METHODS FOR ASSESSING THE SUSCEPTIBILITY OF FRESHWATER ECOSYSTEMS IN SOUTHERN AFRICA TO INVASION BY ALIEN AQUATIC ANIMALS

THESIS

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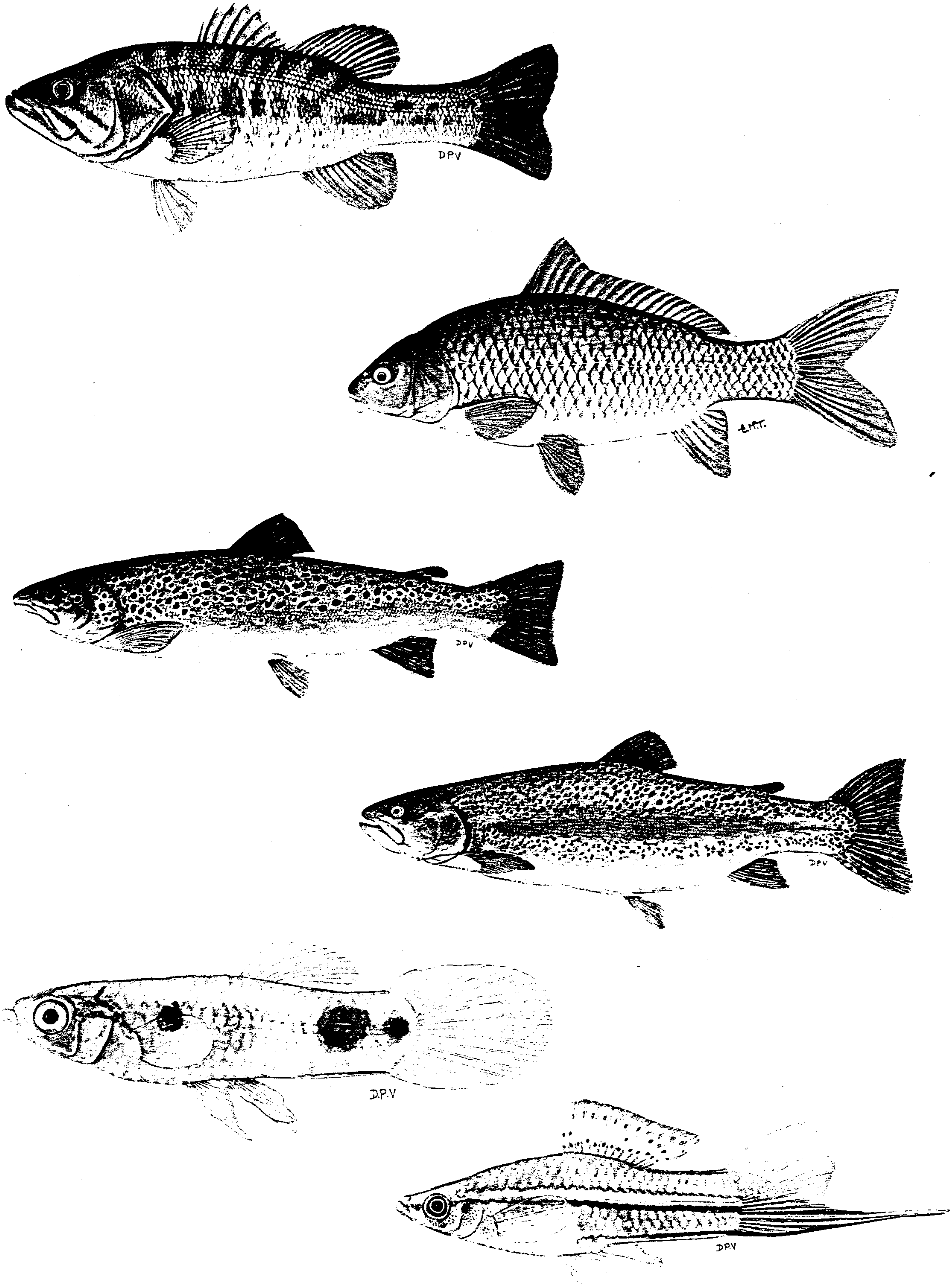

Frontispiece: Some of the alien "indicator species" discussed in this thesis (from top to bottom): largemouth bass, common carp, brown trout, rainbow trout, guppy and swordtail. (Illustrations by D. Voorvelt & E. Tarr from "A complete guide to the freshwater fishes of southern Africa" by P.H. Skelton (1993). Southern Book Publishers.

ABSTRACT

Two methods for predicting regions susceptible to invasion by alien aquatic animals were developed for southern Africa (excluding Zimbabwe and Mozambique).

In the "traditional" (data-poor) approach, distributions of three categories of alien "indicator" species (warm mesothermal, cold stenothermal and eurytopic) were compared to seven existing biogeographical models of distribution patterns of various animals in southern Africa. On the basis of these comparisons a synthesis model was developed which divided southern Africa into seven regions characterised by their susceptibility to invasion by alien aquatic animals with particular habitat requirements.

In the "data-rich," geographic information systems (GIS) approach, the distribution of trout (*Oncorhynchus mykiss* and *Salmo trutta*) in selected "sampled regions" was related to elevation (as a surrogate of water temperature) and median annual rainfall (MAR) (as a surrogate of water availability). Using concentration analysis, optimum conditions for trout were identified. Regions within a larger "predictive area" which satisfied these conditions, were plotted as a digital map using the IDRISI package. Using this method seven models of potential trout distribution were generated for the following regions: northern Natal (two); southern Natal /Lesotho /Transkei (three), eastern Cape (two) and western Cape (two). Since two of the models were used to refine the methods, only five models were considered for the final assessment.

In a modification of the GIS method, another model of potential trout distribution, based on mean monthly July minimum air temperature and MAR parameters, was developed for the region bounded by 29°- 34°S and 26°- 32°E. This model showed marked similarities to another model, developed for the region bounded by 29°- 32°S and 26°- 32°E, which was based on elevation and MAR parameters.

The validity of the models developed was assessed by independent experts. Of the six models considered, four received favourable judgements, one was equivocal and one was judged to be poor. Based on these assessments it was concluded that the GIS method has credibility and could be used to develop a "data-rich" model of the susceptibility of southern Africa to invasion by alien aquatic animals. This method represents an alternative to the bioclimatic matching approach developed by scientists in Australia.

The GIS method has a number of advantages over the "traditional" method: it is more amenable to testing, has greater flexibility, stores more information, produces images of a finer resolution, and can be easily updated. The traditional method has the advantage of being less expensive and requiring a less extensive database.

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DEDICATION

I would like to dedicate this thesis to my husband, Ferdy, who has always encouraged me in my work and given me moral support when I needed it.

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CHAPTER 1: GENERAL INTRODUCTION

"Man, the supreme meddler, has never been quite satisfied with the world as he found it, and as he has dabbled in rearranging it to his own design, he has frequently created surprising and frightening situations for himself."

.... George Laycock (1966).

The composition of the biota of most countries in the world has been changing at an unprecendented rate in the past few decades. This is due primarily to disruptions caused by human activities including the introduction of foreign species into regions where they do not naturally occur. Although many of these species have not survived, many others have invaded their new environments, often resulting in major alterations to the structure and functioning of communities and ecosystems (Mooney & Drake 1986). The magnitude of the problem was first brought to the attention of biologists by Charles Elton (1958) who noted that "if we look far enough ahead, the eventual state of the biological world will become not more complex, but simpler - and poorer. Instead of six continental realms of life (Wallace's realms), with all their minor components of mountain tops, islands and fresh waters, separated by barriers to dispersal, there will be only one world, with the remaining wild species dispersed up to the limits set by their genetic characteristics, not to the narrower limits set by mechanical barriers as well".

Elton (1958) also noted that it was impossible to estimate the number of species which have been introduced by man into new environments, but that it must be in the region of tens of thousands. This is illustrated by a comment appearing in an article written by the United States Office of Plant Introduction in which it is stated that the activities of the organization "had resulted in the introduction of nearly 200 000 named species and varieties of plants from all over the world" (Elton 1958). Mooney & Drake (1986) observed that in some regions, alien species account for a large percentage of the composition of species (for example, nearly 50% of the flora in coastal California are aliens). This illustrates that many of the introductions into the USA have proved to be "successful".

Although migrating people in ancient times were sometimes responsible for the translocation of biota into new areas (Deacon 1986), the frequency of introductions has increased significantly during the last four centuries in association with Anglo Saxon migrations from Europe to other continents (di Castri 1989). It can also be expected that, with the increasing sophistication and speed of modern transportation systems, as well as the forthcoming global climate change which could increase the susceptibility of environments to invasion, the frequency of invasions is likely to increase (di Castri 1989).

Freshwater animals are normally restricted in their distribution, as the land barriers separating different river systems effectively prevent dispersal into new catchments. Elton (1958) notes that the dispersal of aquatic animals depends mostly on the changes of water systems (for example the capture of watersheds by rivers, the joining of river mouths by elevation of the land, etc.). Even when there are renewed land junctions, the pace of redistribution of freshwater fish across such junctions is extremely slow (Elton 1958). Long periods of isolation of river systems from each other can result in the evolution of unique faunal assemblages in different catchments on continents. For example, the rivers of the southern and western Cape belong to the same faunal province characterised by a dominance of cyprinid fish (notably *Barbus* and *Pseudobarbus* species) (Skelton 1990). Nevertheless the species assemblage within each river system is unique (Skelton pers. comm.) and the degree of endemicity in certain regions such as the coastal streams and rivers of the Cape, is very high (Skelton 1986a).

Welcomme (1988) compiled a checklist of international transfers of freshwater animals. This list only includes transfers across political barriers, and not to new catchments within countries. He records a total of 1354 introductions of 237 species into 140 countries, but emphasises that this list is not complete.

Numerous ecological problems have resulted from the introduction of aquatic species into inland waters (Welcomme 1988). These include: degradation of the environment; disruption of the host community chiefly through competition with and predation of indigenous species; deterioration of fish stocks (through stunting of the introduced population); genetic contamination of the host community as a result of interbreeding with the introduced species; and the introduction of parasites and diseases. Welcomme (1988) lists some socio-economic problems which have arisen after the replacement of indigenous fish with alien species. For example, the introduction of *Oreochromis mossambicus* into some reservoirs in India caused dissatisfaction in local communities because the fish proved to be unpopular as a result of their perceived unfavourable taste and small size (Welcomme 1988).

Although there have been some notable economic benefits resulting from the introduction of alien species, such as the establishment of a thriving fishery in Lake Kariba based on the introduced pelagic sardine *Limnothrissa miodon* (Marshall 1988), there have also been some economic and health disasters arising from purposeful as well as accidental introductions. The unintentional introduction of the sea lamprey (*Petromyzon marinus*) into the Laurentian great lakes in North America (via the Welland Canal which connects Lake Ontario to Lake Erie), resulted in the collapse of the economically-important lake trout fishery (Christie 1974). The recent introduction of the zebra mussel *Dreissena polymorpha* into the great lakes region has had even more serious economic impacts. This species has caused widespread economic damage as a result of its prolific growth in the water pipes of electricity-generation and water-treatment facilities (Griffiths et al. 1991). The cost of cleaning encrustations of mussels and replacing equipment in hydro-electrical and other installations is expected to run into billions of dollars (Johnson 1990).

Alien aquatic animals have also sometimes had serious medical and health impacts on human populations. The introduction of the malaria-vector mosquito, *Anopheles gambiae* into South America resulted in a serious malaria epidemic causing the death of over 20 000 people (Soper & Wilson 1943).

1.1. INVASIVE ALIEN AQUATIC ANIMALS IN SOUTHERN AFRICA

A checklist of 93 alien aquatic animals in southern Africa was compiled by Bruton & Merron (1985). This list included some species which had been introduced, but had not yet established successful populations in natural waters. In a subsequent review, de Moor & Bruton (1988) found that 58 alien species had established breeding populations in the southern African region (excluding Zimbabwe and Mozambique). Of these, 33 were from other countries and 25 were transfers of species into new catchments within southern Africa. At least 14 of these species have had a major impact on indigenous animal communities. All major southern African river systems have been invaded by alien or translocated indigenous species and, of the 58 species which were frequently recorded in natural habitats, 37 were considered to be detrimental, three to be beneficial and 18 to be equivocal (i.e. beneficial in some respects, and detrimental in others) (de Moor & Bruton 1988).

Some of the more serious detrimental effects which alien species have had on aquatic ecosystems in southern Africa are summarised below:

1. Parasitism: Four fish parasites have been introduced into southern Africa: whitespot disease (*Ichthyophthirius multifilis*), the trichodina parasite (*Trichodina acuta*), the fish tape worm (*Bothriocephalus acheilognathi*) and the fish louse (*Argulus japonicus*) (van As & Basson 1984). These parasites were all introduced accidentally in association with sport angling, the

aquarium trade or aquaculture. All of these parasites have been found on indigenous fish species in natural waters, with extremely high incidences in some cases (Brandt et al. 1981, Kruger et al. 1983).

2. Habitat destruction: Because of its habit of grubbing in benthic sediments for food, *Cyprinus carpio* (carp) has been reported to have a devastating impact on the habitat. Submerged vegetation is uprooted, and bottom sediments are disturbed. This has the overall effect of making the pond bottom soft and increasing the turbidity and suspensoid load in the water. The altered environment then becomes less suitable for native species (Welcomme 1984). There is however some dispute about the supposed role of carp in causing these effects, and Ashton et al. (1986) regard carp's reputation for having eliminated more desirable fish and fouling the water as being exaggerated.

3. Predation: Certain predatory species such as smallmouth bass and largemouth bass (*Micropterus dolomieu* and *M. salmoides* respectively) have had an extremely detrimental impact on freshwater ecosystems throughout southern Africa, particularly in sensitive ecosystems with a high degree of endemism (de Moor & Bruton 1988). The introduction of smallmouth bass (*M. dolomieu*) into certain rivers in the southern Cape is regarded by Skelton (1987) as being an important factor contributing to the decline of nine of the twelve threatened freshwater fishes in the Cape.

4. Competitive effects: The Mediterranean mussel, *Mytilus galloprovincialis*, a highly invasive, intertidal species, has invaded extensive regions of the west and south coast of southern Africa (Grant et al. 1984) resulting in a decline in the population of the indigenous ribbed mussel, *Aulacomya ater* (Hockey & Schurink 1992). It was noted that *M. galloprovincialis* outcompetes *A. ater* as a result of its greater reproductive output, faster growth rate and greater tolerance to dessication. *M. galloprovincialis* is also a superior competitor to the intertidal limpet, *Patella granularis*, for primary rock space (Hockey & Schurink 1992).

5. Potential medical and veterinary problems: The American red-eared terrapin, *Trachemys scripta elegans*, which has established populations in the Transvaal and Natal, is a potential vector of salmonellosis. This disease could be transferred to humans who drink water in which these terrapins occur (Newbery 1984). No such incidences have as yet been recorded in South Africa (de Moor & Bruton 1988).

The alien freshwater snail, *Lymnaea columella*, which is highly invasive and has been recorded throughout southern Africa, is an intermediate host of the fluke worm (*Fasciola hepatica* or *F. gigantica*) which causes liver fluke disease (fascioliasis) in cattle. The presence of *L. columella* in southern Africa is believed to have resulted in an increase in the incidence of fascioliasis in livestock, partly because *L. columella* is more widespread than the indigenous *L. natalensis* which is also an intermediate host of *Fasciola* spp. (Brown 1980).

6. Genetic contamination of indigenous species: There are fears that alien species will hybridise with closely-related indigenous species, resulting in genetic contamination of wildstock. The following species could be affected:

a. The introduced mallard duck (*Anas platyrhynchos*) is capable of hybridising with three indigenous anatid ducks (*A. undulata*, *A. erythrorhyncha* and *Alopochen aegyptiacus*) (Liversidge 1985). It should however be pointed out that the former species, although widespread in semi-captive situations, has not yet established feral populations in southern Africa (Liversidge 1979).

b. The Mozambique tilapia (*Oreochromis mossambicus*) could hybridise with two indigenous species *O. macrochir* and *O. andersonii* in certain rivers in northern Namibia into which the former species has been introduced (de Moor & Bruton 1988).

c. The Orange River labeo (*Labeo capensis*) which has recently been introduced into the Tugela River via the Vaal-Tugela interbasin transfer scheme (Coke pers. comm.) could hybridise with *L. rubromaculatus* which is endemic to the Tugela system (Skelton pers. comm.; Jubb 1967).

The detrimental impacts mentioned above can be regarded as being very serious in terms of environmental effects. However, alien aquatic animals have not yet caused any serious medical or economic impacts in southern Africa on the scale of some well-known disasters such as the introduction of *Anopheles gambiae* into South America, or the zebra mussel into the great lakes of North America.

1.2. FUTURE PROBLEMS

Macdonald (1991) noted that, because of close historical contacts between South Africa and temperate countries in the northern hemisphere, there have been extensive introductions from these countries of species which are able to survive in the more temperate regions of southern Africa. This suggests that many of the potential invader species from temperate countries have already been introduced into southern Africa. The situation pertaining to alien tropical species is however very different. Historically, southern Africa has had limited contact with many tropical countries, particularly in central Africa and South America, where the number of potential invader species which could survive in southern Africa is vast. As the political and trade contacts between South Africa and many of these countries increase, it is likely that the number of introductions from these countries will also increase.

Pettijean & Davies (1988) highlighted the problem of species transfers via interbasin transfers (IBTs) within southern Africa. A number of these schemes have already resulted in the introduction of species into new catchments, and there are plans to build a number of IBTs which will link such diverse regions as the Zambezi and the Vaal-Orange system. This would result in the mixing of species from two very distinct ichthyofaunal provinces (Skelton 1986a).

There is also considerable potential for the introduction of species via the aquarium trade and the aquaculture industries in southern Africa. This was illustrated by the recent discovery of an extremely undesirable species, the red swamp crayfish (*Procambarus clarkii)*, in the Crocodile River, Transvaal (Schoonbee 1993). Although this species was prohibited for importation via the aquarium trade (Lotz pers. comm.), specimens were periodically found in aquarium shops (Anon 1987; Schoonbee 1993). It is not certain whether the present population is a result of deliberate introductions by aquarium hobbysts or accidental escapes from aquaculture installations. Inadequate control over the importation of such prohibited species could result in the introduction of more undesirable species.

1.3. BENEFITS OF ALIEN AQUATIC ANIMALS

Many economic benefits have resulted from the importation of alien species in southern Africa, even in cases where such species have had a detrimental effect on the environment. In other cases considerable economic benefit can be gained from species which either could not survive in natural waters, or are unlikely to have any serious detrimental effects on freshwater ecosystems should they escape into natural waters.

Certain alien aquatic insects such as the salvinia weevil, (*Cyrtobagous salviniae*) and the water weevil (*Neohydronomus pulchellus*) have proved to be successful biocontrol agents of alien invasive aquatic plants (*Salvinia molesta* and *Pistia stratiotes* respectively) (Schlettwein 1984;

Giliomee 1986; Cilliers 1987a & b). These species can therefore be regarded as having had a beneficial impact on the ecosystem and the economy.

Ashton et al. (1986) point out that sport angling in inland waters in South Africa has benefited immensely from the introduction of alien species, such as trout (*Salmo trutta* and *Oncorhynchus mykiss*) bass (*Micropterus salmoides* and *M. dolomieu*) and carp (*C. carpio*). Numerous socio-economic benefits have arisen from the development of sport fishing in southern Africa, including the recreational aspect, the provision of nutritious food as well as benefits to tourism and the development of the sport-equipment industry (Jackson 1989).

The tropical fish industry in South Africa is an essential part of the pet industry and, with the development of large hatcheries, particularly in Natal, has recently become an exporter (van Zyl 1989). The operation from the Amatikulu Hatchery in Natal alone has an annual turnover of approximately R2.5 million and provides much-needed employment in an impoverished rural area of Natal (Andrews 1989). The trade in alien species is essential for the functioning of this industry (Andrews 1989).

A similar picture emerges in the aquaculture industry. James & Davies (1989) note that most local species have proved to be either unsuitable for aquaculture, or the technology for their use is poorly developed. The industry is therefore dependent on the importation of alien species.

1.4. MANAGEMENT OF ALIEN AQUATIC ANIMALS

It would be counter-productive to place import controls over all alien aquatic species, especially as many alien species are considered to be beneficial and have little chance of surviving in or invading natural waters, or pose a minimal risk to the environment. There is a need for management over the importation and spread of alien aquatic animals, in order to afford adequate protection to the environment without placing undue pressure on industries and recreational activities which are dependent on alien species for their survival. This was emphasised by many delegates to a workshop on the management of alien aquatic animals in southern Africa held in 1988 (de Moor & Bruton 1989).

Bruton & van As (1986) identified two aspects of the management of aquatic invasives: the prevention of further spread and amelioration of the impact of species already in the subcontinent; and the prevention of the importation or translocation, either intentional or unintentional, of further invasives.

1.5. AIMS AND OBJECTIVES OF THE PRESENT STUDY

Managing the importation of alien aquatic animals into southern Africa would involve an assessment of the attributes of the candidate species as well as the susceptibility of the target environment. Since it would not be possible to assess the attributes of all potential future candidate species, it is more practical to concentrate on studying the characteristics of the target environment.

The aim of this thesis is to make use of biogeographical modelling techniques to predict the potential distribution in southern Africa of alien aquatic animals with particular habitat requirements.

In a study of this nature it is important to examine the literature on the ecology and biogeography of alien invasions. Only after the completion of such a literature review is it possible to formulate the specific aims and objectives of the thesis. These are therefore dealt with in more detail in Chapter 3 (on general methodology), following the literature review (Chapter 2).

1.6. DESIGN OF THE PRESENT STUDY

In this thesis both the "traditional" method of biogeographical modelling as well as more sophisticated GIS techniques will be used to achieve the aims as outlined above. Both methods are based on the same basic approach which is described below:

1. It is assumed that the distribution of breeding populations of selected stenotopic alien aquatic animals which have been widely introduced into many different catchments, can be used as an indicator of prevailing abiotic conditions in the regions where they live.

2. A comparison between the distributions of selected alien species (described above) and abiotic conditions in various regions of southern Africa, forms the basis for the compilation of biogeographical models which predict the potential distribution of alien aquatic animals with particular habitat requirements.

Before attempting to undertake the biogeographical analyses described above it was first necessary to examine the theoretical concepts relating to invasive species and environments that are susceptible to invasion as well as the concepts and theories underlying biogeographical modelling techniques. This is dealt with in Chapter 2 which also includes a review of biogeographical models in southern Africa, particularly those which deal with freshwater ecosystems.

Following the literature review, the more specific objectives, basic assumptions and limitations of the present study are discussed in detail in Chapter 3. A "traditional" approach to biogeographical modelling is dealt with in Chapter 4 culminating in the compilation of a model of regions susceptible to invasion by alien aquatic animals with particular habitat requirements. In Chapters 5 & 6 the GIS approach is used to predict the distribution of two alien species (rainbow trout and brown trout) in selected regions of the sub-continent.

The logic and assumptions in the thesis are critically examined in Chapter 7. In the final section (Chapter 8) the results from both types of analyses are assessed and possible applications of the methods developed are discussed.

Details on the locality records where stenotopic alien species have been introduced are listed in Appendices 1-6 and in lotus-compatible files in the attached floppy disc. To facilitate the reading of this thesis the full taxonomic names, authors and dates of species mentioned in the thesis, are listed in Appendix 7.

CHAPTER 2: LITERATURE REVIEW

2.1. INTRODUCTION

The invasion of alien species into new environments where they did not naturally occur is a complex issue which is central to the traditional disciplines of ecology and biogeography. Many issues and debates are pertinent to the study of biological invasions: the definition of niche, habitat and biotope, ecological succession, the characteristics of invasive species, susceptibility of different ecosystems to invasions, the structure of communities and ecosystems and the biogeography of the source and target environments. All these questions must be discussed in order to gain an understanding of the factors which determine the success or failure of biological invasions.

Certain studies reviewed in this chapter, particularly in section 2.6 on biogeographical analyses in southern Africa, are pertinent to the methods used in the present study. For this reason these studies have been described in detail.

2.2. ECOLOGY OF BIOLOGICAL INVASIONS

2.2.1. Ecological concepts of niche, habitat and biotope

Whittaker et al. (1973) noted that it was regrettable that the two most important terms in ecology i.e. "niche" and "habitat" were among the most confused. Historically the term "niche" was used to describe the place of an organism in the environment, but this definition was found to be inadequate because it did not account for the varied role of a species in its environment (Price 1975). Hutchinson (1957) overcame this problem by defining the niche as a quality of the environment rather than a quality of the species (Price 1975). This definition, subject to some modifications, is widely accepted by ecologists today.

Whittaker et al. (1973) described Hutchinson's niche concept as follows: "Hutchinson proposed that the environmental variables affecting a species be conceived as a set of *n* coordinates. For each of these coordinates limiting values exist, within which the species can survive and reproduce. The ranges of the coordinates within the limiting values define an *n*-dimensional hypervolume, at every point within which environmental conditions would permit the species to exist indefinitely. This hypervolume may be called the species' *fundamental niche*. If both physical and biological variables .... are considered, the *fundamental niche* will completely define the species ecological properties...... Because of competition and other interactions, the species may be excluded from some parts of the fundamental niche. The reduced hypervolume in which a species then exists is termed its *realised niche.*"

Because of difficulties in the way in which this (Hutchinsonian) niche concept related to the concept of "habitat", Whittaker et al. (1973) redefined some of the terms put forward by Hutchinson as follows (from Price 1975):

1. The term "niche" should be used only in terms of resource utilisation by a species within a community (intra-community role of species).
2. The term "biotope" should be used to describe the abiotic environment in which a community exists.
3. The term "habitat" describes the abiotic environment in which a species exists.
4. Thus a species' existence and distribution is defined by factors on two variables - its niche and habitat, and where the total resources utilised by the species are considered, the term ecotope was suggested by Whittaker et al. (1973). This term represents the full environmental and biotic variables which affect the species.

An axiom of the above niche concept is the principle that no two species with exactly the same niche can co-exist in a steady-state. Competition for resources will eventually result in the local extinction or displacement of one of the species (Price 1975). In order for two species to co-exist, some aspect of their niche must differ. The question then arises as to how different two species must be in order to permit co-existence.

The number of species which can co-exist depends to a certain extent on the ranges of resources utilised. Each species exploits a section of the range of a particular resource which is not exploited by any other species. This leads to the concept of "species packing" which relates to the utilisation of a particular resource by a number of different species. In some instances certain resources may be under-utilised and fewer species are "packed" along the length of the particular resource. In a more competitive environment species packing may be more intense, in which case the breadth of the niche used by each species would be narrower and more species would be "packed" along the particular dimension of the "niche hypervolume" (Price 1975).

It should be emphasised that, although species in a community have diversified niches, there may be some competition between species where their niches overlap. There is, however, a selective advantage for the evolution of niche differences. For example, if two species overlap broadly in one aspect of the niche such as prey-size, competition between "rival species" would reduce the chances of survival of individuals who choose prey within the range of sizes preyed on by both species. There would thus be a selective advantage in choosing prey from a range of the available sizes which did not overlap with the resource utilisation by the "rival" species. This would lead to a diversification of resource utilisation by the two species involved so that the range of overlap in the niche gradient is reduced to a minimum (Whittaker 1975).

2.2.2. The niche concept and invasive species

The concept of the "vacant niche" has been used to justify many introductions of organisms into new environments (Herbold & Moyle 1986). These workers point out that this concept is meaningless in terms of most definitions of the term "niche". It would be more appropriate to argue that the new invading species re-arranges the community rather than slipping into an empty niche. Introduced species alter the speed or pathway of energy flow in communities. The classic example of the introduction of a new species into a so-called empty niche is that of the introduction of deer into New Zealand, an environment in which no large herbivorous animals existed. Whittaker et al. (1973) point out that, in this instance, saprobic organisms had previously been the primary consumers of vegetation. This role was taken over by the introduced deer which did not fill an empty niche, but did significantly alter the use of available resources.

2.2.3. Characteristics of successful invaders

Ehrlich (1986) observed that certain species such as the house sparrow (*Passer domesticus*), the domestic pigeon (*Columba palumbus*), the Norway brown rat (*Rattus (Rattus) rattus*) and many others have been remarkably successful invaders throughout the world. Other species, despite numerous introductions, have failed to establish populations in new areas. This has led many biologists to investigate the attributes of successful invaders (Ehrlich 1986).

Moyle (1986) emphasised that, although there is no single biological feature that successfully introduced species have in common, they usually have some of the following characteristics: very hardy and thrive in disturbed environments, aggressive, ecologically and behaviourally distinct from native species, reproductive strategies which confer on them an unusual degree of "fitness", pre-adapted to distinctive local environmental conditions and able to colonise new areas rapidly.

The ability to colonise disturbed areas is usually associated with species with a high intrinsic rate of natural increase i.e. *r*-selected species. It can therefore be expected that such species would be successful invaders (Crawley 1986). However Lawton & Brown (1986) also noted that a low mortality rate has been observed to give a species greater colonisation potential than a high birth rate.

Stauffer (1984) noted that *r*-selected species tend to invade species-poor, temperate areas in the USA whereas *K*-selected species are more frequent invaders in species-rich, subtropical areas such as Florida. He also noted that species which were able to combine some "r" and "K" characteristics had the highest chances of success in these species-rich environments.

Bruton (1986) noted that the life-history style adopted by introduced species was an important factor in determining the success or failure of the introduction. He found that altricial fish (which produce small, incompletely developed young and are generalists capable of surviving in an unstable, uncrowded environment) such as rainbow trout *Oncorhynchus mykiss* and the common carp *Cyprinus carpio*, had successfully invaded species-poor, abiotically harsh environments. Precocial species (which produce large, well-developed young and are specialists adapted to survive in a stable, crowded environment), such as the guppy *Poecilia reticulata*, had successfully invaded species-rich, biotically-harsh, competitive environments. Certain other species which are able to alter their life history styles in response to prevailing environmental conditions, have an enhanced invasive ability. Species such as the Mozambique tilapia *Oreochromis mossambicus*, which exhibits a high degree of phenotypic plasticity both in its ability to adopt different life-history options, and to tolerate a wide range of conditions in the abiotic environment, are highly successful invaders.

Ehrlich (1986) noted that species such as detritivores and generalist predators, which were able to utilise a wide variety of food items, had a better chance of successfully colonising a new environment than specialist species with specific food requirements. However, in certain instances where there was an abundant supply of a particular food type (often as a result of disturbance by man), specialist feeders such as phytophagous insects or bloodsucking parasites of man and his livestock, often became invasive pests (de Moor 1992).

Although the general biology and life history style is important in determining the success of a potential invader species, its tolerance to abiotic conditions is of prime importance. Coope

(1986) noted that a climatic match of source and invaded environments was of major importance in determining the success of invader species. It should also be noted that in many instances the invader species has been observed to have a wider tolerance to various abiotic conditions in the environment into which it was introduced than was the case in its native range. For example *O. mossambicus*, a euryhaline species which normally occurs in freshwaters, has established breeding populations in a marine environment near the Fanning Atoll in the Pacific (Maciolek 1984). Bruton (1986) uses the term "invasive vigor" to describe this phenomenon which can be explained in terms of the absence of natural controls (i.e. the lack of co-evolved predators, parasites and competitors) in the new environment, as well perhaps on an enhanced ability to adopt alternative life styles in the environment into which it was introduced. The invasive species is therefore often observed to occupy a broader ecotope in the newly-colonised environment than was the case in its native range. Its "realised niche" could therefore be described as being broader than was the case in its native range.

2.2.4. Susceptibility of environments to invasion

Elton (1958) used the term "ecological resistance" to describe a system of "checks and balances" opposing the invasion of new species into natural ecosystems. This consisted of an array of parasites, predators and competitor species which would hamper (and in many cases prevent) the successful establishment of an invasive species in a new environment. He also noted that ecological resistance was lower in disturbed, simplified environments, and on small islands where biotic diversity was low. These environments were therefore more susceptible to invasion by introduced species. Although Elton did not state the corollary to his hypothesis, his work would seem to imply that complex, diverse, climax environments would have a high ecological resistance to invasion (Macdonald 1991).

In terms of modern definitions of niche and habitat (Whittaker et al. 1973), Elton's (1958) ideas concerning the susceptibility of environments to invasion could be rephrased as follows (from Price 1975): For an invader species to succeed in establishing a population in a new environment, it must be able to utilise some part of the resources which are underutilised by the existing species. The new coloniser must therefore be pre-adapted to the niche it must fill. The potential colonising ability therefore depends to a large extent on which species are already present and how the introduced species is pre-adapted to fitting between existing species. If the species are packed into a biotope quite tightly then it is unlikely that further species could colonise the area (Price 1975). Likewise Stauffer (1984) noted that the success of a potential invasion depended on the amount of niche space and habitat availability in the new environment.

In spite of some criticism concerning Elton's use of such outmoded ideas as "vacant niches", there has been much evidence to support many of his hypotheses. It has been found that, in general, islands are more susceptible to invasion than mainlands (Carlquist 1965; Macdonald et al. 1988; Macdonald 1991). Other workers (Fox & Fox 1986 and others) have also noted the tendency for disturbed environments to be more susceptible to invasions by alien species.

The idea of depauperate environments being more susceptible to invasions has been criticised by Simberloff (1986) who has serious doubts about the validity of observations on which such work is based. In order to validate the contention that invasions have been more successful on islands and disturbed environments, more information is needed on the relative opportunity to invade in each case, and on the number of failed introductions. This would allow for a more rigorous statistical analysis.

Simberloff (1986) also challenged the idea that disturbed environments are more susceptible to invasion. He contends that evidence indicating such a tendency is biased by the fact that disturbed environments have been exposed to a larger number of introductions and have been studied more carefully than is the case for pristine environments.

While some of his criticism (especially concerning the lack of data on failed invaders) is very constructive, it seems that Simberloff (1986), in his sweeping criticisms, has been too dismissive of some valuable studies. In criticising particular workers, he has tended to generalise about all work undertaken in this field and has ignored some rigorous studies carried out by workers such as Macdonald (1984). In studies on the invasion of the fynbos biome by alien species, it was found that the percentage of introduced species in undisturbed sites was significantly less (3.1%) than that of disturbed sites (21.2%) (Macdonald 1984). Fox & Fox (1986) also found a direct correlation between the degree of invasion and the degree of disturbance of the habitat.

Fox and Fox (1986) reject the idea of "vacant niches" and "niche space" stating that "through evolutionary and ecological time (co-existing species) have come to form an inter-connected framework within which available resources are (presumably) fully utilised". Such communities are periodically exposed to disturbances, either "endogenous disturbance" such as flooding, cyclonic damage and other "natural disturbances", or man-induced "exogenous disturbances". The principle characteristic of disturbance was an alteration in resources, either through resource amplification or resource shift. In both cases, the result of the disturbance is the creation of spare (or additional) resources which could then be utilised by existing components of the communities, or by new species invading the community. These workers also propose that no invasion of natural communities can occur without disturbance and that, even in cases where successful invasions have occurred in natural communities, this has always been preceded by some subtle alterations to endogenous regimes. In this way they apparently differ from many other experts on invasions (Elton 1958; Stauffer 1984) who have proposed that disturbed environments are more susceptible to invasion, but do not see disturbance as an essential prerequisite to the successful establishment of alien species. Bruton (1990) proposed that disturbance is a pre-requisite for invasions by altricial, pioneering species, but that precocial, biotically competitive species are able to invade relatively undisturbed environs and thereby create a disturbance. Macdonald et al. (1988) also noted that certain relatively undisturbed environments within nature reserves in Mediterranean-type climatic regions appeared to be particularly susceptible to invasion. This may appear to refute some of the ideas proposed by Fox & Fox (1986).

This apparent difference in opinion may be due to a difference in interpretation of the concept of a "disturbed environment". To many workers in the field, the term refers to man-induced disturbances, whereas Fox & Fox (1986) make the distinction between "endogenous" and "exogenous" disturbances.

Fox & Fox (1986), in a study comparing the degree of invasion to species diversity in different plant communities, found statistically-validated evidence to indicate a negative relationship between community richness and invasion. This implies that complex, species-rich communities are less susceptible to invasion by alien species.

There is however a large body of research which challenges the ideas of Fox & Fox (1986) regarding the resistance of complex, diverse ecosystems to invasion (Bruton 1990; Macdonald 1991 and others). Bruton (1990) notes that the African Great Lakes, which are stable, complex, diverse ecosystems characterised by the presence of large species flocks of cichlid fishes and a high degree of endemism (Greenwood 1984; Coulter et al. 1986), are particularly vulnerable to major perturbations such as the introduction of alien species, overfishing and pollution (Bruton 1990). Because of the isolated nature of these lakes they can be regarded as "inverted islands" and their faunas may therefore have the same vulnerability to extinction as normal island faunas (Bruton 1990). The introduction of the Nile perch (*Lates niloticus*), the Nile tilapia (*Oreochromis niloticus*) and Jordan's St Peter's fish (*Tilapia zillii*) into Lake

Victoria has had a dramatic effect on indigenous haplochromine fishes that were particularly vulnerable to predation by *L. niloticus*, a large voracious predator sometimes reaching a mass of 200 kg. Prior to the introduction of this species there were very few fish in the lake which grew beyond approximately 1 kg. Endemic species had therefore never encountered predation from such a large fish predator, a factor which may partly explain their susceptibility to *L. niloticus* (Coulter et al. 1986). The introduction of *O. niloticus* had a detrimental effect on indigenous species, mainly because of competition, hybridization and overcrowding of indigenous species (Bruton 1990). Two species endemic to Lake Victoria, *Oreochromis esculentus* and *Oreochromis variabilis* have been virtually replaced by the alien species, *O. niloticus* and *T. zillii* (Coulter et al. 1986).

Bruton (1990) postulates that complex ecosystems such as the African Great Lakes have a good capacity to resist low-level natural changes, but may have a low elasticity (ability to recoil to the original state) and low amplitude (the area over which they are potentially stable) than simpler, less predictable environments such as African floodplain rivers. Constant intervention by man (including the introduction of alien species) in such ecosystems results in the breakdown of complex, stable relationships which are replaced by simpler, less stable ones, causing specialised species to become rare or extinct. This can be regarded as a process of "resetting the clock of succession", creating conditions unfavourable for the specialised precocial species and more favourable to the altricial "weedy" species.

In comparative studies of invasions of Mediterranean biomes in seven nature reserves around the world, Macdonald et al. (1988) and Macdonald (1991) come to similar conclusions as Bruton (1990). It is noted that, even though some biomes (such as the fynbos biome in the Cape) have a high degree of species diversity, they are vulnerable to invasions by alien species. It was also noted that reserves on oceanic islands have the highest proportion of alien species, followed by those in Mediterranean-type biomes which occur in isolated patches on larger continents and can be regarded as "quasi-insular". Both of these biomes are characterised by a high degree of endemicity. Continental biome types (e.g. savannas) generally have the lowest proportion of alien invasive species (Macdonald et al. 1988; Macdonald 1991).

Macdonald's work as well as that of Bruton (1990) implies that "insular" (rather than "island") ecosystems with a high degree of endemicity have a low resistance to invasion. Macdonald (1991) contends that in regions where there has been a high degree of adaptive radiation, a number of closely-related species tend to utilize a wide variety of niches from a limited genetic base. In these cases, even though there may be high "diversity", it is likely that such species are susceptible to invasion from continental species adapted to utilize similar niches. The reason for this is that the continental biota have had a much wider genetic base to exploit, with the result that such species are able to utilize all available niches "optimally". This implies that where adaptive radiation has occurred in an isolated environment, the niches are not "optimally" filled, and are more susceptible to invasion. In this context, Macdonald (1991) speculated that, should it be given the opportunity to invade an area, a "continental" woodpecker which had evolved on the mainland, would easily be able to displace one of Darwin's "woodpecker" finches on the Galapagos islands.

To sum up the preceding discussion, it appears that there is some evidence (e.g. Fox & Fox 1986) to support the "corollary" of Elton's ideas i.e. that complex, diverse ecosystems with a high species diversity are resistant to invasions. However, in cases where such ecosystems have evolved in isolation or "quasi-isolation" and display a high degree of endemism, this hypothesis does not hold true. From Macdonald's (1991) discussion, it would seem that, while these systems appear to be very diverse and complex in terms of the number of species present, there is in fact very little variability in the genotypes of species within such communities. In this context, it should be noted that there are indications that the haplochromine fish in Lake Victoria can be broken down into a number of polyspecific but monophyletic lineages (Greenwood 1984).

2.2.5. Other factors influencing the success of invasions

A review of the characteristics of the invader species and the target environment may be useful, but nevertheless does not provide population biologists with a reliable means of predicting whether or not a species will invade a particular environment. Ehrlich (1986) notes that this is one area of population biology in which a comprehensive theory is not possible or desirable.

In order to assess the chances of a species invading a particular area, the characteristics of the invading species and of the target environment should be assessed as well as the climatic conditions in both the source and target environments. The role of chance events should also not be ignored. The general situation regarding the potential to invade has been summed up by de Moor (1992) as follows, "The potential of the invasive species should be seen in the perspective of a combination of suitable attributes, climate and chance events which all play a role in determining whether a species will become an invader or not".

2.3. GENERAL PRINCIPLES AND CONCEPTS IN BIOGEOGRAPHY

2.3.1. Factors influencing the distribution of species

Myers & Giller (1988) noted that the determination of species distribution patterns was the starting point for all biogeographical analyses. Historical biogeographers attempt to reconstruct the sequence of the origin, dispersal and extinction of taxa, whereas ecological biogeographers try to analyse distribution patterns of extant species in terms of their relationships with the physical and biotic environment in the present and recent past. There is clearly a joint role of ecological and historical processes in determining present and past distributions of taxa.

Because the assessment of potential distributions of alien species is concerned with present and future conditions in the environment, this review will be confined to studies in the field of ecological biogeography, which includes biogeographical modelling, as a means of describing and predicting potential distribution patterns.

Brown (1988) noted that the ultimate cause of all deterministic patterns of species diversity is the variation of the physical environment. Even if distribution patterns could be explained in terms of biological factors, the biogeographer must still question what physical characteristics in the environment caused the observed differences in the biological attributes from different regions of the globe. Because of this it should be realised that biological factors such as niche relationships and interspecific interactions, while being important components of the explanation of diversity gradients, all play a secondary role in determining species distribution patterns. The physical environment is thus seen as the primary determinant of species distribution patterns.

2.3.2. The distribution of aquatic animals

While all species are restrained by geographical barriers, these barriers are generally more pronounced in freshwater ecosystems than in terrestrial ecoystems. Palaeogeography plays a major role in determining the distribution of freshwater species. In many instances species are not present in certain catchments or river basins which may adequately fulfill their ecological requirements, because they have not had the opportunity to invade these systems in the geological past. For example the Kapachira Falls on the Shire River in Malawi has presented an insurmountable barrier that has prevented the colonisation of Lake Malawi by a number of species (including *Hydrocynus vittatus*) from the Lower Zambezi River (Tweddle et al. 1979).

It is clear from the above discussion, that the absence of particular stenotopic indigenous freshwater animals cannot always be regarded as a reliable indicator of suitable abiotic conditions in a particular environment.

2.3.3. Environmental gradients and gradient analysis

Biogeographers have identified a number of physical gradients (environmental gradients) such as elevation, latitude or aridity, which have a profound effect on gradients of species richness. These gradients affect a number of physical factors which have a direct influence on the biotic environment. For example latitude is correlated with solar radiation, temperature and seasonality (Brown 1988).

Whittaker (1975) studied the ways in which vegetation changed in relation to changes in environmental variables. He noted that plant communities are generally (but not universally) continuous with one another and that community gradients occur along environmental gradients, i.e. that there is a continuous change in population structures along environmental gradients. Thus plant communities do not form distinct, clearly separated zones. However discontinuities do sometimes occur, usually as a result of some disturbance such as fire.

The assemblage of environmental factors that change through space along a community gradient is called a "complex-gradient". An "ecocline" refers to the combined gradient of the community and the environment (Whittaker 1975). The study of the way in which gradients of species, populations and community characteristics change in response to environmental gradients is called "gradient analysis". This approach represents a major alternative to the approach of early ecologists who regarded ecosystems as being communities with well-defined boundaries. It should also be noted that the community gradient concept does not contradict the descriptions of communities along certain environmental gradients in terms of "life-zones". Whittaker notes that such zones "can be compared to the colours man recognizes, and accepts as useful concepts, within the spectrum of wavelengths of light which are known to be continuous" (Whittaker 1975).

Ward (1986) studied the population response of macro-invertebrates along an elevation gradient in a pristine stream from the alpine tundra to the plains. The elevation gradient is a complex gradient of temperature and physico-chemical changes which are important factors in the structuring of faunal distribution patterns. It was found that changes in the elevation gradient had a gradual, clinal effect on benthic communities, except where the character of the river changed abruptly from a rhithron type to a potomon type. Ward (1986) concluded that temperature, food resources, aquatic plants and possible biotic interactions were largely responsible for structuring downstream patterns of faunal communities. Temperature was found to play a major role in the distribution and abundance of lotic zoobenthos and was especially important where the stream traversed an extensive elevation gradient.

Austin et al. (1984) divided environmental gradients into three types:

a. Indirect gradients (e.g. altitude) are those whose influence on plant growth is indirect

b. Direct gradients (e.g. pH) are those in which the parameter (gradient) has a direct physiological effect on plant growth.

c. A resource gradient (e.g. nitrogen) is one in which the parameter (gradient) is directly used as a resource by the plant. There is no absolute distinction between a direct environmental factor and a resource.

The factors which directly influence plant growth can be represented in the following formula

$$p = f(n, w, t, l)$$

Where p = plant performance
n = nutrients
w = water availability
t = temperature
l = light

These direct gradients are in turn influenced by a number of indirect environmental gradients such as slope, altitude, aspect etc. In order to understand the relationship between vegetation and the environment, Austin et al. (1984) proposed that it was necessary to develop generalised expressions which summarised how indirect environmental factors determine the availability of resources (Fig. 1).

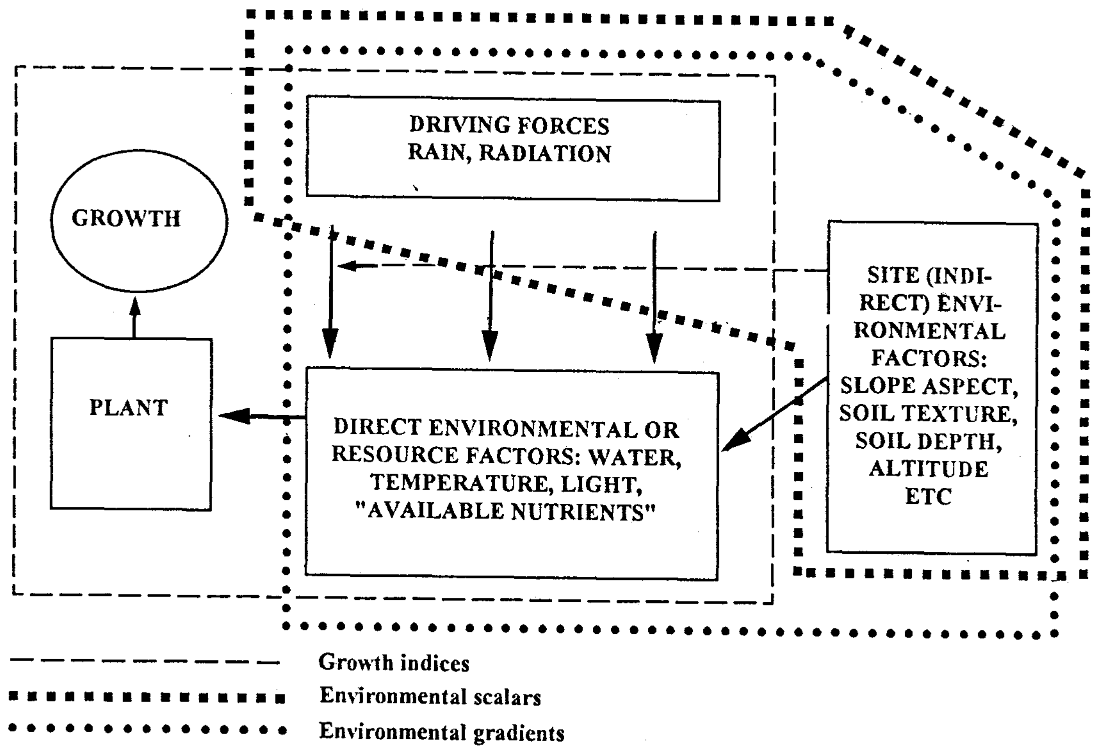


Figure 1: Schematic diagram of the relationship of various environmental variables, types of scalars and the variables they incorporate, which have been used to represent their effects on plant growth (after Austin et al. 1984)

Austin et al. (1984) also studied the individual responses (i.e. presence/absence) of six *Eucalyptus* species to four environmental gradients (mean annual temperature, mean annual rainfall, radiation index and geology). It was found that only a limited number of environmental factors account for a major proportion of the variability in vegetation composition. The significance of this result is that it demonstrates that the distribution of individual species can be reasonably predicted using the four variables examined. It was also found that, in some environments, two or three indirect environmental gradients may summarise much of the observed variation in species distributions (Austin et al. 1984). The measurement of species responses to a limited number of environmental gradients can therefore be used as a basis for drawing up predictive models of expected distributions. Indirect gradients such as elevation, can also be used as surrogate measurements for other direct environmental gradients such as temperature.

2.4. TECHNIQUES IN BIOGEOGRAPHICAL MODELLING

Biogeographical modelling makes use of geographical information to analyse distribution patterns of species, and sometimes to draw up predictive models. The approach is usually to compare distribution patterns of selected groups of plants and animals, particularly stenotopic species, to climatic indices such temperature, elevation or rainfall. Based on such comparisons, synthesis maps are often constructed which are used either as descriptive or predictive models of the distribution patterns of the biota.

2.4.1. Traditional techniques

In the past, geographical information was usually stored in the form of two-dimensional maps. Because there is a severe limitation on the amount of information that can be stored in this way, such "traditional" maps are characterised by the following features (Goodchild & Kemp 1990; Hobson pers. comm.):

1. Cartographic abstraction: Only selected features are represented and in some cases these features are exaggerated (for example a road or river network is usually represented as being bigger than reality in relation to the scale of the map).

2. Static: Maps are representations of the world at a particular time and rapidly become out of date.

3. Generalised: Because of the necessity for cartographers to make fairly arbitrary decisions (e.g. where does a river start?), there are some general rules which cartographers must follow in the compilation of maps.

4. Categorisation: Information is usually condensed and categorised (aggregated). For example elevation, temperature and rainfall values are usually represented in the form of contours, isotherms and isohyets respectively.

2.4.2. Geographical Information Systems (GIS) techniques

Geographical information systems have been described as "systems that can collect, manage, manipulate, analyse and display spatial attribute data. They have the ability to work with many types of data and draw conclusions through the analysis of many data layers" (Carrington

1991).

Because GIS are usually based on extensive computerised databases with a far greater storage capacity than that of the maps used in "traditional" geographical analysis, they have the following advantages (Burrough 1986; Goodchild & Kemp 1990; Hobson pers. comm.):

1. Although data must still be abstracted and generalised to a certain extent, the user has a greater choice regarding the way in which information is generalised.

2. Although the problem of data collection remains, updating information is easier, so the system is less static than is the case for traditional maps.

3. Flexibility in analysis: In GIS there is a greater flexibility in comparing features from different "layers" in the system. The nature of data storage also allows for a greater flexibility. Although aggregate data may be used in GIS, it is possible to store a greater proportion of the data in the raw (disaggregated) form. This means that the user is less constrained by the interpretations, generalisations, and categorisations made by the original collector of the data (e.g. the cartographer or land surveyor).

4. Computer-assisted mapping techniques allow the user to evaluate different aspects of the Earth's surface in a multidisciplinary way. Data from a number of monodisciplinary surveys can be combined to give an integrated overview.

In spite of all the advantages listed above, there are certain disadvantages in using GIS systems compared to traditional methods (Hobson, pers. comm.).

1. GIS are expensive since they rely on the existence of sophisticated hardware and software.

2. The databases required to operate GIS are usually very extensive. If there is a paucity of data, traditional methods may be more appropriate.

3. Skills: GIS require the user to be computer-literate and fairly skilled in the use of sophisticated computer programmes.

GIS systems are either raster-based or vector-based. In raster systems, information is located in "cells" and displayed as "pixels". Sets of cells are located by coordinates and each cell is independently addressed with the value of the attribute to be measured. Raster-based systems produce images which are based on a set of points on a grid (or "raster"), the resolution being dependent on the area represented by a pixel (Burrough 1986). Raster representation assumes that the geographic space can be treated as though it were a flat Cartesian surface. Each pixel or grid cell is then associated with a square parcel of land. A raster map file is built up from what the user perceives as a number of Cartesian overlays. Each geographical attribute is then represented by a separate overlay (Burrough 1986). For example, an attribute such as rainfall may be displayed in one overlay, elevation in the next overlay and soil type in a third overlay.

Vector-based GIS systems make use of points and lines to define and describe areas. These systems are more complex than the raster-based systems and generally require more storage space on computers, but have the advantage of being able to produce cartographic images of a higher quality than those produced using raster-based systems (Burrough 1986).

2.4.3. Coordinate systems and map projections used in GIS

Most GIS systems create flat representations (projections) of the spherical earth in the form of a grid-referencing system in which two sets of straight parallel lines are equally spaced perpendicular to each other (Westervelt 1991). This can be regarded as a conformal projection, which is also the basis for the Universal Transverse Mercator Coordinate system (UTM) (Burrough 1986; Maling 1991), used in government-survey maps in countries such as Britain (West pers. comm.). In South Africa, government-survey maps are based on latitude/longitude coordinate projections (West pers. comm.) in which the grid cells are neither square nor rectangular, because their sides are formed from two meridians and two parallels. In some cases the word "quadrangle" is used to describe such cells (Maling 1991).

The primary source of GIS positional data is usually taken from printed maps. In some cases a number of different maps are used, often with different projections. There is therefore sometimes a need to transform data into a uniform system of positional referencing. A number of different transformations such as Affine, Helmert or numerical transformations can be used for this purpose. The choice of which transformation to use depends on the projection used in the source map (Maling 1991). It may also be necessary to use cartographic transformations in order to change the projection of maps which are the products of GIS analysis. Raster-based systems are however, not amenable to such transformations (Hobson, pers. comm.).

2.5. CHARACTERISTICS OF INLAND WATERS IN SOUTHERN AFRICA

The review of literature in this section is restricted to an analysis of the characteristics of inland waters with respect to water availability and temperature regimes.

2.5.1. Rainfall and water availability

Allanson et al. (1990) note that the southern African region south of the Zambezi can be generally regarded as being water-limited, of which the western side is arid and the eastern and southern regions are wetter. It is also noted that the great majority of southern Africa's water resources are riverine as there are very few natural freshwater lakes south of the Zambezi. The average annual rainfall of southern Africa is about 497 mm per annum which is well below the world average of 860mm (Anon 1986). Only a narrow region along the eastern and southern coastlines is moderately well-watered. Sixty-five percent of the country receives less than 500 mm of rain annually, and twenty one percent receives less than 200 mm. It has also been noted that as the mean annual rainfall (MAR) declines, so the variability in rainfall increases (Alexander 1985). The variability in the rainfall is illustrated in the map (Fig. 2) of the Median Annual Precipitation (after Schulze & McGee 1978).

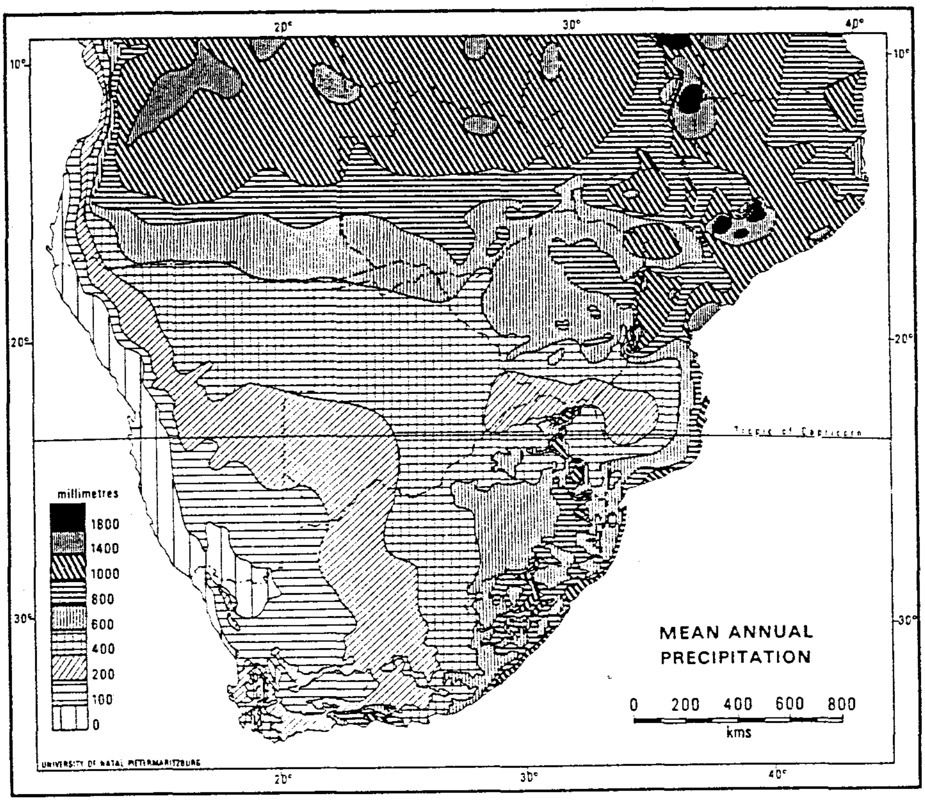


Figure 2: Mean annual precipitation over southern Africa (after Jackson 1961, after Schulze & McGee 1978).

Allanson et al. (1990) noted that rainfall patterns in southern Africa are characterised by the high frequency of drought and the apparent cyclical nature of wet and dry years. The long term cycles of wet and dry years may to a certain extent be predictable, but this is not the case for the short-term yearly climatic cycles. One of the major characteristics of southern African hydrology is therefore its variability. The high evaporation rates associated with fewer rainfall events which contribute to runoff, exacerbates this variability. It should be noted that the average annual rainfall in South Africa is similar to that of Canada which is seemingly a more moist country. There is however a marked difference between the two countries in the percentage of rainfall which is converted to runoff: 65.7% in Canada compared to 8.6% in South Africa (Allanson et al. 1990).

The principle drainage regions and their contribution to mean annual runoff in southern Africa were summarised in a map drawn up by Noble & Hemens (1978), which is reproduced in Fig. 3.

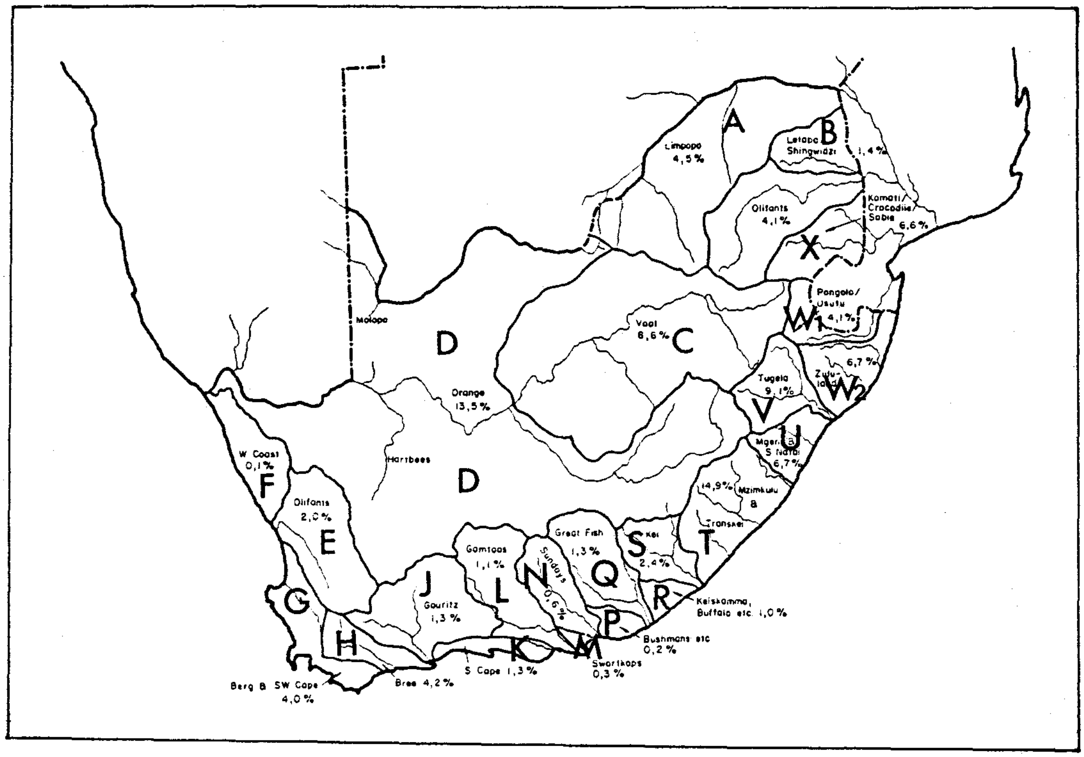


Figure 3: Principle drainage systems in South Africa and their contribution to total mean annual runoff (after Noble & Hemens 1978). Labels for each region follow the code used in Department of Water Affairs publications (Anon 1986)

It is quite clear that such variability in rainfall patterns and runoff will result in a great deal of variation in the flow of rivers through such zones. For this reason many of the rivers in the sub-continent are seasonal or intermittent. Allanson et al. (1990) use the following terms to characterise the flow of rivers:

Perennial rivers - flow throughout the year.
Seasonal rivers - those which cease to flow above ground for a significant part of their length during most years.
Intermittent rivers - typically situated in catchments of less than 300 mm rainfall per annum, and flow above ground only once every few years, following exceptional rainfall.

Allanson et al. (1990) also note that rainfall seasons have important implications for the aquatic biota. The cessation of flow during summer (when biological activity reaches its peak) would be more serious than cessation during winter when organisms may be in dormant stages.

The length of the dry season is obviously of critical importance in determining whether or not rivers would be perennial or seasonal. Balinsky (1962) identified a "drought corridor" which extends from the western Cape and South West Africa (now Namibia) in the south to the Somali peninsula in the north east. This region is characterised by having seasonal rainfall and a dry period of at least three consecutive months when monthly rainfall is less than 10 mm per month. It could be expected that most rivers in this region would be seasonal or intermittent.

Hocutt & Skelton (1983) surveyed the fish fauna in the Sak River (Orange River system), a seasonal river in an arid region of the north western Cape which often dries up to a series of small pools which act as refuges for aquatic organisms. Conditions in these pools were found to be very harsh and only the eurytopic aquatic organisms capable of tolerating extreme conditions of eutrophication, temperature, salinity and oxygen deprivation were able to survive. Allanson et al. (1990) also noted that the fauna in seasonal rivers is generally impoverished compared with that of perennial rivers. Williams (1985) noted that many parameters affecting the survival of the organism such as temperature, salinity and pH showed extreme variability in temporary pools. The volume of water available clearly influences nearly all the biotic and abiotic parameters which affect the ecotope.

From the above description the availability of water is clearly an extremely important factor limiting the distribution of aquatic organisms, particularly in the arid regions of the country.

The availability of water in rivers is indirectly linked to rainfall. Even if the rainfall in an area is low, a perennial supply of water from upper catchments will buffer aquatic organisms from extreme conditions during short dry periods. An example of this phenomenon can be found in large rivers such as the Orange River which flows perennially through extremely arid regions. The flow of rivers in southern Africa has also been significantly altered by man. Allanson et al. (1990) note that "none of the major rivers, and few small streams in southern Africa have escaped from some form of disturbance from Man's influence". A summary of the major impacts of man's interference with the hydrology of rivers is given below:

1. Catchment changes: Factors such as bush clearance, afforestation and urban developments all affect the runoff from catchments, resulting in a loss of storage capacity in the catchment which leads to more intensive floods after heavy rains (Allanson et al. 1990).

2. Regulation by means of impoundments or interbasin transfers: In the past thirty years impoundments have been the dominant form of regulation (Allanson et al. 1990). The character of rivers immediately upstream of impoundments changes from riverine to lacustrine. Downstream effects include the dampening of extremes in flow during the rainy and dry seasons (Chutter 1963).

Pettijean & Davies (1988) noted that existing water transfer schemes in southern Africa divert 1,63 x 10^9 m^3 per year. This is expected to rise to 4,82 x 10^9 m^3 per year when all the planned schemes and those under construction come on stream. Interbasin transfers can result in the alteration of seasonal or intermittent rivers to perennial rivers, e.g. the Great Fish River in the eastern Cape which receives water via the Teebus Tunnel from the Orange River (Allanson et al. 1990).

3. Water abstraction: This has the effect of converting many perennial rivers into seasonal rivers. For example, many rivers flowing through the Kruger National Park (e.g. the Levuvhu, Great Letaba, Olifants, Sabie and Crocodile) were formerly perennial. Of these, only the Sabie still has a natural perennial flow (Allanson et al. 1990).

2.5.2. Temperature characteristics of inland waters, and the distribution of indigenous stenothermal aquatic animals

Air temperatures can be used to predict water temperatures, although these predictions are often inaccurate when dealing with impounded rivers, or in spring-fed water (Nishizawa &

Yamabe 1970; Crisp & Howson 1982). Pitchford (1981) makes the assumption that sufficient correlation exists between air and water temperatures for air temperatures to be a reliable indicator of water temperature when comparing the temperatures of similar waterbodies.

Palmer & O'Keeffe (1989) noted that impoundments induced alterations in the temperature regimes of rivers which were influenced by the size and locality of the impoundment and whether the water was released from the top or bottom of the impoundments. Deep-release impoundments in the headwaters of a river had little effect on the annual temperatures downstream of the impoundment, whereas such impoundments in the middle or lower reaches of rivers would cause a significant reduction in the annual temperature. It could also be expected that small surface-release impoundments in the upper reaches of rivers would cause an increase in the annual temperature range downstream. It was found that surface-release impoundments in the upper reaches of the Buffalo River in the eastern Cape caused increases in temperature of up to 8°C, and recovery to the normal temperature profile was within 6.4 km of the impoundment.

Pitchford & Visser (1975) studied the effect of the building of the HF Verwoerd Dam on the temperature regimes in the Orange River at a site 4km downstream of the impoundment. In comparing the mean monthly temperatures before and after the construction of the dam it was found that the impoundment had caused a dampening of extreme temperatures in winter and summer. Mean monthly maxima were warmer in winter (by as much as 4.3°C in June) and cooler in summer (by as much as 7.2 C°in December). Likewise mean monthly minima were also warmer in winter (by as much as 5.1°C in June) and cooler in summer (by as much as 4.3°C in December).

The assessment of the effect of temperature on a particular species is complicated by the fact that the adaptation of animals to thermal factors is unequal and varied and that refuges can usually be sought away from unfavourable extremes of temperature (Stuckenberg 1969). In the case of aquatic animals this ability to avoid extremes in temperature is directly related to the volume and flow of the water and the nature of the species' preferred habitat.

The use of indigenous species as indicators of abiotic conditions has already been discussed in section 2.3.2.. Although the absence of particular species cannot be used reliably as an indicator of conditions, the presence of certain stenothermal species can be used as indicators of temperature regimes in regions where they have had historical access to catchments. Allanson et al. (1990) provide a checklist of a large number of stenothermal aquatic invertebrates in southern Africa whose distribution is to a certain extent restricted by prevailing temperature regimes. Gabie (1965) noted that the Phongolo River represents the southern limit to the range of a large number of tropical fish species. It is likely that temperature is the most important factor limiting the southward distribution of these species. These observations have been supported by Bowmaker et al. (1978) who regarded temperature as being an important barrier to the southward and upstream dispersal of many tropical species of fish. Other studies on the distribution patterns of Amphibia (Poynton 1962), and of various species of freshwater molluscs whose distributions are restricted to the "tropical" and "temperate" regions of southern Africa (Brown 1978), have suggested that temperature is the paramount biogeographical factor limiting the distribution of these groups of animals particularly in the moist regions of southern Africa.

The presence of any of the above-mentioned species could be used as indicators of certain temperature regimes in inland waters where they have had historical access to invasion. There is a problem however, in that the distribution of many of the aquatic species, particularly invertebrates, in southern Africa is poorly researched. Certain groups of organisms, such as the bilharzia-vector snails, have however been intensively studied as a result of their medical importance (Brown 1978, 1980). Although stream geology may play an important role in limiting the distribution of *Bulinus* spp. and *Biomphalaria* spp. snails (Appleton 1975, 1976), Brown (1978) regarded this influence as being of only local significance. He stressed the importance of temperature as the paramount factor influencing the distribution of both these snails in many regions of southern Africa. Their distribution is also limited by water availability in the arid regions of the subcontinent (Brown 1980).

2.5.3. Classifications of rivers and limnological regions in southern Africa

Harrison (1959) divided the southern African sub-region into 13 hydrobiological provinces. Although temperature regimes were taken into account, this classification system relied extensively on other criteria such as the chemical characteristics of waters in different regions and associated geological features, and was not primarily related to the distribution patterns of any particular group of animals.

Noble & Hemens (1978) proposed a less detailed classification of South African rivers, which was similar to that of Harrison (1959) in that similar criteria were used as a basis for the classification i.e. geological features, water quality and biotic features. The rivers were classified into the following categories, based on the above-mentioned criteria: Cape clear acid waters (south western Cape region); South Cape and acid rivers (southern Cape); southern Karoo rivers (southern & eastern Cape); Transkei & Natal degrading rivers (Transkei & Natal); Escarpment floodplain rivers (eastern & northern Transvaal, northern Zululand); Vaal (southern & western Transvaal, northern & western Orange Free State) and Orange (Lesotho, eastern & southern Orange Free State, northern Cape).

Allanson et al. (1990) concentrated on the characteristics of catchments rather than of rivers, and proposed a classification of southern Africa into five limnological regions. The geomorphological, geochemical and climatological features of southern Africa were used as a basis for this classification.

2.6. BIOGEOGRAPHICAL ANALYSIS OF INLAND WATERS IN SOUTHERN AFRICA

This review is restricted mainly to studies of distribution patterns of species over large regions of southern Africa. The emphasis is also on biogeographical models relating to inland waters. However certain biogeographical studies on other continents or on terrestrial biota in southern Africa have also been reviewed, where the methodologies are of particular importance to the present study.

2.6.1. "Traditional" biogeographical models based on distribution patterns of particular species

2.6.1.1. On aquatic or semi-aquatic animals

The bioclimatic classification systems developed by Bowmaker et al. (1978), Poynton (1964) and Guillet & Crowe (1986) are of particular interest since they deal with aquatic or semi-aquatic animals (Table 1).

Poynton (1964) found that the distribution of Amphibia in southern Africa followed the pattern indicated by certain mean July surface (air temperature) isotherms. In particular he showed that the 18°C isotherm coincided with the belt of precipitous subtraction at the edge of the main concentration of tropical fauna in the north- eastern regions of the country (Maputaland). Likewise the 13°C mean midwinter isotherm on the eastern slopes of the Natal escarpment marked the division between the tropical transitional and the temperate transitional Amphibian fauna.

Table 1. Bioclimatic classifications in southern African based on the distribution patterns of aquatic or semi-aquatic animals.

Animal taxa	Terminology	Abiotic parameters	Reference
1. Amphibia	thermal zones	temperature, rainfall	Poynton (1964)
2. Fish	climatological zones	temperature, rainfall	Bowmaker et al. (1978)
3. Waterbirds	waterbird avifaunal zones	various moisture parameters, temperature, elevation	Guillet & Crowe (1986)*

* This work should not, strictly speaking, be described as a "traditional" method, since some computerised analyses were used in order to define the regions described in the map. However, since this work cannot be described as a GIS analysis, it has been included in this section for convenience.

On the basis of these considerations Poynton divided the country into three thermal regimes bounded by the following mean July surface isotherms:

tropical - temperatures > 18°C isotherm
subtropical - temperatures between 13°C and 18°C isotherms
(warm) temperate - temperatures < 13°C isotherm

Poynton also found that the distribution of Amphibia in the western Cape was not as strongly influenced by prevailing temperatures as was the case in the moist eastern regions of Natal. He concluded that the thermal pattern was of primary importance in determining the distribution of Amphibia in the moist regions of the country, whereas the rainfall regime became increasingly significant as a limiting factor in the drier regions of the country. The annual isohyets of 500 mm and 250 mm were chosen as convenient lines of demarcation whereby the thermal regimes described above, were further sub-divided into moist and arid regions (Fig. 4).

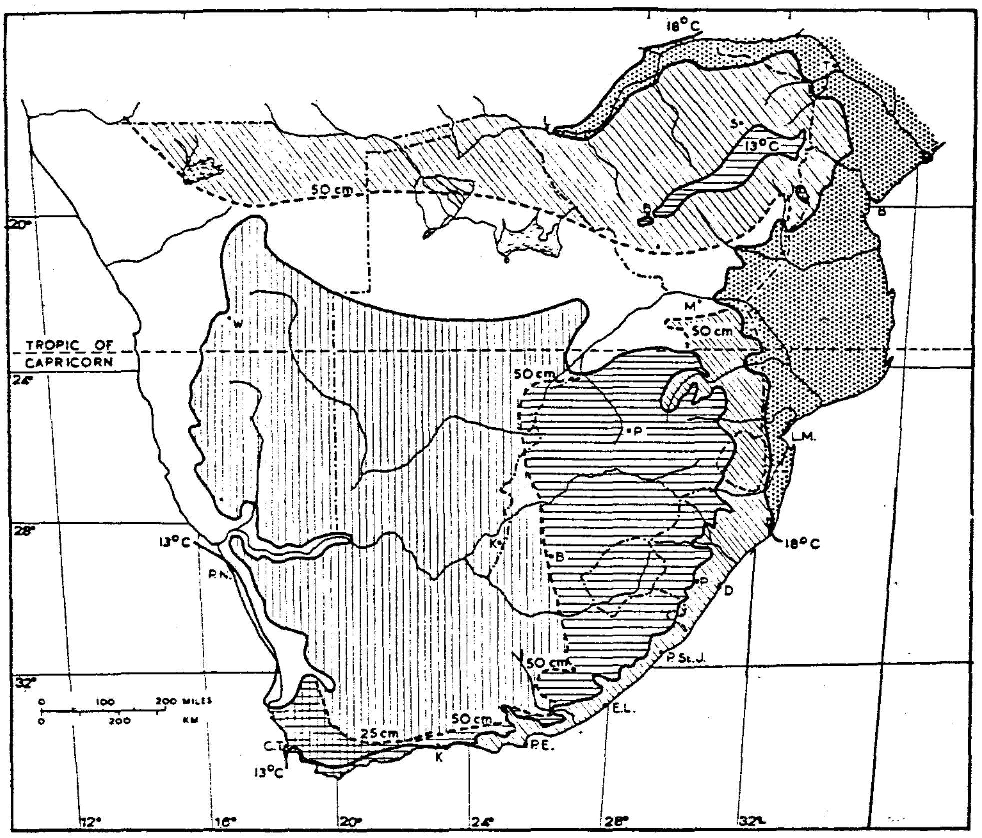


Figure 4: Biotic divisions of southern Africa (after Poynton 1964).

Tropical region. North of the 18°C July surface isotherm

Sub-tropical moist. Between the 13° - 18°C July surface isotherms. Annual rainfall greater than or equal to 500 mm.

Sub-tropical arid. Between 13° - 18°C July surface isotherms. Annual rainfall < 500 mm.

Temperate eastern. Temperature < 13°C July surface isotherm. Annual rainfall > 500 mm.

Temperate western. Temperature < 13°C July surface isotherm. Annual rainfall < 500 mm.

Temperate southern. Winter rainfall region. Bounded by 200mm isohyet in the north and the 13°C July surface isotherm in the south.

Mean surface July isotherm

Isohyets

Based on the distribution patterns of freshwater fish in southern Africa, Bowmaker et al. (1978) divided the southern African sub-region into six zones according to temperature and aridity regimes in the freshwater environment (Fig. 5):

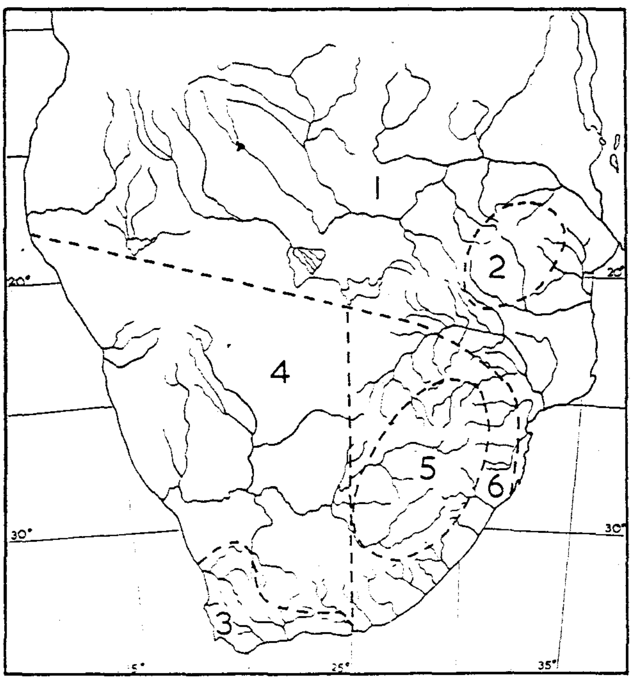


Figure 5: Climatological zones of southern Africa (after Bowmaker et al. 1978).

Zone 1 - Summer rainfall (tropical zone). In this region temperatures are high enough to support warm-water fish. There is an increasing gradient (from the south to the north) in annual rainfall. Most rivers are permanent.

Zone 2 - Highveld zone. Due to altitude, the water temperatures are lower than in Zone 1.

Zone 3 - Winter rainfall zone in the south-western Cape.

Zone 4 - Arid to semi-arid zone west of 25°E. Rainfall is erratic and river flow unreliable. The region is thus characterised by the presence of many intermittent rivers.

Zone 5 - Drakensberg highlands (temperate) region.

Zone 6 - Transitional zone from winter to summer rains. Rivers in the north of this region are predominantly permanent.

It was also noted that, with the southward progression through the regions (Fig. 5), there was a decrease in temperature and an increasing aridity and variability of rainfall, resulting in fewer suitable habitats being available for fish.

Guillet & Crowe (1986) characterised the environment by measuring a number of parameters relating to moisture (median annual rainfall and the size and characterisation of surface water bodies), as well as air temperature and elevation. A number of procedures involving correlations, regressions, stepwise multiple regressions, and cluster analyses, were carried out in order to identify the environmental factors which influenced the species richness of waterbirds. Their results indicated that there was a partitioning of resident waterbird species into two main avifaunal zones in southern Africa. Waterbirds were found to exhibit a longitudinal rather than a latitudinal gradation of species richness, the greatest diversity being in the eastern regions, with a progressive decline in species richness towards the drier western regions. The eastern avifaunal zone was subdivided into two sub-zones, in the region of the Limpopo valley (Fig. 6).

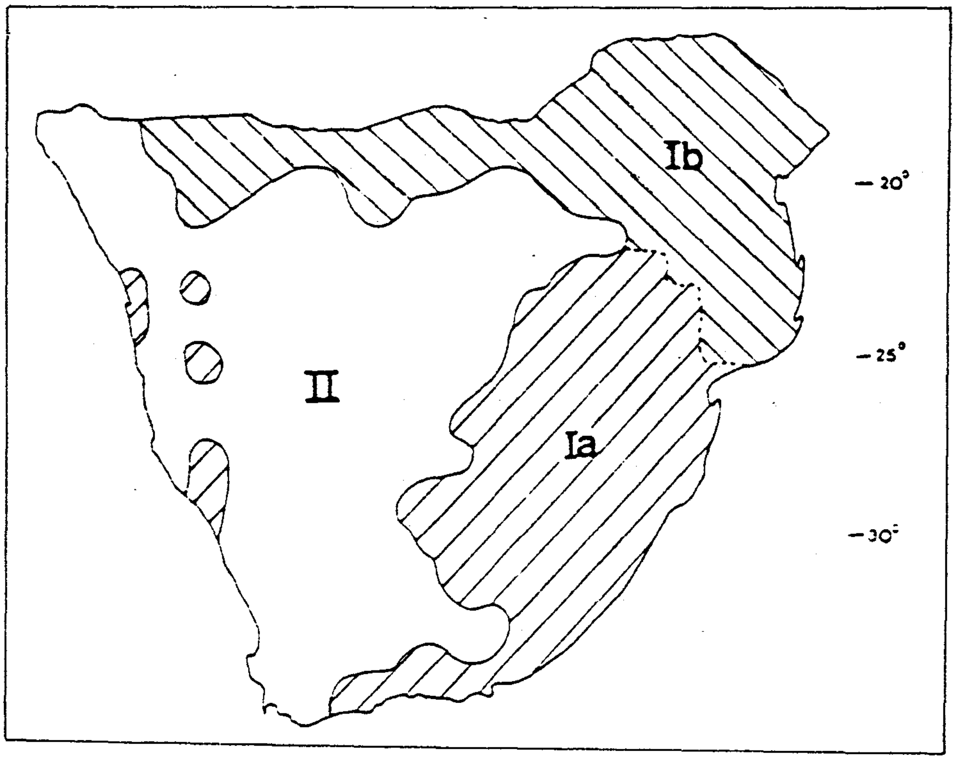


Figure 6: Avifaunal zones of southern Africa for resident waterbirds (after Guillet & Crowe 1986). The moist zone is indicated by the shaded areas which is divided into a northern region (Ia) and a southern region (Ib). The arid region (II) is unshaded.

These results indicate that the dominant environmental variables affecting the distribution of waterbirds was the MAR and the availability of aquatic habitat. The arid western avifaunal zone was described as a "default zone" delimited mainly by range limits of species which do not occur within its boundaries.

Since the entire eastern region of South Africa (extending from the Cape to the Limpopo River Valley) has been classified as a single subzone (Guillet & Crowe 1986), it is apparent that the distribution of waterbirds in southern Africa is not strongly influenced by temperature regimes.

Guillet & Crowe (1986) noted that species richness in certain quadrats (within the eastern and western zones) was much higher than the predicted value. It was proposed that these regions were centres of reliable and diverse aquatic ecosystems which could withstand dry climatic cycles for the longest period of time. These regions were described as "refugia" and represent regions of reliable permanent water (except during exceptionally dry, catastrophic periods) (Fig. 7).

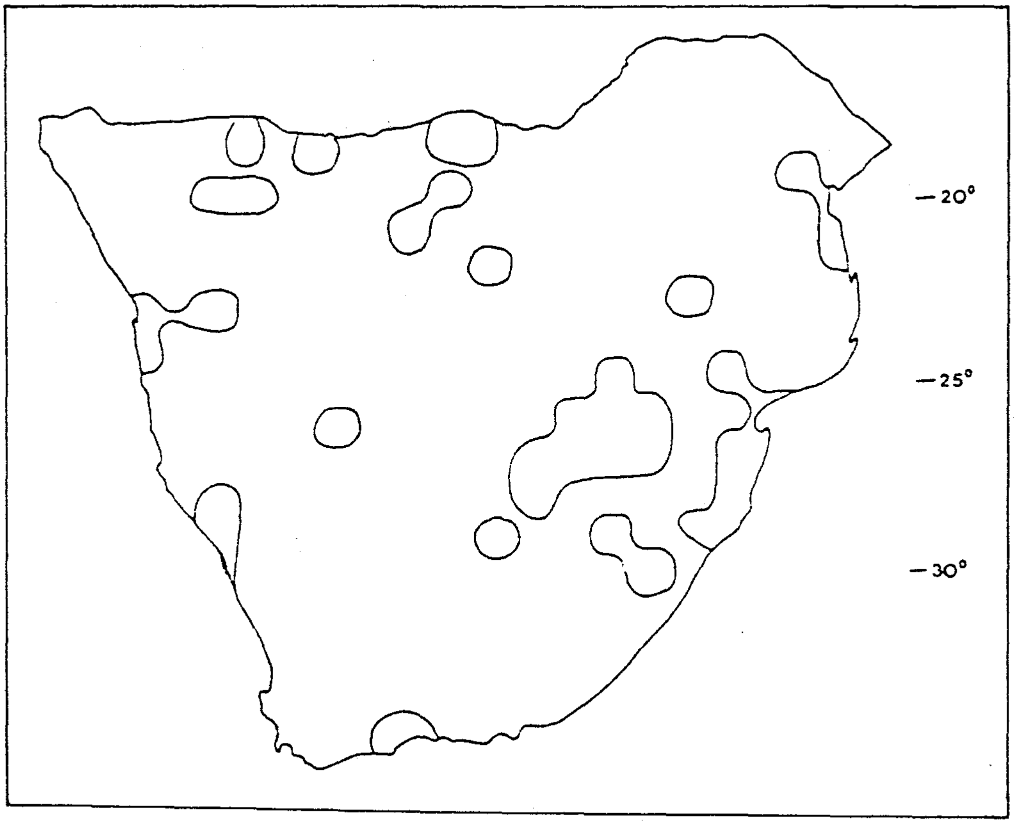


Figure 7: Hypothetical waterbird refugia during dry climatic phases in southern Africa (after Guillet & Crowe 1986).

2.6.1.2. Biogeographical models based on terrestrial animals

An important study using the distribution of snakes and some Amphibia as a means of defining thermal zones in southern Africa was carried out by Stuckenberg (1969). He regarded rainfall as being of greater significance than temperature in determining the distribution of species in the subcontinent, but nevertheless compared the distribution of certain temperature-sensitive species (snakes) to thermal regimes. In this context he regarded the mean surface July isotherm as an arbitrary and unreliable measure of temperature regimes and suggested that the "effective temperature" parameter had more biological significance. Effective Temperature is calculated as follows:

$$ET\ (^\circ C) = \frac{8T + 14AR}{AR + 8}$$

where

ET = effective temperature
T = mean annual temperature
AR = difference between the mean of the warmest and coldest months

The effective temperature parameter represents the temperature at the beginning and end of the warm season. The duration of time over which specific temperatures apply has a strong influence on the calculation of the ET. Therefore an increase in ET implies an increase in the length of summer.

The duration over which temperatures in a particular region are higher than the calculated ET for the region is progressively longer for higher ET measures. For example, at an ET value of 18°C, the mean daily temperatures throughout the year are greater than 18°C. There is effectively no thermal winter. Regions in which ET values are greater than or equal to 18°C can therefore be regarded as tropical. At the 13°C ET, mean daily temperatures are greater than 13°C for approximately half the year.

Stuckenberg (1969) noted that cold spells are biologically significant in the tropics and that the significance of warm spells increases with an increasing distance from the tropics. In southern Africa the ET regime ranges from approximately 13.2 to 18°C. In regions where ET values are greater than 17°C, cold periods are of greater biological significance than warm periods. In the cooler regions, such as those in which ET values are less than 15°C, the biological significance of the summer period increases.

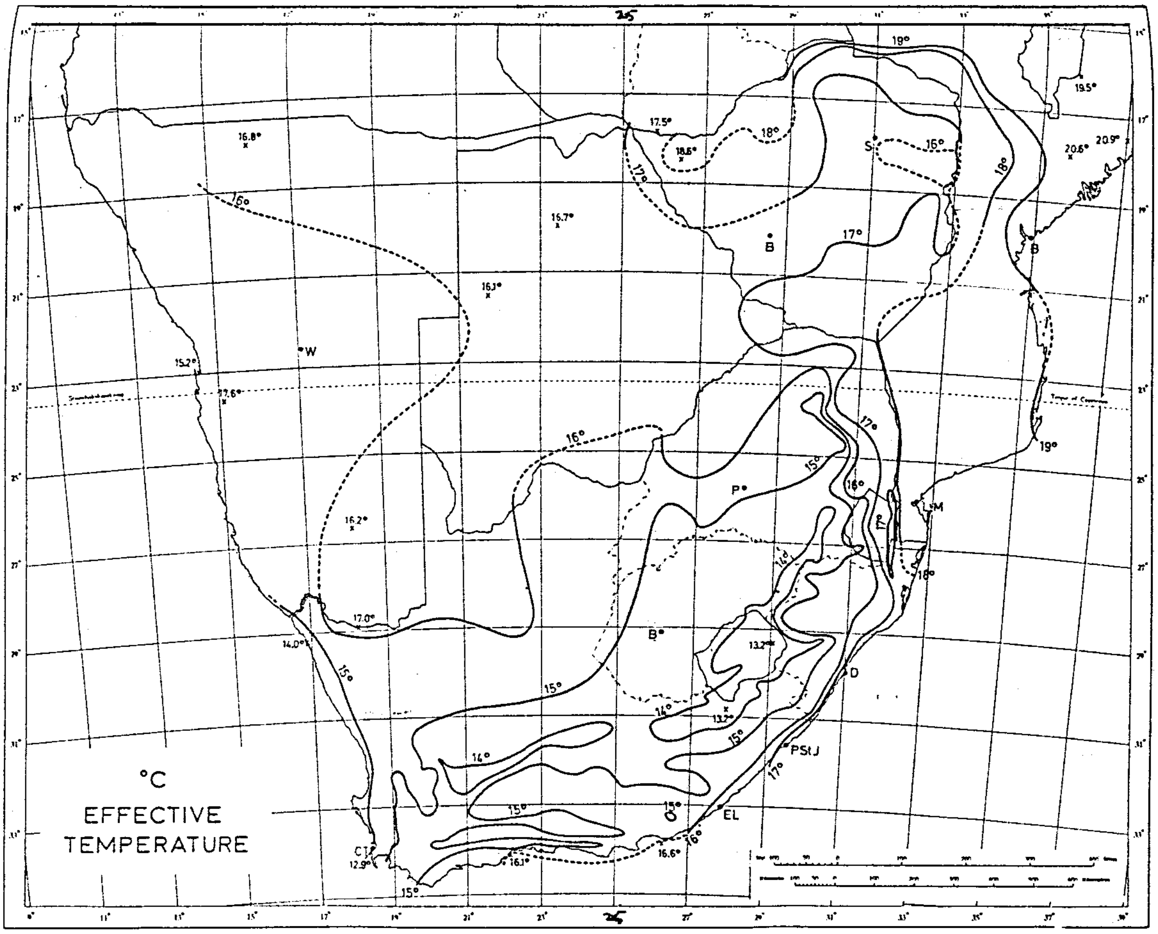


Figure 8: Effective temperature zones in southern Africa (after Stuckenberg 1969).

Based on calculations of Effective Temperature, Stuckenberg (1969) compiled a map indicating ET isolines throughout southern Africa (Fig. 8). A comparison of this map with distribution records of snakes in southern Africa indicated that most tropical species were excluded from regions with temperatures below the 15°C ET isoline, whereas most South African endemic species did not extend into regions with temperatures above the 16°C ET isoline. Many Amphibian species showed similar distribution patterns. The region between the 15°C and 16°C isolines could therefore be described as a transition zone in which both South African endemics and species of tropical origin reached the limits of their distribution (Stuckenberg 1969).

2.6.2. Biogeographical models based on GIS techniques

2.6.2.1. Available databases pertinent to studies on inland waters in southern Africa

The Department of Water Affairs has an extensive database of water-related parameters. A new integrated database, with an emphasis on water-availability parameters, is also being developed. Provision is being made to link this database via a mutual co-ordinate grid to other databases such as the Computing Centre for Water Research (CCWR) database (Anon 1986). It is expected that this database will be available for users throughout South Africa in the near future (Hobson pers. comm.). At present the only large database of geographical parameters in South Africa which can easily be accessed by means of computer link-up is that of the CCWR (Palmer pers. comm.). Much of this data is based on the work of Dent et al. (1989) who carried out an extensive project on the mapping of mean annual rainfall and other rainfall statistics in southern Africa. Although the primary purpose of their project was to identify homogeneous rainfall zones in the subcontinent, other useful accessory information was generated:

a. A response surface of median annual precipitation (MAP) and elevation at a resolution of one minute of a degree. The value at the intersections of the grid is the value for the whole pixel.

b. Physiographic data including preliminary maps of temperature and evaporation.

c. Monthly rainfall data.

d. Regionalisation of rainfall data.

Median annual precipitation (MAP) is regarded by Dent et al. (1989) as being equivalent to median annual rainfall (MAR) because the contribution of fog and snow to the MAP is regarded as being insignificant in the regions of southern Africa covered by the database (South Africa, Lesotho and parts of Swaziland). The two terms are therefore used interchangeably in this thesis.

Dent et al. (1989) generated a minute/minute surface response curve for MAP in southern Africa. The dataset was based on daily and monthly rainfall records from 9409 weather stations throughout southern Africa (in the regions described above).

The following steps were taken to generate the grid map of MAP values:

1. Trend surface analysis and multiple regression techniques (incorporating physiographic data on indices of continentality, exposure, distance to a mountain barrier, surface roughness and aspect) were used to produce a surface response curve of MAP at a minute/minute resolution.

2. The percentage residuals (error) was calculated for each rainfall station by comparison of the observed values with the predicted values generated in step (1).

3. Direct interpolation techniques were used to generate a surface response curve of residual values (at a minute/minute resolution).

4. Each grid point on the regression surface (generated in Step 1) was modified by multiplying the result by a factor calculated from the estimated residual value (generated in step 3) at the point.

5. Step 4 produced a new composite surface response curve based on the original regression surface (step 1) and the residual response curve (Step 3).

This process produced a regional trend map which had been modified to provide local sensitivity to the measured MAP values at rainfall stations. The map had already been adjusted to account for errors measured at different rainfall stations.

The advantage of employing this technique is that the product is a surface which follows the trend exhibited by the regression surface, but also fits the observed MAP exactly at the rainfall station points. The model thus has the predictive capability of a regression analysis in ungauged areas, combined with local sensitivity associated with the use of direct interpolation calculations in the vicinity of the rainfall stations.

The disadvantage of using this technique is that it is not possible to estimate the confidence limits at individual stations. The user may however gain a reasonable insight into the confidence of the estimate of MAP in the vicinity of the station by consulting the extensive appendices in Dent et al. (1989) or referring to the INDEX file on the Computing Centre for Water Research (CCWR) database. Dent et al. (1989) emphasised that it was not possible to obtain the true value of the rainfall in any region, as the original data obtained from weather stations is an estimate of the rainfall in the region and the value of this data varies according to the length of time over which rainfall has been recorded. The margin of error in the original dataset therefore varies from station to station. As a general rule it can be expected that the error in the final map of the surface response curve would be greater in mountainous regions where the distribution of rainfall stations is sparse in relation to the physiographic complexities of the region.

The multiple regression analysis, described above, involved making use of physiographic data (including elevation). This was obtained from various sources and it was also necessary to generate further data using computerised techniques. In the process a grid system (on a minute/minute resolution) formed the framework for the entire physiographic and regional information system. At each point of the grid the variables (including elevation) that are necessary for trend surface analyses were assigned a value. This whole dataset (including a digital terrain map of elevation) is stored with the CCWR and is available to interested users. Data relating to elevation and MAP can already be accessed through computer links to the CCWR.

2.6.2.2. GIS studies carried out in southern Africa and elsewhere which are relevant to the present study

Palmer & van Staden (1992) used the IDRISI geographical analysis programme to predict the potential distribution of plant communities in the north-western Transvaal. In this study floristic surveys of two veld types were carried out. These results were linked to median annual rainfall (MAR) and elevation using the CCWR database. Using contingency tables the optimum conditions for MAR and elevation were defined. A raster-based GIS system (IDRISI) was used to interrogate the dataset from the CCWR for the north western Transvaal, in order to find regions with similar conditions of elevation and MAR. This was used as a basis for predicting the expected distribution of plant communities in the area. The predicted distribution was validated by referring to another source of information (i.e. a digitised version of Acocks' (1970) map of the veld types of South Africa).

A number of GIS programmes have been designed to predict regions which are susceptible to invasion by alien species. These are based on the "bioclimatic matching" approach described by Nix & Wapshere (1986) in which selected parameters of biological significance are used to estimate the "bioclimatic distance" between different regions of the globe. Nix & Wapshere (1986) found the success of invasions was negatively correlated with increasing bioclimatic distance between the native range of a particular species and the region where it is introduced.

The bioclimatic matching approach is not merely an analysis of homoclines, since factors of biological significance are also taken into account in predicting susceptible regions.

Richardson & McMahon (1992) used the BIOCLIM programme to construct bioclimatic profiles of eucalyptus trees (*Eucalyptus nitens*) in their native range and in southern African plantations where the species is thriving. In this method the procedure of identifying "homoclines" (homologous climates) on different continents is used. Using this information potential planting regions in southern Africa have been identified. Results indicate that successful plantations in southern Africa occurred under much warmer and drier conditions than those of the native range. This led to the conclusion that climate on its own is unlikely to be an accurate predictor of distribution. This also indicates that the species does not occupy all potential suitable sites in and around its native range. Competition with similar species results in a restriction of the range. In New South Wales it was found that higher-elevation stands of the congeneric species *E. fastigata* occupy many sites which would be suitable for colonisation by *E. nitens*. Richardson & McMahon (1992) comment that one way of overcoming this problem would be to identify those species that outcompete the species in question (e.g. *E. nitens*) at the edges of its native range. Geocodes (bioclimatic profiles) for these species could then be added to those of *E. nitens* in order to produce a better predictive model for the potential regions of plantations.

The CLIMEX programme has been used to assess the climatic suitability of regions of Australia for invasion by various alien insects and ticks (Sutherst & Maywald 1985; Maywald & Sutherst 1989). This GIS programme is designed for application with poikilothermic animals only. The principle function of CLIMEX is to search locations with climates similar to those of a given location (for example, the native range of a particular problem species). The system then formulates an "ecoclimatic index" based on the favourability of a location for a specified animal. The output consists of a list of locations that best match the given location, together with an index describing the goodness of match for each location (Maywald & Sutherst 1989). This approach has been used to describe regions in Australia susceptible to invasion by the tick *Boophilus microplus*, which correlated well with the known distribution pattern of this species.

Although the bioclimatic matching approach has been used successfully to predict the distribution of a number of terrestrial animals (Sutherst & Maywald 1985), there are certain problems associated with these methods, especially when applied to aquatic animals. There is a large body of evidence (discussed in Section 2.2) to support the contention that the organism in its introduced environment often occupies a broader ecotope than in its native range. This means that predictions based on distribution patterns in the native range of a species can be expected to be too narrow. The results of Richardson & McMahon (1992) add weight to this supposition.

In the case of aquatic animals, there is the added problem that candidate species may not have had the opportunity to invade certain catchments in the source environment, so the climate in the native range would not necessarily be a true reflection of the abiotic conditions suitable for the survival of the species.

2.7. DISCUSSION

On reviewing the biogeographical models which have been used as descriptive and predictive models of distribution patterns of plants and animals in southern Africa and elsewhere, it is clear that a great deal of emphasis has been placed on the effect of moisture and temperature in limiting the distribution of species. This leads to the conclusion that:

a. These factors are of paramount importance in determining distribution patterns and/or

b. Data relating to these two environmental variables is readily available, so they have been used repeatedly in biogeographical analyses.

In some studies on freshwater organisms in southern Africa, physical factors other than temperature or moisture, have been shown to be of prime importance in determining distribution patterns. In a study on the distribution patterns of two temperature-sensitive, bilharzia-vector snails, *Bulinus (Physopsis) globosus* and *Biomphalaria pfeifferi*, Appleton (1976) found that, contrary to expectations, the colonisation of the upper reaches of the stream by these two species was probably limited by current-speed, and not temperature. Likewise, King (1981) concluded that dissolved oxygen, pH and total alkalinity were the most influential variables determining the structure of the invertebrate community in the Eerste River (western Cape).

Debates over the relative importance of various abiotic factors in determining the distribution patterns of species can become counter-productive. It is obvious that if certain basic requirements of a species (e.g. temperature or water availability) are met, then other factors will become limiting. Therefore, it can be expected that different factors would become limiting in different regions, depending on local conditions. It appears that temperature and moisture gradients are particularly useful parameters to consider when studying distribution patterns of species at a large scale, not least of all because databases on these two parameters are readily available.

It may, on the other hand, be more useful to analyse distribution patterns in terms of indirect environmental gradients, such as elevation, which encompass a number of direct gradients. This approach may be more feasible when attempting to discern broad patterns in distributions of species over large regions.

CHAPTER 3: GENERAL METHODOLOGY

3.1. OBJECTIVES, ASSUMPTIONS AND LIMITATIONS TO PREDICTABILITY

A number of points raised in the previous chapter, have a bearing on the basic assumptions and limitations in the present study. Of particular significance are the following:

a. The observation by Brown (1988) that the physical environment should be regarded as the primary determinant of species distribution patterns.

b. That a limited number of indirect environmental gradients account for a major proportion of of the variability in vegetation composition (Austin et al. 1984). Gradient analyses carried out by Ward (1986) on macro-invertebrate populations along an elevation gradient, suggested similar results for aquatic animals.

c. The demonstration by Austin et al. (1984) that "indirect" gradients could be used as surrogate measurements for factors ("direct gradients") which have a direct effect on the growth and survival of species.

d. That many ecological biogeographical studies (Poynton 1964; Stuckenberg 1969; Bowmaker et al. 1978; Austin et al. 1984; Guillet & Crowe 1986; Palmer & van Staden 1992 and others) have placed emphasis on temperature and moisture gradients (or surrogate measurements of these two parameters) in the analysis of distribution patterns of plants and animals. The general consensus therefore appears to be that temperature and moisture gradients are of paramount importance in limiting the distribution of species.

e. That the hydrology of most rivers in southern Africa has been altered due to the building of impoundments, water abstraction, inter-basin transfers and flow regulation. Many rivers are also degraded due to industrial and organic pollution and excessive soil erosion. Alterations in flow regimes may impact on temperature regimes in rivers.

With these points in mind, the basic objectives, assumptions and limitations in the present study are described below:

a. In attempting to predict the potential distribution of alien species in freshwater ecosystems, it would clearly not be possible to consider all aspects of the biotope. It therefore becomes necessary to restrict the level of predictability to a consideration of the most important limiting factors which affect the distribution of species.

b. The objective of the present study is to characterise the different regions of southern Africa in terms of temperature regimes and water availability. It is assumed that these two parameters are factors of primary importance in limiting the distribution of aquatic animals. A more detailed description of the objectives of studies using the traditional and GIS approaches is given at the end of Section 3.3.

c. The predictability of the resultant biogeographical models is therefore also confined to an assessment of the above two parameters only. For example, if the model were to demonstrate that a certain region is susceptible to invasion by alien species with particular requirements in terms of temperature and water availability, this would not mean that the full spectrum of habitat requirements of the candidate species had necessarily been satisfied. The model would merely indicate a potential susceptibility to invasion by species with particular habitat requirements.

d. The corollary of (c) is that the negative image of the predictive models would provide a model of regions where species with particular habitat requirements would have very little chance of surviving.

e. The present study is based on the assumption that the distribution of alien species which have been widely introduced into many different catchments can be used as an indicator of prevailing conditions. To justify this assumption it is necessary to demonstrate that indicator species have had the opportunity of invading most of the major drainage regions in southern Africa. This is dealt with in Section 3.2.3.

f. Man's alterations to the hydrology of inland waters in southern Africa has an impact on the water availability and temperature characteristics of rivers. Since these parameters are used as a basis for drawing up predictive models in the present analysis it is important to be aware of this problem when designing methodologies and interpreting results. This problem is therefore dealt with in more detail in discussions on methodologies used (Chapters 4 & 5) and in the final discussion on results (Chapter 6).

3.2. INDICATOR SPECIES USED IN THE ANALYSIS: THEIR TEMPERATURE TOLERANCES AND DISTRIBUTION RECORDS

3.2.1. Temperature tolerances - definitions of terms

Based on records from de Moor & Bruton (1988) certain alien species which have been widely introduced into many catchments in southern Africa were chosen as indicator species. Table 2 lists these species as well as their temperature tolerance ranges.

In order to carry out biogeographical analyses on distribution patterns of alien species in southern Africa, it was necessary to classify indicator species according to their tolerance to temperature and water-availability conditions. In this context the following definitions are proposed:

Warm stenothermal species: Most "aquarium" species fall into this category. Innes (1966) describes the "tropical" aquarium fishes as generally having a range of tolerance of 21.1° - 26.7 °C, but easily being able to tolerate a drop in temperature to 18.3°C for short periods. These species do not generally tolerate temperatures below 15.6°C.

Warm mesothermal species: prefer warmer waters above 25°C, but are able to tolerate cooler temperatures (to as low as 15.6°C) for short periods. Certain hardy aquarium fish such as *Poecilia reticulata* which can tolerate temperatures in the range of 15.6° - 37.8°C (Innes 1966) would fall into this category.

Eurythermal species can tolerate temperatures below 8°C and have an upper lethal temperature of above 34°C.

Cold stenothermal species. Fish in this category have an upper lethal temperature of below 28°C (Varley 1967). Optimum temperatures for growth are between 7° and 17°C and, for spawning, less than 10°C.

Eurytopic species: tolerate a wide range of extreme environmental conditions, including extreme temperature regimes.

Table 2. Temperature tolerances of species used as indicators in the present analysis.

Species	Temperature tolerance	Reference
Cyrtobagous salviniae	Prefers warm waters. Min. tolerated = 19°C	Thomas & Room (1986)
Hardy aquarium fish (*Poecilia reticulata* & *Xiphophorus helleri*)	Optimum 22°- 24°C Optimum 21.1°- 26.7°C. Lower lethal limit for *P. reticulata* about 15.6°C.	Sterba (1962) Innes (1966)
*Trout (*Oncorhynchus mykiss* & *Salmo trutta*)	Optimum 16°-18°C Detrimental effects at > 21°C. Max. for normal behaviour 24°C. Tolerate up to 30°C for very short periods.	McVeigh (1979a) Hey (1971)
Cyprinus carpio	Optimum: 20-30°C Survives in range 3.3°- 35.6°C	Safriel & Bruton (1984) Hey (1971)
***Lepomis macrochirus*	Broad native range indicates wide temperature tolerances	Scott & Crossman (1973)
Micropterus dolomieu	Optimum 25°C Survives in range from 4° - 35°C	McVeigh (1979b)
M. salmoides	Optimum at 28°C Survive in range from 5° - 36°C	Hey (1971)

* Various strains of the two species of trout have slight differences in temperature tolerance ranges. It is felt that these differences are not significant to biogeographic studies which deal with broad distribution patterns. It was therefore decided that a general outline of the broad temperature requirements of trout would be sufficient for the present analysis.

***L. macrochirus*: The native range of this species extends from the St Lawrence River in Canada southwards to Florida and northeastern Mexico (Scott & Crossman 1973), indicating a broad range of tolerance to temperature.

According to the above definitions, the alien species listed in Table 2 were classified into the following categories:

Warm mesothermal species: *P. reticulata*, *X. helleri*, *C. singularis* and *C. salviniae*.

Cold stenothermal species: *Oncorhynchus mykiss* and *Salmo trutta*.

Eurytopic species: *C. carpio*, *M. dolomieu*, *M. salmoides* and *L. macrochirus*.

The classification of the latter species into the "eurytopic" rather than "eurythermal" category was made because the former term refers to the species' tolerance to a wide range of abiotic conditions including temperature. Since only the most tolerant, eurytopic species would be able to withstand the extreme conditions prevailing in unstable waterbodies of arid environments, this term was used in preference to the term "eurythermal".

3.2.2. Geographic region covered by the analysis, and methods used to collect distribution records

Figure 9 illustrates the geographic region covered in this thesis.

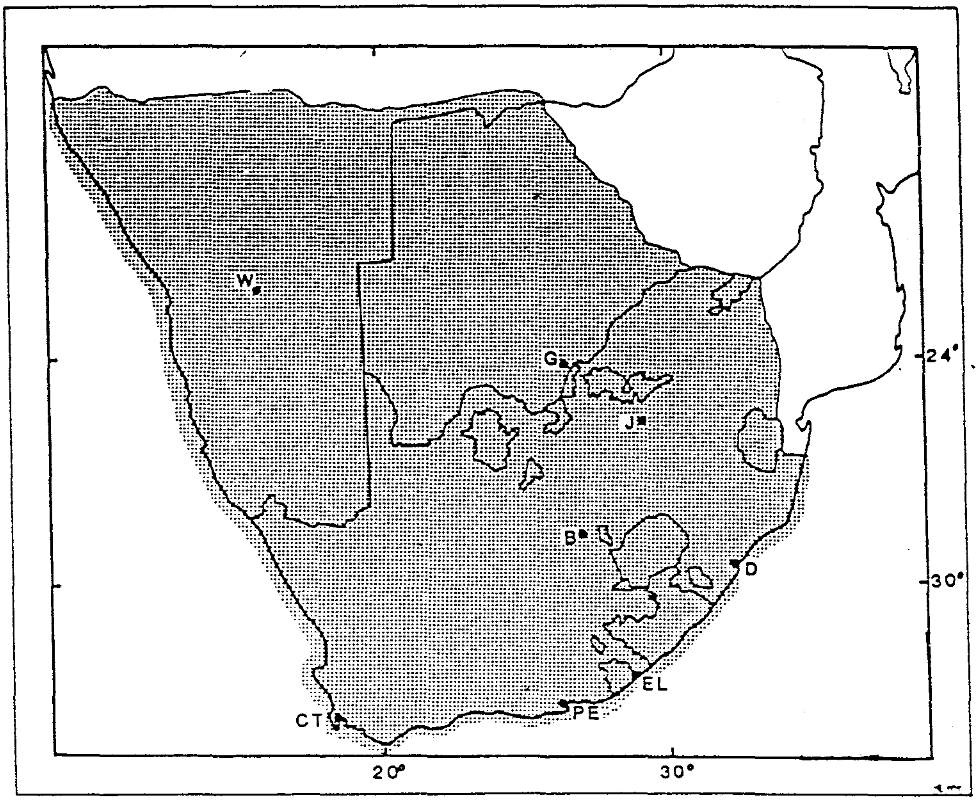


Figure 9: Map of southern Africa showing the geographical area covered by this thesis.

For the purpose of the first analysis using "traditional methods", distribution records for indicator species were based on records obtained from de Moor & Bruton (1988), Schrader (1985), Albany Museum Records (J.A. Cambray pers. comm.), the Jonkershoek Fishery Research Station (A. Smith pers. comm.) and the Department of Ichthyology and Fisheries Science (M.T.T. Davies pers. comm.). Only the precisely-determined and verified "point locality" records of de Moor & Bruton (1988) were used in this analysis and all "approximate" locality records were ignored.

For the purpose of the GIS analysis, detailed distribution records of trout were obtained for selected regions of southern Africa from nature conservation officials and other suitably-qualified people who are familiar with the finer details of trout distributions in their particular regions. The method employed to obtain these records is outlined in more detail in Chapter 5.

3.2.3. Regions where indicator species have been introduced

Many introductions have taken place which are not recorded in the literature. The presence of a species in a river does however indicate that it must have been introduced some time in the past. The distribution of indicator species is described below with reference to the principle drainage regions in southern Africa (Fig. 3).

The predictive region of the biogeographical models drawn up in this thesis (Fig. 9) is more extensive than that shown in Fig. 3 since the latter excludes the Okavango region and Namibia. The introduction of alien species into these regions will be considered in the discussions on each category of species below.

Warm-mesothermal species

While there are definite records of the introduction of *Cyrtobagous salviniae* and *C. singularis* into the Okavango region (de Moor & Bruton 1988), there are no definite records of the releases of the two species of aquarium fish, the guppy (*Poecilia reticulata*) and the swordtail (*Xiphophorus helleri*) in southern Africa. It should be noted however that these two species are extremely popular aquarium fish. The annual retail value of sales of tropical fish in South Africa was estimated to be approximately R10.1 million in 1987 (Andrews 1989). Considering that a large proportion of the trade is accounted for by the more popular species such as guppies and swordtails which sold at a retail price of approximately R2-00 to R3-00 per fish in 1987 (Andrews pers. comm.) it is clear that the above trade figures represent a very large number of guppies and swordtails which are sold in pet shops around southern Africa. When one considers that aquarium hobbyists frequently release unwanted pets into natural waters (McKay 1984) it is likely that large numbers of guppies and swordtails are released in southern Africa on a regular basis. It seems highly probable therefore that these two species have had the opportunity to invade most natural waters in southern Africa except perhaps in the less developed, sparsely populated areas in the western region of the country bounded by 32°S and 23°E.

From the above discussion the assumption is made that *P. reticulata* and *X. helleri* have been released into all the major drainage regions in South Africa except the lower Orange, which is part of the Orange River catchment (Fig. 3: Region D). It is also unlikely that these two species have had the opportunity to invade the Okavango region. Other warm mesothermal species (*Cyrtobagous salviniae* and *C. singularis* have however been released into this region (de Moor & Bruton 1988).

Cold stenothermal indicator species

A detailed account of the drainage regions where the two selected species (*Oncorhynchus mykiss* and *Salmo trutta*) have been released, is given in Appendix 1. This summarises the regions in which there are definite records of stocking of the species in the river (de Moor & Bruton 1988) as well as regions where the presence of the species indicates that they must have been introduced at some time in the past.

Appendix 1 indicates that there is a certainty that trout have been introduced into all principle drainage regions in the country except the Sundays catchment and the West Coast regions. Considering the extremely widespread introduction of trout throughout the country it is likely that unrecorded introductions have been made into the Sundays catchment sometime in the past. It is unlikely that trout would ever have been introduced into the West Coast drainage region (Region F, Fig. 3) or into the Okavango drainage region and Namibia (not illustrated in Fig. 3).

Eurytopic species

A summary of the river systems where there are either records of introductions or present-day locality records is given in Appendix 2.

Appendix 2 indicates that at least one of the four indicator eurytopic species has been introduced into every major drainage region in southern Africa shown in Fig. 3 except the west coast region. De Moor & Bruton (1988) note that none of the four eurytopic indicator species have been introduced into the Okavango region, but there have been numerous introductions into Namibia (Schrader 1985).

3.3. APPROACHES TAKEN IN THE PRESENT ANALYSIS

While it may be widely recognized that temperature and moisture are very important limiting factors influencing the distribution of the biota, a number of problems arise when attempting to use these parameters in biogeographical analysis. Although extensive data have been collected by various environmental monitoring agencies (e.g. the South African Department of Water Affairs) on water flow and temperature characteristics of inland waters, certain problems arise when attempting to use these data for geographical analysis:

a. The geographer may have a problem in deciding which parameter to use in analysis. In the case of temperatures in freshwaters, minima and maxima are seldom available since this would require sophisticated equipment which could record 24-hour recordings at numerous sites.

b. Datasets on water quality, such as those of the South African Department of Water Affairs (DWA), are generally based on information collected at selected measuring weirs on rivers or at selected sites in impoundments. While a large amount of time-series and point-locality data are available (Hughes pers. comm.), this information has not been interpolated so as to present a continuous series, as is the case for the CCWR database on MAR and elevation (Hughes, pers. comm.). It may not be possible to interpolate water-related data (Hughes pers. comm.) Thus the datasets on water quality, even if quite comprehensive, are at present available in a large, cumbersome, disaggregated format which is difficult to use as a basis for biogeographical analysis covering large regions.

Considering the points above, most biogeographers find it necessary to make use of surrogate measurements or aggregate data when analysing distribution patterns of biota on a small scale. One approach (adopted by Poynton 1964 and Austin et al. 1984) is to use the information which is readily available to prepare biogeographical models. The relationship between various direct and indirect environmental variables and species distribution patterns may not be fully understood. Poynton (1964) notes that (mean-midwinter surface) isotherms should be regarded as "reliable climatic indicators, summarising a climatic complex that appears to be decisive in limiting the distribution of amphibians."

In the present study both the "traditional" (data-poor) approach and the "GIS" (data-rich) approach have been used to prepare biogeographical models capable of predicting the potential distribution of alien species in southern Africa. In both instances the approach is to compare the distribution patterns of selected alien aquatic animals (see section 3.2.1) to various geographical parameters. Based on such comparisons, predictions of the potential regions of invasion of alien species are made. The main difference in the two approaches is in the nature of the data-base used in the analyses. In the traditional method, maps which are the result of previous biogeographical models of distribution patterns of plants and animals, are used as a basis for comparison. In the GIS approach, distribution patterns of alien species are compared to a computerised dataset of elevation and Median Annual Rainfall (MAR) at a minute x minute resolution.

The objective of the first approach is to draw up a map describing the regions of the country which are susceptible to invasion by alien warm mesothermal species, cold stenothermal species and eurytopic species. The main shortcoming of this method is that the validity of the resultant model is difficult to assess.

The objective of the GIS analysis is to test a new approach towards predicting potential distribution patterns of species. In this instance, predictions of trout distribution in selected regions of the southern Africa are prepared. Since trout distribution in certain regions of the predictive models are well known, it is possible to test the validity of the predictions using independent data.

CHAPTER 4: BIOGEOGRAPHICAL MODELLING USING "TRADITIONAL" METHODS

4.1. METHODS

4.1.1. Approach

The basic approach to the methods was outlined in the previous chapter. A more detailed description of the method using the "traditional" approach is given below:

1. The distribution of alien aquatic "indicator" species (see section 3.2) is compared to a number of maps which are descriptive models of temperature and water-availability regimes in southern Africa. These maps are described below:

a. Maps illustrating the dry and moist regions of southern Africa.

b. Maps illustrating the distribution of certain temperature-sensitive species.

c. A number of biogeographical models drawn up to describe the distribution patterns of various groups of animals in southern Africa. The biogeographical studies chosen for this purpose were selected according to the following criteria:

* Only ecological biogeographical studies were chosen, in which the model attempted to describe the way in which <u>prevailing conditions</u> limited distributions of species.

* Temperature and moisture regimes were the most important parameters used as a basis for drawing up the biogeographical models.

* With one exception, only studies based on an analysis of the distribution patterns of aquatic or semi-aquatic animals were chosen.

2. On the basis of the comparisons described above, the parameters which gave the "best fit" to the observed distribution patterns of the alien indicator species were chosen. These were used as a basis for drawing up a predictive model characterising regions of southern Africa in terms of temperature regimes and water-availability conditions. These criteria were then used

to predict which regions would be susceptible to invasion by alien aquatic animals with particular habitat requirements.

4.1.2 Biogeographical models chosen for the analysis

Based on the criteria outlined in the previous paragraph, the following biogeographical models were chosen for comparative purposes in the present analysis:

1. Indices of water availability: Arid and moist regions as defined by Balinsky (1962) and models of avifaunal zones and hypothetical waterbird refugia as defined by Guillet & Crowe (1986).

2. Distribution of bilharzia vector snails based on distribution maps of Brown (1978, 1980).

3. Zoogeographical zones described by Poynton (1964), Stuckenberg (1969) and Bowmaker et al. (1978).

Since the distribution patterns of terrestrial animals (mainly snakes) formed the basis for Stuckenberg's (1969) analysis, this study does not strictly follow the criteria for choosing suitable biogeographical models as set out in section 4.1.1.. It should be noted, however, that Stuckenberg's map shows the distributions of effective (air) temperatures which he found to be of particular significance in limiting the distribution of species. It was felt that the use of this map could be justified on the basis that air temperature is a reasonable surrogate measurement for water temperatures.

4.1.3. Procedure

Step 1

The distributions of "indicator" alien species from the three categories described in the previous chapter (section 3.2.1) were compared to the biogeographical indices described above. In each instance three maps were depicted on which the distribution records from each of the three categories of alien "indicator" species was superimposed. The distribution of warm mesothermal species was indicated on all maps labelled "a", cold stenothermal species on maps labelled "b", and eurythermal species on maps labelled "c" (Figs 10 - 16).

In making these comparisons it was necessary to make certain modifications to the maps used as biogeographical indices:

a. It was necessary to draw all maps on the same scale. This entailed modifying the projection of certain maps and was carried out by Mr O. West, Senior Cartographer, Geography Department, Rhodes University) (Figs 10 - 16).

b. Distributions of bilharzia-vector snails: Distribution records of *Biomphalaria* and *Bulinus* obtained from Brown (1978, 1980) were drawn on a composite map (Fig. 13).

c. In the map illustrating effective temperatures (after Stuckenberg 1969) the only temperature isolines illustrated were those which Stuckenberg found to be of significance in influencing the distribution of species (i.e. the 15°C, 16°C & 18°C ET isolines) (Fig. 15).

Step 2

Each of the above comparisons was examined closely and the "best-fit" maps selected as a basis for compiling a new model indicating the potential regions in which alien species with particular habitat requirements may survive according to temperature and water-availability requirements. The criteria used to draw up this map are discussed in the following section.

4.2. RESULTS

The comparison between the distribution of alien species and the bioclimatic indices discussed above is illustrated in Figs 10-16 (a,b,c) and summarised in Tables 3 & 4.

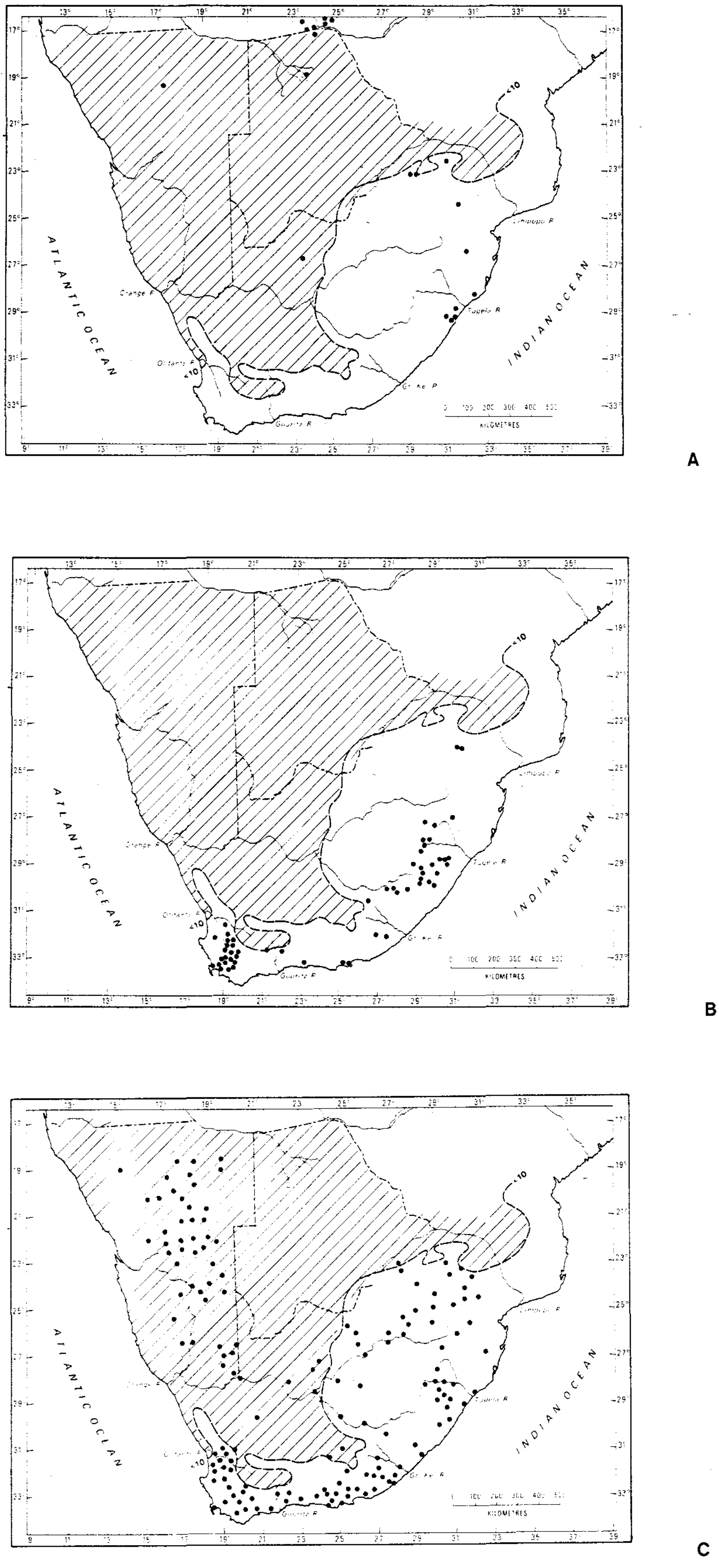


Figure 10: The "drought corridor" of southern Africa (after Balinsky 1962) compared to the distribution of warm mesothermal (a), cold stenothermal (b) and eurytopic (c) alien "indicator" species. (The shaded region represents areas were rainfall is less than 10 mm for at least three consecutive months of the year).

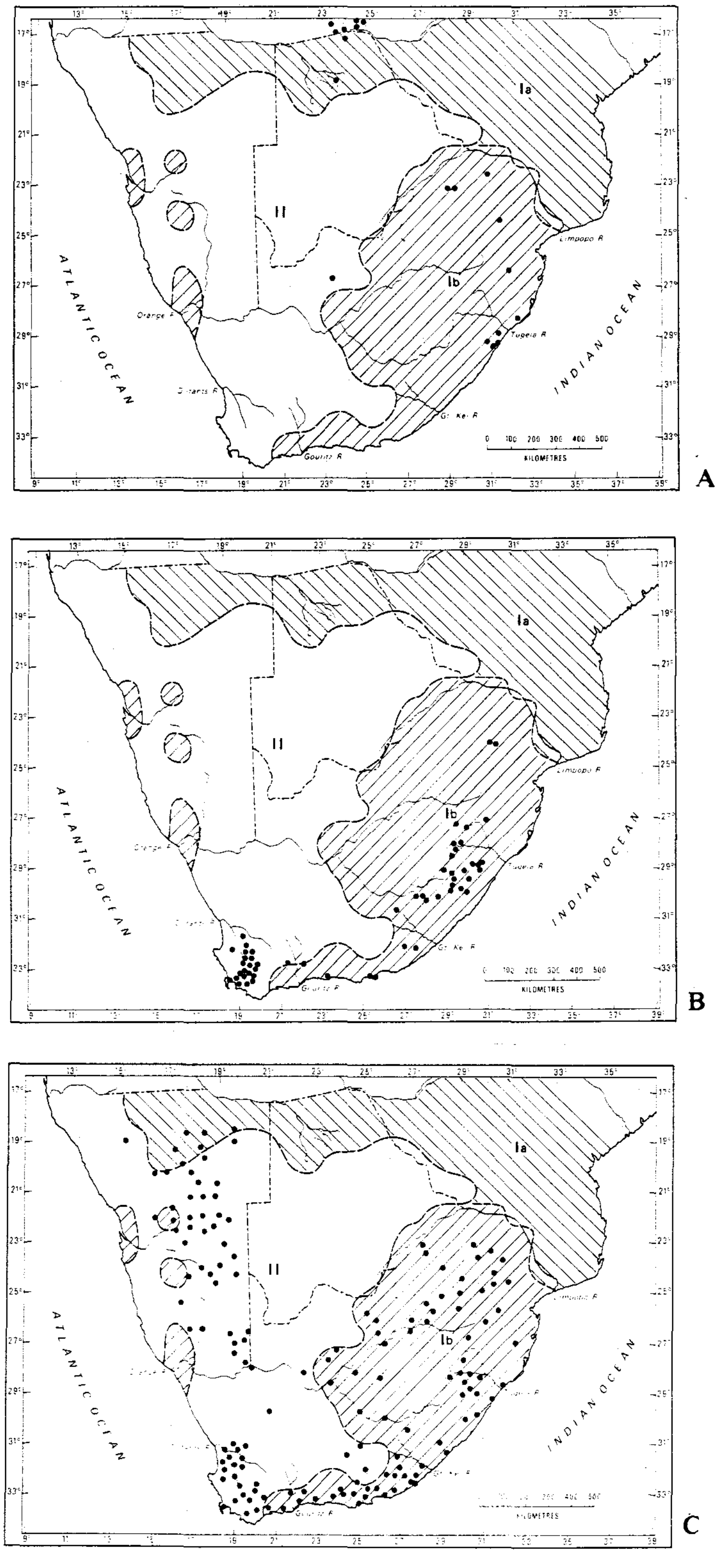


Figure 11: Southern African avifaunal zones for resident waterbirds (after Guillet & Crowe 1986) compared to the distribution of warm mesothermal (a), cold stenothermal (b) and eurytopic (c) alien "indicator" species in southern Africa. The shaded region represents the moist east-north zone, and the unshaded region represents the dry western zone.

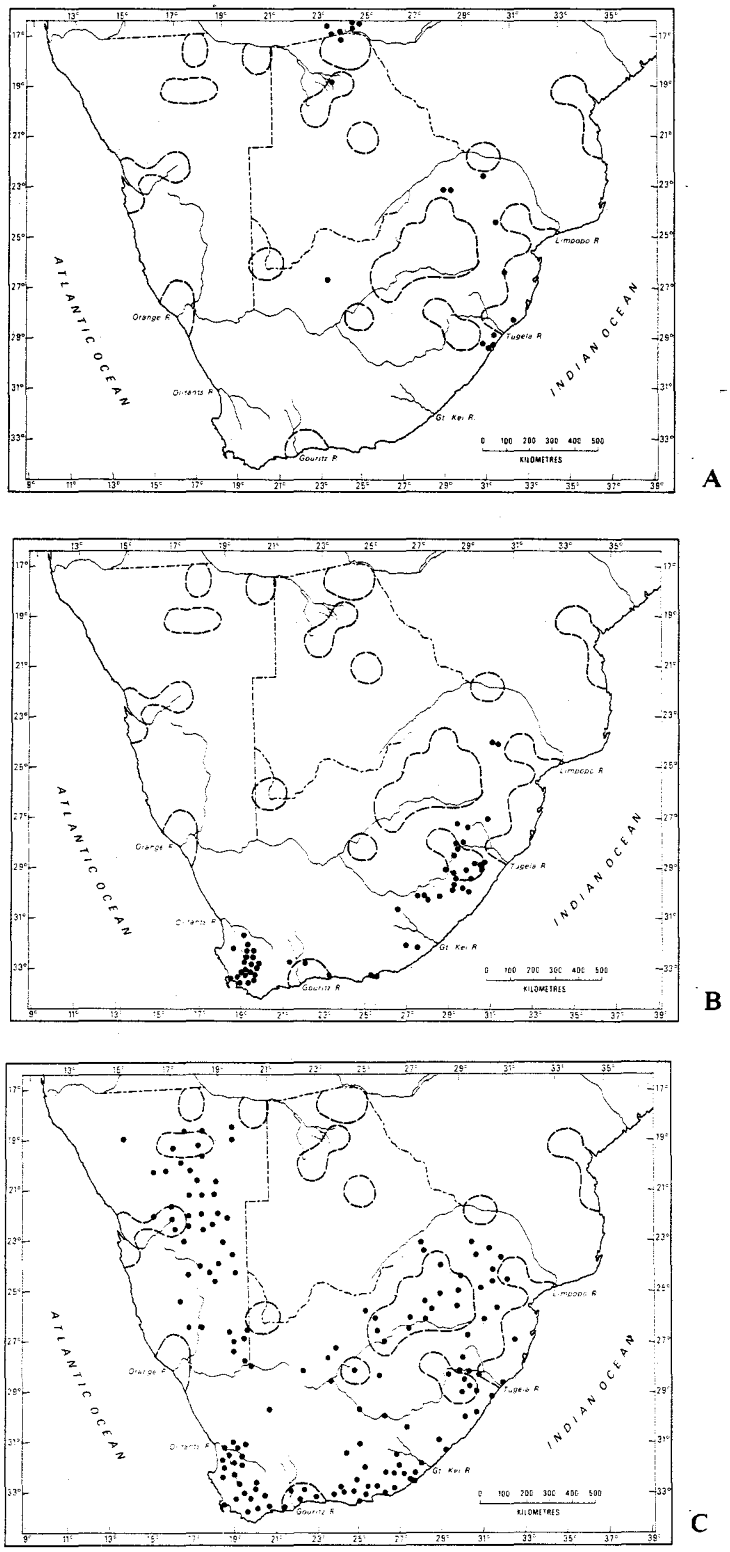
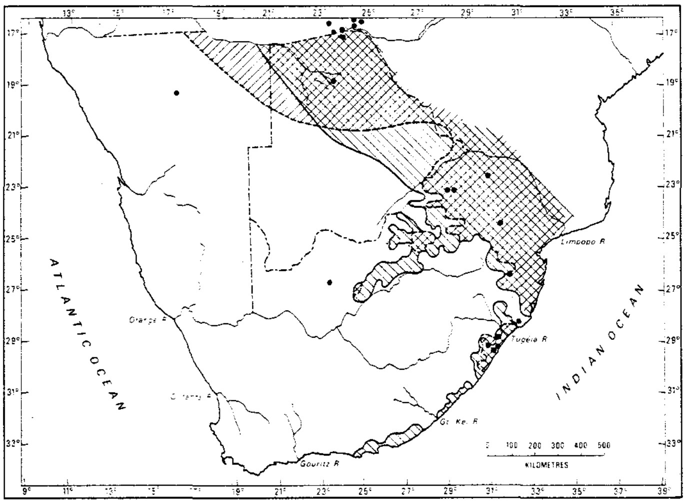
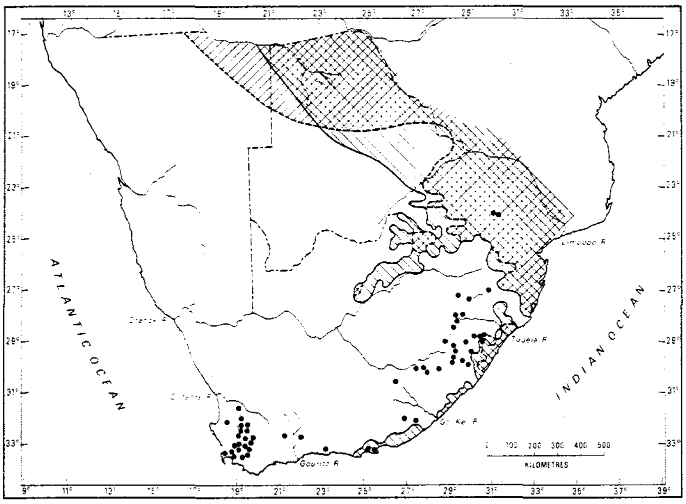


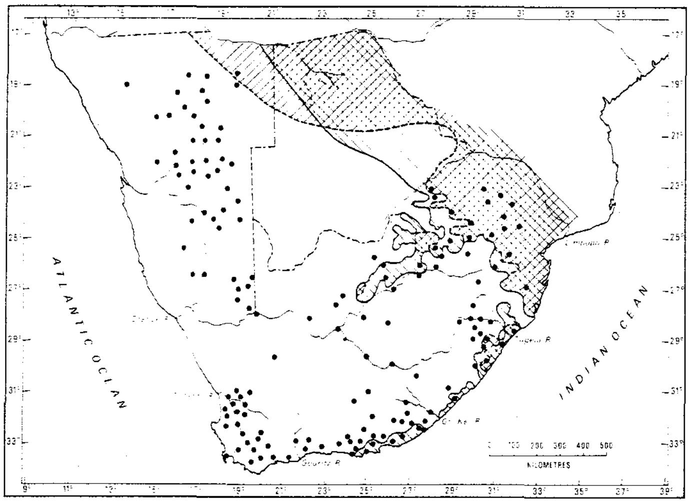
Figure 12: Hypothetical water bird refugia during dry climatic phases (after Guillet & Crowe 1986) compared to the distribution of warm mesothermal (a), cold stenothermal (b) and eurytopic (c) alien "indicator" species in southern Africa.



A



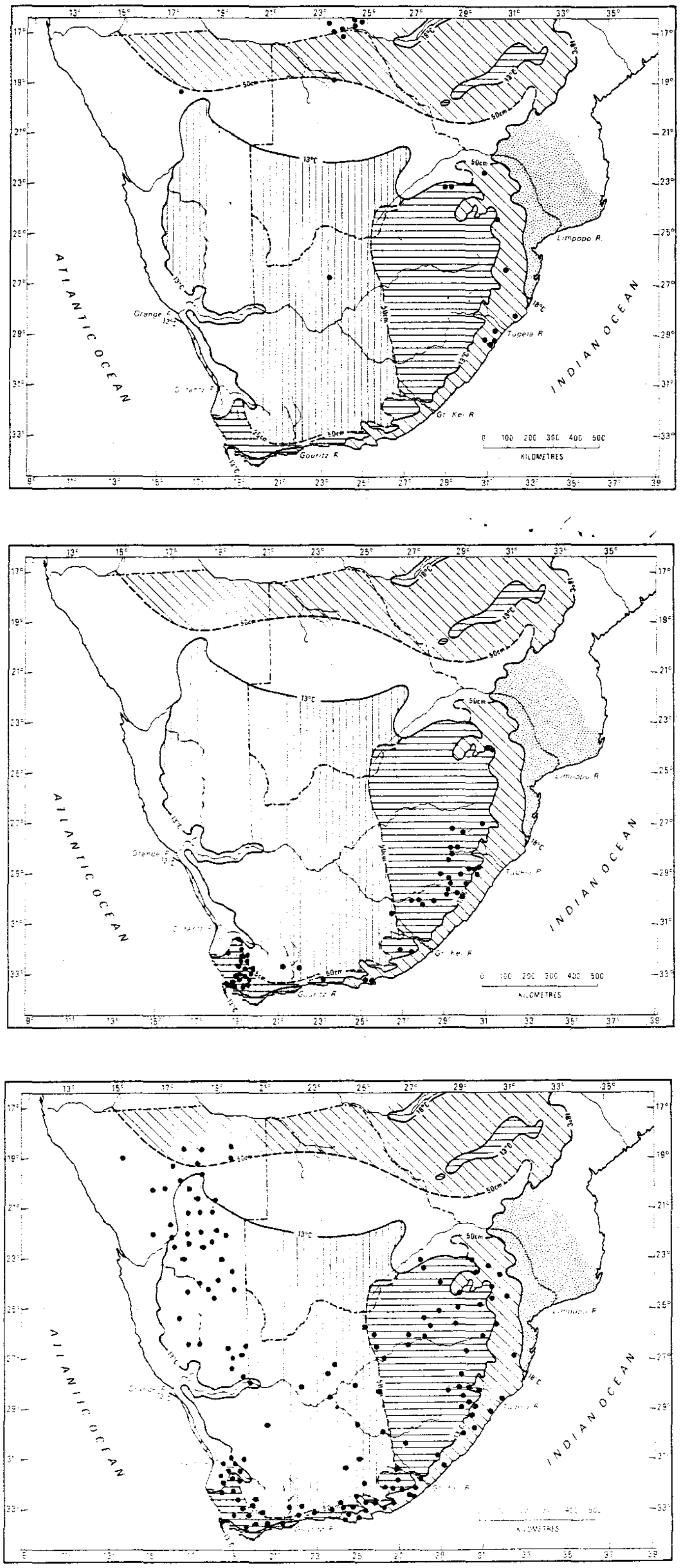
B



C

Figure 13: Distribution of bilharzia-vector snails, *Bulinus* spp. and *Biomphalaria* spp. compared to the distribution of warm mesothermal (a), cold stenothermal (b) and eurytopic (c) alien "indicator" species in southern Africa (after Brown 1978, 1980).

Biomphalaria spp. distribution   *Bulinus* spp. distribution



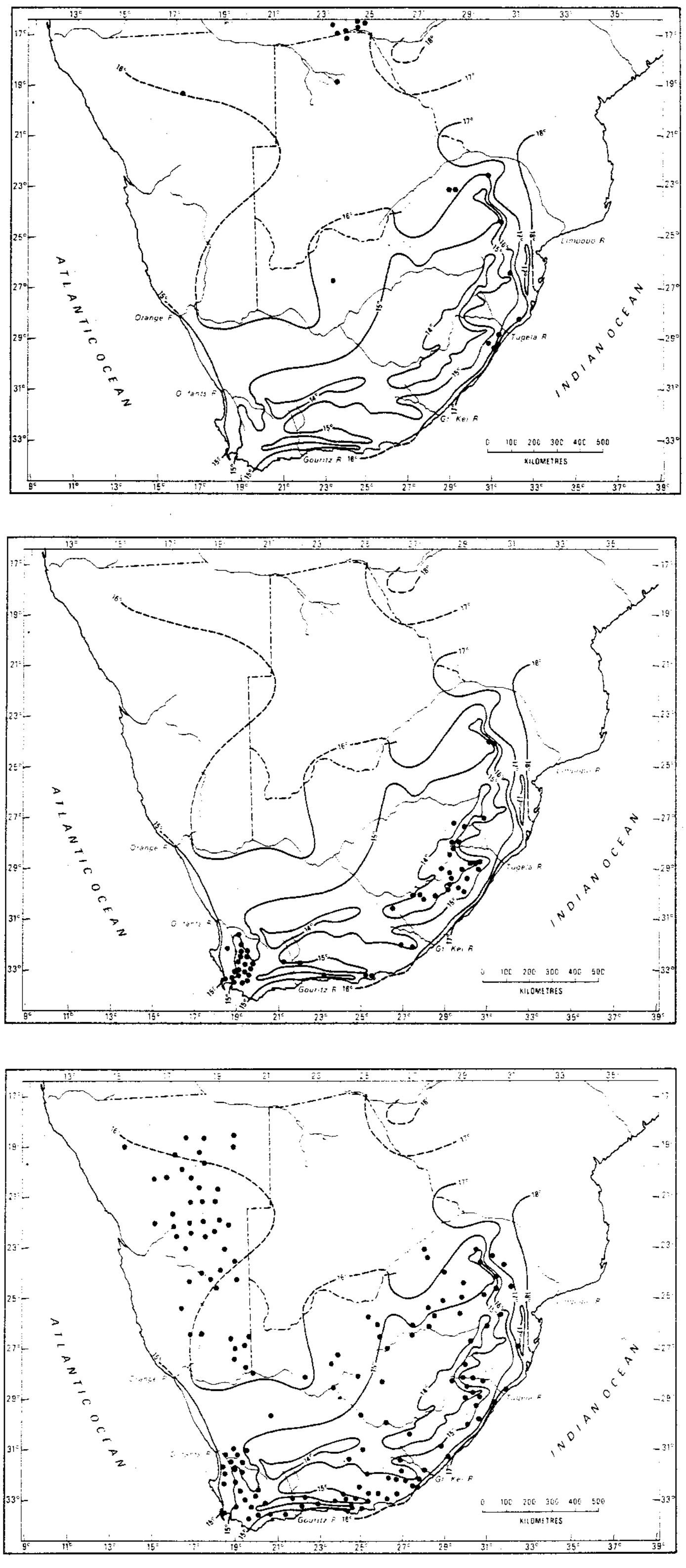
A

B

C

Figure 14: The biotic divisions of southern Africa (after Poynton 1964) compared to the distribution of warm mesothermal (a), cold stenothermal (b) and eurytopic (c) alien "indicator" species in southern Africa.

Temperate western (arid): Annual rainfall <500mm	Temperate eastern (moist): Annual rainfall >500mm
Sub-tropical arid	Sub-tropical moist
Temperate southern	Tropical moist
Mean July isotherm	---- Annual isohytes

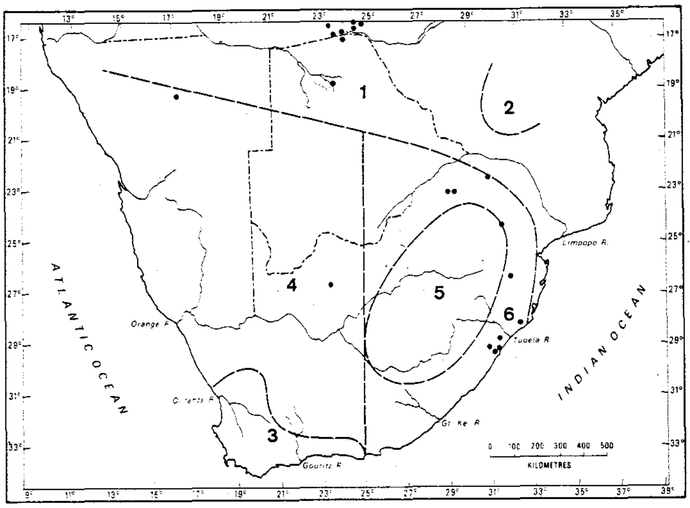


A

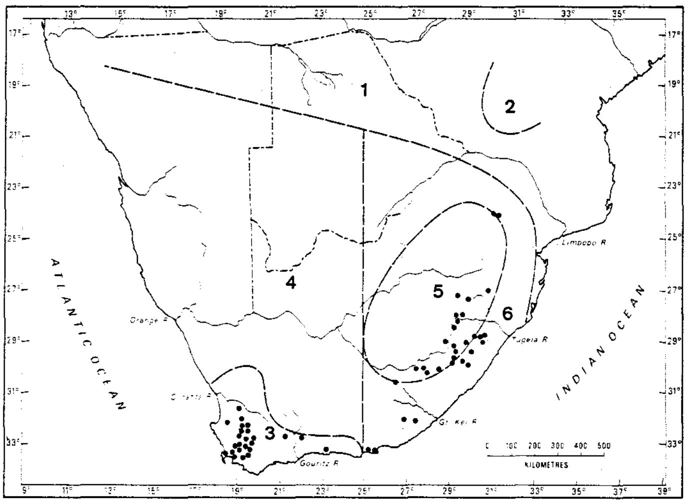
B

C

Figure 15: Effective temperature map (after Stuckenberg, 1969) compared to the distribution of warm mesothermal (a), cold stenothermal (b) and eurytopic (c) alien "indicator" species in southern Africa.



A



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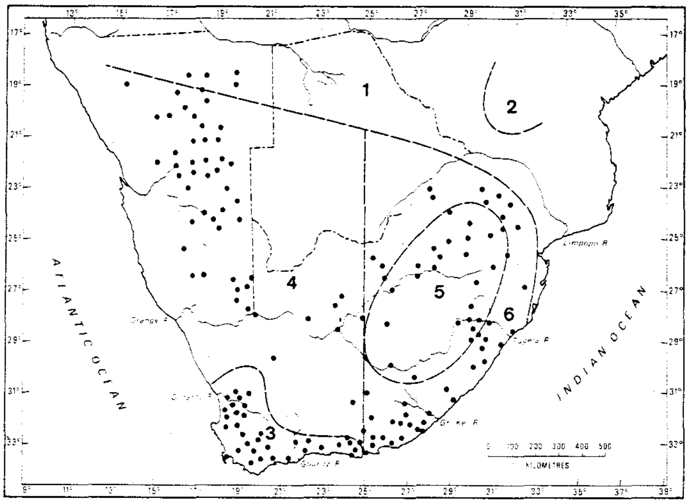

C

Figure 16: The bioclimatic zones of southern Africa (after Bowmaker et al. 1978) compared to the distribution of warm mesothermal (a), cold stenothermal (b) and eurytopic (c) alien "indicator" species in southern Africa.

Legend. Zone 1 - summer rainfall zone;
Zone 2 - summer rainfall - temperate highlands;
Zone 3 - Winter rainfall - temperate;
Zone 4 - semi-arid to arid zone;
Zone 5 - Lesotho highlands - temperate;
Zone 6 - Transition zone. Tropical to temperate climate.

Table 3. Summary of comparisons made (Figs 10 - 13) between the distributions of alien aquatic "indicator" species and various climatic indices (indicating aridity and the distribution of indigenous warm mesothermal species).

Climatic indices	Warm mesothermal species	Cold stenothermal species
a. "Drought corridor" map (Balinsky 1962) (Fig. 10)	Present in "dry" areas in Okavango/Chobe region and isolated localities in Namibia, Botswana and N Cape	Virtually no overlap with "drought corridor"
b. Avifaunal zones (Guillet & Crowe 1986) (Fig. 11)	Present in moist regions in the south, east and north.	Trout present in south western Cape region within the arid western avifaunal zone.
c. Hypothetical waterbird refugia (Guillet & Crowe 1986) (Fig. 12)	Little correlation	Little correlation
d. *Biomphalaria* and *Bulinus* distribution (after Brown 1978) (Fig. 13)	Close correlation with *Biomphalaria* distribution except at Lake Otjiokoto	Little overlap of distribution, except for a small intrusion into *Bulinus* range in the SE Cape coast

Table 4. Summary of the distribution patterns of alien aquatic "indicator" species in relation to various zoogeographic classification systems (illustrated in Figs. 14 - 16).

Classification system	Warm mesothermal species	Cold stenothermal species
Poynton (1964) (Fig. 14)	Predominantly in the sub-tropical moist region. Small intrusion into temperate eastern region and isolated record in Temperate western region.	Very close correlation with the temperate eastern region and southern Cape regions. Some intrusion into the temperate western (arid) region.
Stuckenberg (1969) (Fig. 15)	Most species excluded from areas colder than 16°C ET isoline. Few records in transition zone between 15°and 16°C ET. No records in regions colder than 15°C ET.	Most records lie within regions colder than 15°C ET. Some intrusion into region betwen 15°and 16°C iso-lines. No records in regions warmer than 16°C isoline
Bowmaker <u>et al</u> (1978) (Fig. 16)	Confined to regions 1 and 6. Isolated records in region 4.	Predominantly in regions 3, 5 and south of region 6.

4.2.1. Distribution patterns of alien eurytopic species

It is remarkable that eurytopic alien species have been successful in establishing populations in small, unstable waterbodies in many arid regions of the subcontinent (Fig. 10c & 11c) and appear to have colonised nearly every zoogeographical region in southern Africa (Figs 14c, 15c and 16c). Instead of considering the regions where these species occur, it is probably more pertinent to examine the areas where they have not been recorded in natural waters. A lack of opportunity to invade the Okavango swamps accounts for the absence of alien eurytopic species in this region. Only a few isolated occurrences of alien eurytopic species have been recorded in the north-east of the subcontinent which extends from the mainstream Limpopo in the north, includes the lower Incomati system, Lake Sibaya and the Phongolo floodplain, and extends south as far as the Mkuzi and Mfolozi systems. There have been numerous opportunities for certain eurytopic species (e.g. *Cyprinus carpio* and *Micropterus salmoides*) to invade most of the rivers in this region, particularly the Limpopo, Incomati and Phongolo systems (de Moor & Bruton 1988) (Appendix 2).

As discussed in Chapter 2 there is a large body of literature suggesting that undisturbed, species-rich ecosystems are less susceptible to invasion by alien species than species-poor, disturbed ecosystems. It is likely that biotic factors could have played an important role in excluding alien species from the species-rich waterbodies in the eastern Transvaal and north-eastern Natal. This is however a complex question, which is beyond the scope of the present analysis.

Because alien eurytopic species have such wide tolerances, they occur in many different zoogeographical zones and their distribution is not a sensitive indicator of abiotic conditions in the study area. For this reason the distribution of this group will not be considered further.

4.2.2. Distribution patterns of alien warm mesothermal and cold stenothermal species

Results of the comparison of the distribution of alien aquatic animals to various bioclimatic indices are given below:

a. Aridity

Warm mesothermal and cold stenothermal species are found predominantly in the moist regions of the country (Figs 10 a & b and 11 a & b) with a few notable exceptions: There are isolated records of warm mesothermal species within Balinsky's "drought corridor" (Fig. 10a, Table 3), but these are all in permanent waterbodies within the region (i.e. Lake Otjikoto in Namibia, Malopo Oog in the western Transvaal, and the Okavango region). Cold stenothermal species are not recorded anywhere within the drought corridor. This indicates that rainfall measurements (as described by Balinsky 1962) are useful in describing conditions in small waterbodies over large regions of the country, but notable exceptions must be made where permanent waterbodies are found within arid regions.

The presence of sensitive cold stenothermal species such as trout in regions defined as "arid" (Figs 11b and 14b), suggests that these classifications are not accurate representations of conditions in the aquatic environment of these regions.

Figures 12 a & b indicate that there is very little correlation between the distribution patterns of warm mesothermal and cold stenothermal species and the hypothetical waterbird refugia described by Guillet & Crowe (1986).

b. Distribution of temperature-sensitive indigenous species (Fig. 13 a & b, Table 3)

The distribution of warm mesothermal alien species is closely correlated with that of the subtropical freshwater snail genus, *Biomphalaria*, in southern Africa. There is a small region in the south-eastern Cape where warm mesothermal alien species are found beyond the range of *Biomphalaria*, but still within the range of *Bulinus* (Fig. 13a).

c. Zoogeographical classification systems

A summary of the zoogeographical regions colonised by alien species is given in Table 4. An examination of these data reveals that distribution patterns in the eastern moist regions of the sub-continent tend to broadly follow expected patterns. Warm mesothermal alien species are found predominantly in the sub-tropical moist region of Poynton (1964) (Fig. 14a), in regions warmer than the 16 °C ET isoline of Stuckenberg (1969) (Fig. 15a), and Zones 1 and 6 of Bowmaker et al. (1978) (Fig. 16a). Cold stenothermal species are found predominantly in Poynton's temperate eastern region (Fig. 14b), in regions colder than the 15 °C ET isoline (Stuckenberg 1969) (Fig. 15b), and in temperate Zone 5 of Bowmaker et al. (1978) (Fig. 16b). The region lying between Stuckenberg's 15°C and 16 °C ET isolines is a region of overlap between alien warm mesothermal and cold stenothermal aquatic species (Figs 15 a and b). As suggested by Stuckenberg (1969), this region is a transition zone of marginal suitability to both warm mesothermal and cold stenothermal species.

4.3. SYNTHESIS

As has already been discussed, there is a need for a predictive map indicating the areas of southern Africa which are vulnerable to invasion by alien aquatic animals. The present review of existing bioclimatic classification systems in terms of the areas invaded by alien species, provides a basis on which such a map could be constructed. The rationale behind the compilation of such a map (Fig. 17) is discussed below:

4.3.1. Criteria used in drawing up a model of regions of southern Africa susceptible to invasion by alien aquatic animals

Of all the bioclimatic indices examined (Section 4.1.2.), those used by Balinsky (1962) (Fig. 10: to describe drought zones) and Stuckenberg (1969) (Fig. 15: to describe thermal zones) correlated most closely with the distribution records of selected alien species (Tables 3 & 4). It was therefore decided to use these two studies as a basis for drawing up a map indicating the susceptibility of different regions to invasion by alien aquatic species. Thus aridity was defined according to Balinsky's (1962) "drought corridor" (Fig. 10). Temperature regimes in the eastern regions of the country were defined according to the 15°C, 16°C and 18°C ET isolines of Stuckenberg (1969) (Fig. 15). The arid region was further subdivided according to the following criteria:

a. The regions within the arid zone (as described by Balinsky 1962) which have been colonised by *Biomphalaria* and/or *Bulinus* are regarded as "semi-arid". These regions are indicated in Fig. 17 as shaded areas.

b. Regions within the drought corridor in which there is a permanent supply of water (e.g. the Okavango region and the Orange and Fish Rivers) are regarded as moist zones. These regions are indicated in Fig. 17 as stippled areas.

4.3.2. Description of synthesis map

On the basis of the above criteria the southern African subcontinent can be divided into a number of regions (Fig. 17) described below.

The regions illustrated in Fig. 17 are discussed below:

Zone A: Arid. As defined by Balinsky (1962).

Zone B: Semi-arid: As defined above (4.3.1).

Zone C: Large permanent waterbodies within arid region.

C1. Okavango/ Chobe region.

C2. Orange/Fish Rivers. Small permanent waterbodies such as Lake Otjikoto are not indicated on the map, but would also be placed in this category.

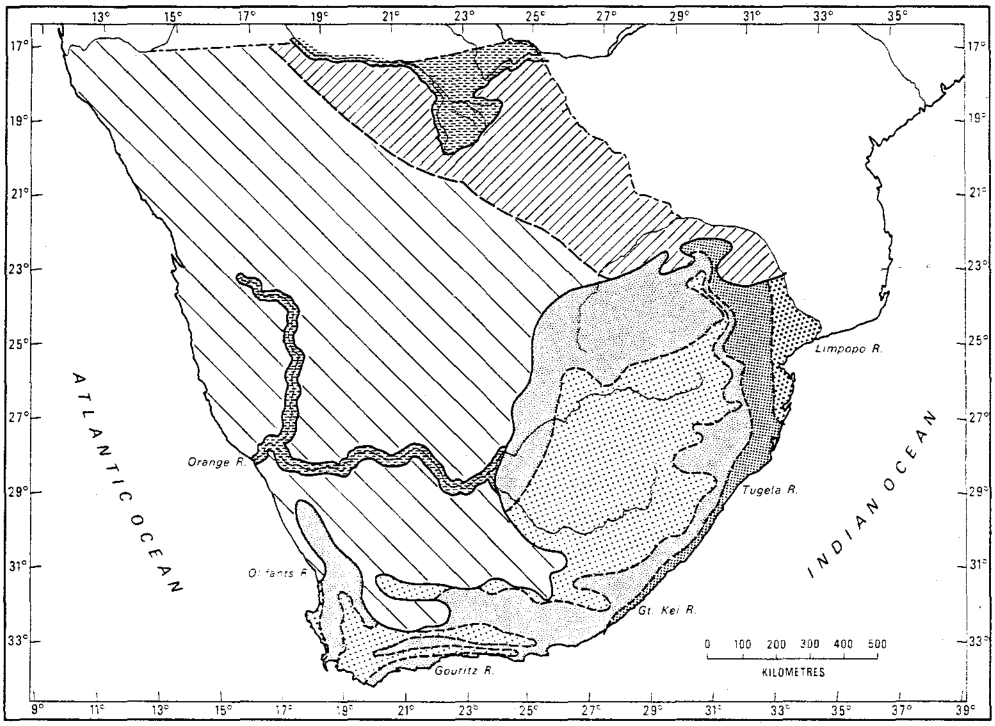

Figure 17: Regions in the study area which are susceptible to invasion by alien species with particular tolerances to temperature and aridity.

Zone A. Arid

Zone B. Semi-arid

Zone C. Large permanent waters within arid region

C1 - Okavango/Chobe region

C2 - Orange/Fish Rivers

Zone D. Moist tropical

Zone E. Moist sub-tropical

Zone F. Moist transition zone

Zone G. Temperate

Zone D: Moist tropical: Warmer than the 18°C ET isoline. This is a region in which no thermal winter occurs. Species unable to tolerate temperatures less than 18°C would be unlikely to survive in regions west and south of this isoline.

Zone E: Moist sub-tropical: Between the 16°C and 18°C ET isolines.

Zone F: Moist transition zone: This region is bounded by the 15°C and 16°C ET isolines. Although conditions may be sub-optimal, it is expected that both warm mesothermal and cold stenothermal species may be able to survive within this region. Severe cold winters or hot summers may result in the eradication of these species (respectively) from this region.

Zone G. Temperate: Cooler than 15°C ET isoline. Warm mesothermal species are not expected to survive in these regions.

The susceptibility of the above regions to colonisation by alien species is summarised in Table 5.

Table 5. The regions (illustrated in Fig. 1) susceptible to colonisation by by different categories of alien aquatic animals.

	Zoogeographical subregions							
Species categories	A	B	C1	C2	D	E	F	G
Warm stenothermal			X		X	M		
Warm mesothermal			X	X	X	X	M	
Hardy warm meso-thermal	M	X	X	X	X	X	M	
Eurytopic	M	X	X	X	M	X	X	X
Cold stenothermal							M	X

M - Marginal
X - Likely to survive according to temperature requirements

It must be emphasised that even if prevailing temperature and rainfall conditions in the target environment appear to suit the habitat requirements of the species, other requirements such as the flow regime, water chemistry or suitable breeding sites, would also have to be satisfied in order for an alien species to establish a population in a new environment. Figure 17 is therefore meant as a guideline merely to indicate the areas of concern in which alien species may survive according to the temperature and aridity regimes.

4.3.3. Discussion

The following criticisms could be levelled at the Model of susceptible regions (Fig. 17).

1. The dataset used in the analysis is based on old information used by other workers in the field a number of years ago. Since the advent of computerised technology more detailed datasets have become available which offer the opportunity to draw detailed maps of a higher resolution.

2. In order to test the validity of the model it would be necessary to compare the predictive map (Fig. 17) to distribution records of a vast number of alien aquatic animals with particular temperature requirements that are present throughout the country. It is clear that this would not be possible.

3. The discontinuous nature of the boundaries between different regions depicted in the map is not an accurate reflection of reality. According to current theories on the response of organisms and communities to environmental gradients (see Chapter 2), it is more likely that there would be a gradual "clinal" change between different regions.

4. The predictive map has a poor resolution and is on a very small scale.

5. Other problems associated with "traditional" maps discussed in Chapter 2 apply to this model (Fig. 17). It has the shortcoming of being static and difficult to update.

In spite of the above criticisms, the model has certain merits that are often associated with "traditional" models.

1. It synthesises previous work and is easy to understand.

2. It may be particularly useful as a broad guideline to susceptible regions. Managers could use this map as a starting point before proceeding with a more detailed analysis on the susceptibility of particular regions to invasion by alien aquatic animals.

3. Considering the paucity of data on distribution records of alien mesothermal species, this model may be the only feasible option for predicting regions that are susceptible to invasion by these species.

CHAPTER 5: GEOGRAPHIC INFORMATION SYSTEM (GIS) APPROACH - METHODS

5.1. INTRODUCTION

5.1.1. General introduction

The principle objective of the GIS analysis is to test the method. Can the distributions of trout (*Oncorhynchus mykiss* and *Salmo trutta*) in certain regions be used as a means of predicting the potential distribution of trout in other regions of the country? Since these two species are used as indicators of prevailing conditions, it is important to have some knowledge of their habitat requirements in order to understand the factors which influence their distribution. For this reason the native ranges and habitat requirements of these two species of trout are reviewed in this chapter.

The general methodology and underlying assumptions have been described in Chapter 3. This chapter gives a more detailed account of the GIS analysis based on the concentration analysis described by Palmer (1991) and Palmer & van Staden (1992) (Chapter 2). In this approach distribution records of selected species are compared to various geographical parameters. Thus two types of data need to be collected:

a. Detailed distribution records of the indicator species (trout).

b. Geographical information (e.g. MAR and elevation).

This chapter deals with the following aspects of the data collection:

a. The choice of data and collection of data.

b. Underlying assumptions associated with the choice of data and methods used.

The factors influencing the choice of sampling regions and predictive regions in the models of the potential distribution of trout are also discussed.

In the analysis use is made of the CCWR dataset on Median Annual Rainfall (MAR) and elevation. Another approach is described in which air temperature records are used as an alternative to elevation as a surrogate measure of water temperatures. The method used to generate the air temperature dataset is described as well as modifications made to the concentration analysis procedure in order to use this dataset. Finally, the methods used to assess the validity of the models generated are also described.

The errors and shortcomings associated with the datasets and methodologies used are discussed in each section.

Since the emphasis of this part of the research is on the development of methods rather the generation of new information, the methods described here are subject to modification. Eight separate models were constructed to describe trout distributions, and in the process errors and shortcomings were identified and modifications made to improve and refine the methods used. The basic methods are described here and the results in Chapter 6.

5.1.2. Native ranges and habitat requirements of the two indicator species

5.1.2.1. Native ranges

Rainbow trout

The scientific name of this species has recently changed. It was previously known as *Salmo gairdneri* and later as *Parasalmo mykiss* (see Skelton 1986b). The species was recently renamed *Oncorhynchus mykiss* by Smith & Stearley (1989). The new classification means that the Asian trout species, previously called *Salmo mykiss*, which occurs north of the Amur River in the Othotsk Sea basin and on Kamchatka and Commander Islands (Lee et al. 1980), is now regarded as the same species as the previously-named "*Salmo gairdneri*".

The native range of rainbow trout therefore includes the area of East Asia described above as well as that of the previously-named *S. gairdneri* from the western United States. The *S. gairdneri* group ranges from the Kuskokwim River to Rio del Presidio, Durango in Mexico, along the Pacific seaboard of North America and inland to the rocky mountain region. Except for the northern and southern extremes of the range, anadromous populations occur in all coastal rivers (Lee et al. 1980).

There are numerous strains of *O. mykiss* that are known by a variety of common names, including the Kamloops trout of British Columbia, Canada, the *mykiss* group from Asia, the anadromous "steelhead" form, the redband trout, Nelson trout, Eagle Lake, Kern River, Shasta, San Gorgonio and Royal Silver. These strains represent inland populations from different regions of the native range. By selective breeding in hatcheries, various new strains with differing tolerances to temperature and other environmental conditions have also been isolated (McClane 1965).

Brown trout

Brown trout is indigenous to Europe as well as parts of north Africa and north-west Asia (Frost & Brown 1967). Since this is an anadromous species, "sea trout" are also found in the various seas of Europe and Asia from Iceland to Scandinavia, the White Sea and Cheshkaya Gulf in the north as well as in the Black, Caspian, Aral, Baltic, and North Seas, the English Channel and the Atlantic Ocean as far south as the Bay of Biscay. *Salmo trutta* also occurs in Corsica and Sardinia (Frost & Brown 1967) and Morocco (Crass 1969).

There are numerous subspecies of brown trout from different regions. The anadromous form is different from the landlocked "lake trout". These varieties and forms (previously classified as different species) are now regarded as the same species, *S. trutta* (Scott & Crossman 1973).

5.1.2.2. Habitat requirements

The various strains of the two species of trout often have slight differences in habitat requirements (including temperature tolerances). It is felt, however, that these differences are more the concern of workers dealing with the finer details of aquaculture and ecology. In biogeographical studies such fine differences are negligible when dealing with broad distribution patterns at a resolution of one minute of one degree. It was therefore decided that a review of the broad requirements of trout would be sufficient for the present analysis. This is summarised below:

Both rainbow trout and brown trout require cold, unpolluted, well-oxygenated waters (Bruton et al. 1982; Safriel & Bruton 1984).

Turbidity: Since trout are visual predators, they require clear waters (preferably to a depth of approximately 3 meters) in order to capture their prey (McVeigh 1979a). High siltation levels have an adverse effect on trout (Alletson 1985).

Temperature requirements: Optimum 16° to 18°C. Beyond 21°C oxygen transfer becomes difficult, and the maximum temperature which can be tolerated for short periods of time is 30°C. Spawning occurs in cold waters at 4°- 6°C. Eggs die if the water temperature exceeds 16°C (McVeigh 1979a; Crass 1986).

Oxygen requirements: Require very high oxygen levels for successful spawning and development of ova. Minimum lethal limit is 45% saturation (i.e. 4.5 ppm) at 17°C. The sublethal effects of low oxygen levels are sluggish movements, decreased metabolic rate and susceptibility to disease (McVeigh 1979a).

pH and carbon dioxide levels: In acid waters carbon dioxide exists in a free form and at high alkalinities it is bound as hydroxide ions. Carbon dioxide concentrations are thus closely related to pH levels in the water. Brown trout can normally tolerate pH values of 5 to 9 (with extreme limits of 4.2 to 11.0) and carbon dioxide levels under 36 ppm. These figures vary with temperature and pH (McVeigh 1979a). Both *S. trutta* and *O. mykiss* have high salinity tolerances and can move from freshwater to the sea (McVeigh 1979a).

Salmo trutta is reported to be less tolerant than *O. mykiss* of adverse environmental conditions such as higher temperatures, excessive water abstraction and high siltation levels. Populations in the Bushmans River (Natal) declined during the drought of 1946-47 and the upper river was almost depopulated during this period (Crass 1969).

Within the confines of temperature and water-quality limitations, trout can survive in a wide range of habitats. In their native range brown trout are found in small streams, large slow rivers, large lakes and in estuaries (Varley 1967). Nevertheless trout are normally predominant in the well-oxygenated upper reaches of streams (Varley 1967) and require stony substrates (i.e. eroding substrates) for breeding (Frost & Brown 1967). Although trout are known to favour fast-flowing waters, there is an upper limit to the gradient tolerated. Frost & Brown (1967) comment that in general few trout are found in the cascade reaches of streams. Their preferred habitat is in the riffles (defined as regions of rapid flowing, broken shallow water with a stable stony bottom) and the runs (greater depth with smooth gliding flow). Trout also prefer streams with adequate cover in the form of submerged rocks or overhanging trees, bushes or grass (Alletson 1985).

5.2. DATA COLLECTION AND ADAPTATION FOR GIS ANALYSIS

5.2.1 Choice of datasets and assumptions made in this choice

As discussed in Chapter 3, the geographical analysis technique of Palmer & van Staden (1992) involves investigating the relationship between distribution patterns of selected species and certain environmental gradients. In the present analysis it was decided to compare trout distributions to Median Annual Rainfall (MAR) and elevation (available as a minute x minute grid matrix in the CCWR database). In making the decision to use this database, the following assumptions were made:

a. That temperature and water availability are the most important variables affecting the distribution of species,

b. That elevation (within confined latitude classes) could be used as a reasonable surrogate measurement of temperature regimes in rivers,

c. That MAR is a reasonable surrogate measurement of water availability.

There are, however, certain disadvantages and shortcomings in making these assumptions:

a. Using elevation as a surrogate for temperature: Because the amount of radiant energy entering the earth's surface varies with latitude, this assumption is only valid within a restricted range of latitude classes. This means that there will be a severe limitation on the latitude range of the model predicted from a particular set of distribution sites. Thus it will be necessary to have a series of distribution points representative of different latitude classes, in order to draw up predictive models for the whole of the study area. Latitude and elevation are not the only factors affecting temperature regimes in rivers. The slope of the river, geological features, the number of impoundments, the nature of fringing vegetation, and whether or not the stream is spring-fed, all have an influence on temperature regimes in freshwaters (Hynes 1970).

b. MAR as a surrogate for water availability: In the case of large rivers flowing through arid regions, or in areas where interbasin transfers have altered the flow regimes of the donor and recipient rivers, this assumption may not always be valid. It is assumed that in regions of high rainfall there will be more surface water available per unit area, implying a greater amount of habitat available for aquatic animals. When considering the tributary streams of most rivers, even in cases where there have been alterations to the flow regime, this assumption seems reasonable.

Because of the problems associated with the use of elevation as a surrogate of temperature, another analysis was performed using air temperature as a surrogate of water temperature. In this case the database was not readily available as a minute x minute matrix of values. It was therefore necessary to generate a data matrix using air-temperature data from weather stations. The methods used to generate this dataset are described in Section 5.3.3.1.

5.2.2. Choice of GIS programmes

After reviewing the GIS packages available at Rhodes University, it was decided that the methods employed by Palmer (1991) and Palmer & van Staden (1992) (including the use of the GIS programme IDRISI) could be applied to the present analysis, subject to certain modifications to account for conditions in the aquatic environment.

The IDRISI programme is a grid-based (raster) geographical analysis system. In IDRISI, spatial data is stored as a fine rectangular matrix. Data are displayed as images where each "cell" or "pixel" (i.e. "picture element") in the grid is displayed in different colours or tones. Images are representations of space in a grid-cell or raster structure. Although IDRISI can be described principally as a raster-based package, it is actually made up of a number of sub-programmes which also include the capability of mapping data in a vector format and supplementing raster routines with some vector aspects (Eastman 1990).

The sub-programmes used in the present analysis are described below:

The DOCUMENT option is used to create a documentation file for newly imported data. Based on the contingency table analysis on the data for elevation and MAR, IDRISI uses the RECLASS file to reclassify the pixels according to user-defined criteria. The CROSSTAB option is then used to cross-classify MAR and elevation images and create new classes of the combinations of these two environmental gradients. The IMAGE-HLJ programme is then used to create a hardcopy image of the cross-classification.

A vector image of the coastline is created by means of reclassifying the elevation image into two classes (> 0 and = 0). The RASLNVEC option of IDRISI then converts the image to a vector format and COLOREVA is used to overlay the vector image of the coast onto the raster image produced in IDRISI. The composite image (which now includes the coastline) is then printed using the IMAGE-HLJ option of IDRISI.

For a complete description of the programmes used, refer to Eastman (1990).

5.2.3. The use of downstream limits in the collection of distribution records

Since trout can easily tolerate water temperatures as low as 4°C (Varley 1967), it can be assumed that low temperatures would not be a limiting factor to trout in any region of the river above the downstream limit. Because of other habitat requirements of trout, it is incorrect to assume that the whole river (including tributaries) above the downstream limit is always suitable for colonisation by trout. Other factors such as slope, bank stability and fringing vegetation can limit the distribution of trout (Crass 1966, 1986). In the Drakensberg region trout are not present in many of the smaller tributaries of rivers in which thriving populations are found in the mainstream. They also disappear from the steeper precipitous headwaters of rivers (Crass pers. comm.).

In terms of the limitations to the predictability described in Chapter 3, this study is only attempting to predict the regions suitable for colonisation by trout (and other cold stenothermal species), according to temperature and water availability requirements. Thus features such as slope, width of rivers and the nature of fringing vegetation are not relevant to the present study. It can therefore be assumed that any region above the downstream limit would satisfy the thermal requirements of trout, subject to water availability.

The downstream limits of trout are subject to seasonal variation and can also be affected by factors such as siltation, slope etc. It can therefore be expected that, even within the same latitude class, there will be some variation in the elevation of downstream limits of trout.

Distribution records close to the downstream limits represent outlying figures at the limits of the range. The present study aims to identify the optimal conditions for breeding populations of trout, which would be expected to occur in the more "central" regions of their distribution range. A variation in values from outlying marginal regions would therefore not be expected to have a profound effect on the results of the analysis.

5.2.4 Definition of terms used for distribution records

The following definitions apply to distribution records of trout:

Established populations: Only distributions of established (breeding) populations are considered. This excludes populations of trout in sub-optimal regions which are dependent on periodic restocking for their continued existence.

Downstream limits: The downstream limit of breeding populations of trout in rivers. Because this may vary with season and climate, it is necessary to describe a lower "marginal zone" (defined below) associated with the downstream limit.

Optimal zone (O): Breeding area for trout.

Marginal zone (M): The region in the vicinity of the downstream limit of trout, where breeding populations of trout sometimes occur, subject to seasonal variations. The upper limit of the marginal zone is the downstream limit of the region where it can be expected that trout would be found throughout the year. The lower limit of the marginal area is the upstream limit of stretches of river which are unsuitable (at any time of the year) for the establishment of breeding populations of trout.

Temperate zone (T): Regions within the optimal thermal regime of trout, which do not satisfy all the habitat requirements of trout but may nevertheless be suitable for colonisation by other alien cold stenothermal species.

Historical records (H): These are records of trout distribution which may or may not still be valid. When extensive historical records exist for a particular region it is likely that the thermal regime is suitable for trout. The disappearance of trout from these regions is usually the result of degradation of the river.

According to the above definitions distribution records were classified into four classes - optimal, marginal, temperate or historical. Historical records (from Lesotho) were only used in Model 8 where they were combined with a number of other records.

5.2.5. Collection of data

Distribution records were needed from different latitudes within the study area in order to obtain representative samples from each latitude class. The ranges of latitude of the sampling areas and predictive models are discussed in Section 5.2.7.

Sampling areas were selected within each region according to the familiarity of scientists with the particular area. A number of experts (from research institutions and conservation authorities) who had an intimate knowledge of trout distributions in particular regions were consulted.

Southern Natal (Himeville- Underberg) region: Downstream and upstream limits obtained from Mr R.S. Crass, previously Principal Scientific Officer of Natal Parks Board: (Mkomazi and Mzimkulu systems.)

Northern Natal: Downstream limits obtained from Mr R.S. Crass (Ncandu, Ngogo, Pivaan and Slang rivers).

Lesotho region: Records for tributaries of the upper Orange River were obtained from Dr J.A. Cambray (from the Loxton-Venn Report 1993) of the Albany Museum and Dr P.H. Skelton of the JLB Smith Institute of Ichthyology for the Senqunyane, Moremoholo, Senqu, Sani, Rafunyane, Bokeng, Tsolotsa, Kao, Malibamatso & Pelaneng rivers. These are point locality records and do not represent downstream limits as is the case for other samples. These records were combined with Natal records in Model 3. For Model 8 additional historical records were obtained from Shortt-Smith (1963) for the Pelaneng, Senqunyane and Maletsunyane rivers. These records represent the historical downstream limits of "trout waters". Although it cannot be assumed that these records represent downstream limits for breeding populations of trout in present-day conditions, it is assumed that temperature regimes upstream of these localities are suitable for trout. A database was thus generated based on these localities, but it cannot be claimed that this represents the full range of the optimal elevation regime as is the case for data obtained from true downstream limits.

Eastern Cape: Mr M.T.T. Davies of the Department of Ichthyology and Fisheries Science, Rhodes University (Wolf, Cata, Tyume, Gubu and Buffalo rivers).

Western Cape: Mr A. Smith and Dr K.C.D. Hamman of the Cape Department of Nature and

Environmental Conservation, Stellenbosch (Olifants, Berg, Jonkershoek and Lourens rivers).

In order to obtain exact distribution records, 1:50 000 maps of the regions concerned were sent to the experts listed above. The downstream limits (including marginal areas) were then marked on the maps, and these were used in further analysis.

5.2.6. Adaptation of distribution records for GIS analysis

Since a river is a linear feature, it is necessary to translate distribution records from rivers into an area-based code suitable for raster-based analysis. The following procedure was adopted in order to convert distribution records from rivers into a "raster" code.

One minute x one minute grids were drawn on transparent paper and overlaid onto 1:50 000 maps. The downstream limit of trout in streams was noted. The river was then followed upstream from this point, and each time the river crossed a grid line a distribution record at the nearest intersection point was registered. In cases where the river crossed the line exactly halfway between two grid intersections, a coin was tossed in order to decide which grid reference point to choose. Distribution points were therefore recorded at a 1 minute x 1 minute resolution, corresponding to the resolution of the CCWR database used in this analysis.

If the river crossed the grid line more than once in one pixel then this was recorded as a duplicate (or triplicate etc.) result at the same distribution point. These records therefore reflect the amount of surface water present in the area. Fig. 18 and Table 6 illustrate the procedure described above.

5.2.7. Choosing latitude classes for the sampling region and the predictive model

A number of decisions need to be taken regarding the relationship between the latitude range of sampling points and predictive models and how distribution data from different latitudes should be combined. A number of factors should be taken into account in making these decisions:

a. The median value of latitude within each sampling class.

b. Sizes of sampling regions, and problems associated with combining distribution records from different regions.

1: 50,000 MAP

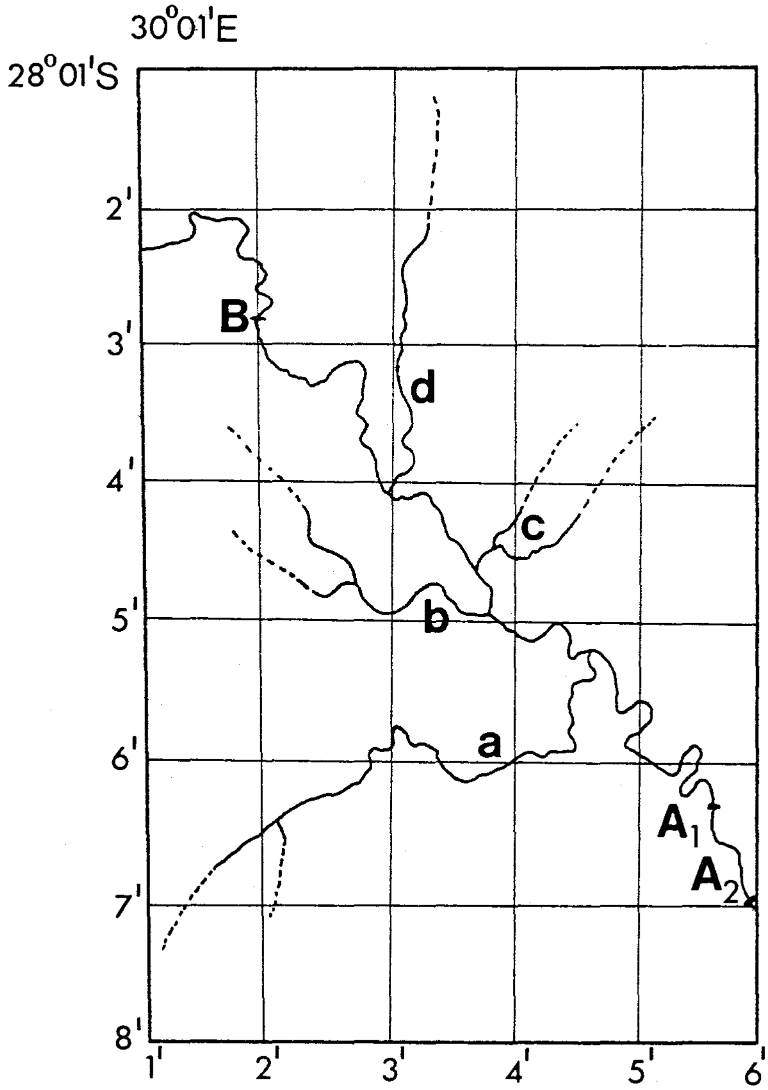

Figure 18: Map of hypothetical river to illustrate the method used in recording distribution records of aquatic organisms for the purpose of GIS analysis (see Table 6 for associated distribution records).

Perennial river

Non-perennial river

a,b,c,d - Tributaries

A_1 - A_2 - Marginal section of river

A_1 - Downstream limit of optimal area for breeding populations of trout

B - Upstream limit of breeding populations of trout

Table 6. Table of distribution records taken from the hypothetical map illustrated in Fig 18.

Record No.	Position	Lat/ Long	No of duplicates	Class	Remarks
1.	Mainstream	28°07'S:30°06'E	1	M	Marginal area*
2.	..	28°06'S:30°05'E	6	O	
3.	..	28°05'S:30°04'E	3	O	
4.	..	28°04'E:30°03'E	2	O	
5.	..	28°03'S:30°02'E	3	O	
6.	..	28°02'S:30°02'E	1	T	Above upper limit(B)
7.	..	28°02'S:30°01'E	1	T	
8.	Tributary a	28°06'S:30°04'E	1	T	
9.	..	28°06'S:30°02'E OR** 28°07'S:30°02'E	3	T	

* The marginal area lies between the two points A1 and A2. Sometimes these are so close as to be recorded as a single grid reference point.
** Since the river crosses the grid reference approximately mid-way between the intersections, a coin is flipped to decide which option to choose.
Classes: O - Optimal; T- Temperate; M - Marginal.

5.2.7.1. Median values of latitudes in the sampling class

Ideally the latitude range of the predictive model should be the same as that of the sampling area since the radiation flux density varies with latitude. Therefore predictions based on elevation data of regions from latitudes which are very different to that of the sampling area would be poor.

The size of the error in the predictive model increases with an increase in the difference between the ranges of latitudes of the sampling area and the range of latitudes of the predictive model. Ideally this difference should be kept to a minimum. This consideration must however be balanced against the consideration that the larger the number of samples used to generate the model, the greater the validity of such a model. Dividing the country into smaller and smaller latitude classes means that the size of samples used to generate each model will become smaller and smaller. A compromise solution must be found. The latitude of the predictive model should be as close to that of the sampling area and should range evenly around the median latitude of the sampling area. The sample size should also be large enough to generate a statistically valid result.

5.2.7.2. Size of sampling area, sampling effort and problems associated with combining distribution records from different regions

An estimate of the size of the areas in which distribution records of trout were recorded was made by measuring the area (on 1: 50 000 maps) subject to comments by experts. This was calculated by estimating the number of grid squares on the transparent overlay map (described in section 5.2.6) which was used to generate distribution data on rivers.

The latitudinal range as well as the area covered and the number of samples recorded for each set of samples at different latitude classes is given in Table 7.

Since more than half of the samples are from southern Natal, it may appear that there has been a greater sampling effort in this region compared to other areas. Table 7 indicates that the area in southern Natal under consideration was comparable in size to that of the western Cape. The

Table 7. Latitude range, number of samples, area of sampling regions and sampling density (for total samples and optimal classes) for each set of samples* at different latitudes.

Latitude range of samples	Area size sq. km.	Total no. samples	Total samples per 100 sq. Km	No. of samples O	T	M	No. of Optimal samples per 100 sq km
29°31'-29°55'S (S. Natal)	2269.55	626	27.32	234	383	9	9.87
32°35'-32°44'S (E. Cape)	901.46	38	4.22	35	3	-	3.88
27°18 -27°50'S (N. Natal)	2322.9	107	4.61	32	71	4	1.38
32°39'-34°03'S (W. Cape)	2694.68	146	5.34	90	56	-	3.34

* Note that area sizes for Lesotho have not been estimated. Because some records from this region were point distribution records rather than downstream limits, it was not possible to calculate the areas and sampling density represented by these distributions.
Classes of samples: O - Optimal; M - Marginal; T - Temperate

large number of samples in the southern Natal region indicates that larger sections of rivers are suitable for trout colonisation in the region. This is illustrated by the significantly higher number of samples (of all classes) per unit area in southern Natal (27.32 samples per 100 km^2) compared to figures from northern Natal, eastern Cape and western Cape (4.61, 4.22 & 5.34 samples per 100 km^2 respectively) (Table 7).

The total area of each sampling region is therefore a better determinant of sampling effort than the number of samples.

Problems arise when data in which there is a large disparity in the numbers of samples are combined. For example, consider the problem of combining data from southern Natal (latitude approximately 29°- 30°S) and the eastern Cape (latitude approximately 32°- 33°S). Since southern Natal has a large number of samples (620 samples) compared to those from the eastern Cape (38 samples), such a combination would result in the "swamping" of eastern Cape results with those from Natal. This would have a marked effect on the frequency crosstabulation analysis, and would affect the decision on the choice of optimal conditions for colonisation by trout.

Table 8. Models of potential trout distributions in various regions of southern Africa drawn up using categorical analysis techniques: Latitude ranges of sampling regions and predictive regions.

Model No.	Latitude range of distribution records used to generate the model	Class* of samples	Predictive Models & latitude ranges
1.	S. Natal 29°31'S - 29°55'S	O	S. Natal, Lesotho, T'kei (29°-32°S)
2.	S. Natal 29°31'S - 29°55'S	OMT	S. Natal, Lesotho, T'kei (29° - 32°S)
3(A&B).	S. Natal & Lesotho 29°31'S - 29°55'S & 29°01'S - 29°34'S	OMT	**A.** S. Natal, Lesotho, T'kei (29° - 32°S) **B.** N. Natal (28°-29°S)
4.	N. Natal 27°18'S - 27°50'E	OMT	N. Natal (27°-29°S)
5	E. Cape 32°34'S - 32°43'S 26°55'E - 27°18'E	OMT	S.E. Cape (32°-34°16'S) (22°-30°E)
6.(A&B).	E. & S.W. Cape 32°34'S - 32°43'S 26°55'E - 27°18'E + 32°40'S - 34°04'S 18°55'S - 19°29'E)	OMT	**A.** S.E. Cape (32°-34°16'S (22°-°30°E) **B.** S.W. Cape (32 - 35°S) (18 - 22°E)
7.	S.W. Cape 32°40'S - 34°04'S 18°55'S - 19°29'E	OMT	S.W. Cape as in Model 6b
8**.	S. Natal, Lesotho & E. Cape (combined samples from latitudes 29° - 32°S)	OMTH	S. Natal, Lesotho, T'kei E. & S.E. Cape (29° - 34°S)

* O=Optimal; M=Marginal; T=Temperate; H=Historical.
** This model was generated using MAR (from the CCWR database) and air temperature records. All other models were based on MAR and elevation data.

5.2.7.3. Decision

It was decided to combine distribution records from different sampling classes in a number of ways, taking the above points into consideration. In this way a number of different models would be generated for each region. Results would then be assessed and, if necessary, the method would be repeated and re-assessed. Reasons for the different combinations used are given in the "Results" section (Chapter 6). A summary of the latitude ranges of sampling regions and predictive models is given in Table 8.

5.3. CONCENTRATION ANALYSIS

5.3.1. Concentration analysis using the CCWR dataset

This method is based on methods developed by Austin et al. (1984) and Palmer (1991). The steps taken in this process are outlined below:

1. The associated MAR and elevation values for each distribution point was extracted from the CCWR database (Dent et al. 1989).

2. Scattergrams were prepared of MAR vs Elevation for each latitude class. This was done in order to assist with the choice of appropriate classes for concentration analysis.

3. Using the statistical programme STATGRAPHICS a contingency table was prepared and a chi-squared statistic obtained as described in Zar (1984). Where the null hypothesis of independence was rejected, cells with the highest frequency were selected as the optimum conditions for trout. Rules applying to the choice of cells which represent optimal conditions are discussed in section 5.3.2.

4. Using the results from (3) a search of the CCWR database was carried out for the same (optimal) conditions of MAR and elevation in the area to be predicted.

5. An image of the results was printed out which indicated the regions susceptible to colonisation by trout. A description of the IDRISI programmes used in this step was given in Section 5.2.2.

5.3.2. Means of reducing potential errors in the method

The results of this analysis depend largely on the way in which classes and optimal conditions are chosen in Steps 2 and 3 (Section 5.3.1) respectively. If these are chosen in a subjective manner, the predictive model may lack credibility. For this reason it is necessary to make certain rules when classes of elevation and MAR are defined (Step 2), and when the sets of optimal conditions for survival of trout are chosen (Step 3).

1. Step 2: Choosing the classes to be used in categorical analysis: Preparing a scattergram to show the spread of distribution points reduces the subjectivity of this step.

2. Step 3: Choosing the classes of elevation and MAR, which indicate optimal conditions for trout, from the contingency table: A problem arises when a decision must be made on which cells in the contingency table should be included in the model and which should be excluded. Palmer (1991) adopted the approach of selecting cells from the highest frequency downwards until more than 60% of the samples were included. This selection was dependent on subjective judgement, and Palmer's approach was meant merely as a guideline in making this decision.

In the present analysis it was decided to adopt Palmer's approach subject to some modifications:

a. Since the sampling method was based on optimum conditions (in terms of MAR and elevation) for trout rather than their mere presence, the total frequency of occurrence should be at least 75% with an upper limit of 95%.

b. In the contingency table the observed frequencies are compared to expected frequencies in each cell of the table as calculated by the following formula:

$$\text{Expected} = \frac{\text{Row total x column total}}{\text{grand total}}$$

Cells in which the observed frequency ($f_{obs.}$) is greater than the expected frequency ($f_{exp.}$) are chosen in most cases, but there are some exceptions to this rule. In some cases cells where $f_{obs.} < f_{exp.}$ were included in the optimum class, and in other cases cells where $f_{obs.} > f_{exp.}$ were excluded. These exceptions are discussed below:

* Inclusion of some cells with a high frequency (when $f_{obs.} < f_{exp.}$), especially where the associated column and/or row frequencies are also high.

* Exclusion of cells with a low frequency (when $f_{obs.} > f_{exp.}$), especially when the associated column and/or row frequencies are also low.

* If there is an observable general trend or gradient in the figures indicating that certain conditions of MAR and elevation (e.g. high rainfall, high elevation) are favourable, then a bias will be shown towards choosing cells indicating these conditions.

* Conversely, if the observable trend indicates unfavourable conditions for trout (e.g. low rainfall) then a bias will be shown against choosing cells indicating these conditions.

* In cases where the general frequency of samples in a particular sampling region is high (e.g. in southern Natal) this is a reflection of a high concentration of suitable habitat for trout in the area. In such cases most of the categories defining cells in the contingency table may represent optimal conditions (of MAR & elevation) for trout. In these instances a bias is shown towards including a large number of cells (some of which have $f_{obs.} < f_{exp.}$) in the analysis, resulting in the sum of frequencies of optimal cells in the contingency table being high (approaching 95%).

5.3.2.1. Collection of representative samples

In the ideal situation for biogeographical analysis, representative samples should be taken at regular intervals over the whole range of conditions of the environmental gradients being measured. This can be represented graphically as follows:

Regular intervals of sampling along the environmental gradient (e.g. MAR).

In practice this ideal is seldom if ever achieved. Distribution records are often concentrated around certain regions of the range which are more accessible to the biogeographer. In the case of studies in freshwater ecosystems where elevation is one of the important environmental gradients being measured, there is a tendency for distribution records to be more concentrated at the lower (more accessible) regions of the study area.

In the present analysis, the problem of covering the full elevation range in rivers is largely overcome by the fact that records are based on downstream limits of trout. Other distribution records were extracted from maps. Nevertheless it is unlikely that the ideal situation will be achieved. Distribution records were taken from a small region and analysed in order to make predictions about probable distributions in a larger region. It is very unlikely that the sample region would cover the full range of conditions (of MAR and elevation) likely to be encountered in the larger (predictive) region. This is a perennial problem in biogeographical studies which cannot be easily overcome. The only solution is to attempt to obtain as representative a sample as possible.

5.3.2.2. "Disjunctions" between adjacent images from two latitude classes

This would arise as a result of the fact that the errors associated with the predictive models are expected to increase at the limits of the range of the predictive model. When two images from adjacent models are aligned together it can be expected that there will be a sharp disjunction at the line at which they join. It is difficult to overcome this problem, except by being aware that the models at the outer limits of the range can be expected to be less accurate than those in the median of the range of latitudes.

5.3.3. Concentration analysis using an (air) temperature database

In this method the concentration analysis is the same as that described above, except that air temperature was substituted for elevation and latitude as an environmental parameter. In making use of air temperature as a surrogate of water temperature, there is no restriction (in principle) on the latitude range of the predictive model as was the case when using elevation as a surrogate. The latitude range of the predictive model (Model 8, Table 8) is therefore much broader (29°00' - 34°00'S) than is the case for the other models generated.

5.3.3.1. Generating a temperature database

Data was obtained using air temperature statistics supplied by the Weather Bureau (Schulze 1986). Mean monthly January maximum and July minimum temperatures were obtained for 750 stations in southern Africa.

These point-data values from weather stations were used in the GRASS s.surf.idw programme to generate a minute x minute grid matrix of values. This programme operates by means of filling a raster matrix with interpolated values generated from a set of irregularly spaced data points using numerical approximation (weighed averaging) techniques. The interpolated value of a cell is determined by values of nearby points and the distance of the cell from those input points (Westervelt 1991).

Using this interpolation technique a surface response curve was generated of mean monthly January maximum temperatures and mean monthly July minimum temperatures for southern Africa. Images of different categories of temperatures were generated using the IDRISI programme in order to assess which would be the most appropriate temperature parameter to use for the analysis.

5.3.3.2. Modifications to the method of concentration analysis in this application

Certain minor modifications were made to the method in this analysis (Model 8: using air temperature as a surrogate) which are described in the results (Chapter 6).

5.4. VALIDATION OF THE MODELS

The following methods were used to evaluate the models:

a. Comparison of the predictive models with known distribution records (other than those used to generate the image) of breeding populations of trout (Appendix 3),

b. Eliciting independent expert opinion on the validity of the predictive models.

The experts consulted are listed below:

Northern Natal/ southern Natal/Lesotho: Messrs. J. Alletson & M. Coke of Natal Parks Board, Pietermaritzburg.

Lesotho/Transkei/north eastern Cape: Dr P.H. Skelton of the JLB Smith Institute of Ichthyology, Grahamstown.

Northern Cape (upper Orange River, region): Mr. M.T.T. Davies of the Department of Ichthyology and Fisheries Science, Rhodes University, Grahamstown.

South eastern Cape: Dr P.H. Skelton of the JLB Smith Institute of Ichthyology and Dr J.A. Cambray of the Albany Museum, Grahamstown.

South western Cape: Messrs. A. Smith and S. Thorne of the Cape Department of Nature and Environmental Conservation, Jonkershoek Fisheries Research Station, Stellenbosch.

In their assessment of the images, the experts were asked to concentrate on the thermal and moisture conditions in the region and to ignore all other considerations such as pH, water quality conditions etc. They were then asked to answer the following questions:

i. Are there any regions in the image indicated as being suitable for colonisation by trout, which in your opinion are unsuitable for colonisation because conditions are too hot and dry?

ii. Are there any omissions in the model? i.e. regions which you regard as being optimal for trout, but which have been excluded from the image?

iii. Where alternative models of the same region were available, the experts were asked to choose the model which they judged to be the best representation of potential trout distributions.

In reply to questions (i) and (ii) the experts were asked to mark the relevant regions on the images.

c. In the case of Natal, models were also compared to the Natal Parks Board (NPB) downstream limits of legal trout waters. Since these records are determined on the basis of administrative and legal considerations as well as actual distribution records of trout, it was decided to use them in conjunction with comments from experts. A list of NPB downstream limits in selected rivers in Natal is given in Appendix 3.

The raster images prepared using the IDRISI programme did not contain sufficient reference points to known localities such as rivers or towns. Such references are essential for a proper assessment of the maps by experts. For this reason it is necessary to overlay maps of major rivers onto the models depicting potential trout distributions. A problem immediately arises in this regard since available maps of rivers in southern Africa are all based on latitude/longitude coordinate projections (West pers. comm.) whereas IDRISI images are based on conformal (flat) grid-referencing projections (see section 2.4.3). This necessitates the construction of a new map of major rivers at the same projection as the IDRISI images. In making use of computer programmes (such as ARCINFO) to digitise the maps of rivers, the appropriate transformations to projections would be made in the computer programme. Unfortunately, such an option was not feasible in the present study since the task of digitising all the rivers in the study area would be extremely time consuming and arduous.

It was therefore decided to enlist an expert cartographer (Mrs. S. Abraham of the Geography Department, Rhodes University) to compile a map of major rivers in which the projection was altered to correspond with the conformal projection used in IDRISI maps. The river conservation map of O'Keeffe (1986) (based on a latitude/longitude coordinate projection) was used as a reference map.

CHAPTER 6: GEOGRAPHIC INFORMATION SYSTEMS (GIS) APPROACH- RESULTS

6.1. INTRODUCTION

A summary of the combinations of sampling data, the classes of samples and the latitude range of sampling areas and predictive models for each analysis was given in Table 8 in the previous chapter. These analyses were based on downstream distribution records of trout from selected regions of the country. Appendix 4 describes the localities of these downstream limits in selected rivers within each sampling area. These records were used to generate the database of 1011 records of trout distributions in streams as described in Section 5.2.6.

Details of the 1011 distribution records of trout are available in the Lotus-compatible file "App5.wk1" (see attached floppy disc). A guide to the use of this file appears in Appendix 5. It should be noted that a discrepancy sometimes exists between the numbers of samples listed in the spreadsheet (of App5.wk1) and the statistical analysis in the associated models. During the process of obtaining MAR and elevation data from the CCWR, certain samples were recognised as duplicates which were then eliminated. The resultant statistical analysis may therefore have fewer samples than those listed in the relevant class in the spreadsheet.

Details of the 757 samples used to generate Model 8 are contained in a separate Lotus file called "Julmin.wk1" (see attached floppy disc). A guide to the use of this file appears in Appendix 6.

Figure 19 illustrates the regions for which models of potential trout distributions (as described in Table 8) have been constructed.

It is notable that no model of potential distributions of trout has been constructed for the Transvaal region. Downstream limits of trout distributions in the Lydenberg district were obtained from Transvaal Nature Conservation officials at the Lydenberg Fisheries Research Station (Engelbrecht pers. comm.). A database of distribution records was generated from these figures and predictive models drawn up. There was however some doubt expressed by Dr C.J. Kleynhans (pers. comm.) about whether the observed downstream limits were of breeding populations, or whether they were the result of periodic stocking. It was decided therefore to abandon any further analysis of potential distributions in this region.

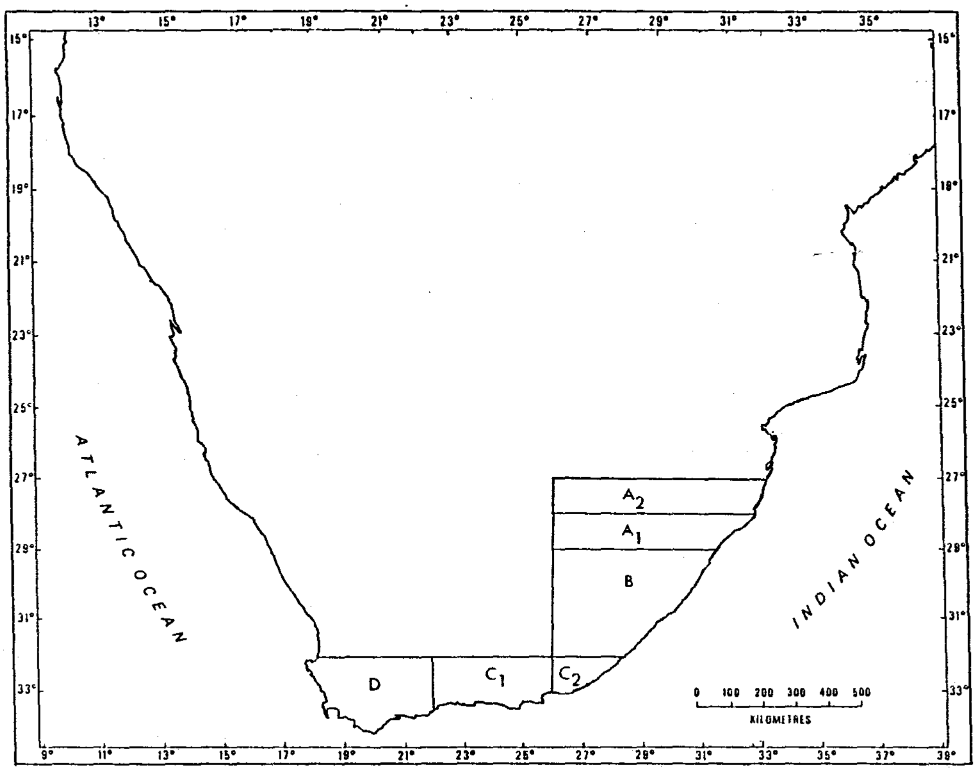

Figure 19: Regions of southern Africa for which predictive models of potential trout distribution have been compiled.

Region A_1 - Model 3B

Region A_{1+2} - Model 4

Region B - Models 1,2 & 3A

Region C_{1+2} - Models 5 & 6A

Region D - Models 6B & 7

Region B + C_2 - Model 8

6.2. RESULTS - SCATTERGRAMS AND CONTINGENCY TABLES FOR MODELS 1 - 7

The same procedure was followed in all the models. This is outlined below:

Scattergrams of MAR vs Elevation for parameters associated with each distribution point were compiled (Figs 20 - 26 for Models 1 - 7 respectively).

Contingency analysis: In each analysis an examination of the scattergram was used as a guideline for choosing appropriate categories of elevation and MAR for the contingency analysis of observed and expected frequencies of distribution of trout. A dependency was demonstrated in all the contingency analyses carried out (Tables 9 - 15 for Models 1 - 7 respectively). The significance levels are indicated in each contingency table (Tables 9-15). High frequency cells in the contingency tables (marked with an asterisk) were selected as indicating optimal conditions for trout. A search for similar conditions in the predictive region for each model, using methods described in Chapter 5, was then carried out in order to generate images of potential trout distributions in different regions.

6.3. RESULTS - IMAGES GENERATED BY MODELS 1 - 7

6.3.1. Southern Natal/Lesotho/Transkei region (Models 1, 2 & 3A)

6.3.1.1. Comparison of two analyses from the same latitude range, but using different classes of samples (Models 1 & 2)

In Models 1 & 2, samples were taken from the same region (S. Natal), in order to compare images generated using only optimal figures (Model 1) to those generated using distribution records from all three classes (optimal, temperate and marginal) (Model 2). The latitude range of the predictive model in this study is from 29-32°S.

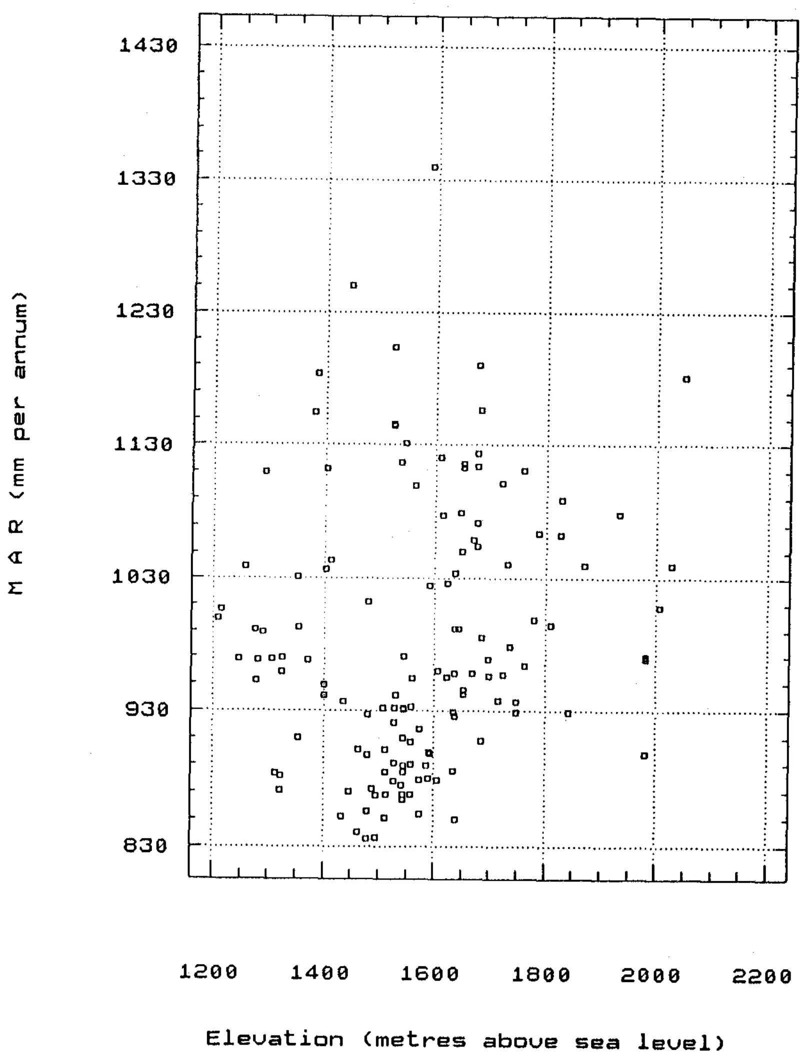

Figure 20: Model 1: Scattergram analysis of MAR vs elevation for parameters associated with each distribution point in the sampling area.

Table 9: Model 1: Contingency table of observed and expected frequencies ($f_{obs.}$ and $f_{exp.}$) of trout distributions in different Median Annual Rainfall (MAR) and elevation conditions.

Elevation (m) Category No.	MAR (mm/annum) 1 830-930	2 930-1030	3 1030-1130	4 > 1130	Row Total
1 1200-1400	$^{1}6$	$^{5}17$*	$^{9}4$	$^{13}3$	30
	12	10	6	2	
2 1400-1600	$^{2}74$*	$^{6}23$*	$^{10}7$	$^{14}7$	111
	45	37	22	7	
3 1600-1800	$^{3}11$	$^{7}34$*	$^{11}27$*	$^{15}4$	76
	30	26	15	5	
4 >1800	$^{4}3$	$^{8}5$	$^{12}8$	$^{16}1$	17
	7	6	3	1	
Column Totals	94	79	46	15	234

$f_{obs.}$ = upper figure in each cell
$f_{exp.}$ = lower figure in each cell
Superscripts indicate the cell number.
* Categories indicating optimal conditions.

Chi-squared statistic = 77.8098

Degrees of Freedom = 9

Significance: $P < 0.0001$

* = 74.8% of the frequency of the total (n)

Cells where $f_{obs.} > f_{exp.}$ were chosen to indicate optimal conditions, with the following exceptions:

Cell 12 was excluded because of its low frequency and the low frequency of Row 4. Cell 6 was included because of its high frequency (approximately 10% of the total n) and the high frequency of Row 2 and Column 2.

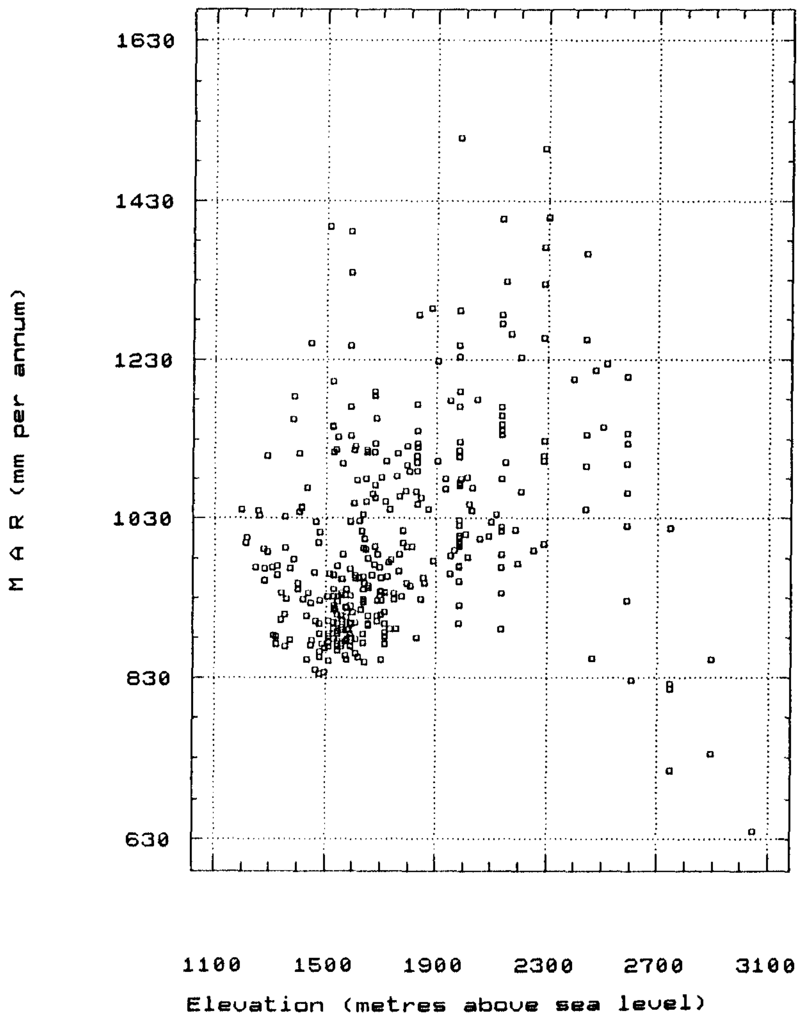

Figure 21: Model 2: Scattergram analysis of MAR vs elevation for values associated with each distribution point in the sampling area.

Table 10: Model 2: Contingency table of the observed and expected frequencies ($f_{obs.}$ and $f_{exp.}$) of trout distribution in different Median Annual Rainfall (MAR) and elevation conditions

Elevation (m) Category No.	MAR (mm per annum) 1 <830	2 830-1030	3 1030-1230	4 >1230	Row Total
1 1100-1500	$^{1}0$	$^{5}98$*	$^{9}24$*	$^{13}2$	124
	1	77	37	9	
2 1500-1900	$^{2}0$	$^{6}233$*	$^{10}85$*	$^{14}10$	328
	3	204	97	24	
3 1900-2300	$^{3}0$	$^{7}45$*	$^{11}55$*	$^{15}29$*	129
	1	80	38	9	
4 >2300	$^{4}5$	$^{8}13$	$^{12}22$*	$^{16}5$	45
	0	28	13	3	
Column Total	5	389	186	46	626

$f_{obs.}$ = upper figure in each cell
$f_{exp.}$ = lower figure in each cell
Superscripts indicate the cell number.
* Categories indicating optimal conditions.

Chi-squared statistic = 107.419

Degrees of freedom = 6.

Significance: P < 0.00001

* = 94.4% of the frequency of the total.

In this contingency analysis, low frequency figures from column 1 were excluded in the calculation of the chi-squared statistic.

Cells where $f_{obs.} > f_{exp.}$ were chosen to indicate optimal conditions, with the following exceptions:

Cells 7 & 9 were included because of their high frequencies and the high frequencies of Columns 2 & 3 respectively. Cells 4 & 16 were excluded because of their low frequencies (<1% of the total n) and the low frequencies of columns 1 & 4 respectively.

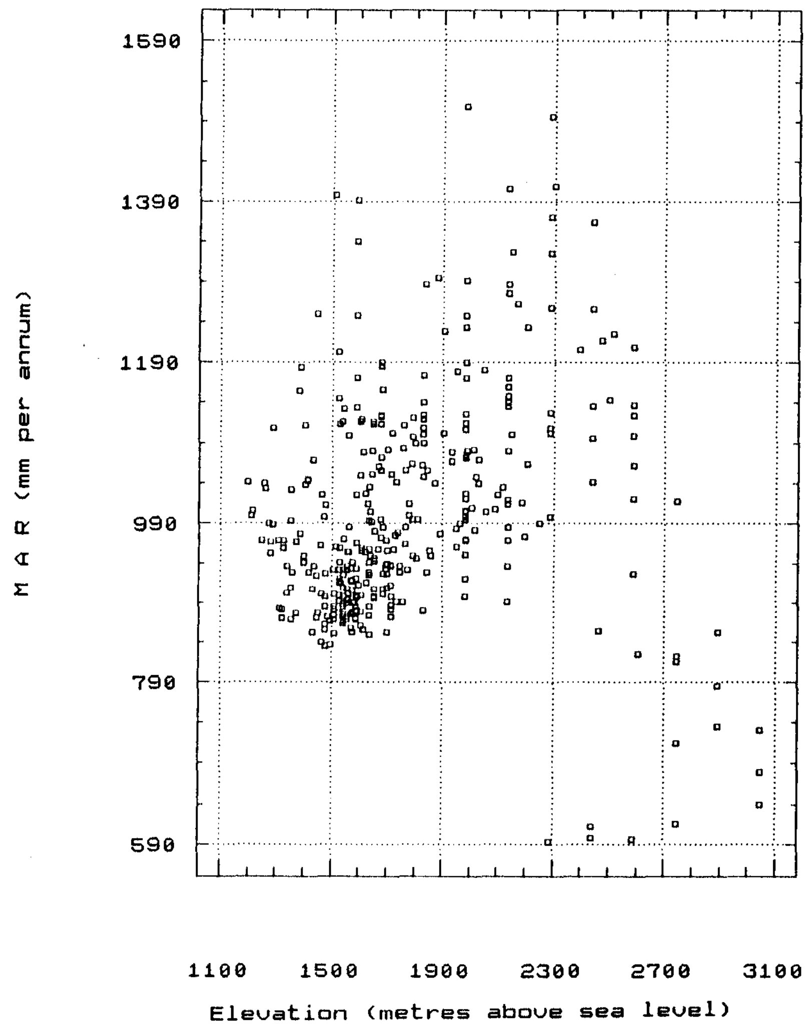

Figure 22: Model 3: Scattergram analysis of MAR vs elevation for parameters associated with each distribution point in the sampling area.

Table 11: Model 3: Contingency table of the observed and expected frequencies ($f_{obs.}$ and $f_{exp.}$) of trout distribution in different Median Annual Rainfall (MAR) and elevation conditions.

Elevation (m) Category No.	MAR (mm per annum) 1 590-790	2 790-990	3 990-1190	4 >1190	Row Total
1 1200-1500	$^{1}0$ 6	$^{5}83$* 63	$^{9}38$* 43	$^{13}2$ 12	123
2 1500-1800	$^{2}0$ 14	$^{6}203$* 149	$^{10}78$* 102	$^{14}12$ 27	293
3 1800-2100	$^{3}7$ 6	$^{7}28$* 60	$^{11}69$* 41	$^{15}14$ 11	118
4 >2100	$^{4}24$* 6	$^{8}23$* 65	$^{12}46$* 44	$^{16}34$* 12	127
Column	31	337	231	62	661

$f_{obs.}$ = upper figure in each cell
$f_{exp.}$ - lower figure in each cell
Superscripts indicate cell numbers.
* Categories indicating optimal conditions.

Chi-squared statistic = 227.961

Degrees of freedom = 9

Significance: P < 0.00001

* = 94.7% of the frequency of the total (n).

In this contingency analysis, low frequency figures from column 1 were excluded in the calculation of the chi-squared statistic. Cells where $f_{obs.} > f_{exp.}$ were chosen to indicate optimal conditions, with the following exceptions:

Cells 7, 8 & 9 were included because of their moderately high frequencies and the high frequencies of Columns 2 & 3 respectively. Cell 15 was excluded because of its low frequency (2.12% of the total n).

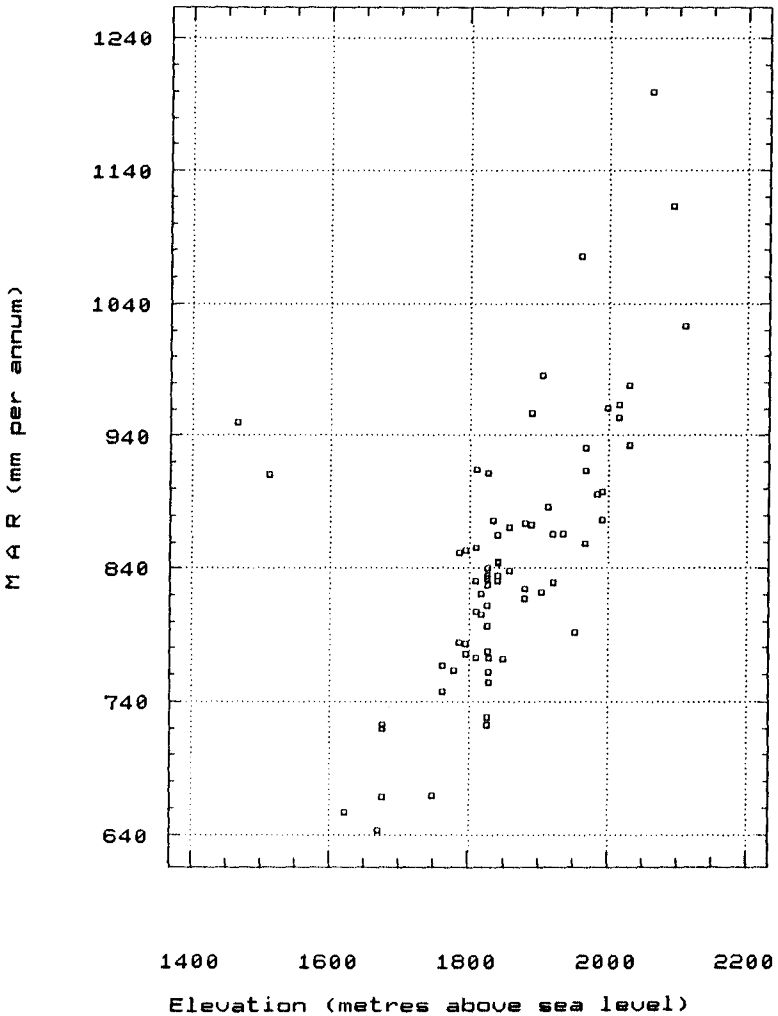

Figure 23: Model 4: Scattergram analysis of MAR vs elevation for parameters associated with each distribution point in the sampling area.

Table 12: Model 4: Contingency table of the observed and expected frequencies ($f_{obs.}$ and $f_{exp.}$) of trout distribution in different Median Annual Rainfall (MAR) and elevation conditions.

Elevation (m)	MAR (mm per annum)				
Category No.	1 <700	2 700-800	3 800-900	4 >900	Row Total
1 1600-1800	$^{1}5$ / 1	$^{4}15$* / 6	$^{7}2$ / 11	$^{10}0$ / 4	22
2 1800-2000	$^{2}0$ / 3	$^{5}14$* / 16	$^{8}39$* / 29	$^{11}4$ / 9	57
3 >2000	$^{3}0$ / 1	$^{6}1$ / 7	$^{9}12$* / 13	$^{12}13$* / 4	26
Column Total	5	30	53	17	105

$f_{obs.}$ = upper figure in each cell
$f_{exp.}$ - lower figure in each cell
Superscripts indicate the cell number.
*Categories indicating optimal conditions.

Chi-squared statistic = 56.8358

Degrees of Freedom = 4

Significance: $P < 0.00001$

* = 88.57% of the frequency of the total (n).

In this contingency analysis, low frequency figures from column 1 were excluded from the calculation of the chi-squared statistic. Cells where $f_{obs.} > f_{exp.}$ were chosen to indicate optimal conditions, with the following exceptions:

Cells 5 & 9 were included because of their high frequency (>10% of total n) and the high frequency of Row 2 & Column 3. Cell 1 was excluded because of its low frequency and the low frequency of Column 1.

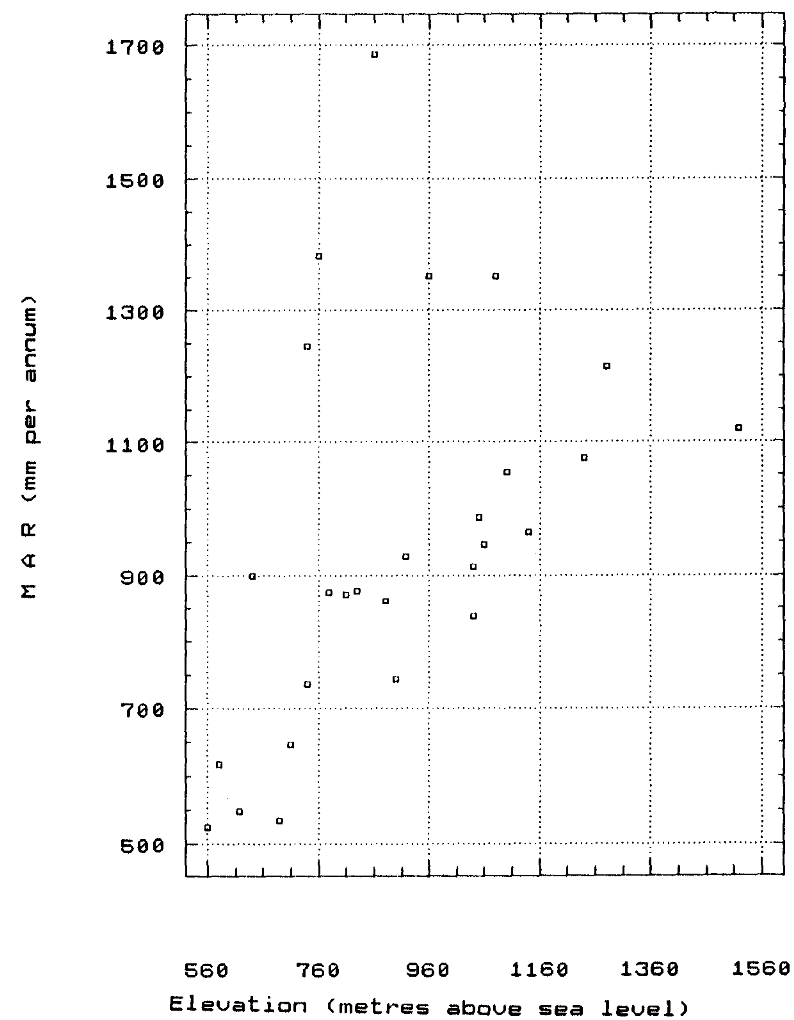

Figure 24: Model 5: Scattergram analysis of MAR vs elevation for values associated with each distribution point in the sampling area.

Table 13: Model 5: Contingency table of observed and expected frequencies ($f_{obs.}$ & $f_{exp.}$) of trout distribution in different Median Annual Rainfall (MAR) and elevation conditions

Elevation (m) Category No.	MAR (mm per annum) 1 <600	2 600-900	3 >900	Row Total
1 (560-810)	[1] 4 2	[4] 10* 8	[7] 3 8	17
2 (810-1110)	[2] 0 2	[5] 7* 7	[8] 8* 7	15
3 (>960)	[3] 0 1	[6] 0 3	[9] 6* 3	6
Column total	4	17	17	38

$f_{obs.}$ = upper figure in each cell
$f_{exp.}$ = lower figure in each cell
Superscripts indicate the cell number (for discussion purposes)

Chi-squared statistic: 9.83590

Degrees of Freedom: 2

Significance: 7.31412×10^{-3}

* = 81.58% of the frequency of the total (n).

In this contingency analysis, Column 1 was ignored in the calculation of the chi-squared statistic. Cells where $f_{obs.} > f_{exp.}$ were chosen to indicate optimal conditions, with the exception of Cell 1 which was excluded because of the low frequency of Column 1.

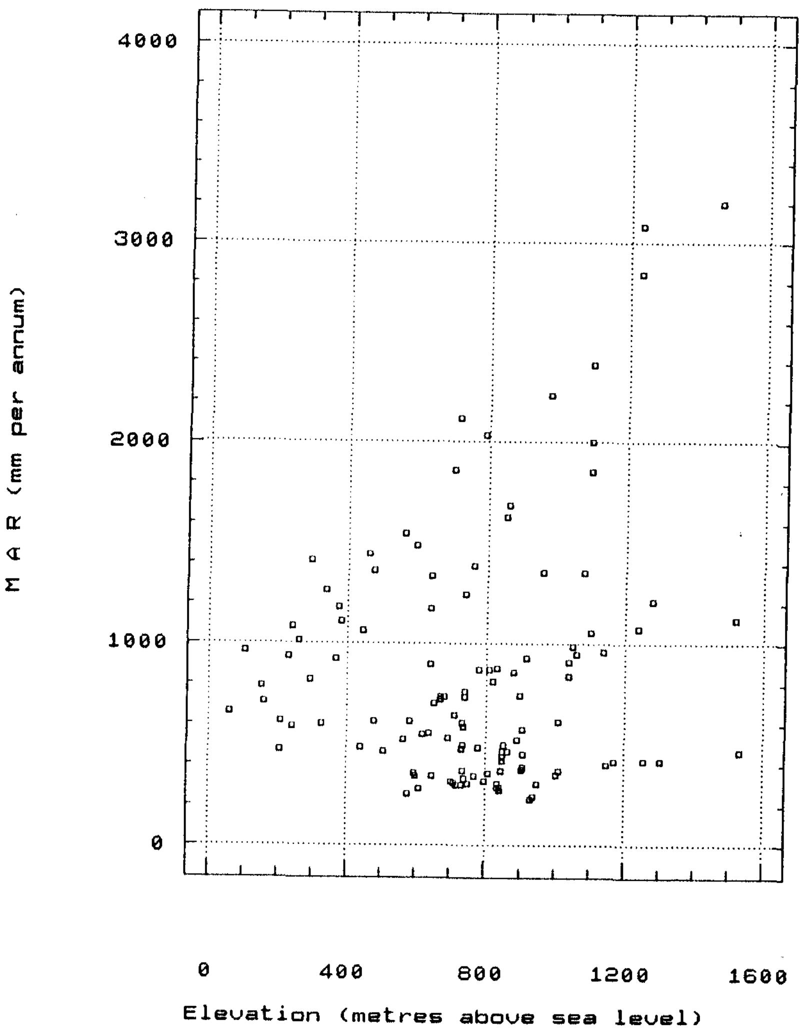

Figure 25: Model 6: Scattergram analysis of MAR vs elevation for values associated with each distribution point in the sampling area

Table 14: Model 6: Contingency table of observed and expected frequencies ($f_{obs.}$ & $f_{exp.}$) of trout distribution in different Median Annual Rainfall (MAR) and elevation conditions

Elevation (m) Category No.	MAR (mm per annum) 1 <300	2 300-650	3 650-1000	4 >1000	Row Total
1	^{1}0	^{5}5	^{9}10*	^{13}14*	29
<400	2	11	6	11	
2	^{2}5	^{6}37*	^{10}12*	^{14}29*	83
400-800	5	31	16	31	
3	^{3}6	^{7}22*	^{11}14*	^{15}14*	56
800-1200	3	21	11	21	
4	^{4}0	^{8}4	^{12}0	^{16}12*	16
>1200	1	6	3	6	
Column Total	11	68	36	69	184

$f_{obs.}$ = upper figure in each cell
$f_{exp.}$ = lower figure in each cell
Superscripts indicate cell numbers
* Categories indicating optimal conditions

Chi-squared statistic = 21.6698

Degrees of Freedom - 6

Significance: $P < 0.0001$

* = 89.13% of the frequency of the total (n).

In this contingency analysis, figures from column 1 were ignored in the calculation of the chi-squared statistic. Cells where $f_{obs.} > f_{exp.}$ were chosen to indicate optimum conditions, with the following exceptions:

Cell 3 was excluded because of the low frequency of Column 1. Cells 10 & 15 were included because of the high frequencies of Row 2 and Column 4 respectively and the general trend indicating optimal conditions in high elevation and high MAR regions.

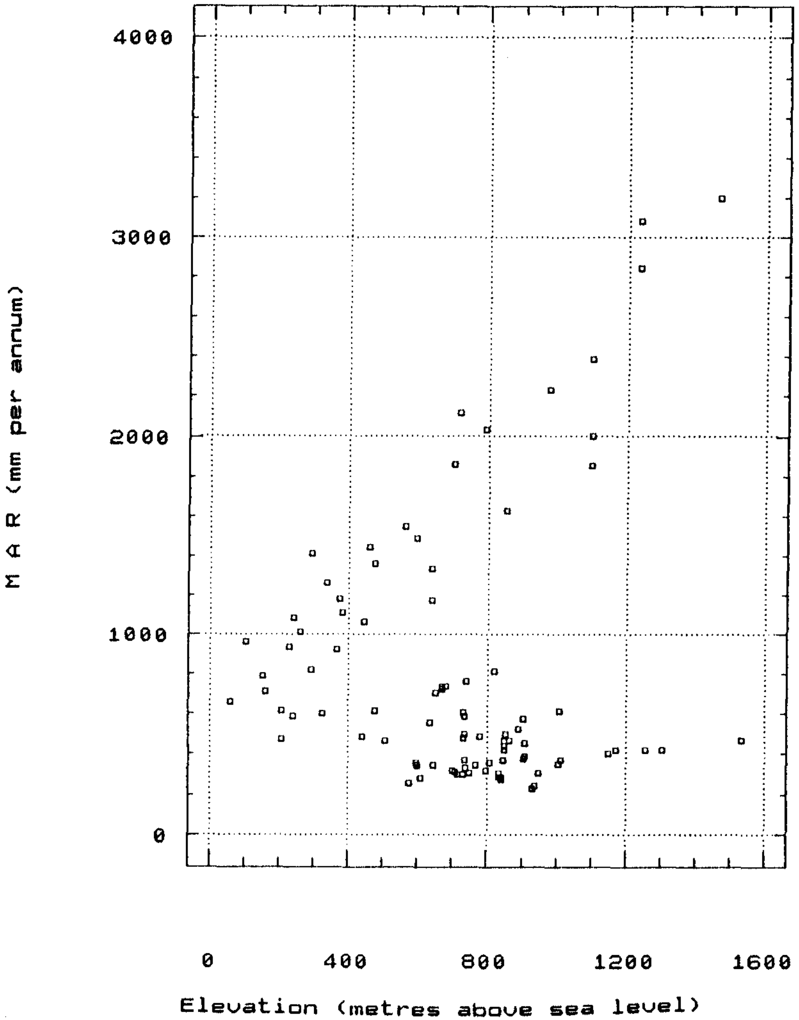

Figure 26: Model 7: Scattergram analysis of MAR vs elevation for values associated with each distribution point in the sampling area

Table 15: Model 7: Contingency table of observed and expected frequencies ($f_{obs.}$ & $f_{exp.}$) of trout distribution in different Median Annual Rainfall (MAR) and elevation conditions

Elevation (m) Category No.	MAR (mm/annum) 1 <300	2 300-600	3 >600	Row Total
1 <400	^{1}0 2	^{4}3 11	^{7}26* 16	29
2 400-800	^{2}5 5	^{5}26* 24	^{8}35* 37	66
3 >800	^{3}6 4	^{6}25* 19	^{9}20* 28	51
Column Total	11	54	81	146

$f_{obs.}$ = upper figure in each cell.
$f_{exp.}$ = lower figure in each cell.
Superscripts indicate cell numbers (for discussion purposes).
* Categories indicating optimal conditions.

Chi-squared = 19.6698

Degrees of freedom = 4

Significance = 5.80199×10^{-4}

* = 90.4% of the frequency of the total (n).

Cells where $f_{obs.} > f_{exp.}$ were chosen to indicate optimal conditions, with the exception of Cell 9 which was included because of its high frequency (13.7% of the total n) and the high frequency of Row 3 and Column 3.

Figures 27 & 28 illustrate the images generated from Models 1 & 2 respectively, together with transparent overlay diagrams illustrating the following: a stylised map of the major rivers, Natal Parks Board (NPB) downstream limits for classified trout waters for selected rivers, point distribution records of known trout waters (Appendix 3), and regions of dispute.

Assessment of Model 1 (Fig. 27): A comprehensive assessment is given in section 6.3.1.3. A brief initial assessment, for the purpose of making adjustments to future models, is given below:

Although the model highlights many well known trout regions in the Drakensberg escarpment, and has excluded many regions, such as the coastal strip, which are obviously unsuitable, there are certain shortcomings in the model. Distribution of trout is indicated as being at lower elevations than the NPB legal limits in the Mkomazi, Bushmans, Pholela and Loteni Rivers (Fig. 27). High-elevation upland regions of the escarpment (Region B, Fig. 27) as well as suitable trout areas in Lesotho (Region A, Fig. 27) have been excluded.

The exclusion of Lesotho from the image probably indicates that the sampling region (in the Himeville/Underberg area) was not representative of the full range of values for the environmental gradients in the predictive region. It is likely that stretches of river in the "temperate" zone above the upper limits for trout occurred in regions in which elevation and rainfall were optimal for trout, but the steep gradient resulted in the exclusion of trout from these sections of the river. The exclusion of these values for elevation and rainfall from the sampling region has resulted in the exclusion of a number of potentially suitable high-elevation regions from the predictive model.

It was therefore decided to repeat this procedure with the inclusion of the (temperate) "T" class of records (i.e. those regions upstream of the present upper limit of trout, which may nevertheless satisfy the thermal requirements of trout).

Assessment of Model 2 (Fig. 28): Model 2 (Fig. 28) is an improvement on Model 1 (Fig. 27) since there is a wider distribution in high elevation regions in the Drakensberg (Region B, Figs 27 & 28) and in Lesotho (Region A, Figs 27 & 28) which are known to be good trout waters (Appendix 3).

Since distribution records in the Drakensberg escarpment and Lesotho are more extensive in

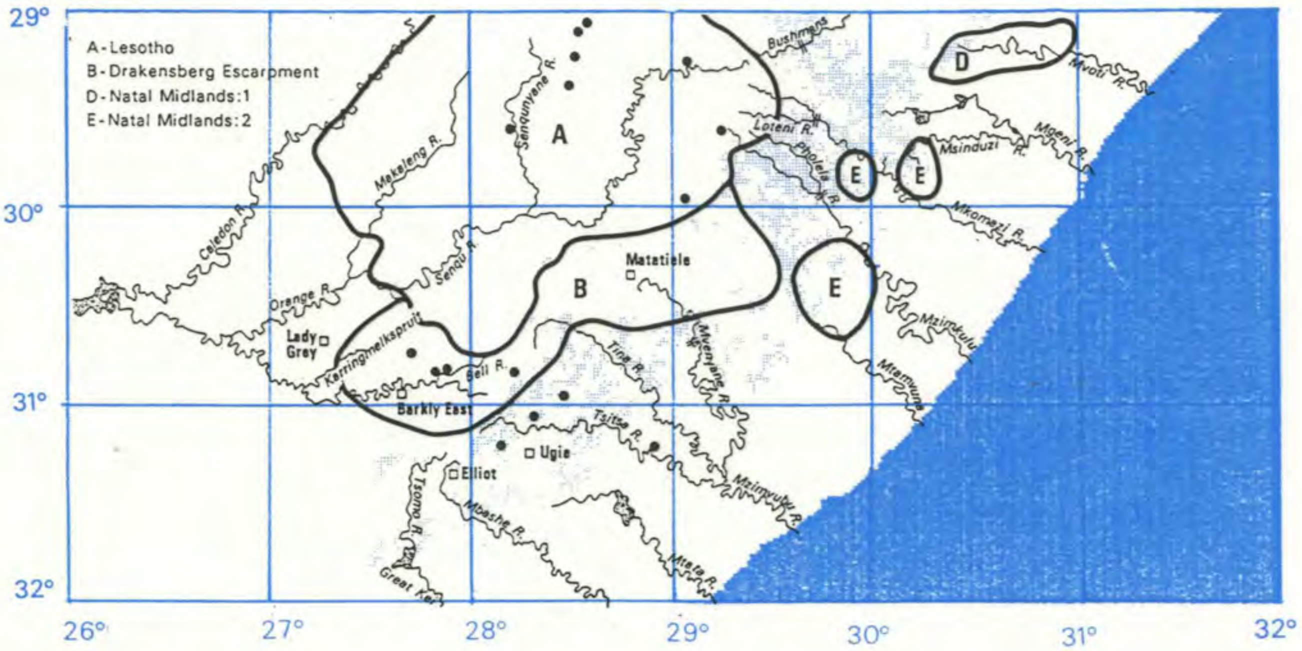

Figure 27: Model 1 (southern Natal/Lesotho/Transkei): Image of regions which are potentially suitable for trout colonisation. The overlay map depicts major rivers, point distribution records of known trout waters, Natal Parks Board legal downstream limits (indicated by) and regions of dispute (A, B, D & E).

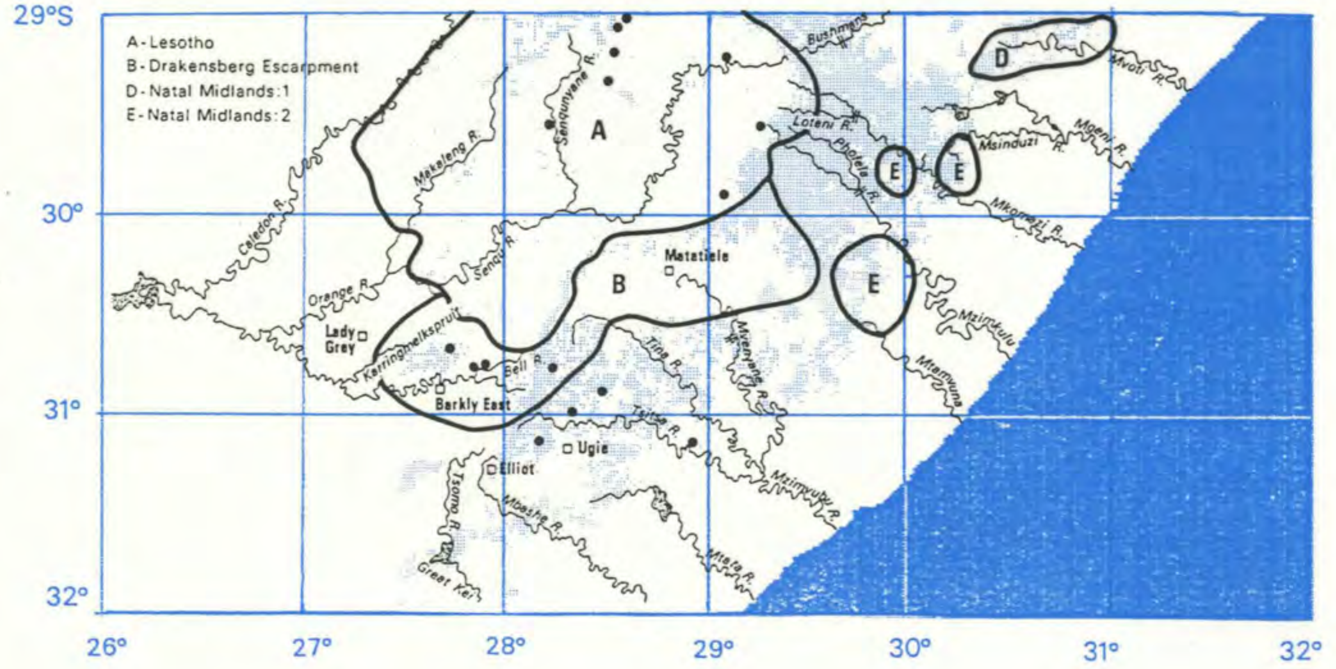

Figure 28: Model 2 (southern Natal/Lesotho/Transkei): Image of regions which are potentially suitable for trout colonisation. The overlay map depicts major rivers, point distribution records of known trout waters, Natal Parks Board legal downstream limits (indicated by) and regions of dispute (A, B, D & E).

Model 2 (Fig. 28) than in Model 1 (Fig. 27) it appears that the problem of the exclusion of high-elevation regions, experienced in Model 1, has been partially overcome with the inclusion of the temperate (T) class of distribution records. It was therefore decided to include this (T) class in all further analyses.

The problem still remains that large regions of high-elevation areas in Lesotho which are known to be suitable for trout colonisation (Appendix 3) are excluded from the model (Region A, Fig. 28). Since Lesotho is at a much higher elevation than the sampling area (i.e. the foothills of the Drakensberg) and also lies in the "rain shadow" of the Drakensberg mountains, it is likely that the full range of elevation and MAR conditions in the predictive area are not represented in the sampling area. One way to overcome this problem is to obtain more samples from the under-represented areas within the predictive region. Trout distribution records from Lesotho were therefore obtained from Dr J.A. Cambray of the Albany Museum (Loxton-Venn report 1993) and from Dr P.H. Skelton (JLB Smith Institute of Ichthyology). These records were from the latitude range of 29°01'S - 29°34'S which is similar to that used for Models 1 & 2 (29°31'S - 29°55'S). For this purpose, point distribution records were obtained from a number of rivers in Lesotho (Appendix 3). As noted in Section 5.2.5, these records are not representative of the full range of suitable elevations within rivers, as is the case for records generated using true downstream limits.

6.3.1.2. Model 3A

Two images were generated by Model 3, the first of which (Model 3A: latitude range of 29 - 32°S) is discussed below. The second image (Model 3B: latitude range of 28 - 29°S) is discussed in section 6.3.2.

Figure 29 illustrates the image generated for the 29 - 32°S latitude region together with a transparent overlay diagram illustrating the following: a stylised map of the major rivers, Natal Parks Board (NPB) downstream limits for classified trout waters for selected rivers, point distribution records of known trout waters (Appendix 3) and regions of dispute.

It is clear that the inclusion of data from Lesotho has improved the model produced, since the image generated by Model 3A (Fig. 29) correlates better with known distribution records in Lesotho, Transkei and the north eastern Cape, than is the case for either of the previous two models (Figs 27 & 28). A comparison of Models 1, 2 & 3A is given in the next section.

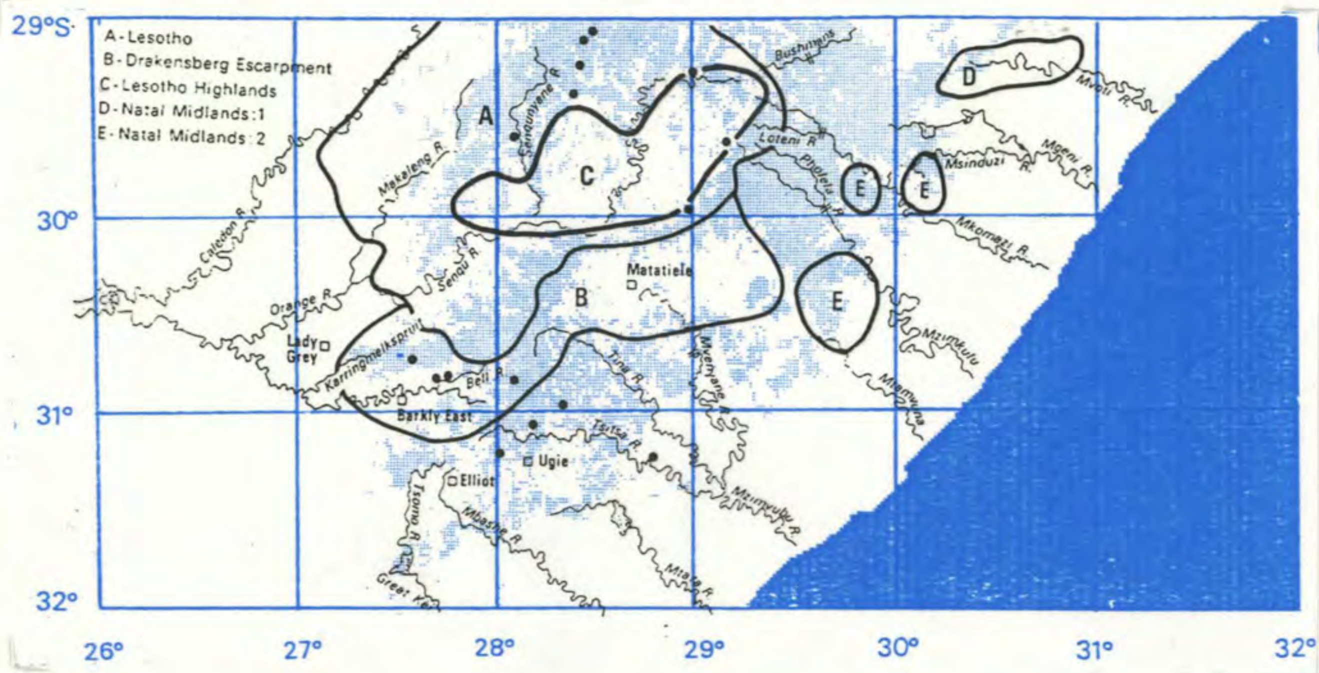

Figure 29: Model 3A (southern Natal/Lesotho/Transkei): Image of regions which are potentially suitable for trout colonisation. The overlay map depicts major rivers, point distribution records of known trout waters, Natal Parks Board legal downstream limits (indicated by) and regions of dispute (A, B, C, D & E).

6.3.1.3. Comparison of Models 1, 2 & 3A

The following experts commented on different regions of the models:

Natal & Lesotho: M. Coke & J. Alletson.

Lesotho, Transkei & North eastern Cape: P.H. Skelton.

Northern Cape (upper tributaries of the Orange): M.T.T. Davies.

Their comments are summarised in Table 16.

Table 16. Comments by experts on the value of images generated by Models 1, 2 & 3A (Figs 27, 28 & 29 respectively) for the southern Natal/Lesotho/Transkei region

Region	Expert opinion	
	Alletson	Coke
Natal midlands	All three models too broad expecially in regions D & E which are too warm for trout.	General agreement with Alletson, but there is a possibility of trout surviving in tributaries of rivers in Region D, but not in mainstream. Nevertheless distribution in this region is too widespread.
	Alletson	Skelton
Drakensb. escarpment /Lesotho	NB trout regions in upper Pholela, Loteni (Region B) & Lesotho (region A), excluded from Models 1 & 2. Model 3A more realistic, but Region C should not be excluded.	Model 3A the most realisitic but Region C should not be excluded.
TransKei & NE Cape		Distrib. in Region B too patchy in Models 1 & 2. Model 3A better in this area. Matatiel region should not be excluded. Image of NE Cape best in Model 3A.
	Davies	
North Cape (Orange R tributs.)	Models 1 & 2 have excluded NB trout waters in upper Orange, including Kraai, Bell & Karringmelkspruit. Model 3A best image.	

6.3.1.4. Summing up assessment of Models 1, 2 & 3A

The overall consensus of opinion is that Model 3A was the best image produced of the expected trout distributions. Models 1 & 2 had a major shortcoming in that large regions of Lesotho were excluded. Alletson also noted that some historical trout waters in the Mvenyane, Bushmans and Umsindusi Rivers are included in Model 3A. Although these were known as good trout waters in historical times, trout are no longer found in these regions, probably as a result of degradation of the rivers. Although Model 3A was judged to be a reasonably good image of expected trout distributions, it did have some shortcomings:

a. In certain areas (Regions D & E) the image is too broad and extends to elevation levels below that of the legal limits of the NPB in many rivers. It is however possible that in many of these regions the upland tributaries flowing into the mainstreams of rivers may be suitable for colonisation by trout, whereas the mainstream (which would be at a lower elevation) may be too warm for colonisation by trout. The resolution of the image (one minute of a degree) is too coarse to represent rivers and their tributaries as separate entities.

b. Some regions (e.g. Region C) which are suitable for trout were excluded from the image.

6.3.2. Northern Natal (Models 3B & 4)

Figures 30 & 31 illustrate the images generated for the 28°- 29°S latitude region (Model 3B) and the 27°- 29°S latitude region (Model 4) respectively. Transparent overlay diagrams associated with these figures illustrate the following: stylised maps of the major rivers, Natal Parks Board downstream limits for classified trout waters in selected rivers, point distribution records of well known trout waters (Appendix 3) and regions of dispute.

Expert opinion on Models 3B & 4 is summarised in Table 17 :

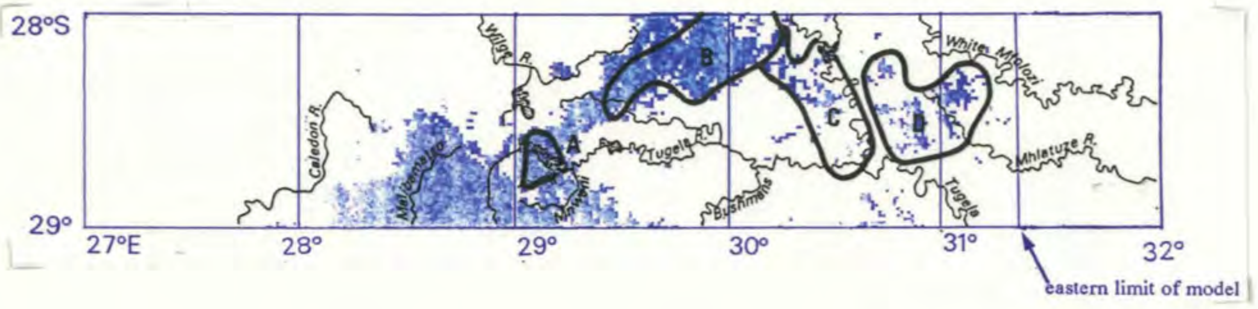

Figure 30: Model 3B (northern Natal; latitudes 28°-29°S): Image of regions which are potentially suitable for trout colonisation. The overlay map depicts major rivers, point distribution records of known trout waters, Natal Parks Board legal downstream limits (indicated by) and regions of dispute (A - D).

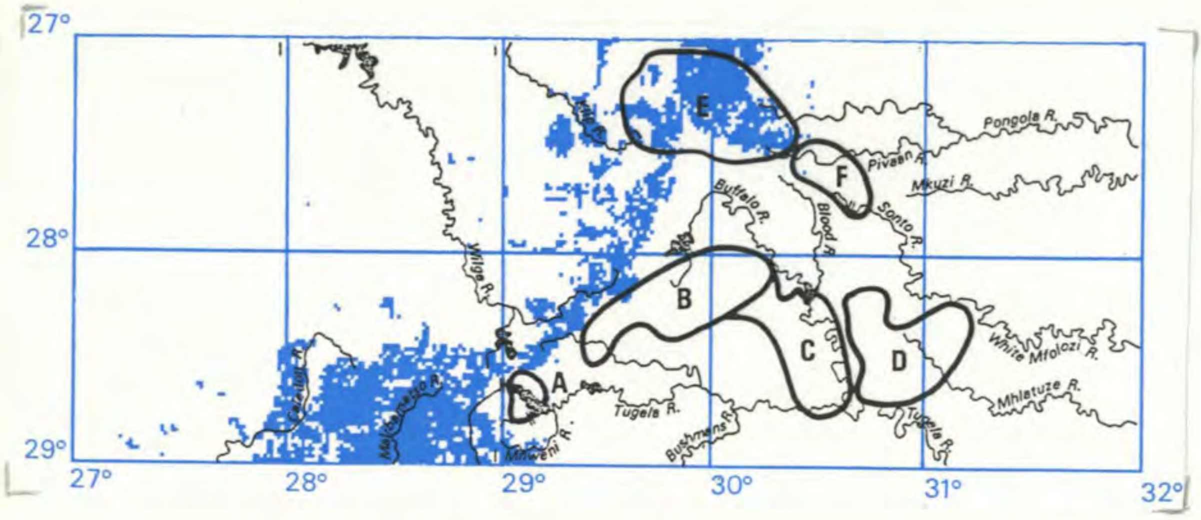

Figure 31: Model 4 (northern Natal; latitudes 27°-29°S): Image of regions which are potentially suitable for trout colonisation. The overlay map depicts major rivers, point distribution records of known trout waters, Natal Parks Board legal downstream limits (indicated by) and regions of dispute (A - F).

Table 17. Summary of expert opinion on the validity of Models 3B & 4 (Figs 30 & 31 respectively) of potential trout distributions in northern Natal

Region	Expert opinion	
	Alletson	Coke
28-29°S section	Image in Model 3B too widespread in regions A, B, C & D. Model 4 a more realistic image for these regions.	Overall agreement with Alletson, except thinks Model 4 may be too "skimpy" in region A.
27-28°S section (Model 4 only)	Overall a good representation	Good overall image, particularly in region E. But too narrow image in Pivaan & Sonto R's. Region F should not be excluded.

It appears from the comments of experts (Table 17) that Model 4 (Fig 31) conforms well with expected distributions of trout, but may be too narrow since the downstream limits are generally at a higher elevation than the NPB downstream legal limits and certain established trout waters (e.g. upper Sonto and Pivaan rivers) are excluded.

There is some evidence (Alletson & Crass pers. comm.) that the distribution of trout in certain rivers in northern Natal (e.g. the Slang River) was more widespread in historical times than at present. This decline in trout has been ascribed to increases in siltation and a general degradation of the river. Since the downstream limit of trout in the Slang River was used to generate distribution records for Model 4, it is likely that this would result in a definition of optimal regions at higher elevations than the true picture, resulting in an image which is too narrow.

6.3.3. South eastern Cape (Models 5 & 6A)

Figures 32 & 33 illustrate the two images generated for the south eastern Cape from Models 5 & 6A respectively, together with transparent overlay diagrams illustrating major rivers, point distribution records of known trout waters (from Appendix 3) and regions of dispute. Because the longitudinal distortion of maps based on a UTM projection (such as IDRISI-generated

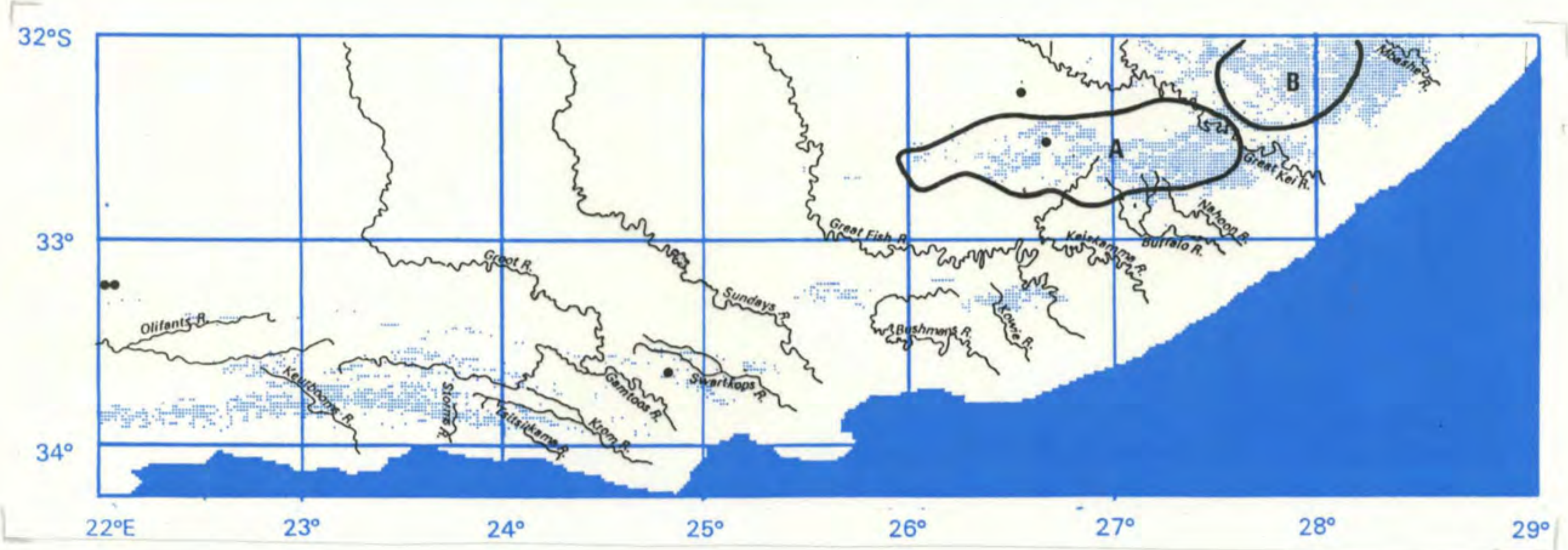

Figure 32: Model 5 (south eastern Cape): Image of regions which are potentially suitable for trout colonisation. The overlay map depicts the upper reaches of major rivers, point distribution records of known trout waters, and regions of dispute (A & B).

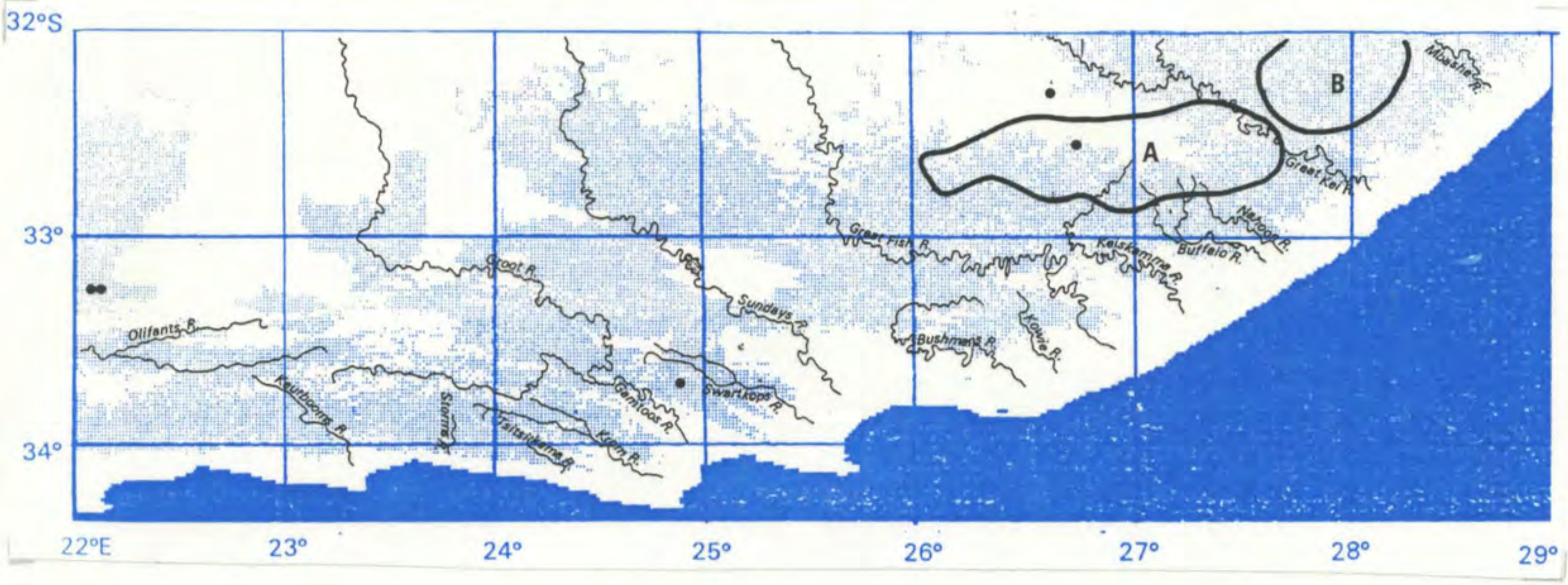

Figure 33: Model 6A (south eastern Cape): Image of regions which are potentially suitable for trout colonisaiton. The overlay map depicts the upper reaches of major rivers, point distribution records of known trout waters, and regions of dispute (A & B).

images) is highest at high latitudes, it was difficult to accurately determine the exact localities of estuaries and lower reaches of rivers on the south-east coast, which extend over a wide longitudinal range. For this reason the coastal sections of rivers were omitted from the overlay maps for Models 5 and 6A. A summary of expert opinion on the value of Models 5 & 6A is given in Table 18.

Table 18. Expert opinion on the value of Models 5 & 6A (Figs 32 & 33 respectively) of potential trout distribution in the south eastern Cape

Region	Expert opinion	
	Skelton	Cambray
S. Cape	Model 5 gives a good image of expected scattered distribution. Model 6A is much too widespread and includes many regions (e.g. mid-Sundays R & Gamtoos R.) which are too warm and arid for trout.	Similar comments to Skelton. Notes the inclusion of regions in the upper Gouritz catchment in Model 6A - too warm for trout.
N E. Cape	Very good image of expected distribution in Region A in Model 5. Distribution in Region B for Model 5 may be too widespread.	Model 5 a good image. Model 6A too widespread in many regions e.g. upper Fish River.

6.3.4. South western Cape (Models 6B & 7)

Figures 34 & 35 illustrate the two images generated for the south western Cape from Models 6B & 7 respectively, together with transparent overlay diagrams illustrating major rivers, point distribution records of known trout waters (from Appendix 3) and regions of dispute.

Expert opinion on the value of Models 6B & 7 was given by Smith & Thorne who demarcated regions A - G on Figs 34 & 35 as being potentially suitable for trout. The following criticisms were noted:

1. Although trout could survive in Regions A - G, the distribution in both Models 6B and 7 within these regions is too widespread.

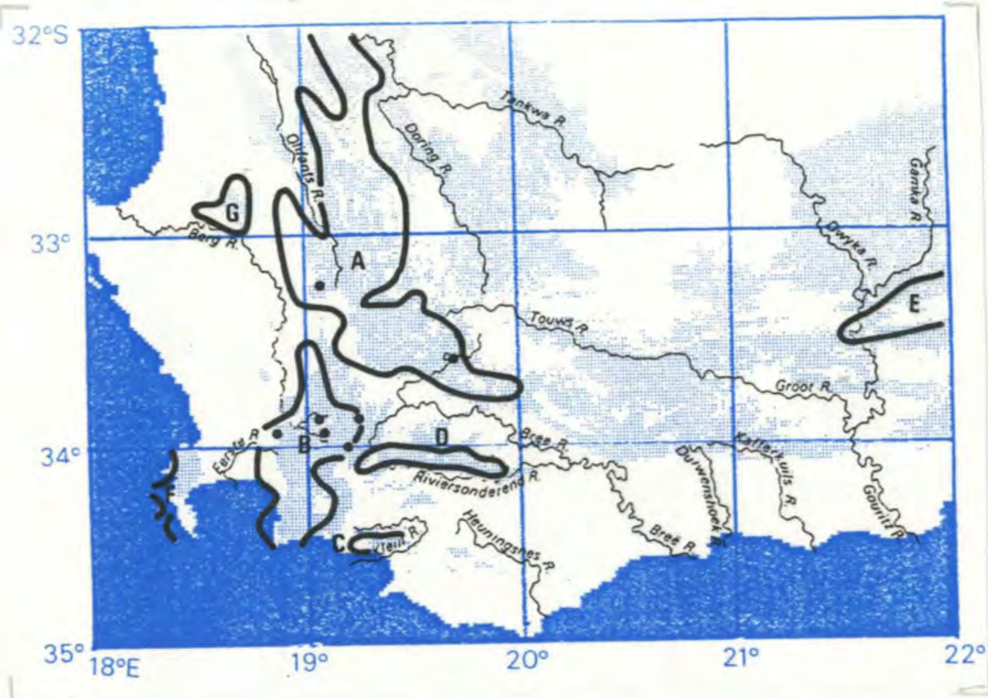

Figure 34: Model 6B (south western Cape): Image of regions which are potentially suitable for trout colonisation. The overlay map depicts the major rivers, point distribution records of known trout waters, and regions of dispute (A - G).

Figure 35: Model 7 (south western Cape): Image of regions which are potentially suitable for trout colonisation. The overlay map depicts the major rivers, point distribution records of known trout waters, and regions of dispute (A - G).

2. It is very unlikely that trout could survive in areas outside the regions (A - G) indicated. Fewer regions outside the potential trout areas (A - G) are indicated in Model 7 than in Model 6B. Model 7 is therefore considered to be a more realistic image than Model 6B. Both models are however considered to be "too widespread".

3. Model 7 does have some merit particularly in regions A, B, C, D & G where it provides a reasonable image of expected trout distributions. The image within these regions should however be more scattered.

Smith (pers. comm.) notes that self-perpetuating populations of trout are rare in the western Cape because winter-rainfall regimes create conditions that are unfavourable for the survival of trout. In summer, temperatures rise and the oxygen tension in the water decreases. A summer rainfall pattern means that greater volumes of water are available during these critical times, and this can offset adverse warm conditions experienced by cold stenothermal species. Winter rainfall patterns mean that the lowest volumes of water are experienced during summer when trout are most vulnerable due to low oxygen tensions in the water. Because of this factor, most regions in the western Cape mountains are marginal for trout, and self-perpetuating populations are only found in isolated pools and shady areas.

Summary of assessments of Models 5, 6 & 7.

The general consensus of opinion is that Model 5 is a more realistic image than Model 6A for the eastern Cape and Model 7 is a better representation than Model 6B for the western Cape. This illustrates that the combination of samples from the eastern and western regions of the same latitude (used to generate Models 6A & B), resulted in an image which was too broad and widespread. The models (5 & 7) in which the sampling region was confined more narrowly to the predictive region, gave more realistic images. This suggests that even when sampling areas are from the same latitude class (as in the eastern and western Cape), it is not advisable to combine samples from widely disparate regions.

6.4.PROBLEMS ASSOCIATED WITH THE USE OF ELEVATION AS AN ENVIRONMENTAL GRADIENT

The problems associated with the use of elevation were discussed in Chapter 5. The main shortcoming is that, since elevation is linked strongly to latitude in determining temperature regimes, predictive regions must be divided into a number of latitude classes.

Making use of air temperature instead of elevation as a surrogate measurement of water temperature would therefore have a number of advantages: sample sizes could be larger as the size of images would not be so severely constrained by latitude considerations. This would mean that models could cover a wider latitudinal range.

6.5. USING AIR TEMPERATURE AND MAR AS ENVIRONMENTAL GRADIENTS

The method used to generate a surface response curve (at a minute x minute resolution) of air temperature data was described in Chapter 5. In this section, two alternative air-temperature datasets were generated - mean monthly January maxima (MJaMax) and mean monthly July minima (MJuMin). Images of these two datasets were produced using the IDRISI programme.

6.5.1. Choosing a suitable temperature parameter

An image of the distribution of a number of arbitrarily-chosen classes of MJaMax temperatures for a region bounded by 29°-34°S and 26°-32°E was generated using the IDRISI programme (Fig. 36).

Maximum temperatures at the coastal regions tend to be more moderate than those in the inland areas (Fig. 36). This is due to the moderating influence of the ocean. The image is therefore not very useful in indicating the temperate regions of the country since inland regions (which are known to be more temperate) often have higher January maximum temperatures than the coastal regions. The (MJaMax) temperatures are therefore not suitable for the present analysis. It was therefore decided to create an image of the mean monthly July minimum (MJuMin) temperatures (Fig. 37) for the same region in order to determine whether this would provide a better representation of temperate regions. This image was created for the southern Natal/Lesotho/eastern Cape region.

The image produced (Fig. 37) appears to be a more realistic representation of temperate zones than that produced using MJaMax temperatures (Fig. 36). Inland regions which are known for their temperate climates are represented as being in the colder regions of the map.

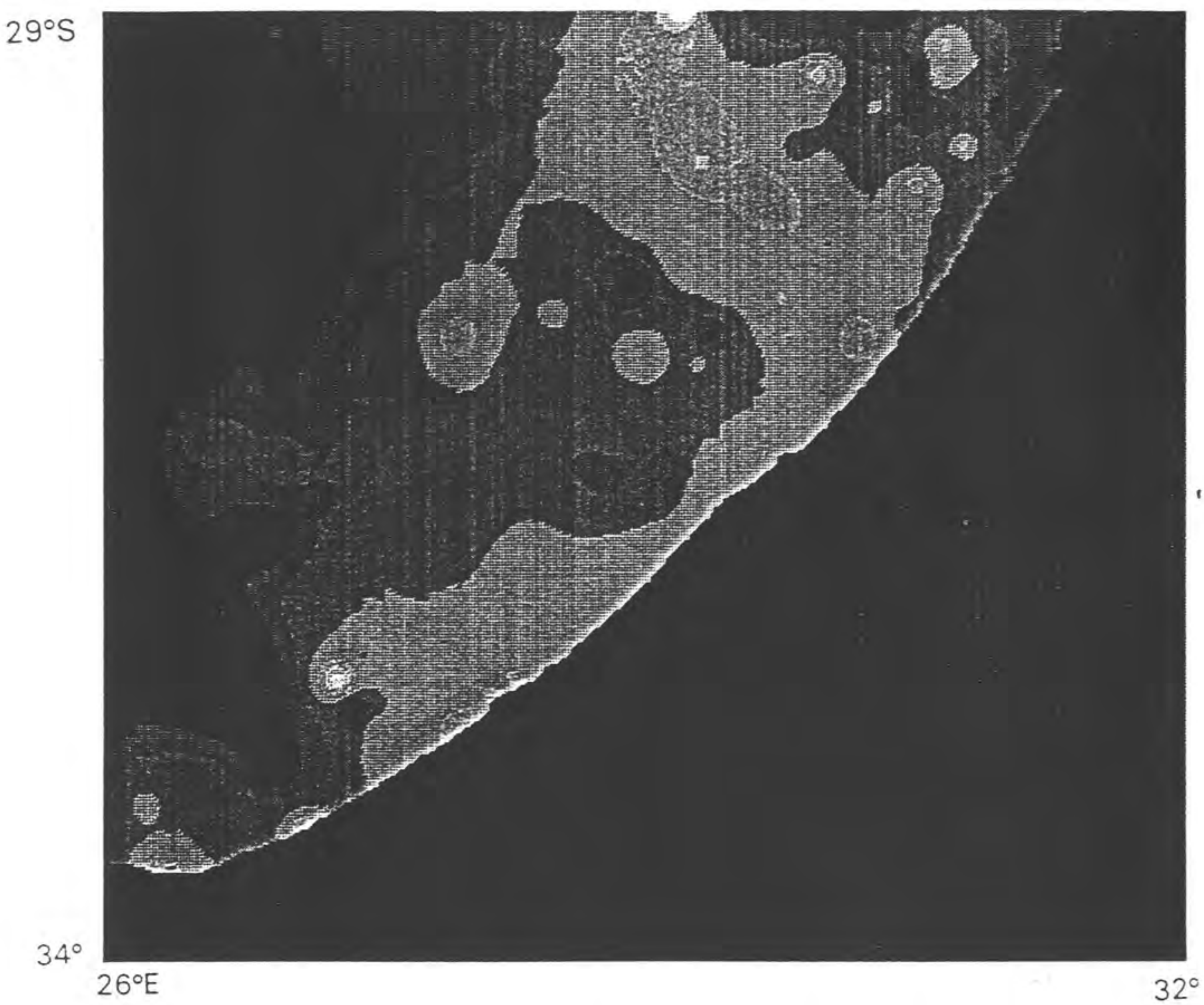

Figure 36: Image of different classes of monthly mean January Maximum (MJMax) temperatures for southern Natal, Transkei and the eastern Cape.

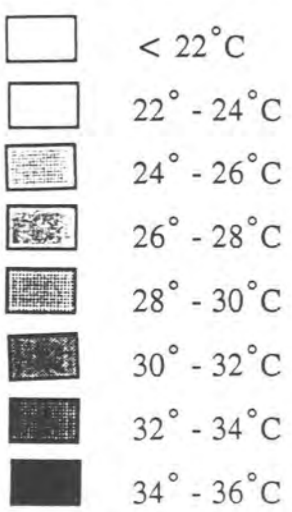

Figure 37: Image of different classes of monthly mean July minimum (MJuMin) temperatures for southern Natal, Transkei and the eastern Cape.

< - 2°C
2° to 0°C
0° to 2°C
2° to 4°C
4° to 6°C
6° to 8°C
8° to 10°C
> 10°C

It was therefore decided to use MJuMin temperatures and MAR as environmental gradients in the analysis. Subject to a few minor modifications (described below), the methods used were the same as those described in Chapter 3 except that temperature was substituted for elevation as an environmental gradient.

6.5.2. Model 8 (southern Natal, Lesotho, Transkei and the eastern Cape)

The latitude ranges of the three sampling regions which were used in this analysis are given below:

Lesotho: range of latitude from 29°01S - 29°52S (36 present-day samples + 57 historical samples from Shortt-Smith 1973).
Southern Natal: range of latitude from 29°31'S - 29°55'S (626 samples).
Eastern Cape: range of latitude from 32°35'S - 32°44'S (38 samples).

A total of 757 distribution records were generated . Some of these which were found to be duplicates, were rejected from the CCWR database. For this reason, the final analysis in the contingency table is based on 748 samples (Table 19).

The range of the predictive map is:

Latitude 29°00'S - 34°00'S
Longitude 26°00'E - 32°00'E.

6.5.2.1. Modifications to the methods used

Because the datasets (for MAR and MJuMin temperatures) were from different sources it was difficult to combine them in order to construct a scattergram showing the frequency of trout distributions in relation to MAR and temperature conditions. For this reason categories (of MAR and MJuMin temperature) suitable for further analysis were chosen independently of each other as described below:

MAR categories were chosen after examination of a frequency histogram (Fig. 38).

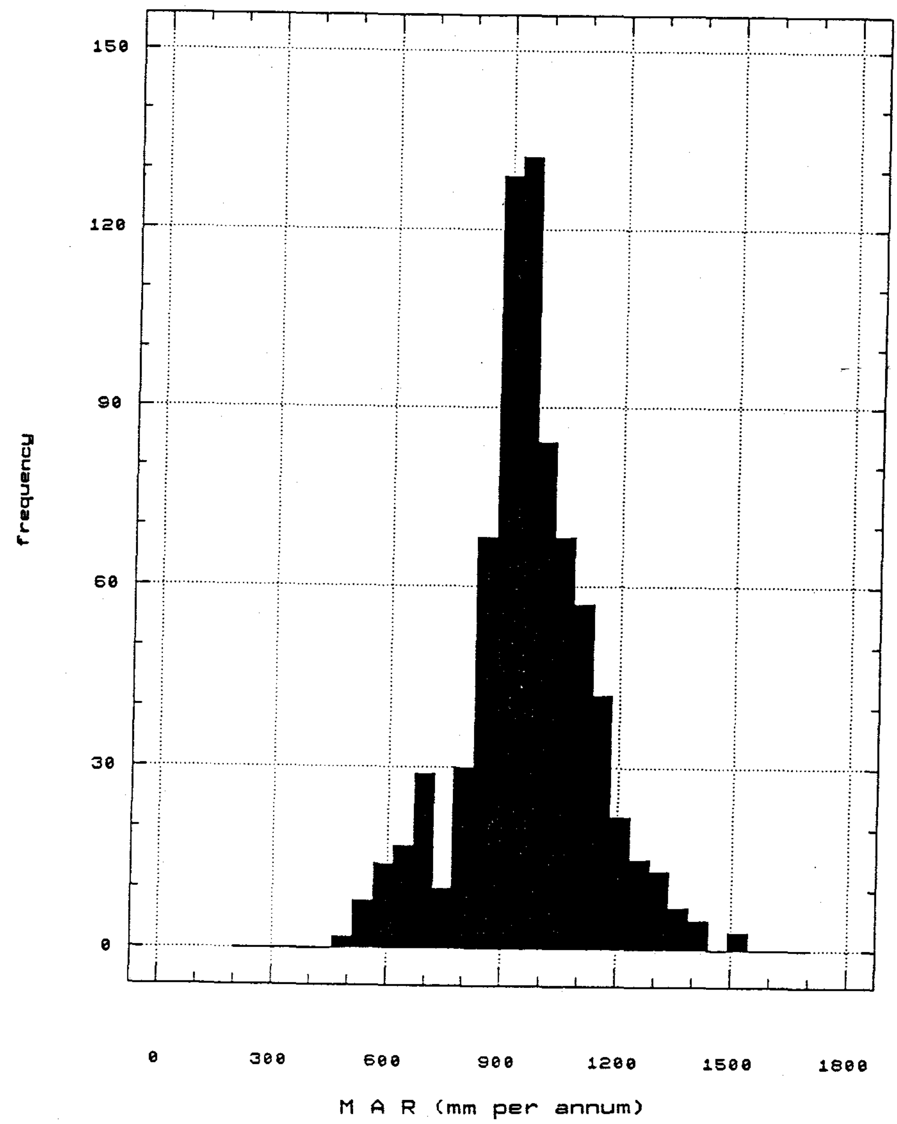

Figure 38: Model 8: Frequency histogram of MAR (mm per annum) associated with distribution records obtained from Natal and the south eastern Cape.

Mean monthly July minimum (MJuMin) temperatures for each distribution record were ranked using a spreadsheet. Categories were assigned after the range and frequency were assessed by examining the database and choosing categories aimed at generating classes with an approximately even frequency of results in each class.

The categories chosen for both MAR and MJuMin temperatures are illustrated in the contingency table of observed and expected frequencies of trout distribution in different MAR and MJuMin temperature classes (Table 19).

Table 19. Model 8: Contingency table of observed and expected frequencies ($f_{obs.}$ & $f_{exp.}$) of trout distribution in different median annual rainfall (MAR) and monthly mean July minimum (MJuMin)(air) temperature conditions.

(MJuMin) Temp (°C)	MAR (mm per annum)					
Category No	1 500 - 600	2 600 - 800	3 800 - 1000	4 1000 - 1200	5 >1200	Row Total
1 -4.0 to -2.0	[1]0 4	[5]0 12	[9]120* 61	[13]0 34	[17]0 10	120
2 -2.0 to 0.0	[2]18 15	[6]7 42	[10]207* 220	[14]160* 121	[18]42* 35	434
3 0.0 to 2.0	[3]4 5	[7]57* 15	[11]39* 80	[15]46* 44	[19]11 13	157
4 2.0 to 6.0	[4]4 1	[8]8 4	[12]14* 19	[16]4 10	[20]7 3	37
Column Total	26	72	380	210	60	748

$f_{obs.}$ = upper figure in each cell.
$f_{exp.}$ = lower figure in each cell.
Superscripts indicate cell number (for discussion purposes)
* Categories indicating optimal conditions.

Chi-squared = 319.473

Degrees of freedom = 12

Significance $P < 0.00001$

* = 91.58% of the frequency of the total (n).

Cells where $f_{obs.} > f_{exp.}$ were chosen to indicate optimal conditions, with the following exceptions:

Cells 10, 11 and 12 were included because of their moderately high frequencies and the high frequency of Column 3. Cell 2 was excluded because of the low frequency of Column 1.

6.5.2.2. Image of susceptible regions

Figure 39 illustrates the image generated (excluding the 31°-32°E region) together with a transparent overlay diagram illustrating a stylised map of the major rivers, point distribution records of known trout waters (from Appendix 3) and regions of dispute.

Assessment of Model 8: Except for one small region in the Katberg area (Region G, Fig. 39) the eastern Cape has been largely excluded from the image (Fig. 39). For a comparative assessment of the Natal/Transkei region of this model a section of the image (from 29 - 32°S) has been enlarged in order to conform with the scale used in the image generated by Model 3 (Fig. 29). This modified image, together with an overlay map illustrating point distribution records of known breeding populations of trout (Appendix 3), major rivers and regions of dispute, is illustrated in Fig. 40.

6.5.2.3. Comparison of Models 3 & 8 (29-32°S section)

The image generated by Model 8 (Fig. 40) was compared with the most suitable model from the southern Natal region (Model 3, Fig. 29). Mr J. Alletson commented on the Natal/Transkei section of the model (29-32°S) and P.H. Skelton commented on the eastern Cape section. A summary of their comments is given below:

Alletson and Skelton both noted that the images are very similar in the Natal region. Model 8 (Fig. 40) was regarded as a more realistic reflection of the expected distribution of trout in the uplands regions of Lesotho (Region C). There is also a denser distribution in the Matatiel region of the Transkei. The overall impression is that the images are very similar, but Model 8 is regarded as being a better image than Model 3 for the Natal/Lesotho/Transkei regions.

Skelton's comments on the eastern Cape section of Model 8: It was noted that, with the exception of one outlying distribution point in the Katberg (Fig. 39 region G), the south eastern Cape is not represented at all. Model 8 is therefore not regarded as a good representation, since many well-known trout regions such as the Hogsback have been excluded.

The overall impression of Model 8 (Fig. 40) is that it provides a good representation of Lesotho, Natal, Transkei and the north eastern Cape, but the image in the south eastern Cape is very poor. This suggests that the results are skewed towards the optimal conditions as

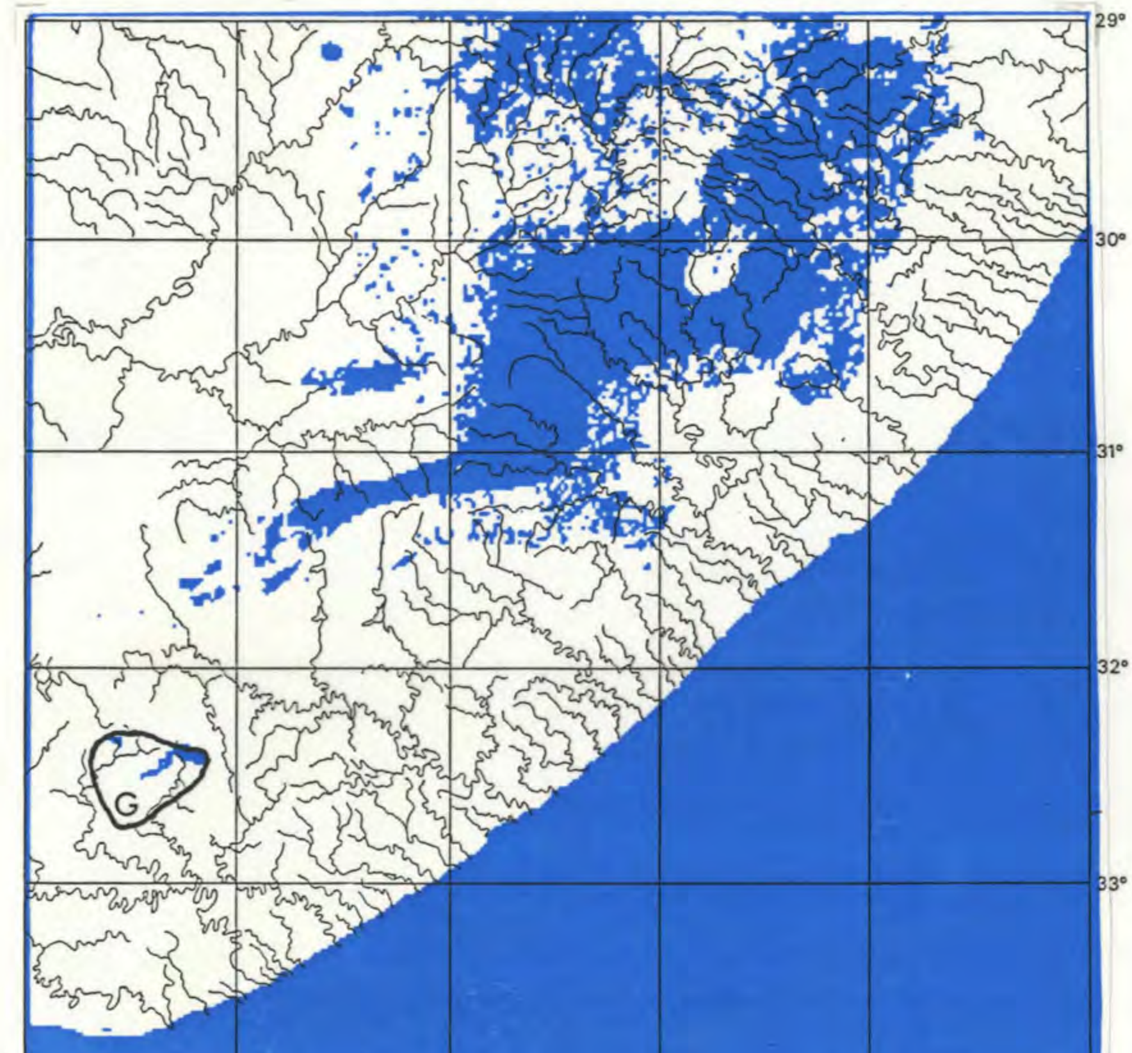

Figure 39: Model 8 (29°-34°S; 26°-31°E section): Image of regions in southern Natal, Lesotho, Transkei, North eastern Cape and south eastern Cape which are potentially suitable for trout colonisation. The overlay map depicts major rivers and a region of dispute (G).

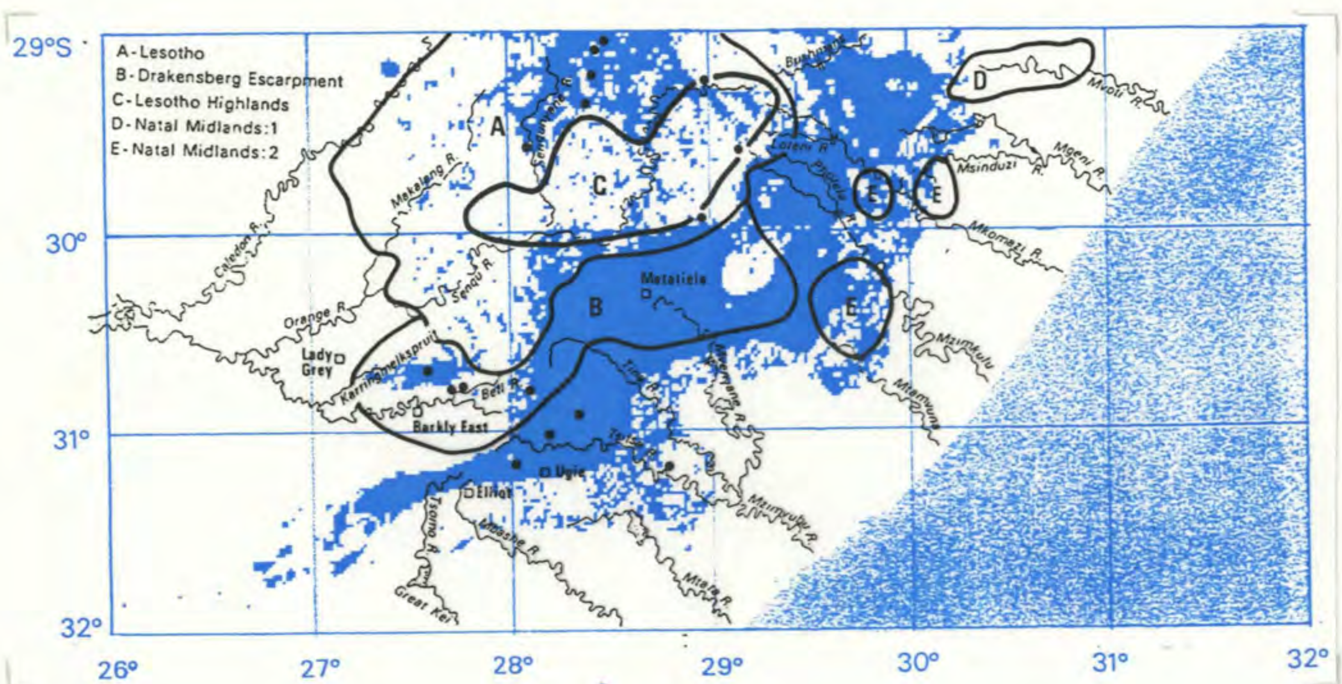

Figure 40: Model 8 (29°-32°S; 26°-32°E section): (southern Natal/Lesotho/Transkei): Image of regions which are potentially suitable for trout colonisation. The overlay map depicts major rivers, point distribution records of known trout waters, Natal Parks Board legal downstream limits (indicated by) and regions of dispute (A, B, C, D & E).

defined in the southern Natal region where most of the distribution records were obtained. Only 38 records were obtained from the eastern Cape region (32-34°S) whereas the remaining 710 records were from the Natal/Lesotho region (29 - 32 S). It is clear that these samples were weighted in favour of the Natal/Lesotho samples.

6.6. OVERALL ASSESSMENT OF MODELS 1 - 8

The following models were chosen by experts as being the most suitable:

Southern Natal/ Lesotho/Transkei: Model 3 or Model 8*

Northern Natal: Model 4
South eastern Cape: Model 5

South western Cape: Model 7

* This model also covered the south eastern Cape, and was found to be suitable for the southern Natal/Lesotho & Transkei regions, but not for the eastern Cape region.

Since the compilation of Models 1 & 2 can be regarded as part of the process of refinement of techniques leading to the development of better models (Model 3), the assessment of the validity of this method should disregard these models.

With the exception of a few problem areas, the overall assessment of Models 3, 4, 5 and 8 by experts was favourable. Model 7 was regarded less favourably, but still had some merit in predicting potential trout waters. The model which received the least favourable assessment was Model 6 (of the south eastern and south western Cape) in which large regions selected by the model as being "potentially suitable for trout" were regarded as being too warm and arid for trout.

Of the six models assessed here, four (Models 3, 4, 5 & 8) were judged favourably, one was judged to have some merit (Model 7) and one was judged to be a poor model (Model 6). This indicates that there is some validity in the GIS methods used.

It is interesting to note that the image of the southern Natal/Lesotho/Transkei region generated by Model 8 (Fig. 40), based on temperature and MAR as environmental gradients, is very similar in general outline to Model 3 (Fig. 29) where elevation and MAR were used as environmental gradients. This demonstrates that making use of two different variables (air temperature and elevation) as surrogates for water temperature made very little difference to the final model. This is a clear demonstration of the flexibility, resilience and redundancy inherent in this approach to biogeographical analysis.

6.7. SUGGESTED GUIDELINES FOR IMPROVING THE METHODS USED

The results suggest certain guidelines which should be adopted regarding the collection of distribution records, the relationship between sampling regions and predictive regions and the reduction of errors. These are described below:

a. Samples should be representative of the full range of conditions in the predictive region. The problem associated with unrepresentative samples is demonstrated by the unsatisfactory image of Lesotho generated by Models 1 & 2.

b. As far as possible sampling should be carried out at the same intensity for all different conditions of elevation and MAR.

c. Although it may be generally desirable to use an environmental gradient (e.g. temperature) which, unlike elevation, is not severely constrained to a limited latitude range, it still appears that combining samples from widely different areas can cause problems due to weighting effects and extraneous factors such as seasonality of rainfall.

d. As far as possible, only rivers with a high conservation status should be used as a basis for generating a database of sampling regions. It may be advisable to consult a reference such as O'Keeffe (1986) on the conservation status of the rivers in the proposed sampling region, prior to making a decision regarding the choice of rivers to be used to generate the database.

e. Decisions relating to the choice of classes (from the contingency table) regarded as representative of optimal conditions must be made very carefully. A choice which is too broad (for example one in which rainfall is defined as "less than 600mm") can lead to images which are too broad. A general criticism of many of the models drawn up is that they were too broad and often included regions which were too warm or arid for trout colonisation. In many of these cases low elevation classes were chosen from contingency tables (for example Cell 9 of

Table 10 for Model 2; Cell 9 of Table 11 for Model 3 and Cell 10 of Table 14 for Model 6) in which $f_{obs.} < f_{exp.}$. These cells were chosen either because of their high frequency or the high frequencies of rows or columns (in the contingency table) associated with the cells. In retrospect, it appears that these choices were not the correct ones. It should be noted that, in this type of analysis, there is a certain amount of redundancy in the system so that the inclusion or exclusion of single classes does not usually make a significant difference to the final image (pers. obs. and Palmer pers. comm.). Nevertheless the models may have generated improved images if these particular cells had been excluded.

f. An analysis is only as good as its database. Some of the shortcomings in the models drawn up can be related to shortcomings in the database. The "gap" (Region C, Fig. 29) in Model 3 for Lesotho may be due to the fact that samples from this region are based on point distribution records and not on downstream limits as is the case for the data in other regions. The distribution records in Lesotho are therefore not representative of the full range of elevations in which trout are found in the rivers. The CCWR database and the temperature database used in Model 8 are both based on weather station data which is more scattered in the inaccessible highland regions of Lesotho. The database in this region is therefore not as reliable as in regions with less complex physiography (Dent et al. 1989). Other problems with the quality of the database will be discussed in Chapter 8.

CHAPTER 7: CRITICAL ANALYSIS OF THE LOGIC AND ASSUMPTIONS IN THE THESIS

The purpose of examining the logic which underlies this thesis is to expose the arguments in their simplest form so that they can easily be evaluated by someone who has a knowledge of the subject.

7.1. DEFINITIONS OF TERMS USED IN ARGUMENTS

In the arguments described below, the following terms have been used:

1. "Survival": the ability to survive and breed in an environment. This is not how the term "survival" has been used in the main body of the thesis, but the term is re-defined here for the sake of brevity in the following arguments.

2. "Thriving": If a species is able to maintain self-sustaining (breeding) populations it is said to be "thriving" in the environment.

3. "Regions": refers to areas of land (including rivers and other waterbodies).

The terms "direct gradients", "indirect gradients" and "surrogate variables" have been described in Chapter 2. A number of other terms are defined in the arguments presented in this chapter. These are: "indicator species", "selected biogeographical models", "close links", "discrepancies" and "suitable habitat for trout".

7.2. ARGUMENTS USED AS A BASIS FOR BOTH METHODS DEVELOPED IN THE THESIS

Argument 1

Premise A: In order for thriving populations of aquatic animals to survive in a particular river system, the following two conditions must be satisfied:

1. The species must have had the opportunity to invade the system some time in the past.

2. Environmental conditions (encompassing abiotic and biotic conditions) must be suitable for

the survival of the species.

Premise B: Species A has had the opportunity to invade all sections of a particular river system.

Conclusion 1A: The presence of breeding populations of Species A in the river or sections of the river indicates that environmental conditions are favourable for the survival of Species A in the regions where it is found.

Conclusion 1B: The prolonged absence of breeding populations of Species A from the river or sections of the river indicates that environmental conditions in these sections are not suitable for the survival of Species A.

Corollary of Conclusion 1A: If the environmental tolerances of species A are well known, then a study of the distribution patterns of Species A tells us something about the environmental conditions (within regions where it is known that species A has had the opportunity to invade) where Species A has survived. If species A is a stenotopic species then it will only survive in restricted conditions, and its presence can be used as an indicator of the distribution of these restricted conditions in different regions.

Argument 2

Premise C: Water availability and temperature regimes are not the only variables affecting the distribution of species in aquatic ecosystems, but they are very important variables affecting such distributions.

Conclusion 2A (Premise D): If a species is to survive in a particular region, then the water availability and temperature conditions in the region must satisfy its habitat requirements.

Conclusion 2B (based on premise D): If the water availability and temperature conditions in a particular region satisfy the habitat requirements of a particular species, then that species has a potential to survive in the region.

Corollary 1 of Conclusion 2B: If the water availability and temperature conditions in a region do not satisfy the habitat requirements of a particular species, then the species will not survive in the region, even if other factors affecting its survival are suitable.

7.3. ARGUMENTS USED AS A BASIS FOR THE DEVELOPMENT OF THE "TRADITIONAL METHOD" (CHAPTER 4)

Argument 3

Premise E (rephrasing of the Corollary of Conclusion 1A): The distribution of stenotopic species can be used as an indicator of prevailing physical conditions in the environment, providing that it can be shown that such stenotopic species have had the opportunity to invade the regions concerned.

Premise F: Certain alien aquatic species have been widely introduced into many catchments in southern Africa. They have therefore had the opportunity to invade most of the river systems in southern Africa.

Premise G: Indigenous aquatic species have not had the opportunity to invade most of the river systems in southern Africa.

Conclusion 3: When studying large regions of southern Africa, stenotopic alien species which have been extensively introduced into many different catchments, are better indicators of prevailing conditions than indigenous species. These alien species are referred to as "indicator species".

Argument 4

Background information relevant to Argument 4:

Certain "traditional" biogeographical models (defined here as "selected biogeographical models") have been selected for the purpose of the present analysis. Although the primary purpose of these models is to describe the distribution patterns of selected groups of aquatic, semi-aquatic or terrestrial animals, the criteria used to separate different biogeographical regions in these models are based on rainfall regimes and/or air temperature regimes.

Premise H: Selected biogeographical models describe the distribution of (air) temperature regimes and/or rainfall conditions in southern Africa.

Premise I: Air temperature can be regarded as a reasonable surrogate variable of water temperature and rainfall can be regarded as a reasonable surrogate variable of water availability in aquatic environments.

Conclusion 4: Selected biogeographical models tell us something about water temperatures and water availability conditions in aquatic environments in southern Africa.

Argument 5

Premise J (Corollary of Conclusion 1A): The distribution of thriving populations of indicator species tells us something about the temperature regimes and/or water availability conditions in aquatic environments in regions where the species is thriving.

Premise K (Conclusion 4): Selected biogeographical models tell us something about the temperature and/or water availability conditions in the aquatic environment in southern Africa.

Conclusion 5: Comparisons can be made between the distribution patterns of indicator species and biogeographical regions in selected biogeographical models.

Argument 6

If the comparisons in Conclusion 5 are acceptable then the assumption is made that such comparisons can be used to evaluate selected biogeographical models in terms of their usefulness in predicting temperature and water availability conditions in freshwater environments in southern Africa.

In this context two terms are defined before proceeding with the next argument:

"Close link": Where there is a close correspondence between the distribution of an indicator species and the biogeographical regions described in selected biogeographical models, this is described as a "close link". An example of a "close link" would be where cold stenothermal indicator species are only found in regions described as "moist temperate" in the selected biogeographical model.

"Discrepancy": Where the distribution of indicator species does not correspond with the biogeographical regions described in selected biogeographical models, this is called a "discrepancy". An example of a "discrepancy" would be if cold stenothermal species were found in regions described as "warm and arid" in the selected biogeographical model.

Argument 6 proceeds from the assumption and definitions described above.

Premise L: The existence of close links in the comparison between the distribution of indicator species and appropriate biogeographical regions in a selected biogeographical model, indicates that the model can be regarded as an acceptable description of temperature and water availability conditions in aquatic environments in regions where such close links occur.

Premise M: The existence of discrepancies between the distribution of indicator species and appropriate biogeographical regions in a selected biogeographical model implies that the model is a not a good description of conditions in aquatic environments in regions where such discrepancies occur.

Conclusion 6: A selected biogeographical model which has many close links and/or few or no discrepancies with distribution patterns of indicator species, can be regarded as an acceptable model in terms of its description of water availability and/or temperature conditions in the aquatic environment.

7.4. ARGUMENTS ASSOCIATED WITH THE GIS ANALYSIS (CHAPTERS 5 & 6)

Argument 7

Premise N: Within the range of temperatures found in rivers in southern Africa, trout are not limited by low temperatures, but are limited by temperatures above approximately 22°C.

Premise O: Temperatures in river systems increase with a decrease in elevation.

Conclusion 7: Daily average temperatures in a river at the downstream limit of the distribution of trout represent the highest daily average temperatures at which trout are found in the river. The temperature regimes of all regions of the river upstream of this point are suitable for the survival of trout.

Assumption and definition relating to suitable habitats for trout:

Based partly on Argument 7, it is assumed in this thesis that all sections of a river (including the mainstream and tributaries) at elevations higher than the downstream limit of trout until the point is reached where the flow of the tributaries becomes seasonal are "suitable habitats for trout in terms of water availability and temperature conditions". This term has been abbreviated as $S_{w,t}$.

Argument 8

Premise P: Conditions in regions with a high concentration of $S_{w,t}$ are more suitable (in terms of water temperature and availability conditions) for trout than in regions with a low concentration of $S_{w,t}$.

Premise Q: Regions with a high concentration of $S_{w,t}$ can be defined as being "optimal trout areas."

Conclusion 8: The temperature and water availability conditions in regions with the highest concentration of $S_{w,t}$ can be defined as being optimal for trout.

Argument 9

Premise R (rephrasing of Conclusion 8): A study of water availability and temperature conditions in regions where there is a high concentration of $S_{w,t}$ tells us something about the conditions (in terms of water availability and temperature) which are favourable to trout.

Premise S: Trout's habitat requirements in terms of temperature and water availability conditions will not change in different regions.

Conclusion 9: If there is a high concentration of $S_{w,t}$ in one region (Region A), then if we find another region (Region B) which has similar environmental conditions (in terms of water availability and temperature conditions) to region A, then we can expect that there will also be a high concentration of $S_{w,t}$ in Region B.

7.5. EVALUATION OF ARGUMENTS

The judgement on whether or not the premises in the above arguments are acceptable, and whether they lend sufficient support to the conclusions, must be made by the reader of the thesis, based on evidence and arguments presented in the thesis. Govier (1988) lists a number of standards by which premises can be judged to be acceptable. It could be contended that all the premises described in the arguments above should be accepted on the basis of one of the following standards of Govier (1988):

a. The premise is defended by a cogent sub-argument,

b. It is common knowledge (to an expert in the field of ecology and/or biogeography),

c. It is based on proper (credible) authority.

CHAPTER 8: DISCUSSION

8.1. COMPARISON OF THE TRADITIONAL AND GIS METHODS

The model which was developed using the traditional approach describes regions which are susceptible to invasion by cold stenothermal, warm mesothermal and eurytopic species. The models developed using the GIS approach are only concerned with potential trout distributions.

Trout can be regarded as an indicator species of temperate conditions. The image generated by one of the GIS models (Model 3) of "potential trout distribution" can therefore be compared to the "temperate regions" described in the model developed using traditional methods. A comparison between Model 3 (Fig. 29) and the equivalent region (bounded by 29°-32°S and 26°-32°E) in the traditional model (Fig. 17) indicates the following:

a. Known trout distributions in the Orange Free State/ Lesotho regions (from de Moor & Bruton 1988) correspond more closely with Model 3 than the traditional model.

b. The boundaries between different zones are more complex in Model 3 than in the traditional model where boundaries are demarcated by smooth lines. This is a feature of scale and indicates that Model 3 (which has a greater scale and higher resolution) has a greater sensitivity to local conditions than the traditional model.

The image generated by Model 3 (Fig. 29) represents an extensive dataset of trout distribution and related information on MAR and Elevation. These data are stored on computer files and can be examined and manipulated. Information on the exact localities of trout distributions is easily retrieved and the database can be refined and updated. Sections of the image can be enlarged in order to produce detailed images of potential distributions of trout in selected localities. Because of these capabilities it is possible to test the model or regions of the model by means of comparison with known distribution records of trout.

The Model developed using the traditional techniques has none of the above-mentioned capabilities. Because of its lack of flexibility and coarse resolution, it is difficult to test the validity of this model. It may be possible to discern gross errors, but it would not be possible to compare the model to distribution records at a finer scale, as is the case for the GIS models.

The GIS model is clearly more accurate, flexible and testable than the "traditional" model. GIS techniques therefore represent a more rigorous and scientific approach to biogeographical modelling than the traditional methods. There are some disadvantages in the GIS approach since it is time-consuming, expensive, and dependent on the existence of large computerised datasets.

If there is no clear advantage in developing an image of such fine resolution, then it may be more desirable to make use of traditional models to predict regions which are susceptible to invasion by alien species. The reliability of such models is however difficult to test.

8.2 CRITICISMS AND SUGGESTED IMPROVEMENTS TO THE GIS TECHNIQUES

A shortcoming of the GIS analysis is that no account has been taken of regions in which there is an absence of trout. A model based on presence and absence data would have more validity than the models developed in the present thesis, which are based only on the presence of trout.

The evaluation of GIS models by means of eliciting expert opinion may be regarded as being too subjective, since experts may sometimes make mistakes in their evaluation of potential trout regions. It may be possible to devise more rigorous methods for the evaluation of models such as the intensive collection of samples along the lengths of certain rivers. This would not test the whole model but may test the validity of the model in selected regions. Such a method of evaluation would also be subject to errors normally encountered in sampling populations from natural waters.

The lack of suitable reference points on IDRISI images represents a major problem in the study. This problem was partially overcome through the compilation of stylised overlay maps of rivers corresponding with the regions described by the models of potential trout distribution. This solution is not entirely satisfactory since it would be preferable to have a more accurate (digitised) map of rivers to use as an overlay map for the models. Problems relating to scale (discussed later in this section) also arise when making use of overlay maps of rivers.

There are many areas of uncertainty in the GIS models generated. These include problems relating to uncertainties in the database (described by Dent et al. 1989) and in seasonal variation in the extent of trout distributions. An attempt was made to account for seasonal differences by defining certain regions close to the downstream limits of trout as being subject to seasonal variation (i.e. marginal areas in the sampling data). No attempt was made to describe seasonal variation in the predictive models.

A problem was also experienced with errors and uncertainties associated with scale in the models. When models of potential trout distribution were shown, together with the overlay map of rivers, to nature conservation officials for assessments, erroneous expectations were created regarding the accuracy of the image. The user was guided into assessing the distributions of trout in particular rivers, whereas the resolution of the image is not fine enough to depict rivers as separate entities. For example, in some regions it may be possible for trout to exist in the highland tributaries of some rivers, but not in the mainstream depicted on the overlay map. The image would be based on CCWR estimates of elevation in the surrounding regions and not on the elevation at the mainstream which would be lower than that of surrounding areas. This represents a problem in the communication of the results. A solution would be to make use of localities such as towns or political boundaries, rather than rivers, as reference points. This would reinforce the impression that the model is "area based" and designed to predict regions where suitable habitats of trout may be found.

In this study it was assumed that there was a sufficient correlation (or congruency) between surrogate variables and direct variables affecting trout distributions. The degree of congruency will vary according to localised conditions. It is difficult to assess the suitability of surrogate variables other than by assessing the validity of the model produced.

Only one out of the six models assessed in Chapter 6 received predominantly unfavourable comments from experts, and another Model was regarded as having some merit. The fact that the remaining four models received favourable comments, suggests that the use of MAR and elevation as surrogate measurements in the present study was acceptable. Nevertheless, some of the problems associated with the use of these surrogates are discussed below. Possible alternative surrogate variables are also examined.

a. *MAR as a surrogate of water availability:* There are problems associated with regions in which there is a high rainfall in the upper catchment and a low rainfall in the lower catchment. The true value of water availability in regions of the lower catchment would be higher than that suggested by measurements of MAR in the region.

In regions where there have been major alterations to the flow rate of rivers, such as excessive water abstraction and interbasin transfers, it can be expected that MAR would not always be a reasonable surrogate measurement of water availability in particular river systems.

There are a number of possible alternative surrogate variables for water availability: median annual runoff is more closely related to the actual amount of water reaching rivers than median annual rainfall (MAR). Data on median annual runoff are available through the Department of Water Affairs, but are not yet accessible as a single dataset through computer networks (Anon 1986).

b. *Elevation as a surrogate of air temperature:* Potential problems associated with the suitability of elevation as a surrogate variable for air temperature were discussed in Chapter 2. Results suggest that these problems were not as great as was first imagined. Provided that the latitude range of the models was restricted, it appeared that latitude effects were not significant. This is demonstrated by the favourable image of the south eastern Cape (latitude 34°S) produced in Model 5 (Fig. 32) which was based on distribution records obtained at latitudes at the extreme northern region of the model (32°25'S). The fact that Model 3 (based on the use of elevation as a surrogate of water temperature) and Model 8 (based on the use of air temperature as a surrogate for water temperature) produced similar images of the southern Natal region suggests that elevation is a reasonable surrogate variable for temperature.

The CCWR has recently developed an air temperature database but the results have not yet been published (Palmer pers. comm.). It is not certain whether or not this database would be a more suitable surrogate variable than elevation. Such a possibility would need to be tested once the data is made available.

8.3. APPLICATIONS OF THE METHODS DEVELOPED USING GIS TECHNIQUES

The GIS method was developed to predict potential regions suitable for colonisation by trout. If it is assumed that trout are suitable indicators of temperate conditions then the models developed in this thesis could also be used to indicate regions which are susceptible to invasion by other alien cold stenothermal species. Using methods described in this thesis, models of the potential distribution of other alien aquatic indicator species (i.e. warm mesothermal species) could be developed. The models of potential distribution of the two different classes (cold stenothermal and warm mesothermal) of indicator species could be superimposed using the IDRISI OVERLAY option. Regions of overlap between the different models could be regarded as "transitional zones". In this way a model of the susceptibility of regions to invasion by alien species could be developed.

Candidate alien species which are considered for importation could be classified into different categories according to their temperature tolerances. If the temperature tolerances of the candidate species are similar to those of the indicator species then it would be assumed that regions which are susceptible to invasion by the indicator species would also be susceptible to invasion by other species in the same "tolerance category" as the indicator species.

The development of such a "model of susceptibility" based on distribution patterns of indicator species represents a major alternative to the bioclimatic matching approach (Nix & Wapshere 1986; Maywald & Sutherst 1989; Richardson & McMahon 1992). In the latter approach (as used in programmes such as BIOCLIM and CLIMEX described in Chapter 2) the assumption is made that species have the potential to invade regions which are climatically similar to their native ranges. The problem with this approach is that the realised niche of a species in an alien environment is often broader than that in the native range, due to the absence of natural competitors, predators and parasites in the new environment. (This phenomenon, observed in many successful invasive species, was discussed in detail in Chapter 2). This means that an analysis of conditions in the native range is not always a good indicator of the range of conditions which the species may be able to tolerate in the new (introduced) environment. In the case of aquatic species, whose range has been severely restricted because of a lack of opportunity to invade potentially suitable catchments, this problem would be further exacerbated. Certain invasive aquatic species have invaded regions which are climatically very different to their native ranges. For example, the largemouth bass (*Micropterus salmoides*) whose native range is in the eastern states of the USA extending from latitudes of approximately 44°N to 25°S, has successfully invaded equatorial regions such as Panama and Colombia (latitude approximately 7°N) (Lee et al. 1980). It is beyond the scope of this thesis to assess the climates in the native range of *M. salmoides* and regions where it has been introduced, but it seems unlikely that there would be a close "climatic match" between these two regions.

Although the bioclimatic matching approach has obvious merits, especially for terrestrial species, the "indicator species approach" described here may be more appropriate for aquatic species whose range has been severely restricted by a lack of opportunity to invade new catchments.

A major drawback in the "indicator species approach" is that the development of predictive models would depend on the presence of suitable stenothermal alien species which had been introduced into many different catchments in the target environment.

There are some other possible applications of the methods developed using GIS techniques:

a. Aquaculture: The methods developed here could be used to predict the suitability of regions for aquaculture of stenothermal species, provided that these species are not considered to pose any threat to the environment.

b. Assessment of the conservation status of rivers: If distribution records of sensitive stenothermal indicator species (such as trout) were taken from a number of rivers with a high conservation status, a model of potential distributions in pristine conditions (within regions where the sensitive species has had the opportunity to invade) could be constructed. Since environmental degradation results in a decline in the distribution of sensitive species, a comparison of actual distributions of the sensitive species with the "pristine" model would give an indication of the conservation status of the rivers concerned. Alternatively, historical records of the distribution of sensitive stenothermal species could be used as a basis for generating a model. This model could then be compared with present distribution records in order to assess the levels of degradation of rivers.

In this respect it was noted that the predictive models for Natal indicated potential trout distributions in some regions, such as the Bushmans River, which are no longer suitable for trout, but were once known to be good "trout waters".

c. Numerous other applications of this method are possible in freshwater biological studies. The method could be used to create temperature profiles of streams in selected regions using the distribution of stenothermal species as a means of generating the database.

d. A comprehensive database has been generated on trout distribution records and the median annual rainfall and elevation values associated with these distributions. Data on the mean monthly July minimum temperatures associated with trout distributions in southern Natal, Lesotho, Transkei and the eastern Cape has also been generated. These databases are available on a floppy disc appended to the thesis and could be used in other analyses.

8.4. CONCLUSION

The main strength of the present study is that it represents an approach to biogeographical analysis of freshwaters in southern Africa that has not been tried before. Since the assessment of many of the models produced has been positive, this indicates that the method has some potential. There are a number of other applications which could be carried out using the methods developed. It is clear that GIS techniques represent a powerful new approach to biogeographical analyses and are likely to develop at an accelerated rate in the future as more programmes become available and the databases improve. It is hoped that the methods described here will make a positive contribution to these developments.

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Appendix 1: Records of the introduction of *P. mykiss* and *S. trutta* into different drainage regions in southern Africa. (Refer Fig. 3 for an illustration of the drainage regions). (After de Moor & Bruton 1988* and Davies pers. comm.).

Drainage region	Rivers where there are definite records of introduction or distribution records exist (in boldface)
A. (Limpopo)	Mutale.
B. Olifants (Limpopo)	**Treur, Blyde, Dorps**
C. Vaal	Wilge, **Slang**
D. Orange	Tsoelikane, Khubelu, **Thamatwe, Tsoelikana, Bell, Kraai, Malibamatso, Mokhoulane, Moremoholo, Senqu**
E. Olifants (W. Cape)	Bokkeveld, Olifants, Hex, Ratel, Kleinkliphuis, **Krom, Leerkloof, Twee, Middeldeur, Driehoek.**
F. West coast	No records
G. Berg & SW Cape	Berg, Eerste, Lourens, Zeekoevlei, Steenbras, Muizenberg, Liesbeeck, Wemmershoek
H. Breede	Breede, de Hoop vlei, **Dwars, Smalblaar, Klein Bree, Molenaars, Elandspad, Holsloot, Witels, Nuy, Elands, Jan du Toits**
J. Gouritz	Dorps, **Huis, Gamka, Sand**
K. S. Cape (Knysna)	Gwaayang, **Keurbooms, Kromme (Sand R. dam)**
L. Gamtoos	**Gamtoos**
M. Swartkops	van Staadens, Baakens, Berg (Loerie Mtns), Swartkops.
N. Sundays	No definite records except historical record that trout were introduced into many streams in Port Elizabeth district (de Moor & Bruton 1988).
Q. Fish	Little Fish
R. Buffalo	Buffalo, Keiskamma (**Wolf, Cata, Lenye, Tyume tributaries).**
S. Kei	Tsomo, **Toise, Klipplaat, Kubusie, Big Thomas, Isidenge.**

Appendix 1 (continued)

T.	S. Natal	Mpendhle, Mzimvubu, Yarrow, Nyamvubu, Illovo, **Mzimkulu, Loteni, Lurane, Mweni, Mshwati, Mvenyane, Pholela, Mkomazi, Mkomozana, Ngwangwana, Ngudweni, Ndodeni, Elands, Nkonza, Nsinga, Mgeni, Mlambonja, Serpentine, Mlaas, Mtamvuna, Mvoti, Weza**
	Transkei	Engcobo, Wildebeest, Tsitsa, Ncomi, Cancele, Xokonxa, Mtata, Gora, Manina (Bashee), Engwali, Mtakatyi, Mgazi, Little Pot, Luzi, Tina, Kanegha, Gingqiskodo, Ibisi, Ncweleni, Nceba, Quteni. **Nyamvubu, Qunu, Bizana, Mzimhlava, Ndowana**
U.	Mgeni	Greytown Lake, Mzimduzi, Mgeni, **Karkloof, Lions, Jacksons**
V.	Tugela	Upper Tugela, Bushmans, Little Mooi, Furth, Klip. **Ncandu, Buffalo, Little Tugela, Bushmans, Pivaan, Ngogo, Sterkspruit**
W.	Phongolo/ Zululand	Poponyani, Records of distribution in many regions in Swaziland particularly in the property of Usutu pulp Mill. **Upper Phongolo.**
X.	Ncomati	**Crocodile, Sabie, Elands**

* For a detailed summary of the literature on dates of original introductions refer appendices in de Moor & Bruton (1988).

Appendix 2: Records of the introduction of eurytopic species (either *C. carpio*, *M. dolomieu*, *M. salmoides* or *L. macrochirus*) into different drainage regions in southern Africa. (Refer Fig. 3 for an illustration of the drainage regions). (After de Moor & Bruton 1988*).

Drainage regions	Rivers where there are definite records of introductions or distribution records exist
A. Limpopo	Limpopo, Mogol, Letaba.
B. Olifants (Limpopo)	Olifants
C. Vaal	Vaal
D. Orange	Upper & Middle Orange, Sak, Caledon, Fish
E. Olifants (W. Cape)	Olifants
F. W. Coast	No record
G. Berg & SW Cape	Berg, Liesbeeck, Eerste
H. Breede	Breede, Dwars, Smalblaar, Holsloot, Riviersonderend
J. Gouritz	Gouritz
K. S. Cape	Rondevlei, Kromme
L. Gamtoos	Gamtoos, Baviaans, Groot
N. Swartkops	Swartkops, Baakens, van Staadens
O. Fish	Fish
R. Buffalo	Buffalo, Keiskamma, Tyume, Nahoon, Cintsa,
S. Kei	Kei, Kubusie
T. S. Natal & T'Kei	Mkomazi, Mzimkulu, Mzimvubu, Mlaas, Msimhlava, Mtata
U. Mgeni	Mgeni
V. Tugela	Tugela, Bushmans, Mooi
W. Phongolo	Phongolo
X. Ncomati	Elands, Sabie.

* For a detailed summary of the literature on dates of original introductions refer appendices in de Moor & Bruton (1988).

Appendix 3: Selected distribution records of trout in southern Africa (not used for the generation of distribution models) used for comparison with models of trout distribution.

River	Lat/ Long coordinates	Reference
Lesotho		
Senqunyane	29°30'S : 28°05'E	Rall pers. comm.
Moremoholo	29°15'S : 29°05'E	Rondorf 1976
Senqu	28°55'S : 29°01'E	..
Sani	29°34'S : 29°13'E	Skelton pers. comm.
Rafunyane	29°11'S : 28°29'E	AMR
Bokeng	29°20'S : 28°29'E	..
Tsolotsa	29°20'S : 28°28'E	..
Kao	29°01'S : 28°33'E	..
Malibamatso	29°11'S : 28°29'E	..
Pelaneng	29°05'S : 28°30'E	..
E. Cape		
Mooi	31°05'S : 28°18'E	Skelton pers. comm.
Hawespoort	30°52'S : 28°12'E	..
Wildebeest	31°10'S : 28°07'E	..
Wildebeest	31°11'S : 28°56'E	..
Tsitsa	30°57'S : 28°27'E	..
Bell (Kraai)	30°49'S : 27°52'E	AMR
Kraai (Orange)	30°53'S : 27°53'E	..
Kraai (Orange)	30°45'S : 27°43'E	..
Klipplaat (S. Kei)	32°32'S : 26°59'E	..
Waterdowm Berry dam	32°17'S : 26°51'E	de Moor & Bruton (1988)

Appendix 3 (cont.)

Karringmelk-spruit (Orange R)	30°48'S : 27°17'E	..	
S Cape			
Gamtoos	33°48'S : 25°01'E	AMR	
Wemmershoek (Berg)	33°50'S : 19°07'E	..	
Franschoek (Berg)	33°56'S : 19°07'E	..	
Klein Berg	33°11'S : 19°09'E	..	
Dwars (Berg)	33°51'S : 18°57'E	..	
Gouritz	33°24'S : 21°24'E	..	
Sand (Gouritz)	33°16'S : 22°02'E	..	
Gamka (Gouritz)	33°18'S : 22°03'E	..	
Witwaters (Nuy)	33°34'S : 19°42'E	..	
Elands (Bree)	33°58'S : 19°18'E	..	
	33°54'S : 19°17'E	..	
Holsloot (Bree)	33°42'S : 19°24'E	..	
Natal Parks Board (NPB) legal downstream limits of trout waters			
Tugela	28°38'50'' S : 29° 02'40'' E		Coke pers. comm.
Mnweni	28°48'20'' S : 29° 11'15'' E		..
Bushmans	29°11'10'' S : 29° 38'15'' E		..
Yarrow	29°20'50'' S : 30° 17'10'' E		..
Mshwati	29°16'20'' S : 30° 21'45'' E		..
Mvenyane	30°30'55'' S : 29° 00'15'' E		..
Mtamvuna	30°44'10'' S : 29° 54'50'' E		..
Sonto	27°44'45'' S : 30° 42'00'' E		..

Appendix 3 (cont.) (NPB legal downstream limits of trout waters)

Ngogo	27°34'50'' S : 29° 52'30'' E	..
Pivaan	27°34'20'' S : 30° 42'00'' E	..
Mkomazi	29°35'35'' S : 29° 40'40'' E	..
Pholela	29°54'15'' S : 29° 40'10'' E	..
Loteni	29°35'35'' S : 29° 40'40'' E	..

Well-known trout districts of the Transkei and north eastern Cape

Barclay East	30°58'S : 27°37'E	Davies pers. comm.
Hogsback	32°35'S : 27°05'E	..
Katberg	32°31'S : 26°38'E	..
Lady Grey	30°43'S : 27°13'E	..
Maclear	31°04'S : 28°22'E	..
Ugie	31°11'S : 28°13'E	..

AMR = Albany Museum Records

Appendix 4: Localities* of downstream limits of breeding populations of trout in selected rivers, used as a basis for generating a database of distribution records for the GIS analysis.

Model No.	River	Downstream limits	Source
S. Natal Models 1, 2 & 3 & 8	Mkomazi	29°36'S: 29°40'E	Crass
	Mzimkulu	29°56'S: 29°38'E	..
	Pholela	29°53'S: 29°39'E	..
Lesotho - current records (Models 3 & 8)	Rufanyane	Point distribution records (See section 5.2.5 & Appendix 1)	Skelton + AMR
	Sani		
	Manguang		
	Malibamatso		
	Bokong		
	Tsolotsa		
	Kao		
	Matsoaing		
	Liphofung		
	Pelaneng		
	Mokhoulane		
Lesotho-historical records** (Model 8)	Senqunyane	29°20'S: 28°13'E	Shortt-Smith (1973)
	Pelaneng	29°05'S: 28°29'E	
	Maletsunyane	29°52'S: 28°03E	
N. Natal (Model 4)	Ncandu	27°50'S: 29°46'E	Crass
	Ngogo	27°40'S: 29°46'E	..
	Pivaan	27°29'S: 29°26'E	..
	Slang	27°26'S: 30°04'E	..
E. Cape (Models 5, 6 & 8)	Wolf	32°43'S: 27°06'E	Davies
	Cata	32°36'S: 27°07'E	..
	Tyume	32°40'S: 26°55'E	..
	Gubu	32°36'S: 27°17'E	..
	Mnyameni	32°36'S: 27°04'E	..
	Buffalo	32°44'S: 27°18E	..
W. Cape (Models 6 & 7)	Berg	33°15'S: 19°06'E	Smith
	Eerste	33°58'S: 18°55'E	..
	Lourens	34°04'S: 18°54'E	..
	Groot	32°40'S: 19°22'E	..
	Twee	32°42'S: 19°19'E	..
	Olifants	32°58'S: 19°11'E	..

AMR = Albany Museum Records

* The localities were taken to the nearest grid reference point on a 1 minute x 1 minute resolution.

** These records are not true downstream limits. (See section 5.2.5.)

Appendix 5: A guide to the use of the Lotus programme "App5.wk1"* containing detailed locality records and associated MAR and elevation figures for all analyses carried out

* This file is available on the attached floppy disk.

A. Column Headings

Column 1: Sample number
Column 2: Latitude (degrees, minutes)
Column 3: Longitude (degrees, minutes)
Column 4: Elevation (m)*
Column 5: MAR (mm per annum)*
Column 6: Class of sample

*Elevation and MAR figures are those associated with the locality record and were obtained from the CCWR dataset.

Code for classes of samples (Column 6) (see Section 5.2.5 for definitions)

1 = Optimal
2 = Marginal
3 = Temperate
4 = Historical

B. Regions and rivers associated with sample numbers

Region	River	Sample numbers
S. Natal	**Mkomazi system**	
	Mainstream	1-32
	Major tributaries	
	Mquatsheni	40-87
	Nhlangeni	134-148
	Loteni	149-211
	Mkomozama	212-300
	Minor tributaries	33-59
		88-133
	Mzimkulu system	
	Mainstream	301-358
	Major tributaries	
	Pholela	385-509
	Mzimude	533-562
	Mzimkulwana	563-591
	Minor tributaries	359-384
		510-532
		592-651

Appendix 5 (continued)

Northern Natal		
	Ncandu	652-654
	Ngogo	655-663
	Pivaan	664-673
	Slang	674-759
W. Cape		
	Berg	760-769
	Eerste (Jonkershoek)	771-796
	Lourens	797-834
	Olifants	835-908
E. Cape		
	Wolf	909-915
	Cata	916-921
	Tyume	922-932
	Gubu	933-936
	Buffalo	937-944
	Mnyameni	945-947
Lesotho		
Current records	Point distribution records in rivers (see Table 11)	1187-1225
Historical records	Senqunyane	1226-1254
	Pelaneng	1256-1263
	Maletsunyane	1267-1285

Total number of samples = 1011

Appendix 6: A guide to the use of the Lotus file "Julmin.wk1" * containing detailed locality records and associated MAR & mean monthly minimum July temperatures (MJuMin) used as a basis for generating Model 8.

*Available on attached floppy disc.

Column 1 - Latitude (degrees, minutes)
Column 2 - Longitude (degrees, minutes)
Column 3 - MAR
Column 4 - Mean monthly July minimum temperatures (MJuMin) x 10**

** Temperatures were multiplied by 10 in order to eliminate the decimal points for the purpose of convenience in handling computer analyses.

Description of samples

No. in spreadsheet	Region	Original Sample Nos. (see Appendix 5)
1-38	E. Cape	909-947
39-757	Natal/ Lesotho	Natal: 1-651 Lesotho current: 1187-1225 Lesotho historical: 1226-1254

Appendix 7: List of taxa and their authors cited in this thesis.

Alopochen aegyptiacus (Linnaeus, 1766)
Anas platyrhynchos Linnaeus, 1758
Anas undulata Dubois, 1839
Anas erythrorhyncha Gmelin, 1789
Anopheles gambiae sensu latu Giles, 1920
Argulus japonicus Thiele 1900
Aulacomya ater (Molina, 1782)
Barbus Cuvier & Cloquet, 1816
Boophilus microplus (Canestrini, 1888)
Biomphalaria pfeifferi (Krauss, 1848)
Bothriocephalus acheilognathi Yamaguthi 1934
Bulinus Muller, 1781
Bulinus (Physopsis) globosus (Morelet, 1866)
Columba palumbus Linnaeus, 1758
Cyprinus carpio Linnaeus, 1758
Cyrtobagous salviniae Calder & Sands 1985
Cyrtobagous singularis (Hustache, 1929)
Dreissena polymorpha (Pallas, 1771)
Eucalyptus fastigata Deane & Maiden, 1901
Eucalyptus nitens (Deane & Maiden) Maiden, 1913 = *E. goniocalyx* var. *nitens*
Fasciola gigantica (Cobbold, 1855)
Fasciola hepatica (Linnaeus, 1758)
Hydrocynus vittatus Castelnau, 1861
Ichthyiopthirius multifilis Fouquet 1876
Labeo capensis (A. Smith, 1841)
Labeo rubromaculatus Gilchrist & Thompson, 1913
Lates niloticus (Linnaeus, 1762)
Lepomis macrochirus Rafinesque, 1819
Limnothrissa miodon (Boulenger, 1906)
Lymnaea columella Say 1817
Lymnaea natelensis Krauss, 1848
Micropterus dolomieu (Lacepede, 1802)
Micropterus salmoides (Lacepede, 1802)
Mytilus galloprovincialis Lamarck, 1819
Neohydronomus pulchellus Hustache, 1926
Oncorhynchus mykiss (Walbaum, 1792)
Oreochromis andersonii (Castelnau, 1861)
Oreochromis esculentus (Graham, 1928)
Oreochromis macrochir (Boulenger, 1912)
Oreochromis mossambicus (Peters, 1852)
Oreochromis niloticus (Linnaeus, 1758)
Oreochromis variabilis (Boulenger, 1906)
Parasalmo mykiss (Walbaum 1792) = *Oncorhynchus mykiss*
Passer domesticus Linnaeus, 1758
Patella granularis Lineaus, 1758
Petromyzon marinus Linnaeus, 1758
Pistia stratiotes Linnaeus, 1737
Poecilia reticulata Peters, 1859
Procambarus clarkii (Girard, 1852)
Pseudobarbus Smith, 1841
Rattus (Rattus) rattus (Linnaeus, 1758)
Salmo gairdneri = *Oncorhynchus mykiss*

Salmo trutta Linnaeus, 1758
Salvinia molesta Mitchell, 1972
Tilapia zilii (Bleeker, 1862)
Trachemys scripta elegans (Schoepff, 1792)
Trichodina acuta Lom 1961
Xiphophorus helleri Heckel, 1848