (Equation 6.4) are based on estimates only. These values should be refined using fish tank experiments, to ascertain more precise temperature tolerance limits. However, it is also recognised that laboratory conditions do not necessarily represent field conditions (Section 5.1.3). Individual organisms *in situ* experience daily, seasonal and annual cycles of environmental change which break the continuity of exposure to extremes. Thus, when conditions become intolerable, fish move to refugia habitats. It therefore follows that barriers to fish movement, such as impoundments and weirs, should be minimized if river systems are to be managed to maximize fish diversity;

- The average condition for *C. anoterus* with downstream distance was based on three years of variable data. It is recognised that there is a need to validate this negative trend with downstream distance, and to determine more empirically how condition changes with water temperature. This can also be achieved using fish tank experiments;
- The water temperature data used are for the period 1 June 2001 to 31 May 2002, and sampling was at a relatively coarse resolution (approximately 20 kilometres between loggers). Therefore, it is not known whether the observed water temperatures are within a larger warm or cold cycle, and it was assumed that water temperatures between sampling sites could be interpolated. A decision on whether the *C. anoterus* MWAT exceedance may be increasing or not cannot be made with confidence, since natural versus anthropogenically-induced changes in thermal regimes are often difficult to distinguish.
- At this stage, the ratio of relative abundances of *C. anoterus* to *C. paratus* as an indicator of thermal change should be used with caution, since these data show a high degree of scatter, and no significant negative association has been shown to exist. Understanding the dispersal-colonization dynamics and the resultant distributional patterns is important if Chiloglanid responses to any significant agent of change are to be simulated. Limited data exists on the migration strategies of both species of Chiloglanids, which could potentially be better understood through monthly electrofishing surveys at a finer sampling resolution. Such a study could potentially elucidate the degree to which both species of *Chiloglanis* respond to thermal (and/or additional abiotic) gradients over time.
- The relationship between *C. paratus* and water temperatures is uncertain.

It is recommended that subsequent May electrofishing surveys be conducted in the Sabie River, to test the stability of the condition factor to downstream distance relationship for *C. anoterus*. It is also recommended that further research be undertaken on the links between ecologically significant flow parameters (Richter *et al.* 1996), in addition to critical cumulative annual water temperatures, and the

presence or absence of *C. anoterus*, so that critical flows can be established. Relevant flow parameters could be established using multiple logistic regression models. Currently, mean daily flow volumes are incorporated into the water temperature model (Chapter 3), so that daily flow volumes are indirectly incorporated into the water temperature TPC. Refinement of the TPC for water temperatures should occur within the framework proposed by Rogers and Bestbier (1997), in consultation with the appropriate managers of the Kruger National Park.

* * * * *

The ratio of relative abundances of *C. anoterus* to *C. paratus*, and the average adult population condition (mass to length ratio) of *C. anoterus* were both shown to be useful to river managers as indicators of changes in cumulative annual water temperatures. While such indices should be used together, the weak negative association between *C. anoterus* and *C. paratus* suggests that more emphasis should be placed on the condition index, in spite of this being a contentious parameter to use. The importance of the link between water temperatures and fish diversity in the Sabie River has been stressed (*cf.* Chapter 4). Since the central vision of the Kruger National Park adaptive management approach is the maintenance of biodiversity, appropriate management of water temperature-related issues, becomes of significance. A useful management tool is the use of simple models in which different environmental scenarios may be considered. The relationships between water temperatures and indicator species of fish in the Sabie River are contextualized within a conceptual simple rule-based modelling system in Chapter 7.

7 THE CONCEPTUAL DESIGN OF A CHILOGLANIS MODELLING SYSTEM AS AN ADAPTIVE MANAGEMENT TOOL FOR USE IN THE SABIE RIVER

"Having gathered these facts, Watson, I smoked several pipes over them, trying to separate those which were crucial from others which were merely incidental."

Memoirs of Sherlock Holmes - "The Crooked Man"

7.1 Introduction

This chapter describes the conceptual development of a *Chiloglanis* modelling system, which is intended to simulate changes in the biological indices (ratio and condition) developed in Chapter 6, in response to annual water temperatures metrics. As a background, different modelling approaches, and how these relate to adaptive management, are discussed. These concepts form the basis for simple cause-and-effect relationships which link metrics of annual water temperature to biotic response, and which are incorporated into a pragmatic modelling system developed as a tool for river managers operating within the Sabie catchment.

7.1.1 Aspects of natural resource management

Natural systems form complex webs of synergies, with species patterns providing a reflection of environmental processes, both "fast" and "slow" (Vannote et al. 1980; Frissel et al. 1986). While the dynamics of complex systems remain difficult to understand and predict, their continued sustainability "depends largely on our insight into the functioning of such complex systems" (Scheffer 1999). Two questions that often arise are "How do we understand seemingly random or stochastic patterns?"; and "How do we manage for system variability, which is necessary for preventing competitive exclusions and promoting system productivity?" While the question of random patterns is likely to remain largely unanswered because of the complex nature of natural systems, the degree of success in managing such systems may vary, depending on the management approach adopted.

The need for management of a natural system implies that it is no longer self-sustaining (Moss1999). In systems that are managed, natural resource management decisions are often based on imperfect data, and an incomplete understanding of system behaviour. However, to restore of sustainability to a system requires a fundamental understanding of it, which can only be achieved through long-term research and large-scale experiments (Moss 1999). An effective management approach under such conditions of uncertainty, which seeks to achieve these goals, is known as adaptive management (cf. Sections 6.1.1-2) (Walters 1986 cited in Lynman et al. 2002). One of the strongest tenets of adaptive management is that it does not advocate rigid management policies (Gunderson et al. 1995). Instead, it is a flexible approach that "is generally accepted as a continuously iterative, learn-by-doing process, in which objectives, activities, monitoring protocols, and evaluative procedures are established and then refined as new information is gleaned from the experimental manipulation of structures or processes" (Lynman et al. 2002). A formal approach to adaptive management is to:

- 1. Define management problems;
- 2. Synthesize current system understanding within dynamic models;
- 3. Identify uncertainties to management;
- 4. Design policies which lead to a better understanding of the system (Gray 2000);
- 5. Monitor and evaluate system response to management actions (Lynman *et al.* 2002).

Policies are designed as hypotheses and management implemented as experiments to test those hypotheses (Gunderson *et al.* 1995).

Gunderson et al. (1995), in a case study of the Florida Everglades, classified management policies over a one hundred year period into different management eras. Transitions between eras coincided with either environmental or human-induced crises and "surprises". These various management policies met their demise largely due to being rigid, reactive and prescriptive, and working against natural system variability. Adaptation, rather than adoption of pre-designed and pre-planned projects was the critical component absent in designing successful environmental management programmes. Shared visions, a commitment to a continuous and iterative learning process, and long-term funding have also been identified as key ingredients to successful natural resource management initiatives. While adaptive management programmes based on the learning-by-doing approach may be more expensive to implement in the short term than traditional

management approaches, the approach should lead to more informed management decisions being taken, which is likely to be a more cost-effective strategy in the long term (Johnson 1999b) (cf. Section 6.1.1).

7.1.2 Modelling approaches for natural systems

According to Quinn (1998), "successful policy [application] requires a 'tool-box' of decision-making and evaluatory techniques". Under management situations where system understanding is critical for effective management, and great uncertainties exist with respect to the consequences of management actions, models are useful tools for integrating science and management, and allow managers to examine the potential impacts of various scenarios before choosing the most appropriate approach (Diamond 1991; Breen 1998). Thus, modelling provides a tool for testing and evaluating management policies prior to their implementation, by providing scenarios of potential consequences of management actions based on the current level of understanding of a system.

Typically, ecologists have adopted a reductionist approach to understanding ecosystems. The quest for the ecological "Holy Grail" – a set of mathematical equations that explain system behaviour, obtained by breaking systems down to their basic units – is ongoing. For example, Stone and Esrati (1996) provided numerous examples where apparently random oscillations could be explained by deterministic chaos, and a small number of equations could model a system precisely. This was recognised by Gunderson *et al.* (1995, p.6), who asserted that "the great diversity of life in ecosystems is traceable to the function of a small set of variables, each operating at a qualitatively different speed from the others".

While reductionism is useful in streamlining ecological model design, deterministic equations are generally not able to adequately explain system behaviour, as they ignore the idea that through synergies, the sum of the individual parts is greater than the whole. Very often too, neither the data nor the ability to represent natural processes as equations exists (Matsinos et al. 1994). Qualitative, rule-based models have been identified as useful tools for systems analyses when data are poor (Starfield 1990). Instead of suites of equations and quantitative data, rules (if...then...else) and data categories (low/medium/high) are used to represent system components and relationships (Starfield et al. 1989; Starfield 1990). Interactions between simple sets of rules create dynamic "systems", such as John

Conway's "Game of Life" (Green 1998), where complex patterns emerge when natural objects are viewed as simple computers with their own sets of rules (i.e. cellular automata). This approach can be applied at larger scales by viewing spatial units (river reach, catchment) as a collection of cells.

The object-oriented modelling approach is useful in simulating natural systems, since the "attributes of inheritance, polymorphism, data protection and modularity, provides a natural framework for simulating real-world phenomena involving individual organisms" (Matsinos et al. 1994). Mooij and Boersma (1996) found that "the object-oriented programming paradigm is well suited for the creation of simulation models of ecological systems". Objects (for example fish, elephant, habitat) interact with each other according to sets of procedures and rules. An object-oriented modelling approach has the advantages that each object falls within a hierarchy of other objects, so that inheritance relationships avoid unnecessary coding (Mooij and Boersma 1996). Objects lower down the hierarchy inherit all the attributes of objects higher up the hierarchy (Budd 1991; Silvert 1993). This approach enables modellers to add new objects to a model with relative ease, and minimize redundancy in programming code (Silvert 1993). As such, object-oriented models tend to be simpler and closer to natural ecosystem structure than models with procedural languages; it is possible to modify and refine these models more efficiently. Ecological processes can be simulated at different scales within the same model, depending on the purpose of the model (Matsinos et al. 1994; Mooij and Boersma 1996). By using rules within an object-oriented programme, "animals" are able to interact with their habitat and with other "animals" (Mueller 1991). Animal objects are assigned characteristics and behaviours; the animal objects live within habitat objects that carry relevant information such as vegetation and soil type (Mueller 1991). The concepts of scale, rules and synergies are embodied in object-oriented models, which have been increasingly used to model ecological systems at various scales (for example Matsinos et al. 1994; Mooij and Boersma 1996; Sekine et al. 1996; Railsback et al. 1999; Railsback and Harvey 2000).

Many object-oriented ecological models operate at the level of the individual (individual-based models or IBMs), such as that of Van Winkle *et al.* (1998), who developed a rule-based IBM for trout to predict the effects of different flow and temperature scenarios on trout populations. Individuals within a population interact with each other and with their environment according to sets of rules, such that complex system-level properties emerge

from the simpler behaviour of individuals (Railsback 2001). Organisms display behaviours that improve their potential fitness (defined as an organism's ability to reproduce successfully); the modeller needs to consider which processes drive expected survival and reproduction and are important enough to include in the model (Railsback 2001). This avoids the pitfalls of using an "average" individual, and makes the model more realistic or natural (Matsinos et al. 1994). Furthermore, the individual-based approach avoids the use of complex differential equations to simulate natural phenomena (Railsback 2001). IBMs are usually spatially explicit, with the habitat or environment represented by cell objects possessing abiotic (for example water temperature, flow) and biotic (such as food availability) attributes (Matsinos et al. 1994). Spatially explicit modelling allows patterns to be quantified and linked to ecological processes and mechanisms (Matsinos et al. 1994). Ecological processes can be modelled at different scales, depending on the purpose of the model. This echoes the approach of "hierarchical reductionism" in understanding complex systems, which advocates breaking an object or system down to the level needed to understand how it works (Dawkins 1986). For example, the objective of the model may be to simulate individual birds (for example Matsinos et al. 1994), which feed on fish; the fish do not need to be individually modelled and could be modelled at a coarser scale (Mooij and Boersma 1996).

7.1.3 Modelling and adaptive management

Currently, there is a perception that "adaptive management has been more influential as an idea than as a practical means of gaining insight into the behaviour of ecosystems utilized and inhabited by humans" (Lee 1999). Criticism has been levelled at the adaptive management paradigm, for having had limited practical success (Johnson 1999b). While institutional barriers and inertia pose the greatest threat to its successful implementation (Walters 1997, Walters *et al.* 2000), additional criticisms include too much focus on the models while ignoring the problems, scale linkages between different models (Walters 1997; Jewitt and Görgens 2000b), and the definition of appropriate goals (Johnson 1999a). Jewitt and Görgens (2000a) highlight that for a fish modelling exercise that was part of the management programme of the Kruger National Park, the main challenge centred on issues of scale and interdisciplinary collaboration.

Models approximate the real world (Beven 2001), and therefore function as hypotheses or problem-solving tools (Starfield and Bleloch 1991; Starfield 1997) for stimulating thinking about a system. Hilborn and Mangel (1997) envisage four components to the modelling process, viz. a set of hypotheses; "good" data; a goodness of fit (how well the description of the world fits the observations); and numerical procedures to explore the goodness of fit of other models. Models should not be seen as the definitive understanding of a system, but rather as tools that help to expose gaps in the data, screen policy options (Walters et al. 2000), and predict the probable consequences of management actions (Quinn 1998). This is of greatest significance under conditions where time is limited and systems are sensitive (Walters et al. 2000). Indeed, "models are nothing but simple theories about the cause of observed patterns" (Scheffer 1999). While model outputs may approximate the real world situation (i.e. there is significant correlation between observed and simulated data), it is important that the mechanisms underlying the model output are also correct (Scheffer 1999; Beven 2001; Snowling and Kramer 2001), which allows for greater confidence when transferring a model to another situation. A model is most useful to natural resource managers if its inputs can be coupled with different scenarios, and the outputs compared against a meaningful threshold.

Newton's first rule of hypothesizing, which states that "we are to admit no more causes of natural things such as are both true and sufficient to explain their appearances" (Forster 1998), and the application of Occam's razor¹ (Forster 1998), reinforce the idea of parsimony, and should guide model development.

Simple, pragmatic models that require relatively fewer parameters than complex models (Jeppesen and Iversen 1987) form a basis for more complex models that are designed to promote management. In this way, suites of relatively simple models can be added together into a "tool-box" of decision-making techniques. However, bringing together different models at different spatial and temporal scales is a daunting task, and involves finding common units, such as fish habitats (biotic models) and geomorphological units (abiotic models) (Jewitt and Görgens 2000b). Lessons learned during the course of a research programme in the Kruger National Park that lasted several years were that in order to achieve efficient interdisciplinary collaboration, model detail may be sacrificed to

¹ Ockham (1285-1347) -"Entities are not to be multiplied beyond necessity"

allow scientists from different disciplines to work within a common framework, at compatible scales, to understand broad-scale catchment patterns (Jewitt and Görgens 2000a). Such an approach has also proved to be useful in highlighting certain management issues within the Colorado River ecosystem (Walters *et al.* 2000), where a suit of small models at multiple temporal and spatial scales were used to assist scientists and managers in "measuring" system response under different scenarios.

The idea of management as a "game" involving different roleplayers, can reveal important general patterns of system behaviour, as illustrated by the "Nonpoint" model developed by Carpenter *et al.* (1999). This simple system model involving few roleplayers, serves to show the interaction between fast and slow variables (multiple time scales), and illustrates that continual learning is crucial for maintaining sustainability in ecosystems.

Finally, model development should be driven by the objectives of the management programme, rather than the available data (Starfield and Bleloch 1991). "In a decision-making context, the ultimate test of a model is not how accurate or truthful it is, but only whether one is likely to make a better decision with it than without it" (Starfield 1997). Thus, the management objectives define the temporal and spatial scales at which a model is developed, with the recognition that the scale of application can restrict the generality and utility of the findings (Lovell et al. 2002). Dominant processes and physical laws change with scale, and thus observations should be made at the scales at which the processes and physical laws are taking place (Lovell et al. 2002). Generic solutions to environmental problems seldom exist, and there should preferably be long-term environmental management programmes, especially in areas with variable climatic or environmental conditions, where short projects may fail to detect processes occurring over longer time scales (Lovell et al. 2002).

7.2 The *Chiloglanis* modelling system

One of the management goals of the Kruger National Park is the maintenance of biodiversity (Rogers and Bestbier 1997). Central to achieving this goal in the adaptive management process is that the rivers of the Kruger National Park conform to a desired future state. Maintaining this state is facilitated through TPCs (cf. Sections 6.1.1-2), which in turn can be monitored using suitably chosen biological indicators. As discussed in Chapter 6, a TPC was

suggested for river temperature in the Sabie River, with two species of Chiloglanid fish chosen to act as indicators of this TPC.

7.2.1 Objectives and conceptual approach

The aim of the *Chiloglanis* modelling system is to provide river managers working within the Sabie catchment with a tool to establish whether the annual water temperature TPC, as defined in Chapter 6, is being exceeded. The importance of water temperatures to aquatic organisms was highlighted in Chapter 4, where water temperatures were shown to be the primary abiotic process determining species distribution patterns within the rivers of the Sabie catchment.

The broad vision of the Kruger National Park requires that managers "maintain biodiversity (sensu Noss 1990) in all its natural facets and fluxes and to provide human benefits in keeping with the National Park, in a manner which detracts as little as possible from the wilderness qualities of the KNP" (Braack 1997). Since biodiversity was identified as being important to maintain, deterioration in the "quality" of water temperatures (both heat units and variability) would pose a threat to such a vision; appropriate management of issues surrounding water temperatures should therefore emerge as a key pillar of any management programme. It was suggested in Chapter 5 that Chiloglanids are suitable indicators of water temperature as an agent of change, having the potential to provide an integrative perspective on changing water temperatures. It was further demonstrated that the presence or absence of these fish could be directly linked to the degree of heating within the Sabie River (cf. Figure 6.5). Biological indices, such as the condition of Chiloglanis anoterus, and the ratio of the relative abundances of C. anoterus to C. paratus, could therefore be used as surrogate measures (or indicators of the agents of change) of TPC exceedance.

Models using such biological indices can be developed to provide a measure of ecosystem functioning (Quinn 1998). In this context, the most pragmatic approach in designing a modelling system using biological indices to assess river state was to integrate a suite of models at different temporal scales, with the potential to draw on many of the ideas described in Section 7.1.2. The model system makes use of simulated daily maximum water temperatures (cf. Section 7.2.3), and simple cause-and-effect relationships at an

annual time scale (cf. Section 7.2.4), and links abiotic drivers to biotic responses. Such a modelling system complements the existing abiotic-biotic models already developed for the Kruger National Park (Weeks et al. 1999; Mackenzie et al. 2000).

To be useful to river managers, this modelling system was developed with the intention of predicting changes in the (a) distribution (as a ratio of relative abundances) of *C. anoterus* (cool water species) and *C. paratus* (warm water species); and (b) condition factor of *C. anoterus*, in response to changing water temperatures for the lowveld section of the Sabie River (downstream of 80km from the headwaters) (cf. Section 6.4.3). The simulated and observed ratios and conditions can be compared, as part of the monitoring process for checking TPC exceedance of annual water temperatures.

7.2.2 Conceptual Chiloglanis modelling system

A necessary first step in developing an objective model, which is common to many modelling approaches, and in accordance with the approach of Mackenzie *et al.* (2000), was to develop a conceptual model of the "entire system world" of Chiloglanids in the Sabie River, which incorporated the main system components and interactions (Figure 7.1). As expressed by Mackenzie *et al.* (2000), "this approach promotes a large multipurpose model that reflects as much of the system dynamics as possible" (p. 39).

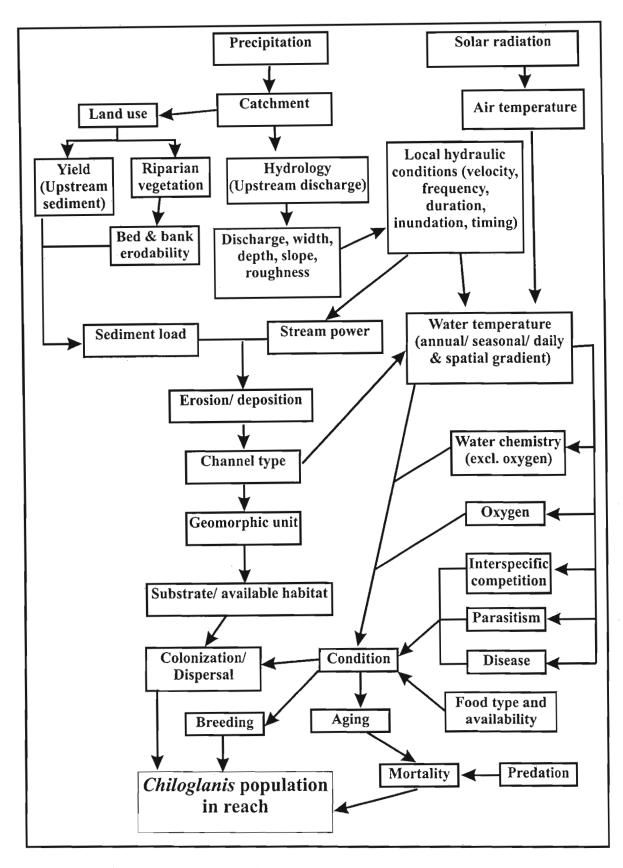


Figure 7.1 "Entire system" model world of Chiloglanis

It was stressed in Chapter 2 that water temperatures provide a measure of the interplay between numerous drivers and buffers at different spatial and temporal scales. Flow volumes and flow velocities are the only directly controllable parameters for indirectly managing water temperatures, which are in turn affected by factors such as impoundments, sedimentation and canalisation. Thus, water temperatures are an indirect measure of these variables. While various environmental variables acting together explain the species patterns observed in the Sabie River (Chapter 4), it has been shown that relative abundances of fish within the Sabie River changed with the downstream water temperature gradient of the Sabie River (cf. Figure 4.6). This is additionally illustrated in Figure 7.2, which shows the May 2001 relative abundances of *C. anoterus* and *C. paratus* versus mean annual water temperature in the Sabie River. Relative abundance curves of both species peaked at different mean annual water temperatures.

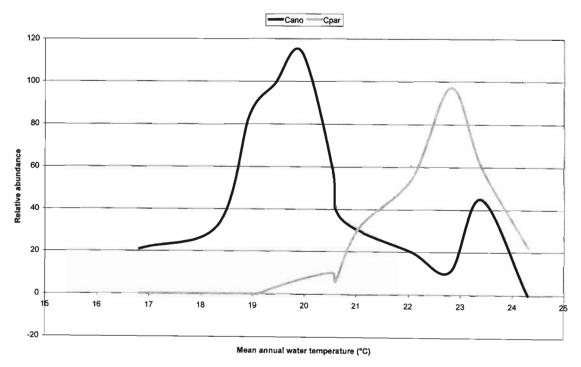


Figure 7.2 Correlative relationship between relative abundances of *C. anoterus* (Cano) and *C. paratus* (Cpar), and mean annual water temperatures in the Sabie River.

Water temperature is a habitat component that changes along the downstream axis of a river. Critical water temperature thresholds (MWATs) for *C. anoterus* and *C. paratus* were calculated to be 25.0°C and 26.4°C respectively (*cf.* Equation 6.1). The cumulative annual frequency of exceedance of the seven-day moving average of daily maximum water temperatures by these values was calculated for the period 1 June 2001 to 31 May 2002. In order to illustrate that thermal habitat quality for *C. anoterus* and *C. paratus* is different along the longitudinal axis of the Sabie River, these were plotted as a function of downstream distance from the headwaters of the Sabie River. Using this approach, the

Sabie River was divided, on a qualitative basis, into areas of "good", "marginal" and "poor" thermal habitat quality, for both Chiloglanid species (Figures 7.3-4). These graphs illustrate that "good" thermal habitat occurs further upstream in the Sabie River for *C. anoterus* than for *C. paratus*.

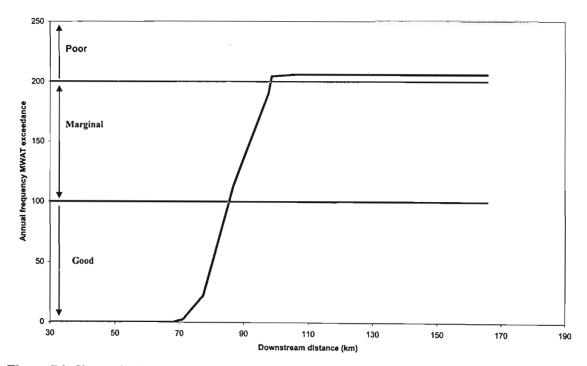


Figure 7.3 Change in thermal habitat quality with downstream river distance on the Sabie River for *C. anoterus* (modified from Poole and Berman 2001)

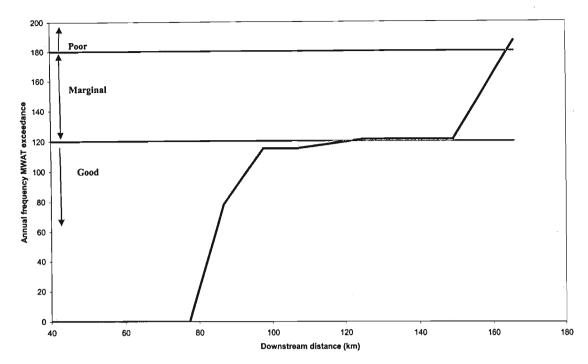


Figure 7.4 Change in thermal habitat quality with downstream river distance on the Sabie River for C. paratus (modified from Poole and Berman 2001)

A primary objective of this research was to provide a problem-specific model producing "a predictive output usable by managers within their operational framework" (Mackenzie et al. 2000, p.41). To this end, the entire system model (Figure 7.2) was "passed" through a TPC-filter (sensu Mackenzie et al. 2000), as a means of highlighting which components were fundamental in establishing a pragmatic conceptual model of the relationships between C. anoterus and C. paratus and water temperature, such that model input, output and internal processes are simplified in order to serve the proposed TPC directly, with the proviso that input and internal functioning are scientifically defensible (Figure 7.5). To keep this model as parsimonious as possible, it was assumed that biotic effects, such as competition and disease, were non-significant.

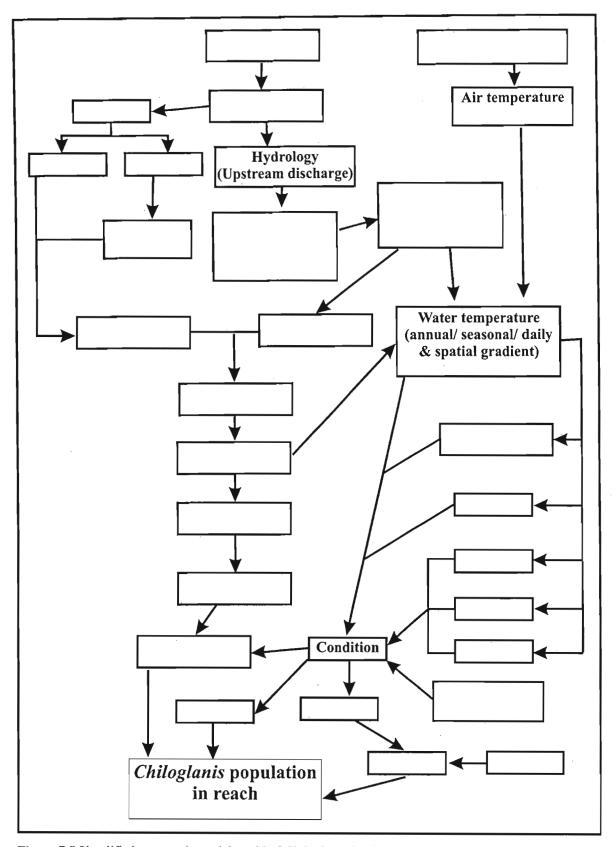


Figure 7.5 Simplified, pragmatic model world of Chiloglanis, having been "passed" though a TPC filter

The resulting pragmatic modelling system builds on the relationships between annual water temperatures and fish considered in Chapters 4, 5, and 6. The biotic component of this modelling system operates at an annual time step, and is spatially explicit, with the Sabie River being divided into thermal reaches. The inputs and outputs of this modelling system, together with the model components and processes, are summarized in Figure 7.6. A flowchart of model processes occurring within selected reaches of the Sabie River, together with associated temporal resolutions, is provided in Figure 7.7. Maximum daily water temperatures are simulated at a daily time step, using a multiple linear regression model derived in Chapter 3. This model, and the derivation of the abiotic inputs used to drive it, is discussed in Section 7.2.3. Output from this model is scaled up into annual water temperature parameters, which are used as inputs in correlative cause-and-effect biotic relationships (cf. Section 7.2.4). This sacrifice in detail, as mentioned in Section 7.1.3, was necessary to enable the output of the water temperature model to be compatible with the Chiloglanis biotic response model.

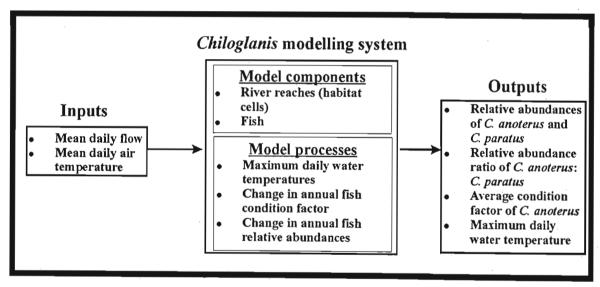


Figure 7.6 Overview of Chiloglanis modelling system inputs and outputs

At this stage, the different model components are encoded within the MS-Excel spreadsheet system. Calculations and simulations were performed using equations and Visual Basic macros. Further options for development include the development of an object-oriented system (cf. Section 7.4).

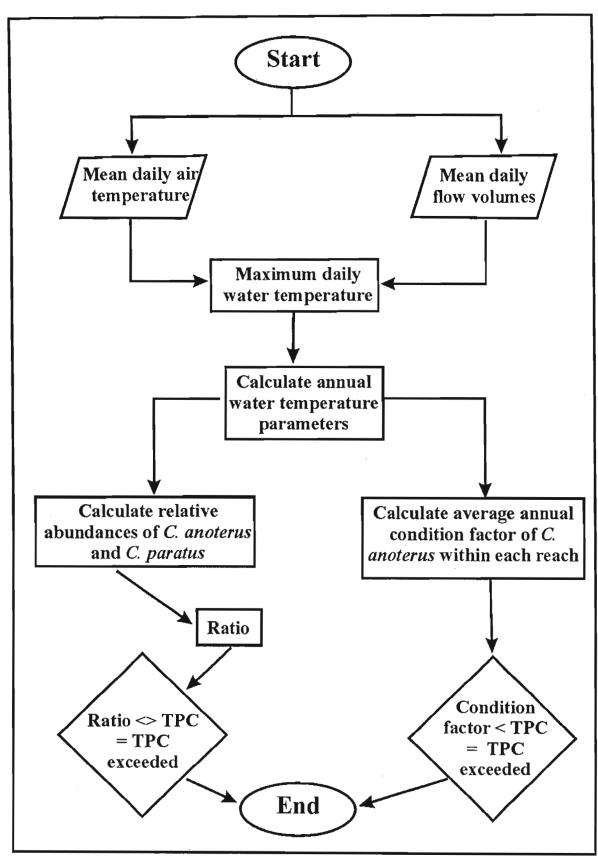


Figure 7.7 Flowchart of biotic response within each thermal reach for the Chiloglanis modelling system

7.2.3 Derivation of daily maximum water temperatures: The abiotic inputs

Physical conditions change constantly over space and time, and to be understood need to be considered at the smallest practical time step. As shown in Figures 7.6 and 7.7, the abiotic inputs to the water temperature model are mean daily air temperatures, and mean daily flow volumes. A multiple linear regression model (Equation 3.21) was used to simulate maximum daily water temperatures, based on inputs of mean daily air temperatures and mean daily flow volumes. Daily maximum water temperatures were simulated at two sites on the Sabie River (WT4 and WT7), which were identified as being relevant to the TPC defined in Chapter 6 (cf. Section 8.2.2).

Mean daily air temperatures for the period 1950-1995 were calculated from maximum and minimum daily air temperatures, extracted from a database of air temperatures for the period 1950 to 1995 (Maharaj and Schulze 2003). Each air temperature time series extracted, and later used in the water temperature model, applies to a degree minute grid, with the coordinates corresponding to the position of each water temperature logger. These daily air temperature values were largely based on observed data, with missing values being patched from adjacent meteorological stations based on weighted values of distance and altitude. In the absence of these data, harmonic analyses were used to fill in missing values.

Since observed flows were not readily available for this corresponding time period at each water temperature site, simulated mean daily flows (m³.s¹) were used in the water temperature model. Mean daily flows at critical sites (WT4 and WT7) were simulated for the period 1950 – 1995, using the ACRU agro-hydrological model (Schulze 1995). This is a daily time step, physical conceptual model that revolves around multi-layer soil water budgeting. It is **conceptual** in that it conceives of a system in which important processes and couplings are idealized, and **physical** in that physical processes are represented explicitly. In large catchments, such as the Sabie, ACRU is applied as a distributed cell-type model. Using this approach, a catchment is subdivided into smaller subcatchments, corresponding to land use and soil types; flows occur according to a pre-determined scheme (Schulze 1995).

The ACRU model has previously been configured, and verified by Pike and Schulze (2000) for use in the Sabie catchment, which was subdivided into 56 subcatchments. Land use was designated as "natural", being based on the Acocks veld types for South Africa (Acocks 1988). These land use categories were used within the ACRU model to simulate reference

mean daily flow volumes for use in the water temperature model, rather than current land use categories, which do not reflect historical land use patterns. In this simulation exercise, the primary concern was to determine the degree to which Chiloglanid fish were responding to changes in annual water temperatures over a forty-five year period under different environmental scenarios (cf. Chapter 8). Thus, the land use type chosen was of secondary importance to this exercise. The aim was also to simulate reference water temperatures, which approximated natural conditions, and consequently a decision was taken to use the Acocks (1988) veld types rather than current land use.

7.2.4 Linking abiotic drivers to biotic response

Although individual fish are exposed to constantly varying river temperatures, mean fish population performance is usually of interest to the researcher. Eaton and Scheller (1996) suggested that a weekly time scale should be adequate to assess changes in fish habitat. Such a temporal scale was not practical for this model, which was based on data collected from annual electrofishing surveys. This constraint dictated that biotic outputs operate at an annual timescale, where the Chiloglanids are assumed to be responding to an annual accumulation of water temperatures exceeding a threshold value.

Cause-and-effect relationships between annual water temperature metrics, and condition and relative abundances, are pragmatic approaches to measuring the exceedance of the water temperature TPC. Note that a correlative relationship does not necessarily reflect a causative relationship. The relationships act as hypotheses, which represent the best understanding of the system, as it relates to water temperatures. Daily maximum water temperatures were aggregated into annual (1 June – 31 May) metrics, on a site-by-site basis:

- Mean annual maximum water temperature;
- Annual frequency of exceedance by the 25°C MWAT for *C. anoterus* of the seven-day moving averages of daily maximum water temperatures.

These measures were used as causative drivers for predicting the average condition factors of adult populations of *C. anoterus* within a reach (Section 7.2.4.1), and relative abundances of *C. anoterus* and *C. paratus* (Section 7.2.4.2), within a biotic response model. The development of these relationships is described in the following sections.

7.2.4.1 Change in condition factor of *C. anoterus* with change in water temperature

The average condition factor of *C. anoterus* populations within the Sabie River was correlated with MWAT exceedance, based on change in condition and MWAT exceedance with downstream distance on the Sabie River (Figure 7.8). Condition factors were rescaled from length to mass ratios to percentage values of condition factor, with condition factors (length to mass ratio) at the top of the Sabie River being rescaled to 100%. The average condition of the adult population of *C. anoterus* for any reach can thus either be changed on a qualitative basis (good, fair and poor) according to a cause-and-effect relationship, or on a continuous basis, based on percent condition, as used in this model.

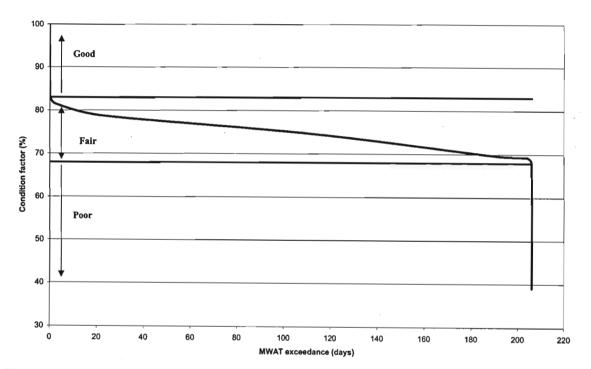


Figure 7.8 Correlative relationship between cumulative annual exceedance of a 25°C MWAT and mean percentage condition factor of adult *C. anoterus* populations

7.2.4.2 Change in relative abundance of Chiloglanids with change in annual water temperature

Cause-and-effect relationships between annual fish relative abundances and metrics of annual water temperatures were defined for *C. anoterus* and *C. paratus*. It is recognised that the incomplete overlap between water temperature time series and relative abundances from electrofishing surveys potentially weakens these relationships. These discrepancies were a result of logistical constraints of this study, as discussed in Chapter 1.

Observed relative abundances of *C. anoterus* peaked at 80-90 kilometres downstream of the headwaters. Above this point, MWAT exceedance was zero, so that other environmental and/or biotic variables, such as water temperatures being too cold, may be determining abundances. MWAT exceedance became critical downstream from this point, as discussed in Section 6.4.2. In terms of the water temperature TPC, the critical length of river is downstream of 80 kilometres from the headwaters, such that the MWAT-abundance correlation is adequate for the management purposes of this model.

It was assumed that while the pattern of daily maximum water temperatures may vary between years, the frequency of annual MWAT exceedances based on a seven-day moving average of daily maximum water temperatures would remain relatively stable between years on a short-term basis, which would ameliorate this incomplete overlap of data. Given this assumption, it was possible to correlate relative abundances of *C. anoterus* for May 2001 with MWAT values for an annual exceedance of MWAT ending on 31 May 2002.

A relationship between MWAT (25°C) and relative abundances of C. anoterus provided a good correlation ($R^2 = 0.86$), and was chosen as the cause-and-effect relationship to simulate changes in the relative abundances of C. anoterus in response to changes in annual water temperatures (Figure 7.9), since this relationship incorporates a measure of cumulative heat over the preceding year. This correlative relationship (Equation 7.1) was based on a combined dataset of relative abundances of C. anoterus for the May 2001 and May 2002 electrofishing surveys, versus an annual frequency of MWAT exceedance for the period 1 June 2001 to 31 May 2002, as calculated from Equation 6.4 (Section 6.3, Chapter 6).

It is recognised that the strength of this relationship appears to depend on the leverage of a single data point (the maximum relative abundance value for *C. anoterus* from the May 2001 electrofishing survey), which occurred at a downstream distance of 86 kilometres. However, based on the October 2000 and 2001 electrofishing surveys, in addition to the May 2001 survey (*cf.* Figures 6.3a,b), this point is relatively persistent, with the relative abundance curves having peaked between 71 and 97 kilometres downstream throughout the survey period. Relative abundances decreased substantially between 97 and 106 kilometres downstream, based on the May and October 2001 survey data, and between 71

and 106 kilometres, based on the October 2000 survey. This reach coincides with the critical thermal reach identified in Section 6.4.3. Additional electrofishing surveys within the 71 - 106 kilometre reach of the Sabie River would add to the strength of the relationship in Figure 7.9.

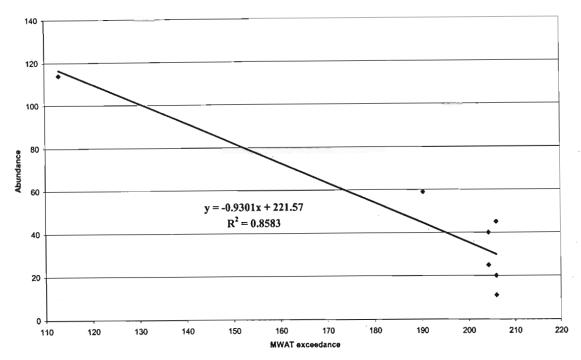


Figure 7.9 Relationship between cumulative annual exceedance of a 25°C MWAT and relative abundance of C. anoterus

$$RA_{Cano} = -0.93*MWAT + 221.57 [7.1]$$

where RA_{Cano} is relative abundance of C. anoterus.

The relationship between C. paratus relative abundances and water temperature is uncertain; consequently it was not possible to link the 26.4°C MWAT to relative abundances. It is possible that cold winter temperatures are impacting on population numbers. Mean maximum annual water temperatures for the period 1 June 2001 to 31 May 2002 were regressed against downstream distance ($R^2 = 0.95$), and mean maximum annual water temperatures predicted for downstream distances using this relationship. A five-point cause-and-effect relationship, based on mean maximum annual water temperatures, was chosen for C. paratus (Figure 7.10). Relative abundances of C. paratus, based on the May 2001 electrofishing surveys, were correlated with the mean maximum annual water temperatures corresponding to each fish survey site.

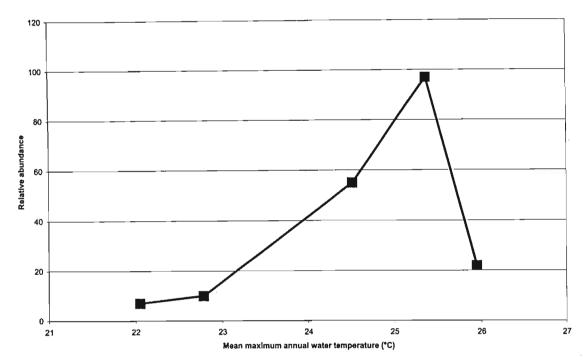


Figure 7.10 Relationship between mean maximum annual water temperature and relative abundance of *C. paratus*

Outputs from the water temperature and biotic response models, which together constitute the "Chiloglanis modelling system", are discussed in detail in Chapter 8.

7.3 Potential for future development

One of the problems with model development is that it is often site specific: Reitsma and Carron (1995) report that fish habitat studies of the Colorado River have shown different empirical relationships between flow and habitat suitability for different sections of the river for the same species of fish. What is true for the Colorado River is also likely to be true for the Sabie River, which remains a weakness of this model. Taking the existing relationships and components, and developing them as an object-oriented application, would improve this model by providing the scope for being applicable at different sites. In spite of providing the same outputs as those from the spreadsheets, an object-oriented model would be more spatially explicit, and would have the capability of coping with site-specific differences. There would also be a more seamless integration of the different models used with the *Chiloglanis* modelling system.

Additionally, an object-oriented design of the *Chiloglanis* modelling system would allow for expandability, such that additional relationships and classes could be added in the future. Should more suitable cause-and-effect relationships emerge with subsequent research, these could be substituted into the model code with relative ease. As with the Nonpoint model of Carpenter *et al.* (1999) referred to in Section 7.1.3, it could be used as a game to stimulate discussion between scientists and managers through the inclusion of different management options and societal values. This would greatly increase the utility value of this model as a tool within the adaptive management framework outlined by Rogers and Bestbier (1997).

According to the object-oriented approach described in Section 7.1.2, different model components could be represented as different classes, arranged in a logical hierarchy. A class contains the structure of an object (an instance of a class) plus a set of procedures for initialising and using it. Inherent in a class are the concepts of inheritance and hierarchy (Silvert 1992; Matsinos *et al.* 1994). In the case of the *Chiloglanis* model, biotic model classes could be designed according to the hierarchy illustrated in Figure 7.11. Classes should be arranged from the broadest, most abstract level ("Organism"), to the most specific level relevant to this model (species-specific age cohorts). These could be further subdivided into actual individuals, whereupon the model would be classed as an individual-based model (IBM). Using this approach, this model is generic enough to be readily convertible between different ecosystems with different sets of drivers and problems.

Associated classes within this hierarchy include those of birth and death rates, and preferred habitats. The inheritance relationships reduces redundancy in coding, since classes lower down the hierarchy inherit attributes and methods common to parent classes. Specific characteristics apply to specific "child" classes, which can be "instantiated" (i.e. by creating unique objects, which are "instances" of a class) to make numerous, unique objects. The associations between the classes are of two types viz. "type of" (arrows), so that objects lower down the hierarchy inherit all the attributes of the objects higher up the hierarchy, and "part of" (diamonds), where objects (relationships, data and processes) not directly part of the hierarchy may be associated with different classes.

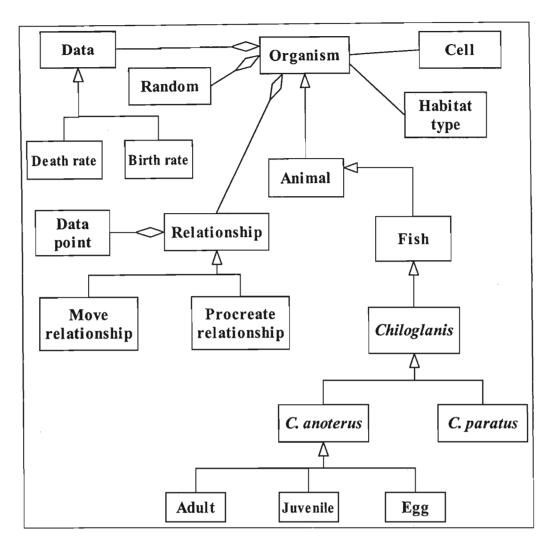


Figure 7.11 Hierarchy of biotic classes within proposed object-oriented Chiloglanis modelling system.

Similarly, spatial units could be arranged hierarchically, as illustrated in Figure 7.12. In this case, classes range from an abstract spatial unit ("Cell") to a specific habitat type. Each class is associated ("part of") with abiotic processes ("Abiotic drivers"), together with different management options ("Management decision") at different scales, which makes provision for the "gaming" element. The fish objects interact with habitat objects through the "part of" associations.

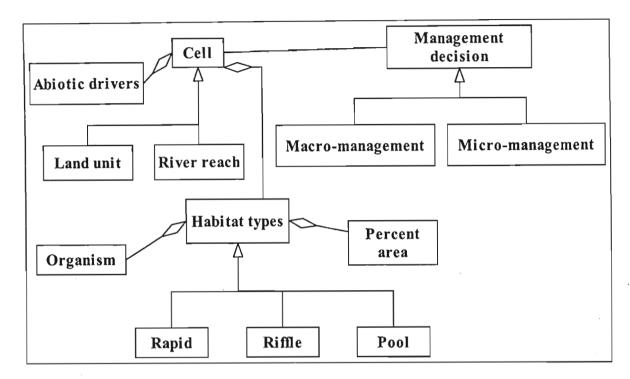


Figure 7.12 Hierarchy of environmental classes within proposed object-oriented *Chiloglanis* modelling system.

The use of objects with inheritance makes it possible to create locale-specific definitions, with different objects representing different locales. The Sabie River could be divided into cells (reaches), with the cell neighbourhood being made up of upstream and downstream cells only (Figure 7.13), together with relevant associated information. Each cell "owns" habitats, and the fish live within the habitats. Output from these cells could be spatially represented as a shapefile, where each cell is associated with a polygon.

At this stage, the additional coding complexity necessary to achieve the same output achieved using MS-Excel spreadsheets did not justify the object-oriented approach. Subsequent research and extended data would make such a conversion worthwhile.

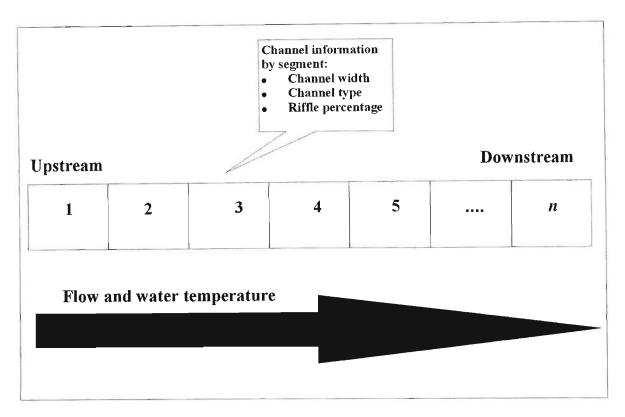


Figure 7.13 Cell-based approach to modelling fish response to seasonal water temperature in the Sabie River

* * * * *

In this chapter, three separate correlative relationships were developed to simulate the mean conditions of *C. anoterus* populations within any particular reach of the Sabie River, and the ratio of *C. anoterus* to *C. paratus*, in response to changes in annual water temperatures. Their potential for future development within a more generic, object-oriented approach was also outlined. The results of the water temperature model, together with their output in the correlative relationships, relative to recommended critical biological thresholds relating to a water temperature TPC, are discussed in Chapter 8.

8 APPLICATION OF THE CHILOGLANIS MODELLING SYSTEM

8.1 Introduction

There is always uncertainty in modelling: Is the model valid (is the numerical solution close to the analytical solution i.e. does the code produces output which is logical)?; Can the simulations be verified (is model output consistent with observed data)? Ultimately, the usefulness of a model is judged on the extent to which it has added to the quality of a management decision. The effectiveness of the biological indices developed in Chapter 6, as a river management tool, is evaluated relative to surrogates for the TPC for annual water temperatures in the Sabie River. This is achieved through the application of the conceptual *Chiloglanis* modelling system discussed in Chapter 7.

8.1.1 Adaptive management and model complexity

Models may be divided into different categories based on their levels of complexity, as well as how they simulate real-world processes. Jewitt (1998) re-emphasised the classification of models into either stochastic or deterministic categories. Deterministic models are further subdivided, based on their levels of mathematical complexity. Mechanistic models involve complex mathematical equations, and are often process-based. Models such as these were discussed in Chapter 3, for modelling water temperatures using complex differential equations. At the opposite end of this spectrum of mathematical complexity are qualitative rule-based models (QRBMs), which were discussed in Chapter 7. Such models make use of simple "If...then...else" rules, or simple cause-and-effect relationships. However, in spite of such apparent simplicity, complex patterns may still be simulated.

Wagenet and Rao (1990, cited in Snowling and Kramer 2001) divide models into 3 basic groups:

- Research models (complex);
- Management models (less complex);
- Screening models (relative comparisons).

Complex (research) models generally have more parameters and variables, and therefore require more data, than simpler (management) models, which often have more simplifying

assumptions. Models of increasing complexity are difficult to validate, since it is often difficult to unambiguously falsify their output. A fundamental reason for choosing a simpler model is that typically data requirements increase with added complexity (Snowling and Kramer 2001). The increased cost of a more complex model may outweigh any benefits, such as greater accuracy, gained through greater model complexity.

As discussed in Chapter 7, management decisions are often taken under conditions of uncertainty and imperfect data. In these cases, models act as hypotheses based on the current level of system understanding, and facilitate discussion surrounding the consequences of different environmental scenarios and management actions. Such models should be relatively simple to use, yet be grounded on research, since the users of these models are often more concerned with trends and orders of magnitude, which can be simulated with confidence, than with high levels of accuracy in simulations.

8.1.2 Aims of Chiloglanis modelling system

The main aims for the development of the *Chiloglanis* modelling system were threefold:

- To provide an objective basis for testing the proposed water temperature TPC using the two biotic indices (ratio and condition) proposed as hypotheses in Chapter 6.
- To provide river managers with a tool to "measure" the effects of changes in annual water temperatures, by simulating the response of two indicator species of fish to the cumulative effects of daily maximum water temperatures over the preceding year, within a critical thermal zone identified in the Sabie River (Chapter 6).
- To generate questions regarding the links between water temperature processes and biotic patterns.

These aims determined the temporal scale of this model, viz. the use of daily inputs that were aggregated into annual metrics to provide an output at an annual time step (cf. Chapter 8). An overarching assumption was that the chosen fish species were responding in a predictable way to changing environmental conditions, which has been discussed in greater detail in Chapter 6. This necessitated quantifying the predictability, or level of cyclical constancy, of the simulated water temperatures, and examining how this changed

with downstream distance. Additionally, the level of predictability between the Marite, Sand and Sabie Rivers, was also compared.

8.2 Methods for assessing the "level of predictability" of water temperature data, and application of the *Chiloglanis* modelling system under different environmental scenarios

The methods were defined in terms of the following two questions:

- How predictable has the thermal regime of the Sabie River been for the period
 1950 to 1995;
- Given a predictable biotic response to "unpredictable" abiotic conditions, how
 useful are the indices of fish response (condition and ratio) to measures of
 annual water temperatures within the TPC zone defined in Section 6.4.2?

Methods were therefore divided into two sections, viz. a quantification of predictability of the daily maximum water temperature regime (Section 8.2.1), and simulating fish response to these water temperatures using the correlative relationships between water temperatures and fish abundance and condition, as defined in Section 7.4.3 (cf. Section 8.2.2).

Model verifications and validations were not explicitly undertaken. The reasons for this are discussed in Section 8.4.2.

8.2.1 Colwell's indices of predictability

Colwell's indices (Colwell 1974) were selected to quantify the predictability of the thermal regime of the Sabie, Sand and Marite Rivers. These indices classify temporal patterns into a measure of predictability, based on the degree of constancy (the system – a river – is the same for all seasons) and contingency (the state of the system is different for each season; but the pattern is the same for all years). Therefore, a high level of predictability is achieved due to either a high degree of constancy or contingency (Colwell 1974). The predictability of any periodic phenomenon is maximal when there is complete certainty with regard to state for a point in time, such as when a tree will be in flower (Colwell 1974). These indices were used by Vannote and Sweeney (1980) to quantify the predictability of a river system in the United States based on daily average river

temperatures over a ten-year period. For this particular system, it was found that "natural stream systems exhibit a pattern of 'predictable variability' with respect to temperature".

In this assessment, simulated daily maximum water temperatures for nine sites in the Sabie catchment were reclassified into water temperature classes (Table 8.1). These were based on n successive standard deviations on either side of the mean for observed water temperatures collected from February 2001 to March 2003 in the Sabie catchment at site WT9 (cf. Chapter 2). This site was specifically chosen, since it exhibited the least variability of the nine sites where water temperatures were collected, which thus allowed for conservative temperature class sizes to be defined.

Table 8.1 Water temperature classes used to reclassify simulated daily maximum water temperatures, based on observed mean and standard deviation values for site WT9 on the Sabie River

Class	Upper	Lower		
1	> 34.04			
2	34.04	32.01		
3	32.01	29.98		
4	29.98	27.95		
5	27.95	25.92		
6	25.92	23.89		
7	23.89	21.86		
8	21.86	19.83		
9	19.83	17.8		
10	17.8	15.77		
11	15.77	13.74		
12	13.74	11.71		
13	< 11.71			

A basic requirement of any data for use in Colwell's indices, particularly involving phenomena with fixed lower bounds, is that the standard deviation and mean are uncorrelated (Colwell 1974). For example, with data that have a fixed lower bound (0), such as hydrological data, there is often a high correlation between mean and standard deviation. While in practice water temperatures do not generally have a fixed lower bound, these data

were tested for correlations between annual mean and standard deviation, since a high correlation between the mean and standard deviation necessitates a log transformation.

Time (columns) by state (rows) contingency tables, corresponding to the nine water temperature sites monitored during this study (WT1-5 and WT7-10) and based on simulated daily maximum water temperatures for the period 1950 to 1995, were calculated using two different approaches:

- The cumulative number of days of each month within different temperature classes;
- The cumulative number of successive days within the same temperature class for each month.

The former contingency tables were based on simple frequency counts. For the latter contingency tables, data were divided into months, and the cumulative numbers of days falling within the same water temperature class for each month were calculated, to provide twelve tables of state (columns) by the successive number of days within the same class (rows) for each site (an example of this is provided in Appendix A4). Row totals from each month were combined to form a single table for each site, with months as columns and successive number of days within the same temperature class as rows (states). In the case of these tables, twenty-eight states were defined.

Colwell's indices of predictability (p), constancy (c) and contingency (m) values were calculated for each site, based on the contingency tables. The percent contribution made to predictability either by constancy or contingency was calculated by dividing the predictability value by either index. The indices of predictability were also compared with the corresponding coefficients of variation for each site.

8.2.2 Application of *Chiloglanis* modelling system

Three broad scenarios of daily maximum water temperatures were predicted for each reach relevant to the TPC defined in Section 6.4.3 (i.e. WT4 and WT7) for the period 1951 to 1995 using a multiple linear regression water temperature model derived in Chapter 3 (Equation 8.1). These were:

- "Reference" conditions (Scenario 1);
- Daily maximum water temperatures assuming a two degree increase in mean daily air temperatures (Scenario 2);

 Daily maximum water temperatures assuming a ten percent reduction in mean daily flow volumes (m³.s⁻¹) (Scenario 3).

$$Wt_{max} = 6.121 + 0.793(Ta_{mean}) - 0.175(1/flow)$$
 [8.1]

Daily maximum water temperatures were aggregated into annual measures (1 June to 31 May; MWAT and mean annual maximum water temperature), which were necessary for the cause-and-effect relationships proposed to predict relative abundances of *Chiloglanis anoterus* and *C. paratus*, and an annual condition factor for *C. anoterus* (Chapter 7, Section 7.4.3). According to the proposed water temperature TPC defined in Chapter 6, the interpolations were only valid at river sites corresponding to the loggers at sites WT3, WT5, WT4, WT7 and WT8. Sites WT9 and WT1 were not simulated, since these sites fell outside the correlative bounds for these relationships. More specifically, the water temperature TPC corresponded to the reach of the Sabie River between sites WT4 and WT7, and consequently, *Chiloglanis* model simulations were for these two sites only. The annual frequency of TPC exceedance at each site for each scenario was calculated, based both on the condition index, and the ratio of *C. anoterus* and *C. paratus*. The effects of different water temperature scenarios were quantified by calculating the coefficients of variation for each index under each scenario.

8.3 Results

8.3.1 Predictability of water temperatures within the Sabie catchment

The correlation between the mean and standard deviation for the calculated water temperatures was non-significant ($R^2 = 0.2$). No transformations of the simulated water temperature data were necessary, and untransformed temperature data were consequently suitable for subsequent classification using Colwell's indices.

Contingency tables for each site showing the cumulative frequency of daily maximum water temperatures falling within each of the thirteen temperature classes (i.e. thirteen states) are given in Appendix A5. Contingency tables for each site showing the cumulative frequency of successive daily maximum water temperatures falling within the same water temperature class for each month (28 states) are given in Appendix A6. Colwell's indices for frequencies within each class (Table 8.2) and successive days within the same class (Table 8.3) suggest that the degree to which a system is classified as predictable depends on how system states were defined. Based on cumulative frequencies, all sites on the Sabie River, together with the site on the Marite River, had low predictabilities. Daily maximum water temperatures on the Sand River were half as predictable as the sites on the Sabie or Marite Rivers. However, while the coefficients of variation did not show any noticeable change between rivers with downstream distance, there was a downstream trend in the percentage contributions of constancy and contingency to the indices of predictability. The contribution of constancy to predictability decreased with downstream distance. In other words, the probability of water temperatures being found within any one state increased with downstream distance. Conversely, contingency increased with downstream distance. According to Colwell (1974), contingency is the degree to which time determines state, and is smallest when all columns are homogenous, or when system state is independent of the effects of seasonality; contingency is highest when the state of the river is different for each season, even though the pattern is the same for all years. In the case of the Sabie River, an increase in contingency with downstream distance suggests an increasing effect of seasonality with downstream distance. The Sand River showed a greater degree of unpredictability than the Sabie River, which is likely to be due to the differences in daily flow volumes (Figure 8.1), with the flow volumes being lower in the Sand River than in the Sabie River. The degree of predictability within the Sand River was largely (98%) due to constancy; i.e. the system state tends towards

the same class for all seasons, and seasonality does not play as big a role in the Sand river as it does in the Sabie or Marite Rivers.

Table 8.2 Colwell's indices, and corresponding coefficients of variation, based on the frequencies of number of simulated daily maximum water temperatures within each of thirteen classes for nine sites for rivers in the Sabie catchment

Site	Downstream distance (km)	Coefficient of variation		Constancy (c)	Contin- gency (m)	Contrib- ution of c to p (c/p)	Contrib- ution of m to p (m/p)
WT9	5.87	15.95	0.41	0.27	0.14	66.15	33.85
WT1	30.09	13.5	0.47	0.32	0.15	67.25	32.75
WT3	57.29	13.36	0.43	0.28	0.14	66.73	33.27
WT5	83.49	13.62	0.43	0.26	0.16	62.21	37.79
WT4	106.94	16.12	0.44	0.22	0.22	50.69	49.31
WT7	125.17	15.83	0.44	0.22	0.22	50.36	49.64
WT8	160.9	15.58	0.44	0.22	0.22	50.56	49.44
WT2	Marite	13.5	0.47	0.32	0.15	67.25	32.75
WT10	Sand	15.85	0.23	0.22	0.01	97.60	2.40

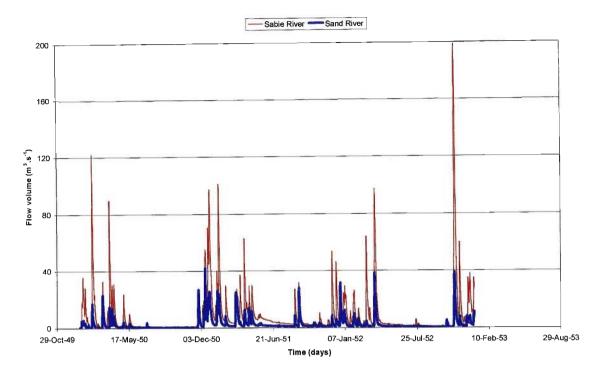


Figure 8.1 Simulated daily flow volumes (m³.s⁻¹) for the period 1950-1952 for the Sand and Sabie Rivers. This represents a subset of the flows for the period 1950-1995, to illustrate the differences in flow volumes between the Sabie and Sand Rivers.

Based on the indices of predictability using the frequency of successive days within the same temperature classes for each month (Table 8.3), predictability was similar for all sites in all rivers. Using this method of state classification, predictability was higher than the previous state classification system. In all instances, the greater determinant of predictability was constancy (98-99%), which did not show any trends between rivers or as a function of downstream distance. The constancy within the system was due to many of the frequencies falling within state one (Appendix A6), which is the state when one day's water temperatures do not fall within the same class as a previous day's water temperatures. Thus, water temperatures within the Sabie River, without exception, could be defined as "predictably unpredictable" using this second method of state classifications in conjunction with Colwell's indices.

Table 8.3 Colwell's indices, and corresponding coefficients of variation, based on the total number of successive days of daily maximum water temperatures within the same temperature class for each month of

the year for nine sites

the year for	Downstream	Coefficient	-	6 4	C	Contrib-	Contrib-
Site	distance	of	Predict- ability (p)	(c)	Contin- gency (m)	ution of c	ution of m
	(km)	variation				to p (c/p)	to p (m/p)
WT9	5.87	15.95	0.63	0.62	0.01	99.01	0.99
WT1	30.09	13.5	0.62	0.61	0.01	97.73	2.27
WT3	57.29	13.36	0.65	0.64	0.01	98.92	1.08
WT5	83.49	13.62	0.64	0.63	0.01	98.85	1.15
WT4	106.94	16.12	0.63	0.62	0.01	98.95	1.05
WT7	125.17	15.83	0.63	0.62	0.01	99.12	0.88
WT8	160.9	15.58	0.63	0.62	0.01	99.09	0.91
WT2	Marite	13.5	0.62	0.61	0.01	97.73	2.27
WT10	Sand	15.85	0.63	0.62	0.00	99.32	0.68

8.3.2 Biotic output from *Chiloglanis* modelling system

Simulated relative abundances of *C. anoterus* exhibited a high degree of variability in response to water temperatures for the period 1951 to 1995 for sites WT4 and WT7 (Figures 8.2-3). Increased water temperatures, due to either an increase in air temperatures or a reduction in flows, resulted in reduced, yet more variable, relative abundances of *C. anoterus*, as shown by the means and standard deviations of relative abundances respectively (Figures 8.4-5). Similarly, relative abundances of *C. paratus* exhibited a high degree of inter-annual variability (Figures 8.6-7). Relative abundances of *C. paratus* increased under conditions of increased water temperatures (Scenarios 2 and 3), in conjunction with an increase in standard deviations (Figures 8.4-5).

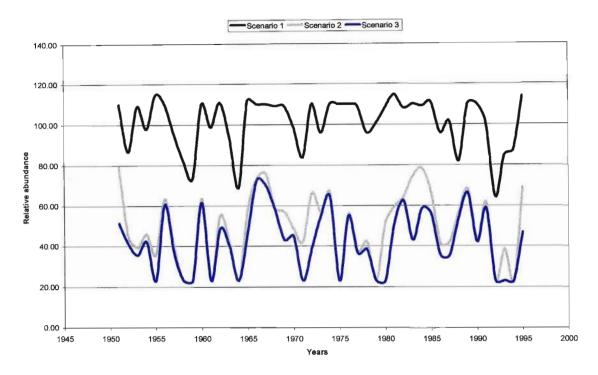


Figure 8.2 Relative abundances of *C. anoterus* at site WT4 for the period 1951 to 1995 for scenarios of 1) reference water temperatures; 2) 2°C increase in mean daily air temperatures; 3) 10% reduction in mean daily flow volumes.

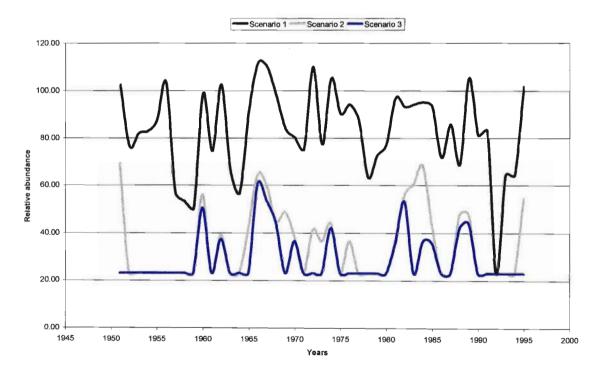


Figure 8.3 Relative abundances of *C. anoterus* at site WT7 for the period 1951 to 1995 for scenarios of 1) reference water temperatures; 2) 2°C increase in mean daily air temperatures; 3) 10% reduction in mean daily flow volumes.

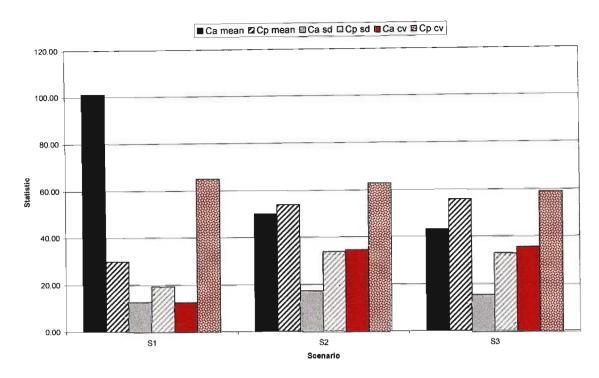


Figure 8.4 Differences between mean, standard deviation (sd) and coefficient of variation (cv) for *C. anoterus* (Ca) and *C. paratus* (Cp) at site WT4 for the period 1951 to 1995 for scenarios of 1) reference water temperatures; 2) 2°C increase in mean daily air temperatures; 3) 10% reduction in mean daily flow volumes.

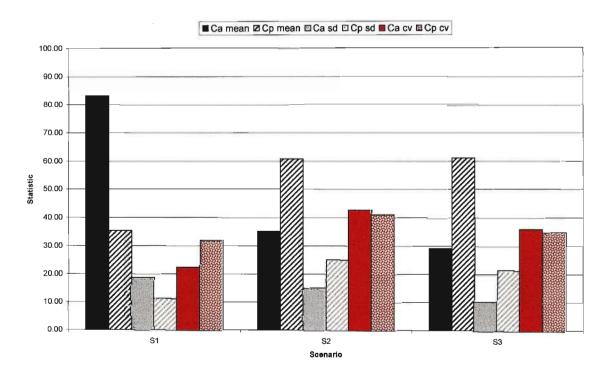


Figure 8.5 Differences between mean, standard deviation (sd) and coefficient of variation (cv) for *C. anoterus* (Ca) and *C. paratus* (Cp) at site WT7 for the period 1951 to 1995 for scenarios of 1) reference water temperatures; 2) 2°C increase in mean daily air temperatures; 3) 10% reduction in mean daily flow volumes.

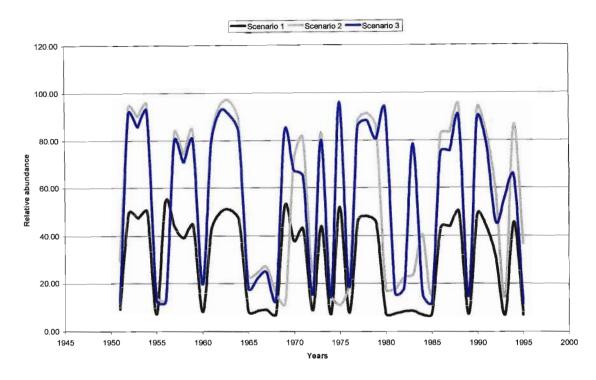


Figure 8.6 Relative abundances of *C. paratus* at site WT4 for three different scenarios of water temperatures for scenarios of 1) reference water temperatures; 2) 2°C increase in mean daily air temperatures; 3) 10% reduction in mean daily flow volumes.

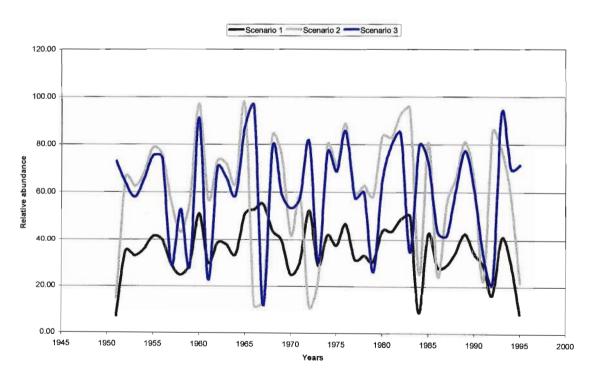


Figure 8.7 Relative abundances of *C. paratus* at site WT7 for three different scenarios of water temperatures for scenarios of 1) reference water temperatures; 2) 2°C increase in mean daily air temperatures; 3) 10% reduction in mean daily flow volumes.

Ratios of relative abundances of *C. anoterus* to *C. paratus* at sites WT4 (Figure 8.8) and WT7 (Figure 8.9), relative to surrogate measures of TPC exceedance (middle, upper and lower ratio bounds determined on a site-specific basis) showed that by using ratios of relative abundances of two species of fish with different water temperature tolerances, TPCs will be exceeded approximately fifty percent of the time under reference conditions (Figure 8.10). Raised water temperatures due to increased air temperatures (Scenario 2) or decreased flows (Scenario 3) resulted in an increase in TPC exceedance (Figure 8.10). Based on these simulations, periodic exceedance of the ratio threshold is to be expected, due to the variable nature of fish relative abundances. River health should be noted by management as deteriorating when these thresholds are exceeded for prolonged periods, as in the case of Scenarios 2 and 3. At both sites, it should be noted that the ratio of *C. anoterus* to *C. paratus* decreases under conditions of water temperature change. This is in agreement with the life histories and niche requirements of both species, as proposed in Chapter 4, viz.:

- Under conditions of river warming, *C. anoterus* retreats upstream while *C. paratus* advances upstream;
- Abundances of *C. anoterus* decrease under conditions of increased water temperatures, while *C. paratus* abundances increase.

Thresholds of relative abundance ratios were calculated using the linear relationships between the ratio of relative abundance of *C. anoterus* and *C. paratus*, and downstream distance (cf. Section 6.3.1), where a mean threshold relative abundance ratio (plus or minus 10%) was calculated based on the linear relationships for October 2000, October 2001 and May 2001. This value appears to be realistic at site WT4, with ratios of relative abundances of *C. anoterus* to *C. paratus* oscillating around this threshold for the period simulated. However, the threshold calculated for WT7 was outside the bounds of the ratio for reference conditions (Figure 8.11). The predicted ratio based on the October 2001 electrofishing survey (cf. Equation 6.7b) was used instead of this value, which established a more realistic threshold and corrected for this anomaly.

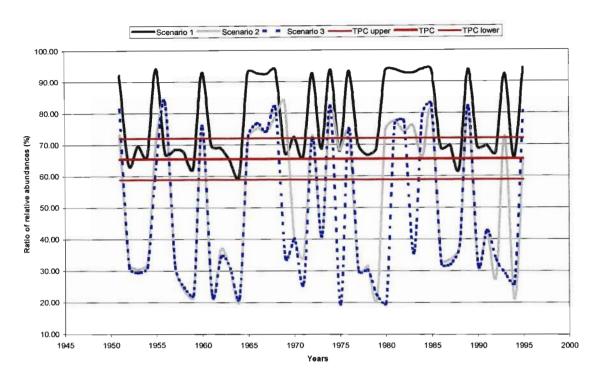


Figure 8.8 Ratio of relative abundances of *C. anoterus* to *C. paratus* for site WT4 for three different water temperature scenarios. Ratios are compared relative to a suggested ratio threshold of 65% *C. anoterus* to 35% *C. paratus* (cf. Table 6.7), with ten percent error margins on either side of this value.

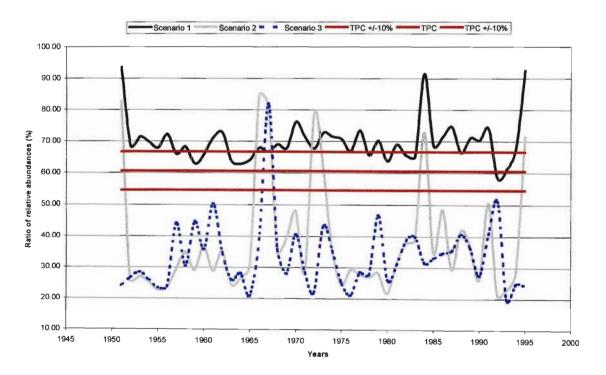


Figure 8.9 Ratio of relative abundances of *C. anoterus* to *C. paratus* for site WT7 for three different water temperature scenarios. Ratios are compared relative to a suggested ratio threshold of 61% *C. anoterus* to 39% *C. paratus* (cf. Table 6.7), with ten percent error margins on either side of this value.

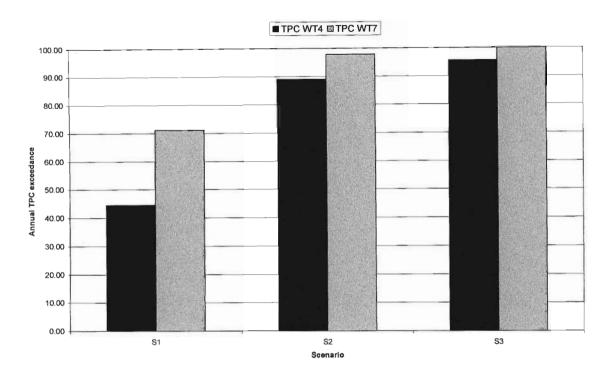


Figure 8.10 Frequency of exceedance for *C. anoterus* to *C. paratus* ratio thresholds at sites WT4 and WT7 for the period 1951 to 1995. The results for three different scenarios of daily maximum water temperatures are presented.

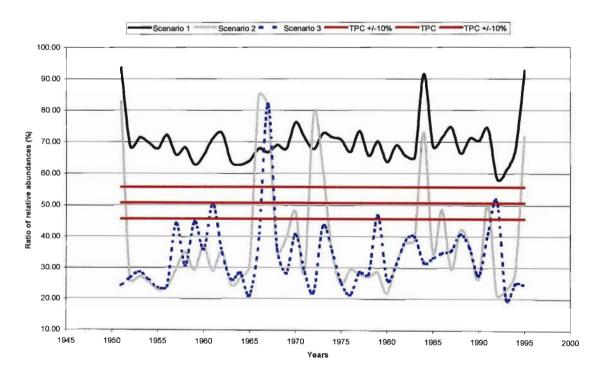


Figure 8.11 Ratio of *C. anoterus* to *C. paratus* for site WT7 for three different water temperature scenarios. Ratios are compared relative to a predicted threshold of 50.55% *C. anoterus* to 49.45% *C. paratus* (*cf.* Table 6.7), and a 10% error on either side of this value.

Using the relationship between MWAT and condition of *C. anoterus* at sites WT4 and WT7, it was shown that under reference condition factors, the threshold defined for the condition factor was not exceeded at sites WT4 and WT7 (Figures 8.12-13). However, under conditions of increased air temperatures (Scenario 2) or reduced flows (Scenario 3), the coefficients of variation for average condition increased more than tenfold (Figure 8.14). In addition, the frequency of exceedance of the suggested site-specific threshold for condition factor increased under conditions of increased air temperatures or reduced flow volumes (Figure 8.15). This index, as a surrogate measure for increased water temperatures, is more sensitive to water temperature changes, and more predictable, than the index for ratio of relative abundances.

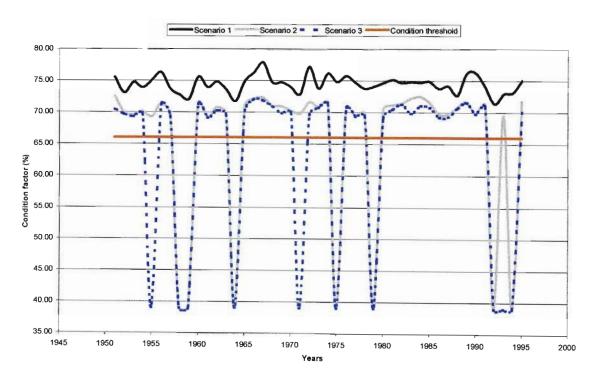


Figure 8.12 Simulated average condition factors of *C. anoterus* population at site WT4 for the period 1951 to 1995 for three different water temperature scenarios. Annual average condition factors were graphed relative to a predicted threshold condition factor, based on a linear regression model of condition factor versus downstream distance.

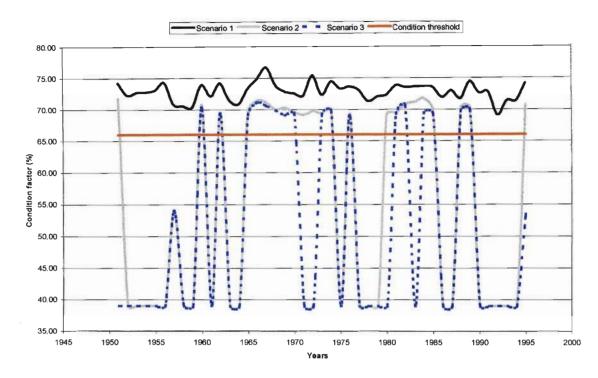


Figure 8.13 Simulated average condition factors of *C. anoterus* population at site WT7 for the period 1951 to 1995 for three different water temperature scenarios. Annual average condition factors were graphed relative to a predicted threshold condition factor, based on a linear regression model of condition factor versus downstream distance

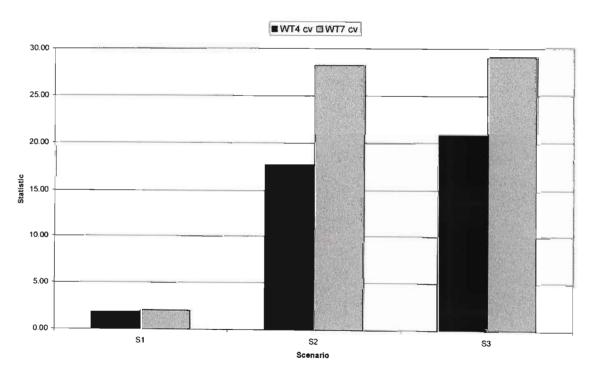


Figure 8.14 Coefficients of variation for the *C. anoterus* condition factor index at sites WT4 and WT7 under three water temperature scenarios.

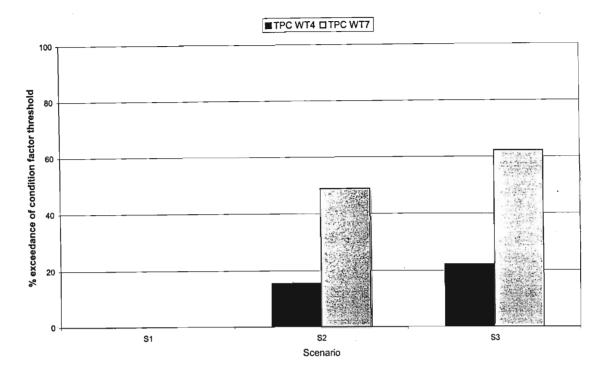


Figure 8.15 Cumulative frequencies of exceedance of the suggested condition factor threshold at sites WT4 and WT7 for the period 1951 to 1995 based on three different water temperature scenarios.

8.4 Discussion and conclusions

8.4.1 Quality of data inputs

It is recognized that the *Chiloglanis* modelling system is based on inputs using imperfect "best-available" data. Sources of error within these simulations are additive, being potentially introduced in the following areas:

- Simulated daily flows; and
- Simulated mean daily air temperatures (*cf.* Section 7.4.3), both of which potentially incorporate error into the water temperature simulations.
- The flow-dependant water temperature model was based on observed mean daily
 flows at two sites for a limited period of time, which may add additional error in
 the simulated water temperatures.
- Observed daily maximum water temperatures in the Sabie catchment exhibited non-constant variance, which could not be removed using data transformations (cf. Section 3.4.2). Multiple linear regression models simulate maximum daily water temperatures with a constant mean and variance, by virtue of the assumptions of linearity inherent within these models. Therefore, simulated

water temperatures are likely to be inherently more predictable than observed water temperatures.

With reference to the last point, Basson *et al.* (1994) recognized similar challenges in simulating seasonal flows using stochastic models (auto-regressive moving average ARMA (1,1)) in a study on the reliability of water resources yields within the Vaal River system of South Africa. These models aimed to represent mean flow behaviour, variability (both interand intra-annual), and persistence within this river system. The sequence of recorded monthly flows was assumed to have a similar appearance between years, even though it varies in a random way. It was recognized that system variability between months in non-humid southern hemisphere regions presented challenges not present in humid northern hemisphere regions. As pointed out in Section 2.1.1, South African rivers are generally more variable than northern hemisphere rivers; this is reflected in the thermo- and hydrographs from such river systems. In spite of these problems, time series models were utilized by Basson *et al.* (1994) since, as with the case of models used to simulate maximum daily water temperatures, the main focus was on mean system behaviour.

Notwithstanding the inherent problems with time series exhibiting non-constant variance, it is nevertheless worthwhile to characterize system variability, since it is this aspect of a thermal regime that enables aquatic organisms with different temperature tolerances to co-exist within a single reach of river. The challenges of classifying system variability in ways that are ecologically relevant are ongoing, and are reflected in the numerous approaches currently under debate in the available literature. Such approaches attempt to measure variability by either agglomerating or decomposing the time series data. Agglomerative techniques make use of techniques such as duration curves, while reductionist approaches make use of indices that focus on state and threshold values using descriptive statistics, and attempt to understand the links between timing, duration and magnitudes of different system states. Harris et al. (2000) proposed characterizing flow and water temperature time series by regimes. This approach uses basic descriptive statistics, such as mean, maximum, minimum and variances of the time series, to define the "shape" of the regime over time for a particular river or group of rivers. System change is measured when the "shape" of the regime curves change. Alternatively, certain indices "measure" variability against abiotic parameters perceived to be ecologically relevant. For example, the Indicators of Hydrologic Alteration (IHA) developed by Richter et al. (1996) measures flow variability against 32 ecologically relevant hydrological parameters. Colwell's indices (Colwell 1974) are appropriate for highlighting hidden periodicities within time series that are of biological significance. Archer (2000) describes these methods as being "perhaps the most focussed existing methods of describing aspects of temporal fluctuation and have been applied both to physical and biological phenomena". However, one drawback in analyses using these indices is that they are constrained by the way in which class intervals are defined to characterize the states of the phenomena occurring (Archer 2000).

8.4.2 Validation and verification of the Chiloglanis modelling system

Starfield *et al.* (1990) defined validation as "the process of assessing correspondence between the output and the rules applied to the model". The simulations from the *Chiloglanis* modelling system provided a measure of model validation, with model output being within limits established by the TPCs, which were objectively defined in Chapter 6.

According to Jewitt and Görgens (2000b), some form of verification is necessary if this model is to be used outside the scope of knowledge used in its development. In the case of the *Chiloglanis* modelling system, verification was not possible, due to a lack of flow and air temperature data succeeding 2000 and 1995 respectively. The water temperature models have been validated, as far as possible, in Chapter 3 (*cf.* Section 3.4.3), but could not be verified due to a lack of observed mean daily flow data subsequent to 2000, with the exception of the flow data used to develop this model (*cf.* Table 3.1).

According to Jewitt and Görgens (2000b), short (3 years) periods of observed data do not offer an adequate data set for verification exercises. Output from the *Chiloglanis* modelling system could not be verified due to a lack of observed fish data and water temperature data. Model verification remains to be undertaken, which can only be achieved by using additional data collected during ongoing monitoring programmes, which should also include comparable time series of either observed or simulated water temperatures. Within the context of this study, the models will only be verified if a monitoring programme is accepted, which in turn depends on the acceptance of the TPC as a river management tool within the Kruger National Park (cf. Section 9.2.1).

8.4.3 Model output and implications for management

Based on the cause-and-effect relationships used in this model, relative abundances of *C. anoterus* and *C. paratus* were highly variable over time. A consequence of this is that the Gaussian distribution curves, as described in Section 6.3, are also likely to be dynamic, changeable and unstable over time. Assuming that the correlative relationships between *Chiloglanis* relative abundances and condition, and indices of water temperatures, provide the basis for the biotic patterns observed, there is considerable variability in fish distribution patterns, and relative abundances, over time. This is occurring in a "predictably unpredictable" river system, where a predictable response (i.e. the cause-and effect relationships) leads to unpredictable patterns.

Based on the outputs of this model under three broad water temperature scenarios, these relationships appear to be sensitive to changing water temperatures. An increase in air temperatures, or a decrease in daily flow volumes, both had similar effects on fish relative abundances and conditions within this model, and in both cases changing abiotic conditions led to increased variability in biotic indices. However, comparing the ratio and condition indices against hypothesised thresholds showed that the ratio index was more unstable than the condition index. It is recommended that the condition index be used in preference to the ratio index for monitoring water temperature change. The non-significance of the negative association between *C. anoterus* and *C. paratus* (*cf.* Section 6.3.1) adds further impetus to the use of the condition index as a stronger alternative.

The use of models within a management context, and in particular their use in improving management decisions, was discussed in greater detail in Section 7.1.2. From a management perspective, the *Chiloglanis* modelling system has value in evaluating the impact of different flow and climate warming scenarios on water temperatures, and how these might affect the distributions of proposed indicator species of fish. Further quantifying of the links between water temperature processes and fish response patterns within the Sabie River system is an important contribution this model makes to the management process of the Sabie River. Changing water temperatures are likely to lead to changes in the distributional patterns of all fish species, but particularly those species with a narrower temperature tolerance range. From a practical perspective, it is not possible to manage water temperatures under conditions of climate change. Concomitantly, it is possible to set and work towards management targets for flow volumes, and thus indirectly

to manage water temperatures. Practical management goals need to ensure that river channels and migration corridors are kept open so that fish are able to move up or down the longitudinal axis of the Sabie River in response to changing water temperatures.

Currently, the model output provides a forum for discussion only, thereby providing a gambit for additional research into these relationships. The accuracy of the model could be improved in the following ways:

- Refining the flow-dependant water temperature linear multiple regression model by obtaining additional daily flow data;
- Obtaining forecast data of mean daily air temperatures using appropriate
 Global Change Models (GCMs). This would make it possible to predict the
 ratios and conditions of Chiloglanids for the appropriate TPC sites on the Sabie
 River, and test the reliability of these relationships with data collected annually
 in May electrofishing surveys.

* * * * *

The Sabie River was shown to be "predictably unpredictable" using Colwell's indices of predictability. Simple cause-and-effect relationships between measures of annual water temperature in the Sabie River and biological indices using two species of *Chiloglanis*, suggest that fish response to changing water temperatures is equally unpredictable. This unpredictability increased with changes in daily maximum water temperatures due to both reductions in mean daily flow volumes and increases in mean daily air temperatures. Exceedances of threshold values (biological indices acting as surrogates for a water temperature TPC) are likely to increase should maximum daily water temperatures increase. While managing for this TPC is difficult, what does emerge from this model is that river managers need to manage the Sabie River for its capacity to allow biota to respond (i.e. the flux of change). A greater understanding of the nature of thermal variability (what is natural versus anthropogenic change) is also necessary before this aspect can be "managed".

9 DISCUSSION AND CONCLUSIONS

"Within any complex system there are certain elements that cannot be deduced from its basic characteristics. This may mean that, even had we known every particular of the circumstances surrounding this journey, we would still have been unable to guard against the unpredictable."

Peter Høeg - Journey into a Dark Heart

9.1 Synthesis

The purpose of this research was to contribute to aquatic ecosystem management, with a focus on the main rivers of the Sabie catchment. This study aimed to provide understanding of the degree to which fish distribution patterns within the rivers of the Sabie catchment are a function of, and to what extent similar rivers might be managed for, changes in annual water temperature regimes. As stated in Chapter 1, the major components of this research were to:

- Describe intra-annual water temperature variation in the Sabie River at a macro-scale;
- Develop a prototype model of water temperature for the Sabie River, which may have broader applications in other South African rivers;
- Develop a model for simulating the responses of two species of the suckermouth catlets *Chiloglanis* (Mochokidae) to changes in annual water temperatures, in order to test the recommendation of Weeks *et al.* (1996) that the spatio-temporal change in ratio of relative abundances of these species provides an index for a proposed TPC for water temperature over the past season;
- Assess how the findings of this model add to the tools available to natural resource managers in the Kruger National Park.

The first two objectives were achieved through collection and analysis of hourly water temperatures along the longitudinal gradient of the Sabie River, and using these as the basis for simulating maximum daily water temperatures using statistical models. The latter two objectives were achieved by linking fish distribution patterns in the Sabie catchment to thermal drivers, and by simulating the responses of two Chiloglanid species to annual changes in water temperature using simple cause-and-effect relationships. Different

statistical techniques were utilized to add to the understanding of fish distribution patterns within the rivers of the Sabie catchment, as obtained by the "snapshots" provided by electrofishing surveys. It is important to stress that the patterns described in this study are a subset of the broader patterns occurring within the catchment, and that the use of different multivariate techniques leads only to a partial understanding of this system; no single interpretation is definitive.

9.1.1 Water temperatures in the Sabie River

The thermal regime of a river is the product of complex multi-scale interactions between different driving variables, such as solar radiation, altitude, air temperatures and flow volumes. Intra-annual water temperatures in the rivers of the Sabie catchment were shown to be complex and highly variable in time and space. A limited degree of thermal stratification and patchiness was shown to occur at the micro scale. The overriding thermal effect observed was a marked downstream gradient in thermal heating, daily range and variability of water temperatures along the longitudinal axis of the Sabie River.

Daily maximum water temperatures, which are generally regarded as being of greatest ecological significance, were simulated using various statistical approaches that incorporate air temperatures as the principal driver of daily water temperatures. Multiple linear regression models were identified as the most pragmatic approach to simulate ecologically meaningful water temperatures within the Sabie River. The usefulness of such models as a management tool was enhanced by the inclusion of a flow-dependant term, since this provided the potential to consider the impacts of impoundments and changes in catchment conditions on water temperatures.

9.1.2 Fish as indicators of thermal change in the Sabie River

Macro-scale ichthyological zonation patterns within the Sabie catchment were primarily in response to water temperatures, as supported by the site and species groupings that emerged from the multivariate ordinations. Diversity indices suggest that species diversity increases concomitantly with a downstream increase in thermal variability.

Measures of mean annual water temperatures were the overriding water temperature parameter relevant to fish communities in general within the rivers of the Sabie catchment. However, each species is likely to respond to seasonal water temperatures in a unique way, determined by specific life histories and tolerance levels to thermal stresses. Therefore, water temperature requirements should be related to each body of water, and to its particular fish community (Essig 1998). A similar approach to that used in this study could therefore be followed in other South African river systems where river "health" is of concern. Such an application would require knowledge of the fish communities occurring within each river system, prior to the identification of suitable indicator species, and the establishment of critical water temperature thresholds. This would also be of merit in refining management approaches within the rivers of South Africa, by showing, in thermal terms, whether river systems could be agglomerated into management groups, or whether each river system should be managed for its uniqueness.

In the case of the Sabie River, the riffle-dwelling fish species *Chiloglanis anoterus* and *C. paratus* are suitable indicators of water temperatures of the preceding season in the Sabie River, based on the analyses of niche dimensions. Logistic regression models made it possible to link the presence or absence of *C. anoterus* within different reaches of the Sabie River to an index of cumulative annual warmth. A negative relationship was shown to exist between the average condition of *C. anoterus* populations and downstream distance, which was also correlated with the index of cumulative annual warmth. Relative abundances of both species were correlated with annual measures of water temperatures. The links between biotic patterns and abiotic processes enabled relative abundances of the two Chiloglanid species, and average conditions of *C. anoterus*, to be simulated on a site-specific basis, through the use of correlative cause-and-effect relationships. These biological indices are suitable as surrogates for a TPC for cumulative annual heat units within the Sabie River.

9.2 Adaptive management implications for rivers

Hydro-ecological studies are increasingly interdisciplinary, with research focussing on, inter alia, the relationships between water quantity and quality, the importance of variability and scale, and the use of biological indicators of river health. A growing awareness of the complexity of natural systems is being encapsulated within management strategies, which are moving away from rigid approaches towards strategies that recognize uncertainty. Within this paradigm is an awareness of the links between pattern and process, and the dynamism of "fast" processes within the confines or constraints of "slow" processes (Frissel et al. 1986; Gunderson et al. 1995). A simple analogy of these complex systems can be drawn from horology, where the second, minute and hour hands (pattern) display the time through a complex interaction of gears moving at different speeds (process).

There is a growing recognition, particularly since the 1980s, of the importance of variability in maintaining river health (see for example Schindler 1987; Gunderson *et al.* 1995; Richter *et al.* 1996; Reynolds 1998). Pickett *et al.* (1992) and Rogers (1997) emphasize the failure of the "balance of nature" paradigm. Scheffer (1999) also refutes this concept, by proposing that natural systems do not seek equilibrium through succession, but rather exist in a state of non-equilibrium where disturbance is important. Thus, an alternative approach – the "flux of nature" – has intuitive appeal, but daunting practical applications (Rogers and Bestbier 1997).

In parallel with this paradigm shift has been the growing popularity of the adaptive management approach, as discussed in Chapter 7. Again, this approach has intuitive appeal, yet to date has had little practical success.

The use of TPCs provides a practical means towards managing for system flux. However, their use assumes a degree of central tendency within systems. While the concept of TPCs remains useful, perhaps what is needed is a reappraisal of the way in which TPC exceedances are measured. This is discussed further in Section 9.2.1, based on the lessons learned from this research.

9.2.1 Management lessons learned from the rivers of the Sabie catchment

Adaptive management initiatives are concerned either with ecological restoration of a system, or managing for a desired future state, preferably based on reference conditions. The Sabie River forms an ideal pilot study for the ongoing implementation of adaptive management, since this river system is relatively pristine, according to Weeks *et al.* (1996).

The principles and concepts of adaptive management, as formalized in the general adaptive management cycle described in Figure 9.1, and why this is applicable to the issues on the Sabie River, were described in detail in Chapters 6 and 7. This management approach is an alternative to "charging blindly ahead" or "being paralyzed by indecision" (Anon. 1999), which often characterizes the so-called "traditional" management approaches.

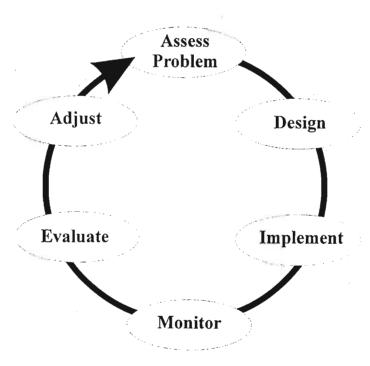


Figure 9.1 Framework for adaptive management (Anon. 1999)

This research is not an end in itself, but rather provides a foundation for further application of adaptive management principles, particularly within the Kruger National Park, where an adaptive management framework exists (Rogers and Bestbier 1999). The following issues beneficial to management have been achieved through this research:

- The problem has been assessed the importance of intra-annual variability in water temperatures has been established (Chapters 2 and 3). Water temperatures have been shown to be a significant agent of change driving fish diversity patterns within the man rivers of the Sabie catchment (Chapter 4);
- Indicators of thermal change have been identified the riffle-dwelling rock catlets *Chiloglanis anoterus* and *C. paratus* have been shown to be suitable indicators of annual thermal change (Chapters 5 and 6);
- Models have been developed a modelling system using multiple linear regression and cause-and-effect relationships, adds to the management tools available to river managers in the Kruger National Park, by highlighting the sensitivity of the Sabie River system to changes in water temperatures at an annual time scale. These models also emphasize the importance of variability and uncertainty in maintaining this system (Chapters 7 and 8).

It has been shown that changes in water temperatures are likely to have substantial impacts on the fish communities in the rivers of the Sabie catchment, and that these will be a consequence of changes in the drivers and buffers of this thermal regime, including, *inter alia*, flow volumes and air temperatures. The broader scientific context of the abovementioned points, assuming a need for management of the Sabie catchment's rivers, will be a cycle of ongoing assessment, application/rejection, and refinement of the management approach, supported by these models, as advocated by the adaptive management cycle (Figure 9.1). This iterative approach aims to reinforce the fundamental science that should underpin effective management of natural systems, as emphasised by Moss (1999) (cf. Section 7.1.1). Two pertinent questions arising from this research are:

- How meaningful are these findings for managing water temperatures in the rivers of the Sabie catchment?
- How do these findings add to the adaptive management tools available to natural resource managers within the Kruger National Park? (i.e. are TPCs valid for abiotic drivers over which there is little direct management control?).

From a management perspective, streamflow within the rivers of the Sabie catchment is the most manageable abiotic parameter. Water temperature is a critically important water quality variable, which cannot be managed directly. However, indirect management of water temperatures is possible by targeting those drivers and buffers of thermal regimes (cf. Section 2.1.1) that can be directly managed. Such drivers and buffers would include appropriate management of riparian zones, the maintenance of natural flow variability, and addressing a general problem of sedimentation in rivers. A TPC for water temperature within the Sabie River nevertheless remains useful to river managers, as it provides an additional indication of system stress. However, as Essig (1998) points out, "the current state of affairs is that we cannot reliably distinguish management-caused temperature exceedances from natural conditions". According to Schindler (1987), "the fact is that we usually do not know the normal range for any variable, at least for any time period greater than a few years." Furthermore, "even if well-designed monitoring programs were magically emplaced tomorrow, it would be years before we could confidently distinguish between natural variation and low-level effects of perturbances in ecosystems" (Schindler 1987). Thus, to make greater use of the proposed water temperature TPC, the observed water temperature time series should be extended for as long as possible. These longer times series would be appropriate for use in stochastic time series models. Future research should focus on further understanding seasonality and variability, as well as the relationships between these and "manageable" components, of the thermal regimes of the main rivers of the Sabie catchment.

As was demonstrated using the *Chiloglanis* modelling system, a critical problem related to the TPC is deciding how often exceedance is natural, versus what constitutes declining river health. Management should focus on understanding how different fish species respond to changes in water temperatures, and ensuring that movement corridors are open for fish to respond to changes in water temperatures. An additional management focus should be on further understanding the nature of water temperature variability. This could be related to the water temperature TPC by recommending successive upper and lower limit values, together with associated degrees of confidence in these thresholds.

Monitoring of the indicators discussed in Chapter 6 is a logical extension of this research, in order to determine whether the hypothesized relationships presented in Chapters 7 and 8 are valid for forming the basis for future forecasts. Monitoring allows scientists and managers to assess how actions affect indicators, and provides the basis for model validation. Long-term monitoring is critical in distinguishing natural from anthropogenic stress (Schindler 1987). It also leads into the subsequent adaptive management process of evaluation, where the heuristic value of the different hypotheses is assessed. New insights gained during these phases should then be incorporated into the models in the adjustment phase, and the entire process begun again (Anon. 1999).

This research provides the impetus for the management of the Kruger National Park to institute a small-scale adaptive management programme that focuses on the maintenance of fish diversity within the Sabie River. Given the financial implications of field experiments, initial research should focus on further development of object-oriented models that incorporate scenarios of loss of variability in flow volumes and daily maximum water temperatures. This is particularly important if the adaptive management process is to gain credibility, since adaptive management has been previously criticized for having no practical examples of success. Such an approach should aim to include the establishment of long-term experiments, and could consider the use of artificial intelligence approaches, such as Bayesian networks, to evaluate the confidences that can be placed in the different hypotheses.

Successful adaptive management programmes have a degree of inbuilt redundancy, and implicit in this is the use of a suite of TPCs and their associated models, which provide management with the ability to assess a multitude of system components at different temporal and spatial scales. This would add robustness to the management approach, since as Schindler (1987) pointed out, widespread use of single-species bioassays, complicated models, and impact-statement studies have been unsuccessful at predicting the effects of human-induced stress on biological systems.

9.2.2 Adaptive management in South African rivers: The way forward

Two scientific approaches are recognised in understanding natural systems, namely reductionism versus integration (or holism). The former approach assumes that in order to understand a system, it should be broken down into its constituent components. An inevitable consequence of this is that management approaches based on reductionism become static. The latter approach recognises that the whole is greater than the sum of the individual parts, and assumes that knowledge is always incomplete, surprise is inevitable, and there is a need to recognise unpredictability in management approaches. An emerging belief system in the integrative approach recognises that management, as with natural systems, is both evolutionary and adaptive (Gunderson *et al.* 1995). Complex non-linear system behaviour, chaos and order, and adaptive evolving systems are embodied in this belief system. It challenges the entrenched ideas of systems seeking a stable equilibrium state. Based on these ideas, contemporary understandings of ecosystems serve as hypotheses by which to define management policies.

Hydro-ecological science and management should aim to understand species patterns, as a reflection of abiotic and biotic processes acting on individuals at the micro scale (Vannote et al. 1980; Frissel et al. 1986). Unravelling these complex species patterns in the context of environmental drivers has been described "ecological detection", which "is a craft that requires the right tools as well as the skills and materials to use the tools" (Hilborn and Mangel 1997, p. 10). Hilborn and Mangel (1997) also comment that "for the ecological detective the problem is paramount. Because of that, we bring to the problem whatever techniques – from wherever they come – needed to solve it. And if the techniques do not exist, then we must invent them" (p. 11). Given the financial and spatio-temporal constraints in managing natural systems through a process of experimentation, scenario modelling that focuses on the major components of a system, and which promotes thinking and discussion of systems rather than attempting to replicate the "real" world, is becoming an increasingly used tool within adaptive management. The discussions in Chapters 7 and 8 contribute in this regard. However, experimental ecosystem perturbation does provide a relatively short-term approach to understanding system variability (Schindler 1987), and should not be ignored as an adaptive management tool, through undue emphasis on scenario modelling.

Traditionally, natural resource management has aimed to control the variability of a target (for example insects at low levels, trout at high levels). Gunderson *et al.* (1995) point out that reducing the variability of ecosystems inevitably leads to:

- Reduced resilience;
- Increased vulnerability;
- More spatially homogenized ecosystems, which are more likely to decline into a persistent degraded state;
 - More rigid management institutions, and
 - More dependant societies.

This exposes a fundamental flaw in traditional ecosystem management, since there is no other way to manage for reliable yield targets, than through reducing variability and increasing short-term predictability. Rigid policies and a narrow focus place emphasis in the economic element of systems management, and in the short term will maximise yields. However, given the hierarchical scales of patterns and processes driving all natural systems, such exploitative management approaches inevitably result in crisis, conflict and gridlock. Management regimes will often respond reactively to environmental or anthropogenic crises, as highlighted by Gunderson *et al.* (1995) based on a number of case studies that focussed on management eras associated with different ecosystems.

Gunderson et al. (1995) argue that "sustainable development", in the traditional sense, is not achievable. Adaptive management is not about being reactive in times of crisis, but rather in getting "people together ahead of time to define experiments" (Anon. 2000), which are aimed at providing insights into system functioning which in turn guide management. It is recognized as "a process for developing hypotheses about how components of an ecosystem function and interact, and for using management actions at a large scale to test those hypotheses and to learn more about our management options. It is different from 'muddling through', however, in that it inherently presumes pre-experiment design, and follow-up monitoring are needed in order to evaluate whether management has accomplished what is intended, and if outcomes are consistent with our understanding of ecosystem structure and function" (Anon. 2000). Successful management programmes are based on applied science at appropriate scales, which relies on monitoring leading to corrective responses, and an understanding of human behaviour (Gunderson et al. 1995).

Effectively managed systems are associated with flexible and diverse management policies, rather than a procedural approach of institutional control. The interdependencies of ecosystems, economics and society in setting holistic management goals are recognised.

Anon. (2000) emphasizes that adaptive management is based on the acceptance that comprehensive predictive knowledge is not possible. Consequently, it is about acknowledging and working through management challenges in the presence of uncertainty and change (Anon. 1999), and disturbance and renewal. Such ecosystem uncertainties concern:

- Ecological process and function;
- Impacts of human use and management;
- The future;
- The social/political arena regarding stakeholder values and conflicts (Anon. 2000).

This uncertainty should form the basis for any adaptive management policies. Multidisciplinary workshops play a critical role in identifying gaps in understanding, where models that synthesize existing knowledge can be developed (Anon. 1999). A subsequent step is to define the scope of the management problem (i.e. range of factors to be considered), and then set goals. This provides the context for defining the spatial and temporal scales of the models and management units. The approach should be to "think globally but act locally", through small-scale experiments that can evolve into pilot phases, and ultimately into large-scale programmes (Anon. 2000). Barriers to success – financial, institutional, knowledge - are important to consider at this stage. Management experiments and associated monitoring allow for the discrimination between alternative hypotheses by providing information about key ecosystem linkages and cause-and-effect pathways (Anon. 2000).

"Adaptive management of large river systems is unique in that it addresses large, [catchment]-scale threats to aquatic, wetland and bottomland biological diversity in a setting where economic, recreational, and other cultural values also matter and where because of the ["catchment"] feature, contact of many people with the river is low" (Anon. 2000). It is an evolutionary approach for maintaining sustainable river systems, because it recognizes and values the role of natural variability in structuring and renewing these

systems. It is about finding the river's energy and working with it rather than against it; learning how to adapt to the river rather than adapting the river to us; learning to live with and profit from the natural variability of a river (Anon. 2000). Given the variable nature of river systems within southern Africa, the questions that really need to be addressed are:

- How can adaptive management be applied, in practical terms?
- Are the correct questions currently being asked?

The abovementioned questions are broad and difficult to answer. A mindset that will facilitate answering these questions should include the following considerations:

- Management for the preservation of adequate system variability and connectivity;
 - Avoid managing to maintain assumed minimum system requirements;
- An acceptance that river systems are less manageable than previously assumed;
- Inclusive management, where society is seen as part of the system, and not adjacent to it;
- A recognition that TPCs form a useful approach for detecting system stress, and are flexible enough to incorporate system flux. However, research emphases need to shift away from TPCs, *per se*, towards a greater understanding of system variability and how this is measured relative to TPCs;
- Greater emphasis on long-term baseline studies. Schindler (1987) asserts that if low-level, sensitive methods for detection of river "stress" are a management goal, there needs to be increased emphasis on ecosystem-level studies, such as population dynamics (life-table methods) and food web organization;

Perhaps most importantly of all, river management should be underpinned by a humble approach: "We have not yet developed an ecological science capable either of detecting the stresses imposed upon natural ecosystems by anthropogenic activities, or of predicting the long-term effects of such stresses" (Schindler 1987).

9.3 Future research requirements

The proposed cause-and-effect relationships of fish response to changes in water temperature and streamflow in the Sabie River form hypotheses based on the available data, and represent the current level of understanding between thermal drivers and biotic Within Popper's (1979) classical view of the scientific method, these responses. hypotheses remain valid until proven otherwise, and each hypothesis is tested against the data in confrontation with a null hypothesis. An alternative approach of more direct relevance to managers for placing belief in the strength of hypotheses is the application of Bayesian statistics. It is suggested that these are well suited for the analysis of the contest between competing hypotheses and data, where hypotheses are tested against each other, using the data to evaluate the degree of belief that should be accorded to each of the hypotheses (Hilborn and Mangel 1997), and should be investigated further. In "classical" science there is acceptance or rejection of a hypothesis, while in Bayesian statistics there are "degrees of belief" associated with each hypothesis. Bayesian theory is useful in incorporating prior information in the testing of hypotheses (Hilborn and Mangel 1997). The Bayesian approach may provide a useful basis for testing future hypotheses between abiotic drivers and biotic response within the Sabie system.

The strength of these abiotic-biotic relationships have been partially validated, by comparison with the "snapshots" of the fish communities within the rivers of the Sabie catchment, over a period of three years. However, a 24-month record of hourly water temperatures is too short to make long-term predictions of thermal trends. Future areas of research in this regard should focus on the following areas:

- The significance (degree and nature) of the contribution of tributaries to the thermal regime of the rivers they flow into, as well as the role of tributaries as thermal refugia for aquatic biotia (cf. Sections 2.3.2 and 2.4);
- Ongoing development of water temperature models, which incorporate nonconstant variance of water temperatures. The generic nature of such models should be validated through studies on other river systems within southern Africa;

- Basic ecological studies of key fish species, focussing on a greater understanding of their life histories and tolerances to environmental stress, such as changes in flow volumes and water temperature. This should include laboratory studies, although it is recognised that results may not be directly transferable to river systems due to the potential influence of modifying factors not easily mimicked by laboratory studies (Dunham *et al.* 2003). However, while laboratory studies may not be able to replicate a species environment (i.e. its realized niche), they are useful in quantifying a specie's response to individual abiotic variables, thereby providing a measure of the fundamental niche space for each variable;
- Further development of predictive models, which incorporate additional abiotic-biotic relationships, such as flow volumes, changes in the habitat template (geomorphology), and dissolved oxygen. In an object-oriented framework, the efficacy of these models as management tools could be enhanced by using the models as gaming tools that involve different role-players (ecological, economic and societal sectors), to promote the development of hypotheses and controlled research experiments for increasing the level of system understanding. Additionally, these models should be verified through ongoing sampling of fish together with the collection of concurrent records of water temperature and flow volume time series. The existing models need to incorporate forecasts of daily maximum water temperatures, based on GCM forecasts of air temperatures, as part of the model verification procedure. In this way, model outputs can be compared with observed fish data collected during monitoring surveys on the Sabie River;
- Impacts of impoundments and global warming on water temperatures and fish distributions.

These foci of research call for an interdisciplinary approach, where a mix of fundamental and applied scientific research, and an emphasis on predictive modelling, continues to underpin sound environmental management. A continued need exists for the ongoing development of suites of pragmatic models that provide long-term predictions of system response under different management and/or environmental scenarios. Such models bridge different scientific disciplines, by providing the breadth needed to begin to understand the complexities of natural systems. In the case of ecologically relevant research of water temperatures, basic scientific research should focus on ongoing collection of data (time series), together with further understanding the relative significance of the drivers and

buffers of water temperatures, including the role of the hyporheic zone. The success of such endeavours will depend heavily on a commitment to long-term ecological research programmes. While this may not yield immediate dividends, the merits of such an approach will be seen in the future, both through the provision of a sound foundation of data, and also by providing a means of validating models with a greater degree of confidence.

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APPENDICES

Appendix A1 Species list, and relative abundances of fish species by site for May electrofishing surveys.

Table A1.1 Fish species list, and species name abbreviations used.

AURA Amphilius uranoscopus AMOS Anguilla mossambicus BAFR Barbus afrohamiltoni BANN Barbus annectans BBRE Barbus breviceps BEUT Barbus eutaenia BPAL Barbus pallidus BPOL Barbus polylepis BRAD Barbus radiatus BTRI Barbus trimaculatus BUNI Barbus unitaeniatus BVIV Barbus viviporus BIMB Brycinus imberi CANO Chiloglanus anoterus CPAR Chiloglanus paratus CSWI Chiloglanus swierstrai CGAR Clarias gariepinus GCAL Glossogobius callidus GGIU Glossogobius giuris HVIT Hydrocynus vittatus LMOL Labeo molybdinus LMAR Labeobarbus marequensis MMAC Marcusenius macrolepidotus MBRE Mesobola brevianalis MACU Micralestes acutidens OPER Opsaridium perengii OMOS Oreochromis mossambicus PCAT Petrocephalus catastoma		Fish species list, and species hame
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BPOL Barbus polylepis BRAD Barbus radiatus BTRI Barbus trimaculatus BUNI Barbus unitaeniatus BVIV Barbus viviporus BIMB Brycinus imberi CANO Chiloglanus anoterus CPAR Chiloglanus paratus CSWI Chiloglanus swierstrai CGAR Clarias gariepinus GCAL Glossogobius callidus GGIU Glossogobius giuris HVIT Hydrocynus vittatus LMOL Labeo molybdinus LMAR Labeobarbus marequensis MMAC Marcusenius macrolepidotus MBRE Mesobola brevianalis MACU Micralestes acutidens OPER Opsaridium perengii OMOS Oreochromis mossambicus PCAT Petrocephalus catastoma PPHI Pseudocrenilabrus philander SINT Schilbe intermedius SMER Serranochromis meridianus TREN Tilapia rendalli TSPA Tilapia sparrmanii	BEUT	
BRAD Barbus radiatus BTRI Barbus trimaculatus BUNI Barbus unitaeniatus BVIV Barbus viviporus BIMB Brycinus imberi CANO Chiloglanus anoterus CPAR Chiloglanus paratus CSWI Chiloglanus swierstrai CGAR Clarias gariepinus GCAL Glossogobius callidus GGIU Glossogobius giuris HVIT Hydrocynus vittatus LMOL Labeo molybdinus LMAR Labeobarbus marequensis MMAC Marcusenius macrolepidotus MBRE Mesobola brevianalis MACU Micralestes acutidens OPER Opsaridium perengii OMOS Oreochromis mossambicus PCAT Petrocephalus catastoma PPHI Pseudocrenilabrus philander SINT Schilbe intermedius SMER Serranochromis meridianus TREN Tilapia rendalli TSPA Tilapia sparrmanii		
BTRI Barbus trimaculatus BUNI Barbus unitaeniatus BVIV Barbus viviporus BIMB Brycinus imberi CANO Chiloglanus anoterus CPAR Chiloglanus paratus CSWI Chiloglanus swierstrai CGAR Clarias gariepinus GCAL Glossogobius callidus GGIU Glossogobius giuris HVIT Hydrocynus vittatus LMOL Labeo molybdinus LMAR Labeobarbus marequensis MMAC Marcusenius macrolepidotus MBRE Mesobola brevianalis MACU Micralestes acutidens OPER Opsaridium perengii OMOS Oreochromis mossambicus PCAT Petrocephalus catastoma PPHI Pseudocrenilabrus philander SINT Schilbe intermedius SMER Serranochromis meridianus TREN Tilapia rendalli TSPA Tilapia sparrmanii	BPOL	Barbus polylepis
BUNI Barbus unitaeniatus BVIV Barbus viviporus BIMB Brycinus imberi CANO Chiloglanus anoterus CPAR Chiloglanus paratus CSWI Chiloglanus swierstrai CGAR Clarias gariepinus GCAL Glossogobius callidus GGIU Glossogobius giuris HVIT Hydrocynus vittatus LMOL Labeo molybdinus LMAR Labeobarbus marequensis MMAC Marcusenius macrolepidotus MBRE Mesobola brevianalis MACU Micralestes acutidens OPER Opsaridium perengii OMOS Oreochromis mossambicus PCAT Petrocephalus catastoma PPHI Pseudocrenilabrus philander SINT Schilbe intermedius SMER Serranochromis meridianus TREN Tilapia rendalli TSPA Tilapia sparrmanii	BRAD	Barbus radiatus
BVIV Barbus viviporus BIMB Brycinus imberi CANO Chiloglanus anoterus CPAR Chiloglanus paratus CSWI Chiloglanus swierstrai CGAR Clarias gariepinus GCAL Glossogobius callidus GGIU Glossogobius giuris HVIT Hydrocynus vittatus LMOL Labeo molybdinus LMAR Labeobarbus marequensis MMAC Marcusenius macrolepidotus MBRE Mesobola brevianalis MACU Micralestes acutidens OPER Opsaridium perengii OMOS Oreochromis mossambicus PCAT Petrocephalus catastoma PPHI Pseudocrenilabrus philander SINT Schilbe intermedius SMER Serranochromis meridianus TREN Tilapia rendalli TSPA Tilapia sparrmanii	BTRI	Barbus trimaculatus
BIMB Brycinus imberi CANO Chiloglanus anoterus CPAR Chiloglanus paratus CSWI Chiloglanus swierstrai CGAR Clarias gariepinus GCAL Glossogobius callidus GGIU Glossogobius giuris HVIT Hydrocynus vittatus LMOL Labeo molybdinus LMAR Labeobarbus marequensis MMAC Marcusenius macrolepidotus MBRE Mesobola brevianalis MACU Micralestes acutidens OPER Opsaridium perengii OMOS Oreochromis mossambicus PCAT Petrocephalus catastoma PPHI Pseudocrenilabrus philander SINT Schilbe intermedius SMER Serranochromis meridianus TREN Tilapia rendalli TSPA Tilapia sparrmanii	BUNI	Barbus unitaeniatus
CANO Chiloglanus anoterus CPAR Chiloglanus paratus CSWI Chiloglanus swierstrai CGAR Clarias gariepinus GCAL Glossogobius callidus GGIU Glossogobius giuris HVIT Hydrocynus vittatus LMOL Labeo molybdinus LMAR Labeobarbus marequensis MMAC Marcusenius macrolepidotus MBRE Mesobola brevianalis MACU Micralestes acutidens OPER Opsaridium perengii OMOS Oreochromis mossambicus PCAT Petrocephalus catastoma PPHI Pseudocrenilabrus philander SINT Schilbe intermedius SMER Serranochromis meridianus TREN Tilapia rendalli TSPA Tilapia sparrmanii	BVIV	Barbus viviporus
CPAR Chiloglanus paratus CSWI Chiloglanus swierstrai CGAR Clarias gariepinus GCAL Glossogobius callidus GGIU Glossogobius giuris HVIT Hydrocynus vittatus LMOL Labeo molybdinus LMAR Labeobarbus marequensis MMAC Marcusenius macrolepidotus MBRE Mesobola brevianalis MACU Micralestes acutidens OPER Opsaridium perengii OMOS Oreochromis mossambicus PCAT Petrocephalus catastoma PPHI Pseudocrenilabrus philander SINT Schilbe intermedius SMER Serranochromis meridianus TREN Tilapia rendalli TSPA Tilapia sparrmanii	BIMB	Brycinus imberi
CSWI Chiloglanus swierstrai CGAR Clarias gariepinus GCAL Glossogobius callidus GGIU Glossogobius giuris HVIT Hydrocynus vittatus LMOL Labeo molybdinus LMAR Labeobarbus marequensis MMAC Marcusenius macrolepidotus MBRE Mesobola brevianalis MACU Micralestes acutidens OPER Opsaridium perengii OMOS Oreochromis mossambicus PCAT Petrocephalus catastoma PPHI Pseudocrenilabrus philander SINT Schilbe intermedius SMER Serranochromis meridianus TREN Tilapia rendalli TSPA Tilapia sparrmanii	CANO	Chiloglanus anoterus
CGAR Clarias gariepinus GCAL Glossogobius callidus GGIU Glossogobius giuris HVIT Hydrocynus vittatus LMOL Labeo molybdinus LMAR Labeobarbus marequensis MMAC Marcusenius macrolepidotus MBRE Mesobola brevianalis MACU Micralestes acutidens OPER Opsaridium perengii OMOS Oreochromis mossambicus PCAT Petrocephalus catastoma PPHI Pseudocrenilabrus philander SINT Schilbe intermedius SMER Serranochromis meridianus TREN Tilapia rendalli TSPA Tilapia sparrmanii	CPAR	Chiloglanus paratus
GCAL Glossogobius callidus GGIU Glossogobius giuris HVIT Hydrocynus vittatus LMOL Labeo molybdinus LMAR Labeobarbus marequensis MMAC Marcusenius macrolepidotus MBRE Mesobola brevianalis MACU Micralestes acutidens OPER Opsaridium perengii OMOS Oreochromis mossambicus PCAT Petrocephalus catastoma PPHI Pseudocrenilabrus philander SINT Schilbe intermedius SMER Serranochromis meridianus TREN Tilapia rendalli TSPA Tilapia sparrmanii	CSWI	Chiloglanus swierstrai
GGIU Glossogobius giuris HVIT Hydrocynus vittatus LMOL Labeo molybdinus LMAR Labeobarbus marequensis MMAC Marcusenius macrolepidotus MBRE Mesobola brevianalis MACU Micralestes acutidens OPER Opsaridium perengii OMOS Oreochromis mossambicus PCAT Petrocephalus catastoma PPHI Pseudocrenilabrus philander SINT Schilbe intermedius SMER Serranochromis meridianus TREN Tilapia rendalli TSPA Tilapia sparrmanii	CGAR	Clarias gariepinus
HVIT Hydrocynus vittatus LMOL Labeo molybdinus LMAR Labeobarbus marequensis MMAC Marcusenius macrolepidotus MBRE Mesobola brevianalis MACU Micralestes acutidens OPER Opsaridium perengii OMOS Oreochromis mossambicus PCAT Petrocephalus catastoma PPHI Pseudocrenilabrus philander SINT Schilbe intermedius SMER Serranochromis meridianus TREN Tilapia rendalli TSPA Tilapia sparrmanii	GCAL	Glossogobius callidus
LMOL Labeo molybdinus LMAR Labeobarbus marequensis MMAC Marcusenius macrolepidotus MBRE Mesobola brevianalis MACU Micralestes acutidens OPER Opsaridium perengii OMOS Oreochromis mossambicus PCAT Petrocephalus catastoma PPHI Pseudocrenilabrus philander SINT Schilbe intermedius SMER Serranochromis meridianus TREN Tilapia rendalli TSPA Tilapia sparrmanii	GGIU	Glossogobius giuris
LMAR Labeobarbus marequensis MMAC Marcusenius macrolepidotus MBRE Mesobola brevianalis MACU Micralestes acutidens OPER Opsaridium perengii OMOS Oreochromis mossambicus PCAT Petrocephalus catastoma PPHI Pseudocrenilabrus philander SINT Schilbe intermedius SMER Serranochromis meridianus TREN Tilapia rendalli TSPA Tilapia sparrmanii	HVIT	Hydrocynus vittatus
MMAC Marcusenius macrolepidotus MBRE Mesobola brevianalis MACU Micralestes acutidens OPER Opsaridium perengii OMOS Oreochromis mossambicus PCAT Petrocephalus catastoma PPHI Pseudocrenilabrus philander SINT Schilbe intermedius SMER Serranochromis meridianus TREN Tilapia rendalli TSPA Tilapia sparrmanii	LMOL	Labeo molybdinus
MBRE Mesobola brevianalis MACU Micralestes acutidens OPER Opsaridium perengii OMOS Oreochromis mossambicus PCAT Petrocephalus catastoma PPHI Pseudocrenilabrus philander SINT Schilbe intermedius SMER Serranochromis meridianus TREN Tilapia rendalli TSPA Tilapia sparrmanii	LMAR	Labeobarbus marequensis
MACU Micralestes acutidens OPER Opsaridium perengii OMOS Oreochromis mossambicus PCAT Petrocephalus catastoma PPHI Pseudocrenilabrus philander SINT Schilbe intermedius SMER Serranochromis meridianus TREN Tilapia rendalli TSPA Tilapia sparrmanii	MMAC	Marcusenius macrolepidotus
OPER Opsaridium perengii OMOS Oreochromis mossambicus PCAT Petrocephalus catastoma PPHI Pseudocrenilabrus philander SINT Schilbe intermedius SMER Serranochromis meridianus TREN Tilapia rendalli TSPA Tilapia sparrmanii	MBRE	Mesobola brevianalis
OMOS Oreochromis mossambicus PCAT Petrocephalus catastoma PPHI Pseudocrenilabrus philander SINT Schilbe intermedius SMER Serranochromis meridianus TREN Tilapia rendalli TSPA Tilapia sparrmanii	MACU	Micralestes acutidens
PCAT Petrocephalus catastoma PPHI Pseudocrenilabrus philander SINT Schilbe intermedius SMER Serranochromis meridianus TREN Tilapia rendalli TSPA Tilapia sparrmanii	OPER	Opsaridium perengii
PPHI Pseudocrenilabrus philander SINT Schilbe intermedius SMER Serranochromis meridianus TREN Tilapia rendalli TSPA Tilapia sparrmanii	OMOS	Oreochromis mossambicus
SINT Schilbe intermedius SMER Serranochromis meridianus TREN Tilapia rendalli TSPA Tilapia sparrmanii	PCAT	Petrocephalus catastoma
SMER Serranochromis meridianus TREN Tilapia rendalli TSPA Tilapia sparrmanii	PPHI	Pseudocrenilabrus philander
TREN Tilapia rendalli TSPA Tilapia sparrmanii	SINT	Schilbe intermedius
TSPA Tilapia sparrmanii	SMER	Serranochromis meridianus
	TREN	Tilapia rendalli
VNEL Varicorhinus nelspruitensis	TSPA	Tilapia sparrmanii
	VNEL	Varicorhinus nelspruitensis

Table A1.2 Relative abundances of species for May 2000 electrofish
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SPECIES	3	5	21	7	20	11	19	14	26
AMOS	0	0	0	0	0	0	0	0	0
AURA	0	5	0	0	0	0	0	0	0
BAFR	0	0	0	0	1	0	0	0	0
BANN	0	0	0	2	1	0	0	44	5
BBRE	0	0	1	0	0	0	0	0	0
BEUT	0	0	0	0	0	5	1	0	1
BMAR	0	0	4	20	9	10	2	1	35
BPAL	0	0	0	0	0	0	0	1	0
BPOL	0	0	0	0	0	0	0	0.	0
BRAD	0	0	0	0	0	0	0	5	0
BTRI	0	1	0	12	8	5	1	12	42
BUNI	0	0	0	0	0	0	0	2	0
BVIV	0	0	0	4	28	2	3	64	54
BIMB	0	0	0	0	1	0	0	0	0
CANO	7	31	11	4	0	29	14	0	11
CPAR	0	0	0	11	13	0	1	5	61
CSWI	0	0	0	7	4	1	0	0	4
CGAR	0	1	0	3	0	1	0	0	0
GCAL	0	0	0	0	0	0	0	0	1
GGIU	0	0	0	0	1	0	0	0	0
HVIT	0	0	0	0	0	0	0	0	0
LMOL	0	1	0	16	7	11	2	14	14
MMAC	0	0	0	0	1	0	0	0	0
MBRE	0	0	0	0	0	0	2	1	2
MACU	0	0	0	0	1	7	1	3	14
OPER	0	0	0	9	0	0	0	0	2
OMOS	0	0	0	0	1	0	3	7	0
PCAT	0	0	0	0	0	0	0	0	0
PPHI	0	1	0	0	0	0	0	0	0
SINT	0	0	0	0	0	0	0	0	0
SMER	0	0	0	0	0	0	0	0	0
TREN	0	0	0	0	0	0	0	0	0
TSPA	0	0	0	0	0	0	0	0	0
VNEL	8	0	0	0	0	0	0	0	0
Total individuals	15	40	16	88	76	71	30	159	246
Total species	2	6	3	10	13	9	10	12	13

CPUE (fish.min⁻¹) 22.53 20.00 15.00 20.00 21.00 30.00 20.17 20.17 33.83

Table A1.3 Relative abundances of species for May 2001 electrofishing survey in the Sabie catchment

Table A1.3 Relative										bie cateni
SPECIES	3	5	21	7	9	20	11	19	14	
AMOS	0	0	1	0	0	0	0	0	0	
AURA	0	6	6	0	0	0	0	0	0	
BAFR	0	0	0	0	0	0		0	0	
BANN	0	0	0	3	0	0	0	0	2	
BBRE	0	0	0	0	0	0	0	0	0	
BEUT	0	1	0	0	0	0	4	8	0	
BMAR	0	1	1	54	4	8	41	14	16	
BPAL	0	0	0	0	0	0	0	0	0	
BPOL	0	0	1	0	0	0	0	0	0	
BRAD	0	0	0	0	0	0	0	0	0	
BTRI	0	0	0	15	3	2	0	9	28	
BUNI	0	0	0	0	0	0	0	1	0	
BVIV	0	0	0	2	4	0	0	10	44	
BIMB	0	0	0	0	0	1	0	0	0	
CANO	36	32	47	40	0	0	15	34	0	
CPAR	0	0	0	6	0	22	0	8	29	
CSWI	0	0	0	8	4	7	0	1	0	
CGAR	0	0	0	0	3		0	2	0	
GCAL	0	0	0	2	1	7	0	0	0	
GGIU	0	0	0	0	0	2	0	0	0	
HVIT	0	0	0	0	0	0	0	0	0	
LMOL	0	0	0	7	0	5	8	7	29	
MMAC	0	0	0	2	0	0	1	0	9	
MBRE	0	0	0	0	0	0	0	8	0	
MACU	0	0	0	0	0	1	0	3	5	
OPER	0	21	0	8	0	0	0	1	0	
OMOS	0	0	0	0	27	25	0	15	14	
PCAT	0	0	0	1	0	0	0	0	0	
PPHI	0	3	0	0	2	1	0	0	0	
SINT	0	0	0	0	0	0	0	0	0	
SMER	0	0	0	0	0	0	0	0	1	
TREN	0	0	0	0	8	10	0	1	1	
TSPA	0	0	0	0	0	0	0	0	0	
VNEL	18	2	0	0	0	0	0	0	0	
Total individuals	54	66	5 6	148	56	92	69	122	178	
Total species	2	7	5	12	9	13	5	15	12	

Total individuals 54 66 56 148 56 92 69 122 178 Total species 2 7 5 12 9 13 5 15 12 CPUE (fish.min⁻¹) 21.72 22.62 27.05 28.22 17.32 28.00 30.00 41.13 28.53

Table A1.4 Relative									n the Sa	bie catc	hment
SPECIES	3	5	21	7	9	20	11	19	14	26	
AMOS	0	0	0	0	0	0	0	0	0	0	
AURA	0	2	3	0	0	0	0	0	0	0	
BAFR	0	0	0	0	0	0	0	0	0	0	
BANN	0	0	0	0	0	0	0	0	3	3	
BBRE	0	0	0	0	0	0	0	0	0	0	
BEUT	0	0	0	0	0	0	7	0	0	0	
BMAR	0	2	0	66	13	2	86	1	2	0	
BPAL	0	0	0	0	0	0	0	0	0	0	
BPOL	0	0	0	0	0	0	0	0	0	0	
BRAD	0	0	0	0	0	1	0	0	1	1	,
BTRI	0	0	0	1	4	1	19	0	10	6	
BUNI	0	0	0	0	0	0	2	0	0	2	
BVIV	0	0	0	12	0	7	0	4	14	6	
BIMB	0	0	0	0	0	0	0	0	0	0	
CANO	20	34	61	25	1	0	31	10	0	0	
CPAR	0	0	0	11	3	2	0	6	32	0	
CSWI	0	0	0	4	23	3	0	9	0	0	
CGAR	0	0	0	0	0	0	0	0	0	4	
GCAL	0	0	0	0	0	1	0	0	2	0	
GGIU	0	0	0	0	0	0	0	0	0	0	
HVIT	0	0	0	0	0	1	0	0	0	0	
LMOL	0	2	0	16	0	0	11	0	10	0	
MMAC	0	0	0	4	1	0	0	1	32	2	
MBRE	0	0	0	6	0	0	0	0.	0	0	
MACU	0	0	0	2	0	0	2	0	3	0	
OPER	0	0	0	0	0	0	0	0	0	0	
OMOS	0	0	0	1	27	23	1	7	9	16	
PCAT	0	0	0	1	0	0	0	0	6	0	
PPHI	0	0	0	1	0	0	0	2	0	10	
SINT	0	0	0	0	0	0	0	0	0	1	
SMER	0	0	0	0	0	0	0	0	0	0	
TREN	0	0	0	3	12	11	0	0	2	0	
TSPA	0	0	0	0	0	0	0	2	0	0	
VNEL	11	0	12	0	0	0	0	0	0	0	
Total individuals	31	40	76	153	84	52	159	42	126	51	
Total species	2	Λ	2	4 =	0	140	_	_			

 Total individuals
 31
 40
 76
 153
 84
 52
 159
 42
 126
 51

 Total species
 2
 4
 3
 15
 9
 10
 8
 9
 13
 10

 CPUE (fish.min⁻¹)
 27.62
 17.02
 22.97
 17.23
 37.78
 39.42
 33.67
 20.42
 25.18
 18.78

Appendix A2 Environmental data for May electrofishing surveys in main rivers of the Sabie catchment

Table A2.1 Environmental data for sites fished in May 2000

Environmental variables	3	5	21	7	20	11	19	14	26
NTUs	6.3	4.4	27.7	17.5	28.1	34.2	60	39.2	18
DO	94.8	90.5	93.5	95	97.4	95	98.8	104	98.5
pH	8	7.9	7.5	8	8.2	7.8	7.9	8.1	8
Dissolved organic carbon as C (mg/l)	3.1	1.8	1.4	1.4	2.4	1.6	2.9	2.4	1.1
Kjeldahl nitrogen as N (mg/l)	0.37	0.29	0.29	0.35	0.48	0.33	0.48	0.44	0.29
Ammonium as N (mg/l)	0.06	< 0.04	0.06	< 0.04	0.05	0.05	0.07	0.06	< 0.04
Nitrate + Nitrite as N (mg/l)	0.39	0.39	0.23	0.4	0.27	0.27	0.45	0.25	0.39
Flouride as F (mg/l)	<0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.1
Alkalinity as calcium carbonate (mg/l)	39	32	17	41	88	25	44	54	45
Sodium as Na (mg/l)	3	6	6	8	30	9	12	15	9
Magnesium as Mg (mg/l)	3	3	2	3	10	2	2	3	4
Silicon as Si (mg/l)	5.2	6.9	8.7	8.5	9.9	12.6	12.2	11.6	8.3
Orthophosphate as P (mg/l)	0.026	0.019	0.015	0.013	0.028	0.028	0.04	0.026	0.02
Sulphate as SO ₄ (mg/l)	10	10	6	6	12	9	13	11	9
Chloride as Cl (mg/l)	<10	<10	<10	<10	44	<10	13	13	11
Potassium as K (mg/l)	0.7	0.9	1	1	2	0.9	1.2	1.1	1
Calcium as Ca (mg/l)	9	8	4	7	17	5	7	6	8
Electrical Conductivity (25°C, mS/m)	11.2	9.9	6.6	13.7	37.1	9.6	14.5	15.8	15.7
TDS (mg/l)	81	73	47	87	225	66	104		100
Spot temperature	15.6	15	16.7	- 20.2	18.8	18.9	20.8		14.4
Mean temp	17.82	19.14	20.71	22.65	24	19.14	22.65		22.71
SD temp	2.3	3.21	3.82	3.97	4.5	3.21	3.97	3.97	4.88
CV temp	12.92	16.79	18.44	17.53	18.76	16.79	17.53		21.48
mean temperature (3 month)	18.63	20.39	22.18	24.2	25.81	20.39	24.2	24.2	25.01
Max temp	23.24	25.95	30.31	32.76	34.85	25.95	32.76		36.57
Min temp	10.99	9.82	9.42	10.6			10.6		
Mean max temp	18.98	20.49	22.66	24.92		20.49	24.92		28.03
Mean min temp	16.73	18	18.87	20.71	21.71	18	20.71	20.71	20.61

Degree days > 25°C for last 4 months	0	0	9.5	39.5	62.5	0	39.5	39.5	54
Mean flow	1.01	8.31	4.45	19.92	19.92	4.45	4.45	13.86	13.86
SD flow	1	15.01	6.18	16.9	16.9	6.18	6.18	63.45	63.45
CV flow	99.67	180.66	138.94	117.63	117.63	138.94	138.94	457.84	457.84
Max flow	13.18	100.21	83.39	88.48	88.48	83.39	83.39	1236.59	1236.59
Min flow	0.13	0.99	0.18	1.79	1.79	0.18	0.18	0.21	0.21

Table A2.2 Environmental data for sites fished in May 2001

Environmental variables	3	5	21	7	9	20	11	19	14
NTUs	0.2	1.5	9	3.3	6.7	7.5	7	28.4	7.4
DO	91.1	100.1	96	104.1	92.5	95.7	105.2	88.8	90.4
pH	7.8	7.4	7.1	7.7	7.6	8	7.4	7.5	7.8
Dissolved organic carbon as C (mg/l)	1.9	5.5	7.2	1.7	5.5	6.1	4.6	4.9	4.1
Kjeldahl nitrogen as N (mg/l)	0.22	< 0.19	< 0.19	0.59	< 0.19	< 0.19	0.26	< 0.19	< 0.19
Ammonium as N (mg/l)	<0.04	<0.04	< 0.04	< 0.04	< 0.04	< 0.04	0.08	< 0.04	< 0.04
Nitrate + Nitrite as N (mg/l)	0.23	0.32	0.19	0.26	0.24	0.17	0.27	0.25	0.08
Flouride as F (mg/l)	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.2
Alkalinity as calcium carbonate (mg/l)	43	32	20	38	4.3	85	32	44	49
Sodium as Na (mg/l)	7	4	5	7	9	29	_ 9	15	15
Magnesium as Mg (mg/l)	5	4	1	5	5	12	2	4	5
Silicon as Si (mg/l)	7.4	6.6	9.4	7.4	7.5	8.4	12.9	12	10.4
Orthophosphate as P (mg/l)	0.185	0.184	0.43	0.189	0.219	0.357	0.326	0.175	0.248
Sulphate as SO ₄ (mg/l)	4	7	6	7	8	7	6	6	6
Chloride as Cl (mg/l)	<10	<10	<10	<10	10	40	<10	12	13
Potassium as K (mg/l)	0.8	0.5	0.8	0.9	0.9	1.4	. 0.9	1	0.9
Calcium as Ca (mg/l)	9	7	4	8	7	16	5	. 7	7
Electrical Conductivity (25°C, mS/m)	12.3	9.1	5.9	11.1	12.8	31.7	9.3	14	14.9
TDS (mg/l)	88	69	50	82	96	211	71	99	107
Spot temperature	18.3	18.4	18.6	21.7	17.8	21.6	21.1	19.6	20.6
Mean temp	17.82	19.14	20.71	22.65	23.1	24	19.14	22.65	22.65
SD temp	2.3	3.21	3.82	3.97	3.97	4.5	3.21	3.97	3.97
CV temp	12.92	16.79	18.44	17.53	17.19	18.76	16.79	17.53	17.53
mean temperature (3 month)	18.5	20.34	22.06	23.89	24.48	25.19	20.34	23.89	23.89
Max temp	23.24	25.95	30.31	32.76	31.93	34.85	25.95	32.76	32.76
Min temp	10.99	9.82	9.42	10.6	11.38	11.38		10.6	10.6
Mean max temp	18.98	20.49	22.66	24.92	24.9	26.54	20.49	24.92	24.92
Mean min temp	16.73	18	18.87	20.71	21.46	21.71	18	20.71	20.71
Degree days > 25°C for last 4 months	0	0	10	35	40	46		35	35
Mean flow	1.01	8.31	4.45	19.92	19.92	19.92	4.45	4.45	13.86
SD flow	1	15.01	6.18	16.9	16.9	16.9	6.18	6.18	63.45

CV flow	29.66	180.66	138.94	117.63	117.63	117.63	138.94	138.94	457.84
Max flow	13.18	100.21	83.39	88.48	88.48	88.48	83.39	83.39	1236.59
Min flow	0.13	0.99	0.18	1.79	1.79	1.79	0.18	0.18	0.21

Table A2.3 Environmental data for sites fished in May 2002

Environmental variables	3	5	21	7	9	20	11	19	14	26
NTUs	0.1	0.05		0.2	1.6			6.4		
DO*	9.31E-19	2.95E-18	8.64E-21	1.35E-18	2.56E-20	3.86E-21	4.67E-20	1.12E-19		
рН	7.98	8.55	8.2	8.27	8.38	7.85	8.7	7.89	7.96	7.9
Dissolved organic carbon as C (mg/l)										
Kjeldahl nitrogen as N (mg/l)										
Ammonium as N (mg/l)										
Nitrate + Nitrite as N (mg/l)	0.36	0.24	0.07	0.23	0.06	0.05	0.08	0.08	0.05	< 0.05
Flouride as F (mg/l)										
Alkalinity as calcium carbonate (mg/l)										
Sodium as Na (mg/l)										
Magnesium as Mg (mg/l)										
Silicon as Si (mg/l)										
Orthophosphate as P (ug/l)	26.5	15.1	17.9	15.3	16.1	26.2	25.2	21.5		
Sulphate as SO ₄ (mg/l)	4.89	3.19	0.64	3.89	3.61	3.12	0.76	1.19	1.89	1.89
Chloride as Cl (mg/l)										
Potassium as K (mg/l)										
Calcium as Ca (mg/l)										
Electrical Conductivity (25°C, mS/m)	118.7	90	71.1	123.1	143.1	216	87.2	126.7	156.7	167.3
TDS (mg/l)										
Spot temperature	15.5	17	16	21	23	19.5	18			
Mean temp	17.82	19.14	20.71	22.65	23.1	24				
SD temp	2.3	3.21	3.82	3.97	3.97	4.5	3.21	3.97		
CV temp	12.92	16.79	18.44	17.53	17.19	18.76	16.79			
mean temperature (3 month)	18.76	20.43	22.31	24.52	25.05	26.43	20.43	24.52		_
Max temp	23.24	25.95	30.31	32.76	31.93	34.85	25.95	32.76	32.76	
Min temp	10.99	9.82	9.42	10.6	11.38	11.38	9.82	10.6	10.6	
Mean max temp	18.98	20.49	22.66	24.92	24.9	26.54	20.49	24.92	24.92	
Mean min temp	16.73	18	18.87	20.71	21.46	21.71	18	20.71		
Degree days > 25°C for last 4 months	0	0	_		53	79				
Mean flow	1.01	8.31	4.45	19.92	19.92	_				
SD flow	1	15.01	6.18	16.9	16.9	16.9	6.18	6.18	63.45	63.45

CV flow	99.67	180.66	138.94	117.63	117.63	117.63	138.94	138.94	457.84	457.84
Max flow	13.18	100.21	83.39	88.48	88.48	88.48	83.39	83.39	1236.59	1236.59
Min flow	0.13	0.99	0.18	1.79	1.79	1.79	0.18	0.18	0.21	0.21

A dissolved oxygen meter was unavailable for this survey. According to Lorentz (2003), DO levels can be approximated using techniques employed to estimate oxygen levels in soils. According to this technique, the relationship between pH and redox potentials ($pe = -\log of$ electron activity) differs according to oxygen levels at a pressure of one atmosphere. Thus, relative oxygen levels between sites can be calculated using the relationship between pH and pe (Lindsay 1979, pp. 23-28). The acidity of water is readily measured using a pH meter, while redox potentials can be calculated from the electrical conductivity of a solution.

Appendix A3 Correlation matrices for environmental data for May 2000, May 2001 and May 2002 electrofishing surveys.

Table A3.	1 Correlation	matrix for en	nvironmenta	l data for M	ay 2000		
Cond	1.000						
DO	0.359	1.000					
Fcv	0.003	0.655	1.000				
Fmax	0.062	0.712	0.992	1.000			
Fmean	0.663	0.313	0.280	0.329	1.000		
Fmin	0.594	-0.229	-0.343	-0.314	0.773	1.000	
N	-0.149	-0.170	-0.117	-0.131	-0.086	0.064	1.000
NTUs	0.140		0.078	0.094	-0.075	-0.278	-0.118
P	0.283	0.441	-0.075	-0.069	-0.317	-0.323	0.186
pН	0.723	0.492	0.273	0.324	0.616	0.452	0.220
SO4	0.507	0.449	0.111	0.101	-0.063	-0.104	0.198
Subs	0.718	0.512	0.095	0.161	0.713	0.516	-0.316
Tcv	0.298		0.532	0.530	0.543	0.136	-0.140
Tdd	0.749		0.396	0.460	0.775	0.405	0.061
Tmax	0.542	0.585	0.488	0.533	0.715	0.282	-0.024
Tmean	0.659		0.346	0.396	0.771	0.423	-0.055
Tmean3	0.641	0.599	0.394	0.442	0.769	0.394	-0.050
Tmin	0.593	0.251	-0.400	-0.336	0.239	0.450	0.049
Tmmax	0.573	0.598	0.514	0.561	0.727	0.284	0.027
Tmmin	0.663	0.615	0.344	0.392	0.783	0.441	-0.036
	Cond	DO :	Fev]	Fmax	Fmean]	Fmin I	N
NTUs	1.000						
P	0.696	1.000					
pН	-0.069	0.269	1.000				
SO_4	0.442	0.872	0.555	1.000			
Subs	0.373	0.212	0.591	0.233	1.000		
Tcv	0.236	-0.187	0.004	-0.102	0.314	1.000	
Tdd	0.350	0.154	0.604	0.296	0.644	0.669	1.000
Tmax	0.400	0.003	0.326	0.094	0.517	0.850	0.938
Tmean	0.484	0.108	0.429	0.205	0.654	0.719	0.954
Tmean3	0.455	0.078	0.409	0.181	0.630	0.778	0.958
Tmin	0.145	0.42	0.626	0.489	0.453	-0.504	0.248
Tmmax	0.361	0.028	0.400	0.138	0.530	0.839	0.956
Tmmin	0.494	0.131	0.458	0.232	0.682	0.706	0.949
	NTUs	P	pH S	SO ₄	Subs	Γcv	Γdd
Tmax	1.000						
Tmean	0.959	1.000					
Tmean3	0.980	0.995	1.000				
Tmin	-0.051	0.192	0.110	1.000			
Tmmax	0.994	0.172	0.971	-0.035	1.000		
Tmmin	0.946	0.997	0.991	0.208	0.937	1.000	
			rmean3			1.000 Γ mmin	

1 4010 1 4012	2 Correlation	matrix for er	ivironmental	data for Ma	ıy 2001		
Cond	1.000						
DO	-0.240	1.000					
Fcv	0.000	-0.284	1.000				
Fmax	0.077	-0.325	0.985	1.000			
Fmean	0.516	0.127	0.101	0.184	1.000		
Fmin	0.455	0.276	-0.313	-0.255	0.886	1.000	
N	-0.399	0.500	-0.680	-0.766	-0.232	0.169	1.000
NTUs	0.096	-0.441	0.001	-0.006	-0.192	-0.284	-0.065
P	0.139	0.200	-0.036	-0.023	-0.037	-0.113	-0.380
pН	0.783	-0.258	0.165	0.272	0.521	0.412	-0.397
SO_4	0.190	0.275	-0.051	-0.056	0.776	0.780	0.161
Subs	0.689	0.228	0.201	0.288	0.632	0.416	-0.391
Tcv	0.275	0.167	0.169	0.162	0.512	0.353	-0.255
Tdd	0.633	-0.341	0.164	0.268	0.786	0.578	-0.458
Tmax	0.533	-0.218	0.213	0.288	0.715	0.484	-0.487
Tmean	0.580	-0.241	0.180	0.264	0.784	0.570	-0.444
Tmean3	0.541	-0.212	0.185	0.262	0.781	0.567	-0.425
Tmin	0.698	-0.456	-0.094	0.030	0.570	0.536	-0.254
Tmmax	0.585	-0.241	0.194	0.278	0.761	0.540	-0.469
Tmmin	0.563	-0.229	0.175	0.257	0.809	0.602	-0.399
	Cond	DO	Fev I	Fmax I	Fmean I	Fmin N	V
NTUs	1.000						
P	-0.034	1.000					
рH	-0.034	-0.302	1.000				
SO4				1.000			
	11 (177	1111144	_0 1177				
	0.022	0.033	-0.027 0.600		1 000		
Subs	0.086	0.203	0.600	0.341	1.000	1 000	
Subs Tev	0.086 0.375	0.203 0.505	0.600 -0.174	0.341 0.693	0.482	1.000	1 000
Subs Tev Tdd	0.086 0.375 0.380	0.203 0.505 -0.053	0.600 -0.174 0.538	0.341 0.693 0.543	0.482 0.634	0.566	1.000
Subs Tcv Tdd Tmax	0.086 0.375 0.380 0.454	0.203 0.505 -0.053 0.179	0.600 -0.174 0.538 0.300	0.341 0.693 0.543 0.579	0.482 0.634 0.615	0.566 0.794	0.936
Subs Tcv Tdd Tmax Tmean	0.086 0.375 0.380 0.454 0.414	0.203 0.505 -0.053 0.179 0.090	0.600 -0.174 0.538 0.300 0.385	0.341 0.693 0.543 0.579 0.638	0.482 0.634 0.615 0.639	0.566 0.794 0.733	0.936 0.975
Subs Tcv Tdd Tmax Tmean Tmean3	0.086 0.375 0.380 0.454 0.414 0.421	0.203 0.505 -0.053 0.179 0.090 0.114	0.600 -0.174 0.538 0.300 0.385 0.328	0.341 0.693 0.543 0.579 0.638 0.672	0.482 0.634 0.615 0.639 0.625	0.566 0.794 0.733 0.769	0.936 0.975 0.960
Subs Tcv Tdd Tmax Tmean Tmean3	0.086 0.375 0.380 0.454 0.414 0.421 0.003	0.203 0.505 -0.053 0.179 0.090 0.114 -0.350	0.600 -0.174 0.538 0.300 0.385 0.328 0.846	0.341 0.693 0.543 0.579 0.638 0.672 0.167	0.482 0.634 0.615 0.639 0.625 0.413	0.566 0.794 0.733 0.769 -0.148	0.936 0.975 0.960 0.673
Subs Tcv Tdd Tmax Tmean Tmean3 Tmin	0.086 0.375 0.380 0.454 0.414 0.421 0.003 0.429	0.203 0.505 -0.053 0.179 0.090 0.114 -0.350 0.112	0.600 -0.174 0.538 0.300 0.385 0.328 0.846 0.382	0.341 0.693 0.543 0.579 0.638 0.672 0.167 0.601	0.482 0.634 0.615 0.639 0.625 0.413	0.566 0.794 0.733 0.769 -0.148 0.745	0.936 0.975 0.960 0.673 0.969
Subs Tcv Tdd Tmax Tmean Tmean3	0.086 0.375 0.380 0.454 0.414 0.421 0.003	0.203 0.505 -0.053 0.179 0.090 0.114 -0.350 0.112 0.038	0.600 -0.174 0.538 0.300 0.385 0.328 0.846 0.382 0.388	0.341 0.693 0.543 0.579 0.638 0.672 0.167 0.601 0.684	0.482 0.634 0.615 0.639 0.625 0.413 0.645 0.636	0.566 0.794 0.733 0.769 -0.148 0.745 0.712	0.936 0.975 0.960 0.673 0.969 0.975
Subs Tcv Tdd Tmax Tmean Tmean3 Tmin	0.086 0.375 0.380 0.454 0.414 0.421 0.003 0.429 0.399	0.203 0.505 -0.053 0.179 0.090 0.114 -0.350 0.112 0.038	0.600 -0.174 0.538 0.300 0.385 0.328 0.846 0.382	0.341 0.693 0.543 0.579 0.638 0.672 0.167 0.601 0.684	0.482 0.634 0.615 0.639 0.625 0.413 0.645 0.636	0.566 0.794 0.733 0.769 -0.148 0.745 0.712	0.936 0.975 0.960 0.673 0.969
Subs Tev Tdd Tmax Tmean Tmean3 Tmin Tmmax Tmmin	0.086 0.375 0.380 0.454 0.414 0.421 0.003 0.429 0.399 NTUs	0.203 0.505 -0.053 0.179 0.090 0.114 -0.350 0.112 0.038	0.600 -0.174 0.538 0.300 0.385 0.328 0.846 0.382 0.388	0.341 0.693 0.543 0.579 0.638 0.672 0.167 0.601 0.684	0.482 0.634 0.615 0.639 0.625 0.413 0.645 0.636	0.566 0.794 0.733 0.769 -0.148 0.745 0.712	0.936 0.975 0.960 0.673 0.969 0.975
Subs Tev Tdd Tmax Tmean Tmean3 Tmin Tmmax Tmmin	0.086 0.375 0.380 0.454 0.414 0.421 0.003 0.429 0.399 NTUs	0.203 0.505 -0.053 0.179 0.090 0.114 -0.350 0.112 0.038	0.600 -0.174 0.538 0.300 0.385 0.328 0.846 0.382 0.388	0.341 0.693 0.543 0.579 0.638 0.672 0.167 0.601 0.684	0.482 0.634 0.615 0.639 0.625 0.413 0.645 0.636	0.566 0.794 0.733 0.769 -0.148 0.745 0.712	0.936 0.975 0.960 0.673 0.969 0.975
Subs Tev Tdd Tmax Tmean Tmean3 Tmin Tmmax Tmmin Tmax Tmean Tmean Tmean3	0.086 0.375 0.380 0.454 0.414 0.421 0.003 0.429 0.399 NTUs 1.000 0.984 0.984	0.203 0.505 -0.053 0.179 0.090 0.114 -0.350 0.112 0.038 P	0.600 -0.174 0.538 0.300 0.385 0.328 0.846 0.382 0.388 pH	0.341 0.693 0.543 0.579 0.638 0.672 0.167 0.601 0.684	0.482 0.634 0.615 0.639 0.625 0.413 0.645 0.636	0.566 0.794 0.733 0.769 -0.148 0.745 0.712	0.936 0.975 0.960 0.673 0.969 0.975
Subs Tcv Tdd Tmax Tmean Tmean3 Tmin Tmmax Tmmin Tmax Tmean Tmean3 Tmin	0.086 0.375 0.380 0.454 0.414 0.421 0.003 0.429 0.399 NTUs 1.000 0.984 0.984 0.386	0.203 0.505 -0.053 0.179 0.090 0.114 -0.350 0.112 0.038 P	0.600 -0.174 0.538 0.300 0.385 0.328 0.846 0.382 0.388	0.341 0.693 0.543 0.579 0.638 0.672 0.167 0.601 0.684	0.482 0.634 0.615 0.639 0.625 0.413 0.645 0.636	0.566 0.794 0.733 0.769 -0.148 0.745 0.712	0.936 0.975 0.960 0.673 0.969 0.975
Subs Tev Tdd Tmax Tmean Tmean3 Tmin Tmmax Tmmin Tmax Tmean Tmean Tmean3 Tmin Tmean3 Tmin	0.086 0.375 0.380 0.454 0.414 0.421 0.003 0.429 0.399 NTUs 1.000 0.984 0.984 0.386 0.993	0.203 0.505 -0.053 0.179 0.090 0.114 -0.350 0.112 0.038 P 1.000 0.998 0.513 0.997	0.600 -0.174 0.538 0.300 0.385 0.328 0.846 0.382 0.388 pH \$5	0.341 0.693 0.543 0.579 0.638 0.672 0.167 0.601 0.684 SO ₄	0.482 0.634 0.615 0.639 0.625 0.413 0.645 0.636	0.566 0.794 0.733 0.769 -0.148 0.745 0.712	0.936 0.975 0.960 0.673 0.969 0.975
Subs Tcv Tdd Tmax Tmean Tmean3 Tmin Tmmax Tmmin Tmax Tmean Tmean3 Tmin	0.086 0.375 0.380 0.454 0.414 0.421 0.003 0.429 0.399 NTUs 1.000 0.984 0.984 0.984 0.993 0.963	0.203 0.505 -0.053 0.179 0.090 0.114 -0.350 0.112 0.038 P	0.600 -0.174 0.538 0.300 0.385 0.846 0.382 0.388 pH 1.000 0.464 0.994 0.994	0.341 0.693 0.543 0.579 0.638 0.672 0.167 0.601 0.684 50 ₄	0.482 0.634 0.615 0.639 0.625 0.413 0.645 0.636 Subs	0.566 0.794 0.733 0.769 -0.148 0.745 0.712	0.936 0.975 0.960 0.673 0.969 0.975

I able A3.	3 Correlation	matrix for e	nvironmenta	al data for M	ay 2002		
Cond	1.000						
DO	-0.367	1.000					
Fcv	0.318	-0.193	1.000				
Fmax	0.392	-0.273	0.991	1.000			
Fmean	0.667	-0.092	0.165	0.226	1.000		
Fmin	0.400	0.219	-0.390	-0.349	0.818	1.000	
N	-0.370	0.707	-0.445	-0.461	-0.341	0.039	1.000
NTUs	0.085	-0.668	0.363	0.361	-0.194	-0.499	-0.751
P	0.296	-0.421	-0.063	-0.024	-0.326	-0.341	0.024
pН	-0.665	0.409	-0.340	-0.400	-0.121	0.144	0.176
SO_4	0.273	0.467	-0.290	-0.247	0.321	0.544	0.698
Subs	0.646	-0.394	0.106	0.169	0.616	0.419	-0.434
Tcv	0.375	-0.338	0.531	0.531	0.470	0.094	-0.793
Tdd	0.886	-0.450	0.245	0.320	0.799	0.524	-0.56
Tmax	0.674	-0.479	0.456	0.507	0.687	0.294	-0.721
Tmean	0.717	-0.464	0.271	0.332	0.788	0.489	-0.673
Tmean3	0.732	-0.468	0.289	0.350	0.788	0.480	-0.687
Tmin	0.472	-0.100	-0.439	-0.368	0.381	0.566	0.205
Tmmax	0.725	-0.471	0.469	0.525	0.714	0.317	-0.701
Tmmin	0.708	-0.441	0.246	0.306	0.813	0.531	-0.664
	Cond	DO	Fcv	Fmax]	Fmean]	Fmin 1	N
NTUs	1.000						
P	0.241	1.000					
pН	-0.141	-0.330	1.000				
pH SO4	-0.141 -0.831	-0.330 -0.044	-0.086	1.000			
pH SO4 Subs	-0.141 -0.831 0.240	-0.330 -0.044 0.373	-0.086 -0.156	-0.071	1.000		
pH SO4 Subs Tcv	-0.141 -0.831 0.240 0.620	-0.330 -0.044 0.373 -0.376	-0.086 -0.156 -0.227	-0.071 -0.508	0.316	1.000	
pH SO4 Subs Tcv Tdd	-0.141 -0.831 0.240 0.620 0.148	-0.330 -0.044 0.373 -0.376 -0.013	-0.086 -0.156 -0.227 -0.589	-0.071		1.000 0.580	1.000
pH SO4 Subs Tev Tdd Tmax	-0.141 -0.831 0.240 0.620 0.148 0.380	-0.330 -0.044 0.373 -0.376 -0.013 -0.238	-0.086 -0.156 -0.227	-0.071 -0.508	0.316		1.000 0.893
pH SO4 Subs Tcv Tdd Tmax Tmean	-0.141 -0.831 0.240 0.620 0.148 0.380 0.202	-0.330 -0.044 0.373 -0.376 -0.013 -0.238 -0.185	-0.086 -0.156 -0.227 -0.589	-0.071 -0.508 0.089	0.316 0.654	0.580	
pH SO4 Subs Tcv Tdd Tmax Tmean Tmean3	-0.141 -0.831 0.240 0.620 0.148 0.380 0.202 0.231	-0.330 -0.044 0.373 -0.376 -0.013 -0.238 -0.185 -0.181	-0.086 -0.156 -0.227 -0.589 -0.547 -0.478 -0.487	-0.071 -0.508 0.089 -0.230 -0.105 -0.115	0.316 0.654 0.506 0.609 0.611	0.580 0.840 0.677 0.706	0.893
pH SO4 Subs Tcv Tdd Tmax Tmean Tmean3	-0.141 -0.831 0.240 0.620 0.148 0.380 0.202 0.231 -0.537	-0.330 -0.044 0.373 -0.376 -0.013 -0.238 -0.185 -0.181 0.350	-0.086 -0.156 -0.227 -0.589 -0.547 -0.478 -0.487 -0.222	-0.071 -0.508 0.089 -0.230 -0.105 -0.115 0.598	0.316 0.654 0.506 0.609 0.611 0.375	0.580 0.840 0.677 0.706	0.893 0.952 0.957
pH SO4 Subs Tcv Tdd Tmax Tmean Tmean3 Tmin	-0.141 -0.831 0.240 0.620 0.148 0.380 0.202 0.231 -0.537 0.362	-0.330 -0.044 0.373 -0.376 -0.013 -0.238 -0.185 -0.181 0.350 -0.224	-0.086 -0.156 -0.227 -0.589 -0.547 -0.478 -0.487 -0.222 -0.551	-0.071 -0.508 0.089 -0.230 -0.105 -0.115 0.598 -0.163	0.316 0.654 0.506 0.609 0.611 0.375 0.513	0.580 0.840 0.677 0.706 -0.474 0.822	0.893 0.952 0.957 0.413 0.915
pH SO4 Subs Tcv Tdd Tmax Tmean Tmean3	-0.141 -0.831 0.240 0.620 0.148 0.380 0.202 0.231 -0.537 0.362 0.164	-0.330 -0.044 0.373 -0.376 -0.013 -0.238 -0.185 -0.181 0.350 -0.224 -0.206	-0.086 -0.156 -0.227 -0.589 -0.547 -0.478 -0.487 -0.222 -0.551 -0.415	-0.071 -0.508 0.089 -0.230 -0.105 -0.115 0.598 -0.163 -0.075	0.316 0.654 0.506 0.609 0.611 0.375 0.513	0.580 0.840 0.677 0.706 -0.474 0.822 0.643	0.893 0.952 0.957 0.413 0.915 0.946
pH SO4 Subs Tcv Tdd Tmax Tmean Tmean3 Tmin	-0.141 -0.831 0.240 0.620 0.148 0.380 0.202 0.231 -0.537 0.362	-0.330 -0.044 0.373 -0.376 -0.013 -0.238 -0.185 -0.181 0.350 -0.224 -0.206	-0.086 -0.156 -0.227 -0.589 -0.547 -0.478 -0.487 -0.222 -0.551 -0.415	-0.071 -0.508 0.089 -0.230 -0.105 -0.115 0.598 -0.163 -0.075	0.316 0.654 0.506 0.609 0.611 0.375 0.513	0.580 0.840 0.677 0.706 -0.474 0.822 0.643	0.893 0.952 0.957 0.413 0.915 0.946
pH SO4 Subs Tcv Tdd Tmax Tmean Tmean3 Tmin Tmmax Tmmin	-0.141 -0.831 0.240 0.620 0.148 0.380 0.202 0.231 -0.537 0.362 0.164 NTUs	-0.330 -0.044 0.373 -0.376 -0.013 -0.238 -0.185 -0.181 0.350 -0.224 -0.206	-0.086 -0.156 -0.227 -0.589 -0.547 -0.478 -0.487 -0.222 -0.551 -0.415	-0.071 -0.508 0.089 -0.230 -0.105 -0.115 0.598 -0.163 -0.075	0.316 0.654 0.506 0.609 0.611 0.375 0.513	0.580 0.840 0.677 0.706 -0.474 0.822 0.643	0.893 0.952 0.957 0.413 0.915 0.946
pH SO4 Subs Tcv Tdd Tmax Tmean Tmean3 Tmin Tmmax Tmmin	-0.141 -0.831 0.240 0.620 0.148 0.380 0.202 0.231 -0.537 0.362 0.164 NTUs	-0.330 -0.044 0.373 -0.376 -0.013 -0.238 -0.185 -0.181 0.350 -0.224 -0.206	-0.086 -0.156 -0.227 -0.589 -0.547 -0.478 -0.487 -0.222 -0.551 -0.415	-0.071 -0.508 0.089 -0.230 -0.105 -0.115 0.598 -0.163 -0.075	0.316 0.654 0.506 0.609 0.611 0.375 0.513	0.580 0.840 0.677 0.706 -0.474 0.822 0.643	0.893 0.952 0.957 0.413 0.915 0.946
pH SO4 Subs Tcv Tdd Tmax Tmean Tmean3 Tmin Tmmax Tmmin	-0.141 -0.831 0.240 0.620 0.148 0.380 0.202 0.231 -0.537 0.362 0.164 NTUs	-0.330 -0.044 0.373 -0.376 -0.013 -0.238 -0.185 -0.181 0.350 -0.224 -0.206	-0.086 -0.156 -0.227 -0.589 -0.547 -0.478 -0.487 -0.222 -0.551 -0.415	-0.071 -0.508 0.089 -0.230 -0.105 -0.115 0.598 -0.163 -0.075	0.316 0.654 0.506 0.609 0.611 0.375 0.513	0.580 0.840 0.677 0.706 -0.474 0.822 0.643	0.893 0.952 0.957 0.413 0.915 0.946
pH SO4 Subs Tcv Tdd Tmax Tmean Tmin Tmmax Tmin Tmmax Tmmin	-0.141 -0.831 0.240 0.620 0.148 0.380 0.202 0.231 -0.537 0.362 0.164 NTUs	-0.330 -0.044 0.373 -0.376 -0.013 -0.238 -0.185 -0.181 0.350 -0.224 -0.206 P	-0.086 -0.156 -0.227 -0.589 -0.547 -0.487 -0.222 -0.551 -0.415 pH	-0.071 -0.508 0.089 -0.230 -0.105 -0.115 0.598 -0.163 -0.075	0.316 0.654 0.506 0.609 0.611 0.375 0.513	0.580 0.840 0.677 0.706 -0.474 0.822 0.643	0.893 0.952 0.957 0.413 0.915 0.946
pH SO4 Subs Tcv Tdd Tmax Tmean Tmin Tmmax Tmmin Tmax Tmean Tmean Tmean3	-0.141 -0.831 0.240 0.620 0.148 0.380 0.202 0.231 -0.537 0.362 0.164 NTUs 1.000 0.945 0.956 -0.001	-0.330 -0.044 0.373 -0.376 -0.013 -0.238 -0.185 -0.181 0.350 -0.224 -0.206 P	-0.086 -0.156 -0.227 -0.589 -0.547 -0.487 -0.222 -0.551 -0.415 pH	-0.071 -0.508 0.089 -0.230 -0.105 -0.115 0.598 -0.163 -0.075 SO ₄	0.316 0.654 0.506 0.609 0.611 0.375 0.513 0.613	0.580 0.840 0.677 0.706 -0.474 0.822 0.643	0.893 0.952 0.957 0.413 0.915 0.946
pH SO4 Subs Tcv Tdd Tmax Tmean Tmin Tmmax Tmin Tmax Tmean Tmean Tmean Tmean Tmin	-0.141 -0.831 0.240 0.620 0.148 0.380 0.202 0.231 -0.537 0.362 0.164 NTUs 1.000 0.945 0.956 -0.001 0.993	-0.330 -0.044 0.373 -0.376 -0.013 -0.238 -0.185 -0.181 0.350 -0.224 -0.206 P	-0.086 -0.156 -0.227 -0.589 -0.547 -0.487 -0.222 -0.551 -0.415 pH	-0.071 -0.508 0.089 -0.230 -0.105 -0.115 0.598 -0.163 -0.075 SO ₄	0.316 0.654 0.506 0.609 0.611 0.375 0.513 0.613 Subs	0.580 0.840 0.677 0.706 -0.474 0.822 0.643	0.893 0.952 0.957 0.413 0.915 0.946
pH SO4 Subs Tcv Tdd Tmax Tmean Tmin Tmmax Tmmin Tmax Tmean Tmean Tmean3	-0.141 -0.831 0.240 0.620 0.148 0.380 0.202 0.231 -0.537 0.362 0.164 NTUs 1.000 0.945 0.956 -0.001 0.993 0.917	-0.330 -0.044 0.373 -0.376 -0.013 -0.238 -0.181 0.350 -0.224 -0.206 P	-0.086 -0.156 -0.227 -0.589 -0.547 -0.487 -0.222 -0.551 -0.415 pH 1.000 0.257 0.954 0.990	-0.071 -0.508 0.089 -0.230 -0.105 -0.115 0.598 -0.163 -0.075 SO ₄	0.316 0.654 0.506 0.609 0.611 0.375 0.513 0.613 Subs	0.580 0.840 0.677 0.706 -0.474 0.822 0.643 Fev	0.893 0.952 0.957 0.413 0.915 0.946
pH SO4 Subs Tcv Tdd Tmax Tmean Tmin Tmmax Tmin Tmax Tmean Tmean Tmean Tmean Tmin	-0.141 -0.831 0.240 0.620 0.148 0.380 0.202 0.231 -0.537 0.362 0.164 NTUs 1.000 0.945 0.956 -0.001 0.993	-0.330 -0.044 0.373 -0.376 -0.013 -0.238 -0.181 0.350 -0.224 -0.206 P	-0.086 -0.156 -0.227 -0.589 -0.547 -0.487 -0.222 -0.551 -0.415 pH 1.000 0.257 0.954 0.990	-0.071 -0.508 0.089 -0.230 -0.105 -0.115 0.598 -0.163 -0.075 SO ₄	0.316 0.654 0.506 0.609 0.611 0.375 0.513 0.613 Subs	0.580 0.840 0.677 0.706 -0.474 0.822 0.643 Fev	0.893 0.952 0.957 0.413 0.915 0.946

Appendix A4 Successive simulated daily maximum water temperatures falling within the same class

Table A4.1 Water temperatures states (columns) versus number of successive days within each class (rows), for the month of January at site WT4, using simulated maximum daily water temperatures for the period 1950-1995.

	.,,,,,,,				Te	mpe	ratur	e cla	ss				
Day	1	2	3	4	5	6	7	8	9	10	11	12	13
1			38	121	122	103	40	7					
2			10	39	81	51	11						
3			4	29	28	17	4						
4			0	5	22	6	1						
5			2	2	8	1							
6				2 2 2	8 5	1							
7				2	4	1							
8					1								
9					0								
10					0								
11					1								
12					0								
13					0								
14					0								
15					0								
16					0								
17					0								
18					0								
19					0								
20					0								
21					0								
22					0								
23					0								
24					2								
25						,				-			
26													
27													
28													
29													
30													
31													

Appendix A5 Cumulative number of days of each month within different water temperature classes for the period 1950 to 1995

Table A5.1 Frequency data for simulated water temperatures at site WT9

Class	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0
3	1	0	0	0	0	0	0	0	0	0	0	0
4	3	3	0	1	0	0	0	0	0	0	5	1
5	80	36	24	8	0	0	0	0	7	39	41	51
6_	448	343	227	82	18	0	0	10	87	174	243	361
7	597	586	602	314	110	10	11	59	226	357	456	573
8	233	291	456	531	311	67	83	243	382	410	340	329
9	62	46	89	317	483	269	257	411	380	246	205	88
10	2	4	18	115	381	539	529	406	189	130	70	22
11	0	0	0	12	111	385	423	226	88	58	16	1
12	0	0	0	0	12	93	107	62	17	10	4	0
13_	0	0	0	0	0	17	15	9	5	2	. 0	0

Table A5.2 Frequency data for simulated water temperatures at site WT1

Class	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0
3	0	1	0	0	0	0	0	0	· 0	0	0	0
4	6	3	1	0	0	0	0	0	2	5	3	7
5	132	83	47	7	4	0	0	2	17	50	62	87
6	575	697	412	94	23	1	0	34	93	166	215	356
7	572	405	728	497	142	32	26	98	225	285	603	732
8	126	114	186	582	495	143	152	309	615	582	280	194
9	14	6	41	180	578	638	632	611	250	207	171	50
10_	1	0	1	20	161	430	466	260	133	100	35	0
11	0	0	0	0	23	116	131	97	42	30	11	0
12	0	0	0	0	0	20	18	14	4	1	0	0
13	0	0	0	0	0	0	. 0	1	0	0	0	0

Table A5.3 Frequency data for simulated water temperatures at site WT3

Class	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0
3	15	7	3	0	. 0	0	0	0	2	9	6	15
4	205	132	71	13	2	0	0	3	19	52	98	126
5	556	553	472	141	23	0	0	27	109	234	295	471
6	473	457	609	515	167	33	18	102	281	371	426	510
7	155	151	219	491	461	146	155	328	435	367	333	233
8	21	9	40	198	535	445	439	479	303	254	161	70
9	1	0	2	22	201	558	594	334	179	111	47	1
10	0	0	0	0	36	170	189	132	48	26	13	0
11	0	0	0	0	1	28	30	19	5	2	1	0
12	0	0	0	0	. 0	0	0	2	0	0	. 0	0
13	0	0	0	0	0	0	0	0	0	0	0	0

Table A5.4 Frequency data for simulated water temperatures at site WT5

Class	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0
3_	95	54	29	1	1	0	0	0	4	24	45	68
4	435	431	248	55	6	0	0	9	51	127	183	308
5_	599	527	646	311	53	2	1	43	161	279	432	579
6	237	255	379	605	292	54	37	159	415	475	381	335
77	54	40	104	321	540	210	226	396	386	288	231	115
8	6	2	10	82	400	579	538	476	251	169	82	21
9	0	0	0	5	116	376	470	238	95	58	25	0
10	0	0	0	0	18	145	142	88	18	5	1	0
11	0	0	0	0	0	14	11	17	0	1	0	0
12	0	0	0	0	0	. 0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0	0

Table A5.5 Frequency data for simulated water temperatures at site WT4

Class	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0
3	80	41	18	0	0	0	0	0	0	6	24	52
4	342	395	171	21	0	0	0	0	8	61	141	265
5	621	517	602	200	0	0	0	3	67	259	397	498
6	298	287	459	525	92	0	1	35	254	390	421	447
7	78	64	149	433	353	37	23	168	520	419	272	133
88	7	5	17	175	566	224	207	522	334	216	97	31
9	0	0	0	26	342	597	639	460	155	62	23	0
10	0	0	0	0	70	426	449	189	42	11	5	0
11	0	0	0	0	3	86	98	42	1	. 2	0	0
12	0	0	0	0	0	10	7	7	0	0	0	0
13	0	0	0	0	0	0	1	0	0	0	0	0

Table A5.6 Frequency data for simulated water temperatures at site WT7

Class	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1	0	0	0	0	0	0	0	0	0	0	0	0
2	1	1	0	0	0	0	0	0	0	1	1	.0
3	152	86	33	0	0	0	0	0	0	13	48	101
4	451	490	284	48	0	0	0	0	13	94	196	346
5	578	480	622	274	17	0	0	5	116	302	458	576
6	196	220	368	586	138	0	2	65	328	486	364	293
7	41	30	102	348	451	67	46	240	492	316	224	98
8	5	2	7	114	546	287	302	546	290	163	73	12
99	0	0	0	10	239	638	692	405	116	46	14	0
10	0	0	0	0	34	329	322	138	26	4	2	0
11	0	0	0	0	1	52	55	24	0	1	0	. 0
12	0	0	0	0	0	7	6	3	0	0	0	0
13	2	0	0	0	0	0	0	0	0	0	0	0

Table A5.7 Frequency data for simulated water temperatures at site WT8

Table A5.7 Fr	equency data			iperatures a						<u> </u>		Dan
Class	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1	0	0	0	0	0	0	0	0	0	0	0	0
2	3	2	0	0	0	0	. 0	0	0	2	2	1
3	222	128	53	3	0	0	0	0	2	18	65	144
4	530		404	72	0	0	0	1	23	144	259	412
5	490			352	27	0	1	11	155	328	455	547
6	152	167	273			3	.4	82	392	470	351	239
7	25	17	76	290		103	76	305	449	298	178	76
8	2	2	3	90		383		557	257	127	59	7
9	0	- 0	0	3	179	605	-		90	35	11	0
10	0	0	0		17	249			13	4	0	0
11	0	0	0		1	33				0	0	0
12	0	0	0	0	0	4	4	2	0	0	0	0
13	2	0	0	. 0	0	0	0	0	0	0	0	0

Table A5.8 Frequency data for simulated water temperatures at site WT2

Class	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0
3	0	1	0	0	0	0	0	0	0	0	0	0
4	6	3	1	0	0	0	0	0	2	5	3	7
5	132	83	47	7	4	0	0	2	17	50	62	87
6	575	697	412	94	23	1	0	34	93	166	215	356
7	572	405	728	497	142	32	26			285	603	732
8	126	114	186	582	495	143	152	309			280	194
99	14	6	41	180	578	638	632	611		207	171	50
10	1	0	1	20	161	430	466	260			35	0
11	0	0	0	0	23	116	131	97		30	11	0
12	0	0	0	0	0	20	18			1	0	0
13	0	0	0	0	0	0	0	1	0	0	0	0

Table A5.9 Frequency data for simulated water temperatures at site WT10

Class	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1	0	0	0	0	0	0	0	0	0	0	0	0
2_	0	0	0	0	0	1	1	0	0	0	0	0
3	37	27	54	18	34	28	53	18	21	45	31	31
44	121	149	156	163	166	124	156				191	162
5	242	301	289	276	260	277	252	325			293	327
6	248	234	283	197	213	248	266	317			255	288
7	_225	167	189	230	222	232	242	177		238	204	181
8	233	198	176	209	204	207	196	166	184		183	184
9	201	145	168	200	169	193	167	239		150	173	203
10	99	73	8.6	78	127	60	88	38	102	56	46	42
11	20	10	13	9	29	10	4	2	27	8	3	7
12	0	4	2	0	2	0	0	0	7	0	1.	0
13	0	1	0	0	0	0	0	0	0	0	0	1

Appendix A6 Cumulative number of successive days within the same temperature class for simulated maximum daily water temperatures for the period 1950-1995.

Table A6.1 Cumulative number of successive days within each temperature class for simulated maximum

daily water temperatures at site WT9

dany	water	rtem	beratu	res a	t site V	<u> </u>						
	Jan	Feb	Mar	Apr	May	Jun	Jul		Sep	Oct	Nov	Dec
1	425	319	327	327	389	378	416	557	587	632	532	450
2	162	163	141	156	159	156	162	188	162	197	176	185
3	76	69	92	80	78	74	78	86	63	57	82	83
4	36	42	49	34	46	44	45	26	26	28	27	42
5	_23	22	18	25	23	19	19	15	12	. 9	12	10
6	3	10	12	9	11	11	8	1	6	3	7	8
7	8	8	8	8	3	7	6	6	4	1	2	5
8	5	2	2	4	5	5	3	1	0	2	1	2
9	0	1	5	5	_2	1	4	0	0	0	2	1
10	2	1	3	1	3	1	1	0	0	0	0	2
11	0	0	0	0	1	1	0	0	0	0	0	1
12	0	0	1	0	0	1	0	0	0	0	0	0
13	0	1	0	1	0	0	0	0	0	0	0	0
14	0	0	1	0	0	0	0	0	0	0	0	0
15	1	1	0	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	1	0	0	0	0	0
17	1	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0	0	0
21	0	. 0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	0
24	1	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	1	0	0	0
27	0	0	0	0	0	0	0	0	1	0	0	0
>28	0	0	0	1	0	0	0	0	0	1	0	0

Table A6.2 Cumulative number of successive days within each temperature class for simulated maximum daily water temperatures at site WT1

daily					t site v			· ·				
	Jan		Mar			Jun		Aug	Sep		Nov	Dec
1	318	235	268	313	357	331	358	465	524	546	507	413
2	139	110	140	105	121	135	136	160	150	150	163	152
3	60	68	54	71	61	59	56	50	47	41	. 39	56
4	37	33	40	32	21	26	41	26	14	23	22	25
5	20	15	10	15	25	17	11	8	10	13	6	16
6	5	5	11	. 7	10	6	4	4	0.	1	2	5
7	4	11	11	4	2	3	5	5	2	1	1	1
8	3	1	7	5	5	5	1	5	2	0	1	0
9	3	3	2	2	1	2	3	0	1	0	1	1
10	1	0	3	1	0	0	2	0	0	0	1	0
11	1	2	0	2	1	0	0	0	0	0	0	1
12	3	0	0	2	0	0	0	0	0	0	0	0
13	4	0	0	6	0	0	0	1	0	0	0	0
14	1	0	1	0	0	0	0	1	0	0	0	0
15	0	0	0	5	9	0	0	0	0	0	0	0
16	0	0	0	0	9	0	1	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0	0	0
18	4	0	0	0	0	0	0	0	0	0	0	0
19	3	0	0	2	0	0	0	0	0	0	0	0
20	1	0	0	0	0	0	0	0	0	1	0	0
21	1	0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	3	1	0	0	0	0	0	0	0
23	0	0	5	0	0	0	0	2	0	0	0	0
24	0	1	5	0	0	0	0	4	0	0	0	0
25	0	0	0	0	0	0	0	1	0	0	0	1
26	0	0	0	0	0	0	0	1	0	0	0	0
27	0	0	0	0	0	0	0	0	0	1	0	0
>28	0	9	0	0	0	10	9	1	8	8	9	9

Table A6.3 Cumulative number of successive days within each temperature class for simulated maximum daily water temperatures at site WT3

dany	wate	tem	Jeraiu	res a	t site v	V 13						
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1	422	324	340	387	424	392	437	560	634	664	633	538
2	173	168	169	145	148	162	159	197	200	208	217	205
3	80	69	69	92	83	75	67	65	56	_56	51	64
4	43	39	46	42	37	32	43	37	18	19	24	30
5	16	21	18	19	30	21	20	11	10	15	7	19
6	10	7	8	6	8	17	10	4	2	2	1	8
7	4	9		3	5	6	4	3	1	1	1	1
8	2	3	8	4	5	3	3	1	1	1	2	2
9	_4	1	2	1	4	2	4	0	0	0	0	0
10	0		2	3	0	2	1	0	0	0	0	0
11	0	1	4	1	0	0	0	0	0	0	0	0
12	1	0	0	1	0	0	0	0	0	0	0	0
13	0	1	0	1	0	0	0	0	0	0	0	0
14	1	0	0	0	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	1	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	1	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	1	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0	0	0
_ 26	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0
>28_	0	0	0	0	0	0	0	0	1	0	0	0

Table A6.4 Cumulative number of successive days within each temperature class for simulated maximum daily water temperatures at site WT5

daily	water	r temp	peratu	res a	site V	VT5						
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1	433	308	361	362	376	371	404	509	600	638	589	515
2	180	154	171	149	150	180	160	188	178	164	201	194
3	80	85	64	73	75	63	89	75	59	69	57	63
4	32	38	42	41	32	31	31	26	23	20	24	30
5	18	21	17	12	31	22	32	17	8	9	11	12
6	7	11	10	11	14	9	8	6	7	6	5	9
7	6	5	9	12	6	8	3	. 3	3	0	1	5
8	1	3	5	1	3	4	1	1	0	0	0	1
9	1	0	2	1	2	1	1	0	1	0	1	0
10	1	0	2	1	4	1	2	0	0	0	0	0
11	0	1	0	1	0	2	0	1	0	0	0	1
12	0	0	1	0	0	0	0	1	0	1	0	0
13	1	0	1	2	0	1	1	0	0	0	0	0
14	0	0	0	1	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	. 0	0	0	0	2
16	0	0	0	0	0	0	0	0	0	0	0	1
17	0	1	0	0	_2	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	1	0	0
19	0	0	0	1	0	0	0	1	0	0	0	0
20	0	0	1	0	0	0	0	1	0	0	0	0
21	0	0	0	0	0	0	0	0	1	0	1	0
22	0	0	1	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	1	0	0	0
24	1	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0	0	0	0
27	1	0	0	0	0	0	0	0	0	0	0	0
>28	0	1	0	_ 1	0	1	1	0	0	2	0	0

Table A6.5 Cumulative number of successive days within each temperature class for simulated maximum daily water temperatures at site WT4

dany					t site \							
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1	431	327	358	400	374	334	357	424	507	606	532	523
2	192	152	168	186	162	140	158	184	183	187	187	184
3	82	86	74	64	68	92	79	96	75	59	61	75
4	34	44	31	34	42	43	35	27	25	25	24	33
5	13	16	26	21	19	22	18	19	8	6	13	16
6	8	8	12	13	17	13	17	9	8	7	9	0
7	7	5	4	4	6	4	9	0	4	1	1	3
8	1	2	5	2	2	2	2	1	1	1	0	2
9	. 0	0	3	_ 1	2	1	2	1	0	0	1	0
10	0	1	2	1	2	2	2	1	0	0	0	4
11	1	0	0	1	2	0	2	0	0	0	0	0
12	0	1	1	0	1	0	0	0	0	1	0	0
13	0	0	0	0	0	1	1	0	0	0	0	0
14	0	0	0	0	1	1	0	0	0	0	1	0
15	0	0	1	0	1	0	0	2	0	1	2	0
16	0	0	2	0	0	0	0	2	0	1	1	0
17	0	1	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0	1	0	0
20	0	0	0	0	0	0	0	0	0	1	Q	0
21	0	0	0	0	0	0	0	0	0	0	0	1
22	0	0	0	0	0	0	0	0	0	0	0	0
23	-0	0	0	1	0	0	0	0	0	0	0	0
24	. 2	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0	0	0
26	0	1	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	Ō	0	0
>28	0	0	0	0	0	1	1	0	2	0	0	0

Table A6.6 Cumulative number of successive days within each temperature class for simulated maximum daily water temperatures at site WT7

dany	water	n Feb Mar Apr May Jun Jul Aug Sep Oct Nov E										
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1	436	367	368	411	381	357	387	445	515	571	545	498
2	157	143	184	151	183	134	142	175	173	189	189	190
3	79	73	73	_63	57	76	88	82	82	64	72	76
4	36	36	33	42	40	38	35	34	32	27	_16	32
5	23	19	21	16	16	26	23	26	10	13	12	14
6	7	10	6	12	16	11	10	5	2	2	8	7
7	4	5	5	3	. 7	6	4	1	1	0	1	2
8	1	3	2	4	4	3	2	1	1	1	1	1
9	1	1	3	1	1	3	3	1	2	0	1	0
10	2	1	3	1	1	1	3	1	0	0	0	2
11	1	0	1	4	0	2	1	1	1	1	0	0
12	0	0	. 2	0	1	2	0	1	0	0	0	0
13	0	0	1	1	0	0	1	0	0	0	0	0
14	1	0	1	0	2	0	0	0	0	0	0	0
15	0	1	0	0	0	0	0	0	0	0	0	1
16	0	0	0	0	2	0	0	2	0	0	0	0
17	0	1	0	0	0	0	0	0	0	0	0	0
18	0	0	1	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	1	0	1	1	0	0
20	0	0	0	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	1	0	1	0
22	0	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	1
24	2	0	0	0	0	0	0	0	0	0	1	0
25	0	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0
>28	0	1	0	1	0	1	1	0	0	2	0	0

Table A6.7 Cumulative number of successive days within each temperature class for simulated maximum daily water temperatures at site WT8

daily		_			site v	ATO						
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1	409	337	341	397	377	412	402	407	470	564	564	506
2	173	149	167	145	188	149	163	179	186	191	195	188
3	78	63	72	69	87	69	70	94	72	64	74	69
4	35	32	44	41	33	41	40	38	30	35	20	35
5	19	27	20	_18	15	_23	18	13	14	3	10	14
6	10	11	9	14	11	10	6	5	4	6	5	7
7	6	5	12	4	4	3	5	9	2	2	1	3
8	7	3	4	3	2	4	3	3	1	0	1	1
9	0	1	_1	1	2	0	6	0	3	0	0	0
10	1	2	2	_ 2	1	3	2	0	0	1	0	1
11	0	1	0	0	1	0	1	1	1	1	0	0
12	0	1	0	2	0	0	0	0	1	0	0	0
13	0	0	0	1	0	0	2	0	0	0	0	0
14	1	0	1	0	4	0	0	0	0	0	0	0
15	0	0	1	0	0	0	0	0	0	0	0	1
16	0	0	0	0	0	1	0	0	0	0	0	0
17	0	1	0	0	0	0	0	2	0	0	0	0
18	0	0	0	0	0	0	0	0	1	0	0	0
19	0	0	0	0	0	0	0	0	1	0	0	0
20	1	0	0	0	0	0	0	0	0	0	0	0
21	0	0	1	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	1	0	0	0	0	Ö	0
26	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0
>28	0	1	0	1	0	0	1	0	0	2	1	1

Table A6.8 Cumulative number of successive days within each temperature class for simulated maximum daily water temperatures at site WT2

daily water temperatures at site W12												
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1	318	235	268	313	357	331	358	465	524	546	507	413
2	139	110	140	105	121	135	136	160	150	150	163	152
3	60	68	54	71	61	59	56	50	47	41	39	56
4	37	33	40	32	21	26	41	26	14	23	22	25
5	20	15	10	15	25	17	11	8	10	13	6	16
6	5	5	11	7	10	6	4	4	0	1	2	5
7	4	11	11	4	2	3	5	5	2	1	1	1
8	3	1	7	5	5	5	1	5	2	0	1	0
9	3	3	2	2	1	2	3	0	1	0	1	1
10	1	0	3	1	0	0	2	0	0	0	1	0
11	1	2	0	2	1	0	0	0	0	0	0	1
12	3	0	0	2	0	0	0	0	0	0	0	0
13	4	0	0	6	0	0	0	1	0	0	0	0
14	1	0	1	0	0	0	0	1	0	0	0	0
15	0	0	0	5	9	0	0	0	0	0	0	0
16	0	0	0	0	9	0	1	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0	0	0
18	4	0	0	0	0	0	0	0	0	0	0	0
19	3	0	0	2	0	0	0	0	0	0	0	0
20	1	0	0	0	0	0	0	0	0	1	0	0
21	1	0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	3	1	0	0	0	0	0	0	0
23	0	0	5	0	0	0	0	2	0	0	0	0
24	0	1	5	0	0	0	0	4	0	0	0	0
25	0	0	0	0	0	0	0	1	0	0	0	1
26	0	0	0	0	0	0	0	1	0	0	0	0
27	0	0	0	0	0	0	0	0	0	1	0	0
>28	0	9	0	0	0	10	9	1	8	8	9	9

Table A6.9 Cumulative number of successive days within each temperature class for simulated maximum daily water temperatures at site WT10

	Jan 478 169 82 37	74 28		366					_	Oct	Nov	Dec
2 3 4	169 82 37	173 74	195			441	C47					
3 4	82 37	74		154	470		517	296	466	510	433	400
4	37		61		179	165	161	128	187	177	183	159
		20		65	90	75	80	66	74	78	56	88
	19	20	36	26	36	31	33	29	33	36	_43	33
5		18	13	19	18	18	13	19	16	19	16	27
6	10	8	6	7	7	11	7	9	7	5	7	10
7	1	2	5	2	4	6	6	6	6	2	6	3
8	3	5	4	2	4	3	3	1	0	2	2	3
9	1	2	2	0	0	2	2	3	1	1	2	3
10	1	1	0	1	1	0	0	1	0	2	1	3 3 2 1
11	1	0	0	1	0	0	1	2	0	0	3	1
12	0	0	1	0	0	0	1	2	0	0	0	0
13	0	0	1	2	0	0	0	2	0	0	0	0
14	0	0	0	1	0	0	0	0	1	0	0	1
15	0	1	0	1	0	0	0	0	0	0	0	0
16	0	0	0	2	0	0	0	2	0	0	0	0
17	0	0	0	1	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0	0	0
19	0	0	0	1	0	0	0	3	0	0	0	0
20	0	0	0	0	0	1	0	0	0	0	0	0
21	0	0	0	1	0	0	0	0	0	0	0	0
22	0	0	0	1	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	1	0	0	0	1	0	0	0	0
25	0	0	0	0	0	0	0	2	0	0	0	0
26	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0		0	0	0	0
>28	0	0	0		0		0		0	0	0	0