COLONISATION THEORY AND INVASIVE BIOTA: THE GREAT FISH RIVER, A CASE HISTORY.

by

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FOR DEB

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ABSTRACT

Colonisation theory relative to introduced populations was examined with a view to determining the usefulness of theoretical concepts in the prediction of the success of an invasion by a species. To this end, the Great Fish River, with reference to species introduced by the Orange/Fish Tunnel, was used as a case history. It was concluded that theoretical descriptions of population growth, control and decline are useful only when considering individual ecosystems or species. The highly variable nature of species and environments nullifies attempts to simplify behavioural characteristics into a predictive framework.

There is an abundance of terminology associated with introduced organisms and frequently many of these terms are used synonymously. Eleven terms have been defined in this thesis with a view to standardising terminology. Characteristics of species and environments which enhance their susceptibility to invasions by exotic ichthyofauna were discussed and summarised.

Distribution data concerning exotic fish introduced into the Great Fish River by the Orange/Fish Tunnel has demonstrated that, with the exception of Clarias gariepinus, all remaining exotics have restricted distributions. Only Barbus aeneus appears to be extending its range down the drainage. Age, Growth, reproduction and condition data support the conclusion that, excluding B. aeneus and C. gariepinus, invasive species in the drainage are not performing well. Of the five invasive species (B. aeneus, Labeo capensis, L. umbratus, Gephyroglanis sclateri and Cyprinus carpio), only two have established populations (B. aeneus and C. gariepinus). Labeo umbratus and C. carpio were present on the Great Fish River prior to the construction of the tunnel and populations of the species could not be distinguished.

It was conluded that there is no evidence to suggest that exotic species introduced into the Great Fish River are having a deleterious effect on indigenous, endangered ichthyofauna. Monitoring of the drainage should be continued to ensure that a danger to indigenous species does not develop.

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CHAPTER I

1.1 INTRODUCTION

The awareness of the need to manage exotic or transplanted species has been nurtured in South Africa by publications such as Moran & Moran (1982), Siegfried & Davies (1982), Scott (1982a,b) Ferrar & Kruger (1983) and Bruton & Merron (in prep.). However, far more attention has historically been given to vascular plants than fauna, particularly fishes. Increasingly, there is worldwide concern over the impact assessment and management of altered ecosystems, with attention being given to invasive biota as well as to chemical and physical habitat degradation (e.g. see Courtenay & Stauffer, 1984). Successful management of impacted systems requires a clear understanding of the status and behaviour of introduced species. A sound knowledge of theory inevitably enhances practical applications. Thus, with emphasis on aquatic systems, it is the aim of this thesis, using the Great Fish River as a case history, to (a) evaluate the characteristics of a successful invader species, (b) identify those properties of a habitat which enhance its susceptibility to invasion and, (c) relate these theoretical concepts to the Great Fish River, an invaded environment. In Chapter I theoretical aspects of colonisation processes are examined, including topics ranging from introductions and the niche concept, to population growth and control. Island patterns of colonisation are introduced and related to riverine patterns to show their similar characteristics. A detailed description of the study area is presented in Chapter II. Chapters III, IV and V examine the colonisation of the Great Fish River by fishes and evaluates the success of exotic species in the system. Chapter VI relates the theoretical concepts discussed in Chapter I to the observed environmental and biological data presented in Chapters III, IV and V.

1.2 Colonisation Theory and Invasive Biota

1.2.1 Terminology

The literature abounds with many terms, sometimes used synonymously, which for the purposes of this thesis requires clarification. Ten definitions of frequently used terms in colonisation theory and invasive biota (and related topics) are defined with a view to standardising the terminology presently in common use.

Shafland & Lewis (1984) proposed standardising terminology presently used in association with introduced organisms (as does this thesis and Laurenson & Hocutt, in press). A fundamental difference between the terminology proposed by Laurenson & Hocutt (in press) and Shafland & Lewis (1984) is that the former authors premise their definitions on biological rather than the political criteria accepted by the latter. This thesis (and Laurenson & Hocutt, in press) follows the views of Hubbs (1977) for sound ecological and genetic reasons (see Hocutt, 1984). Synonymy of terms is demonstrated in some of the following definitions, however, there is no value in recommending that certain terms not be used as there is already an established literature which frequently makes use of them. The definitions presented are summarised in Table 1.

Alien species: Belonging to another place; a foreign organism.

Foreign species: A species from a different biogeographical region (sensu stricto Pielou, 1979), continent or subcontinent (Siegfried & Davies, 1982).

Table 1: Some definitions of important terminology regarding invasive biota.

Alien species	Belonging to another place; a foreign organism.
Colonisation	The result of the translocation or the natural dispersion of a breeding population into a new environ outside its natural (extant) geographic range. The colony may or may not be successful.
Endemic species	A species that is restricted in its distribution, be it in reference to a particular spring, lake, drainage system or biogeographical region.
Established species	A reproductively successful species.
Exotic species	Any species deliberately or inadvertently introduced to a location outside its natural (extant) geographic range by man (Hubbs 1977).
Foreign species	A species from a different biogeographical region (<u>sensu stricto</u> Pielou 1979), continent or subcontinent.
Indigenous species	A native species, but (as compared to an endemic) not necessarily restricted in its distribution to a particular spring, lake, drainage system or biogeographical province.
Introduced species	A species deliberately or inadvertently transferred by man to an area outside its (extant) native range.
Invasive species	Species expanding their ranges either as a consequence of a natural phenomenon or as a result of man's deliberate or inadvertent action.
Translocated species	Species moved from one environment (spring, lake, drainage system or biogeographical province) to another by man, either deliberately or inadvertently (as opposed to natural faunal transfers through, e.g. stream capture).
Transplant	A species deliberately introduced from one environment (spring, lake, drainage system or biogeographical province) into another.

Exotic species: Any species deliberately or inadvertently introduced to a location outside its natural (extant) geographic range by man (after Hubbs, 1977). The terms alien and foreign species differ from exotic species in that an exotic species does not necessarily have to be transferred from a different biogeographical province or continent. Rather it is introduced into an area outside its natural range, this translocation can even be an intradrainage transfer.

Endemic species: A species that is restricted in distribution, be it in reference to a particular spring, lake, drainage system, or biogeographical province.

Indigenous species: A native species, but (as compared to an endemic) not necessarily restricted in its distribution to a particular spring, lake, drainage system or biogeographical province. The definitions of indigenous and endemic species, although superficially the same, differ significantly in scope. A species may be indigenous to a system but not endemic, e.g. Barbus anoplus is indigenous to the Orange River but also occurs naturally in the Fish River.

Transplant: A species deliberately introduced from one environment (spring, lake, drainage system or biogeographic province) to another, e.g. many salmonids have been transplanted for recreational reasons.

Translocated: Species moved from one environment (spring, lake, drainage system or biogeographical province) to another by man, either deliberately or inadvertently (as opposed to natural faunal transfers through e.g. stream capture), e.g. inadvertent releases of aquarium fishes.

Colonisation: The result of the translocation or natural dispersion of a breeding population into a new environ outside its natural (extant) geographic range. The colony may or may not be successful.

Established species: A reproducing successful species.

Introduced species: Species deliberately or inadvertently transferred by man to an area outside its (extant) native range.

Invasive species: Species expanding their ranges either as a consequence of a natural phenomenon or as a result of man's deliberate or inadvertent action.

1.2.2 Introductions of Species

The introduction of species into other aquatic systems often results in some form of environmental change within that system which is usually detrimental. A classic example is the introduction of Clarias batrachus into Florida, USA (Courtenay & Miley, 1975). However, not all introductions are detrimental, especially when socio-economic, as well as biological factors are considered. For instance, trout (Salmonidae) and bass (Centrarchidae) introductions into many areas worldwide provide valuable recreational potential for anglers and this may outweigh any deleterious effects that the introduction might have on the environment. When propounding the philosophical point of view that an introduction may result in the addition of, rather than the replacement of species in the environment, then presumably the community is enriched (structurally or functionally) and should be more stable.

Prior to large scale interference by man, successful transfers of fish from one watershed to the next were rare and extensions of the geographic range of a species were mainly a function of the geological stability and physical characteristics of the region. However, with the development of rapid transport the translocation of fishes from one watershed to the next and even between continents has become common practise (Lachner et al., 1970; Courtenay & Robins, 1975).

In this thesis factors which may influence the survival and success of an exotic have broadly be subdivided into intrinsic and extrinsic (Table 2). Intrinsic factors are those which are a function of the genotype of the species and individuals, whereas extrinsic factors are a function of the environment into which the species has been translocated. Successful colonisation is rare as conditions must be extremely favourable (see Table 3 for proposed characteristics of an aquatic ecosystem that make it susceptible to invasions by exotics) for a species to become established. When a species enters an environment the probable time until extinction is directly proportional to the number of individuals translocated (MacArthur, 1972).

Fish populations behave (i.e. population growth, control, decline, etc.) in a manner which is characteristic of the species and usually can be described theoretically as has been done for many commercial species, for example, Barbus aeneus in South African Lake Le Roux (Tomasson, 1983) and the southern African horse mackerel (Trachurus trachurus) (Haigh, 1971; Geldenhuys, 1973; Hecht, 1976). Usually data concerning reproductive potential, growth rates of individuals and resistance to environmental stress etc. are available only in heavily sampled or intensively studied populations. It is usually possible to determine from data collections how effective a species has been at invading and colonising an environment. However, prediction of the success of an exotic is difficult.

Table 2. Proposed factors influencing the survival and success of an exotic species.

Intrinsic	Extrinsic
Fecundity	Physico-chemical features
Growth rate	Competition
Age and size at maturity	Disease
r/K strategy	Injury during translocation
Reproductive guild	Predation
Genetic plasticity	Parasitism
Trophic level	Food availability
Rate and mode of dispersal	

Table 3. Some characteristics of an aquatic ecosystem which make it susceptible to invasion by exotic species.

Biotic	Abiotic
Depauperate fauna	Large size
Few predators	Range of habitats
Few parasites, diseases, etc.	Unstable environment
Abundant food supplies	Disturbed by man
Structural and functional redundancy of indigenous fauna	Post-stress conditions
	Lentic or lotic conditions, including stream order and flow dependability

1.2.3 Island Patterns

It is proposed, by analogy, that the distribution of fishes in lotic ecosystems may be thought of in terms of island patterns of colonisation. That is, drainages (or sub-drainages) are divided into a continuum (Vannote et al., 1980) of microhabitats, each with its own set of environmental conditions and characteristic fauna (longitudinal distribution). In systems such as the Great Fish River, characterised by marked seasonal changes in volume of water flow, the latter phenomenon may be accented. In the absence of introduced species, riverine systems are homeostatic with respect to resident community structures, and fluctuations in populations are characteristically within certain bounds which are defined by the physical, chemical and biological characteristics of the ecosystem.

MacArthur (1972) contended that every population will become extinct at some stage. He moreover contended that the time to extinction is directly proportional to population size. For successful establishment a population must grow past this vulnerable stage quickly. Successful colonizers, therefore, generally have a rapid rate of population increase. However, the same rate of population increase can just as easily be obtained from a low death rate as from a high birth rate (MacArthur, 1972). Of these alternatives the former is appreciably more favourable as demonstrated by the remarkable success of man.

Populations which cannot exceed small sizes (N) due to environmental constraints, are likely to become extinct more rapidly than populations of large sizes (large N). Figure 1 shows the expected time in terms of birth rates (λ), death rates (μ) and population size (N) that a founding population will take to become extinct and shows

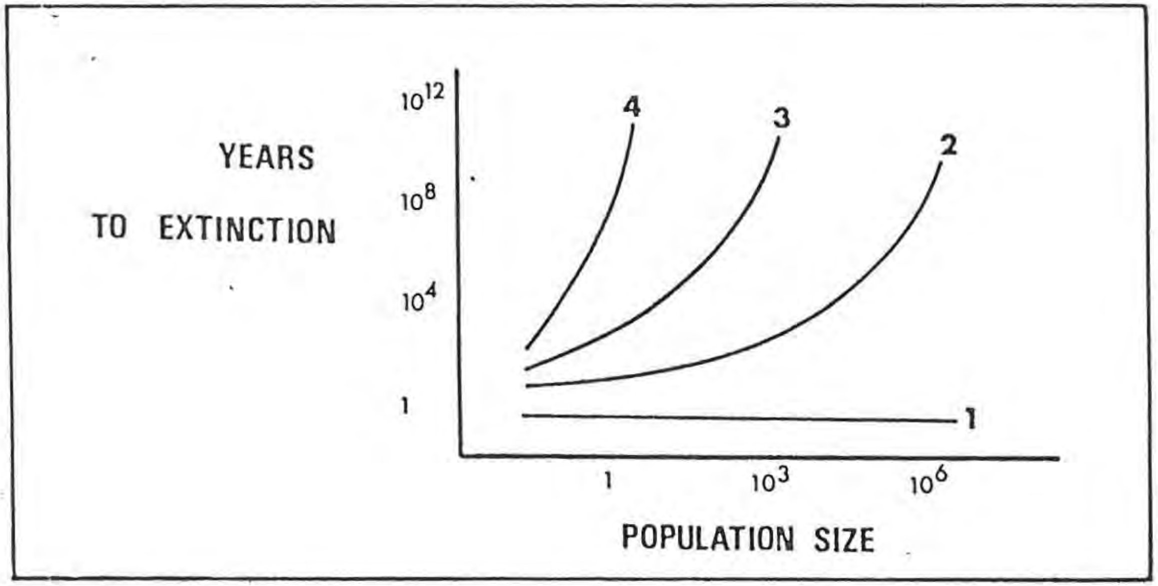


Figure 1: The time to extinction of populations ranging from small to large numbers of individuals (MacArthur, 1972).

1. Birth rate and death rate equal.
2. Birth rate marginally greater than death rate.
3. Birth rate twice as large as death rate.
4. Birth rate 1000X larger than death rate.

that the switch from vulnerable, small populations to safe, large populations can occur quite rapidly.

The immigration and extinction rates of established isolated communities are theoretically usually close to equilibrium. That is, the rate of immigration of species is balanced by an equal rate of extinctions (Fig. 2) (MacArthur, 1972). The explanation for this is two-fold, (1) there are more species after immigration, and (2) greater competition for resources increases the probability of extinction for individual species. Diamond et al. (1982) contend that colonisation and extinction rates are a function of island area, distance from the source of colonising species and to a lesser extent, shape. These factors tend to ignore the intrinsic variability of species but are nevertheless useful as guidelines when attempting to quantify the effects of an introduction on an aquatic system.

1.2.4 The Niche Concept

All organisms occupy an ecological niche which is determined by the particular environmental requirements needed to effectively survive and reproduce in the system as a whole. Hutchinson (1958) defined niche as a multi-dimensional hypervolume which depicts the conditions under which a species can exist. Whittaker et al. (1973) defined niche three ways: (a) "... as the position or role of a species within a given community - the functional concept of niche; (b) the niche as the distributional relation of a species to a range of environments and communities - the niche as a habitat, or the place niche concept; and (c) the niche as an amalgam of both these ideas, and thus defined by both intracommunity and extracommunity factors".

Central to the problem of exotic species is that theoretically no two sympatric species can occupy the same ecological niche for an extended period of time (Gause,

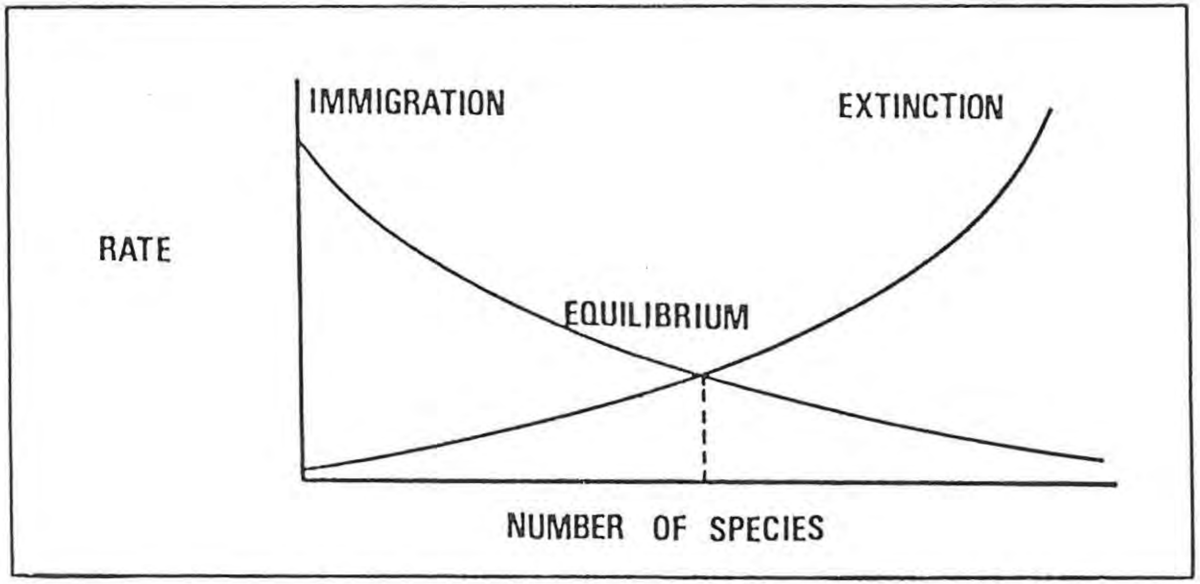


Figure 2: The rates of immigration and extinction of island communities (MacArthur, 1972)

1934; Hardin, 1960). Thus the successful invasive species must either outcompete indigenous fauna, or at a minimum, be sufficiently opportunistic to partition the niche to its advantage. Tillman (1979) categorised a resource as "a factor which, through some range of availabilities, leads to higher population growth rates as its availability is increased and which is consumed, in the broad sense, by the population". While specifically directed toward nutritive resources, Tillman's (1979) definition of a resource is applicable whether one thinks in terms of the functional role of a species or its distribution in space and time.

In reality, the competitive exclusion model is more theoretical than practical as a researcher will invariably find differences between ecological requirements of species regardless of the results of experiments designed to demonstrate the concept (Koopman, 1950; Lewis, 1961; Ayala et al., 1974). Hardin (1960) in a discussion on the classical competitive exclusion principle expressed similar misgivings. Usually when two species are sympatric they differ in at least one dimension of their multi-dimensional ecological requirements, i.e. "complete competitors cannot coexist" (Hardin, 1960). Stauffer (1984) stated that any one dimension has a limit of compressability where the number of species utilising the resource is limited and inextendible. That is, any one resource has a maximum number of species which it can support and this level cannot be extended. Since any resource must be limited, intuitively its utilisation must also eventually be limited although this level in practice may never be reached. Limitations such as these have been demonstrated in competition studies (Chapman, 1966; Everest & Chapman, 1972; Keast, 1978; Fausch & White, 1981).

The niche concept has been divided into various broad categories which make it of greater use to the working ecologist, for example, reproductive niche and feeding niche. Whittaker et al. (1973) emphasises the importance of these distinctions in terms of their practical applications and he defines terminology such as ecotope to include the above distinctions. The utilization of a resource may be limited by the lack of some other resource characteristic of Hutchinson's (1957) multidimensional hypervolume. For example, the lack of available reproductive sites may limit the size of a species population in the presence of abundant food supplies or the abundance of any other required resource. Many studies demonstrate this type of population regulation (Lindstrom & Nilsson, 1962; Everest & Chapman, 1972; Shustov et al., 1981). In regions where species richness is high the multitude of available resources is usually divided amongst the members of the community with community richness being a function of competition and ability to partition the available resources. Conversely, competition may be more intraspecific in environments where there is a low species richness (Odum, 1971). However, lower species richness can be accompanied by increased productivity and resource utilization by those species which occur.

1.2.5 Population Growth and Control

The size of a fish population is subject to many temporal control factors such as fecundity, survival, growth rate and mortality. Broadly, population growth in terms of numbers is governed by the intrinsic rate of natural increase and any environmental resistance (Weatherley, 1972; Everhart & Youngs, 1981; Stauffer, 1984). The growth of a population where theoretically there is no environmental resistance is exponential but takes the form of a J- or S-shaped curve in the presence of environmental resistance (Fig. 3) (Odum, 1971). "Environmental resistance" combines both biotic (parasitism, disease, old age, etc.) and abiotic factors (drought, flooding, etc.) and effectively is the sum of all sources of

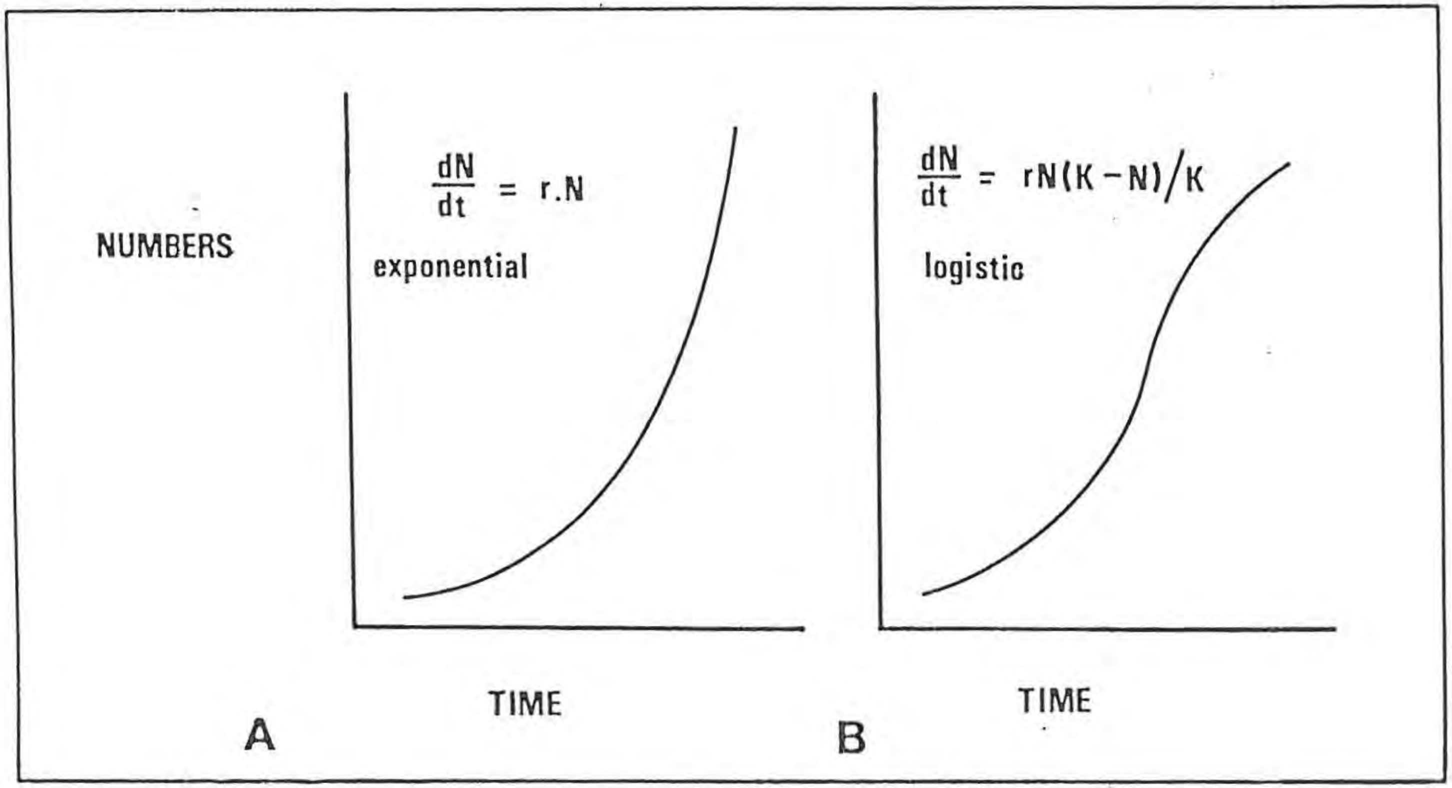


Figure 3: Two types of population growth curves. A - exponential or J - shaped curve. B - logistic or S - shaped curve (MacArthur, 1972).

mortality to the population.

Obviously, there are variations on this theory (for example, curve oscillations) but the basic patterns described do not differ considerably. The J-shaped curve (Odum, 1971) is a simple exponential relationship with a maximum limit of the form:

$$\frac{dN}{dt} = r.N \qquad \text{with a definite limit on } N$$

Whereas the sigmoid pattern is normally expressed by

$$\frac{dN}{dt} = r.N(K-N)/K \quad \text{or} \quad N = {}^{K}/_{1+e^{(\frac{r}{k}-r.t)}}$$

where $\frac{dN}{dt}$ is the change in population size (N = numbers) with time (t), r is the specific growth rate and K is the maximum population size possible. These relationships can be expressed by a number of different equations similar to the above logistic equations and data may or may not fit these examples (Odum, 1971; Weatherley, 1972).

The shape of the population growth curve is a function of the reproductive strategy of the species in question. There are two generally accepted forms of maximising reproductive potential, i.e. r- and K- selection (Pianka, 1970). True r-strategists and K-strategists lie at opposite ends of a continuum in which grades of both forms exist. No species can reasonably be described as totally adapted to one or the other end in this continuum. For example, a species may maximise its reproductive potential by producing large numbers of offspring and contributing little further in terms of parental care to enhance the survival of the juveniles (r-strategist), or it may invest heavily in enhancing the survival of fewer offspring through increased parental care (K-strategists). Table 4 (expanded from Pianka, 1970) compares some of the characteristics of typically r- and K-selected species.

The r-strategists generally colonise environments where competition and predation are at a minimum and are characterised by rapid increases and declines in population size (Gunderson, 1980). K-strategists are usually found in stable, equilibrium environments where selection favours long generation time and allocation of resources into ensuring survival through increased competitiveness (Stauffer, 1984).

Caswell (1982) argued that Pianka's (1970) system is impractical as the extremes on the r-/K- continuum are unlikely and its applications in ecology are limited. The system uses descriptions which have theoretical value, but are too broad in practicality and cannot be applied to dynamic living systems.

As shown by the population growth curves (Fig. 3) the size of a population can increase until the carrying capacity of the environment is reached (r max.), i.e., the point where the environment cannot support more individuals. The r-strategists are density independent and show rapid growth in numbers until environmental conditions become adverse at which stage population growth usually ceases and a decline begins (Gill, 1974). By contrast, typical K-strategists in equilibrium communities are density dependent having constant natality and mortality rates (Gill, 1974; Stauffer, 1984).

Mortality curves are characteristic of where a species finds itself on the r-/K- continuum. If the logarithm of mortality is plotted against age (Fig. 4) an interesting trend is demonstrated (Ricklefs, 1973). Of significance is that

Table 4. Some factors which distinguish between r-selected and K-selected species (after Pianka, 1970)

r-selected species

a. Rapid development
b. Early maturity and reproduction
c. Small size
d. Reduced life span
e. Mortality is controlled by extrinsic environmental factors and is frequently cataclysmic in ecological vacuums (density independant)
f. Show little parental care
g. Tend to dominate in highly variable environments or those recovering from stress.
h. Adapt to adverse environmental conditions through reproductive potential (i.e. high fecundity) and genetical avenues.

K-selected species

a. Slow development
b. Late maturity and reproduction
c. Generally larger in size than r-selected species
d. Longer life span
e. Mortality is density dependant and usually fairly constant
f. Show higher levels of parental care
g. Likely to dominate under constant environmental conditions, characteristic of climax communities
h. Adapt to adverse conditions through physiological or behavioural changes.

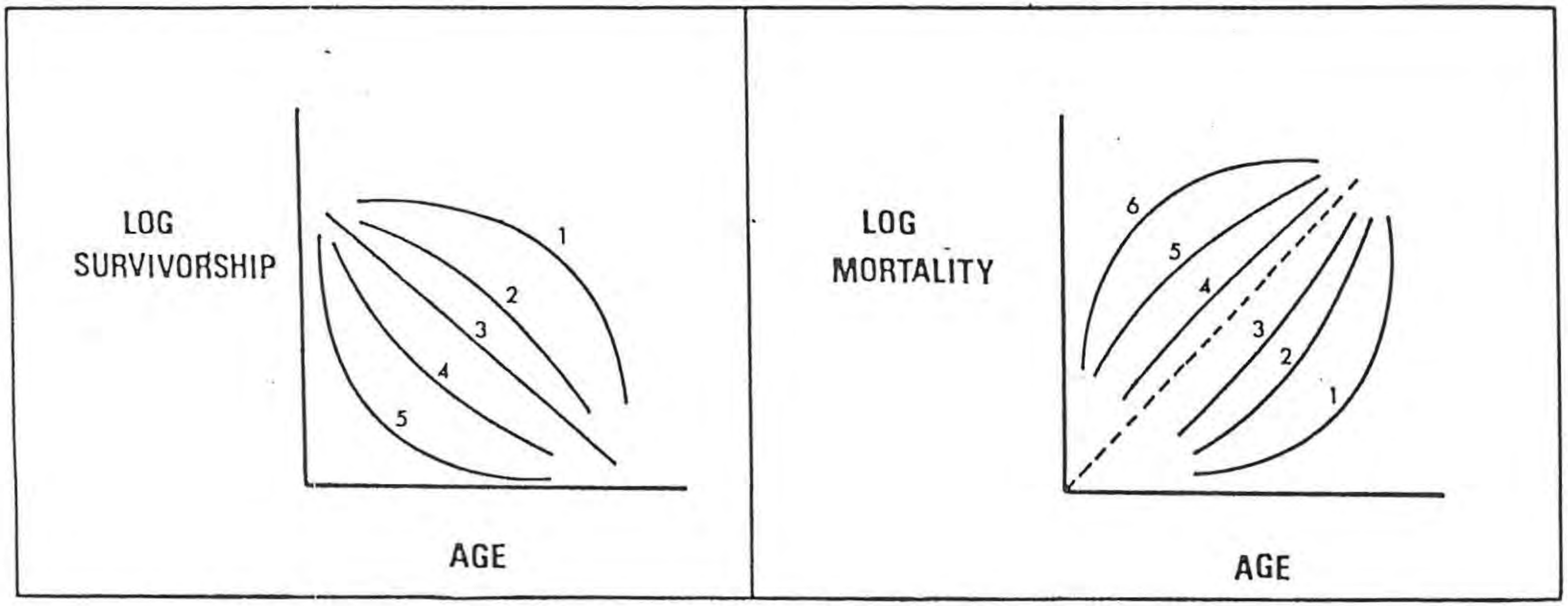


Figure 4: A plot of Log to the base 10 of survival (from Ricklefs, 1973) and mortality against age.

species tend from K- to r-adapted as the curves shift from position 1 to position 6. In these examples only the form of the curves is important and not the scale. Simply, K-adapted species have a proportionally increasing mortality with age, whereas r-strategists, by contrast, have a proportionally decreasing mortality with age. K-adapted species have an increased likelihood of mortality as the density (which can be related to age) rises (i.e. density dependent) whereas the opposite is true for r-strategists (i.e. density independent).

Figure 4 shows that the shape of mortality curves between the extremes on the r-/K-continuum are inverse of one another. Gill (1974) stated that the intrinsic rate of natural increase is exponential for all species given the right conditions. This is clearly demonstrated by the logistic equations and population growth curves (Fig. 3). Growth of populations is similar under ideal conditions but mortality differs considerably. The mechanisms for population growth and decline are, therefore, usually not the same (Stauffer, 1984), although at times they may be (i.e. population decline in both strategies may become density dependant). The scenario of this is demonstrated easily, r-strategists colonise altered or new environments and the size of their populations grow until r max (i.e. the carrying capacity of the environment) is reached. At this stage, a decline may begin or population control may become <u>density dependant</u> (i.e. K-strategy) for a short while. This follows from Gill's (1974) argument that if individuals are not in competition with each other for resources, then they are density independent and vice versa. For r-strategists with random birth and death rates (Karlin, 1966; Stauffer, 1984) the probability for extinction (μi) is estimated by:

$\mu i = (\frac{\lambda}{\mu})$ where the probability of death is greater than the probability of birth

As the probability of birth (λ) increases the probability of death (μ) decreases which results in a reduced probability of extinction (μ_i). When the probabilities of birth and death are equal, the probability of extinction for r-strategists is 1. Effectively this means that r-strategists cannot maintain populations in established communities by utilising an r-strategy. The argument is acceptable when dealing with extremely r-selected species, but is otherwise limited. The limitations result from the equation being a highly simplified description of the real environment and holds true where a species is located in the extreme r-selected range of the r/K continuum. In addition, the equation does not incorporate the intrinsic variability of species.

1.3 Summary

In conclusion, the factors used to define the characteristics of successful invasive species or environments susceptible to invasion are at best theoretical and are more useful in describing the events occurring during and after an invasion rather than the prediction of how successful an invasion will be. The intrinsic variability of species, environments, the associated communities and available resources are amongst the great many parameters which influence the success of an invasion by a species. *Oreochromis aureas* and *Sarotherodon melanotheron* are good examples of the inherent variability within a species. As invaders in Florida (Hocutt, *pers. comm.*) they exhibit tendencies of r-selected species (high fecundity, survival and growth), which in combination with their natural K-adapted traits synergistically allow them to out compete native fauna (Stauffer, 1984).

Theoretical descriptions of population growth, control and decline are useful only when considering individual ecosystems or species. The highly variable nature of species and environments nullifies attempts to simplify behavioural characteristics into a predictive framework, and as such, each case must be individually examined and evaluated. Invasive species are opportunistic and the form that exploitation may take is dependant on intrinsic and extrinsic environmental and species characteristics. It is in this context that invasive fishes in the Great Fish River were viewed.

CHAPTER II

THE STUDY AREA

2.1 INTRODUCTION

Southern African drainages have been divided into four broad regions (Fig. 5), namely the East Coast, South Coast, Orange and Limpopo (Midgley & Pitman, 1969). The Limpopo and Orange River drainages are by far the most dominant (i.e. largest in terms of water flow and size), whereas the east and south coast regions contain many small rivers. A major characteristic feature of southern African rivers is their paucity of indigenous fish fauna (Table 5) and endemism (Skelton, 1983). Species richness in African rivers has been shown to decrease with increasing southerly latitude (Livingstone et al., 1982) with a marked decrease in numbers of species occurring at the tropical/subtropical boundary (Skelton, 1983). Rivers of the southern coastal drainage region (Fig. 5) are particularly depauperate south of the Pongolo River in the east and around the Cape to the Orange River in the west (Skelton, 1983). Livingstone et al. (1982) related the size of indigenous fish fauna in rivers to discharge and catchment area and found a positive correlation for both but with discharge showing the better relationship. Southern coastal rivers characteristically have small discharges, catchment areas (Midgley & Pitman, 1969) and, therefore, have relatively small indigenous fish faunas.

It has been demonstrated that fish diversity in South Central African rivers decreases significantly south of the Zambezi, with diversity related to size of drainage (Livingstone et al., 1982). South African rivers proper harbour relatively few species, however, a high percentage of endemism is evident (Skelton,

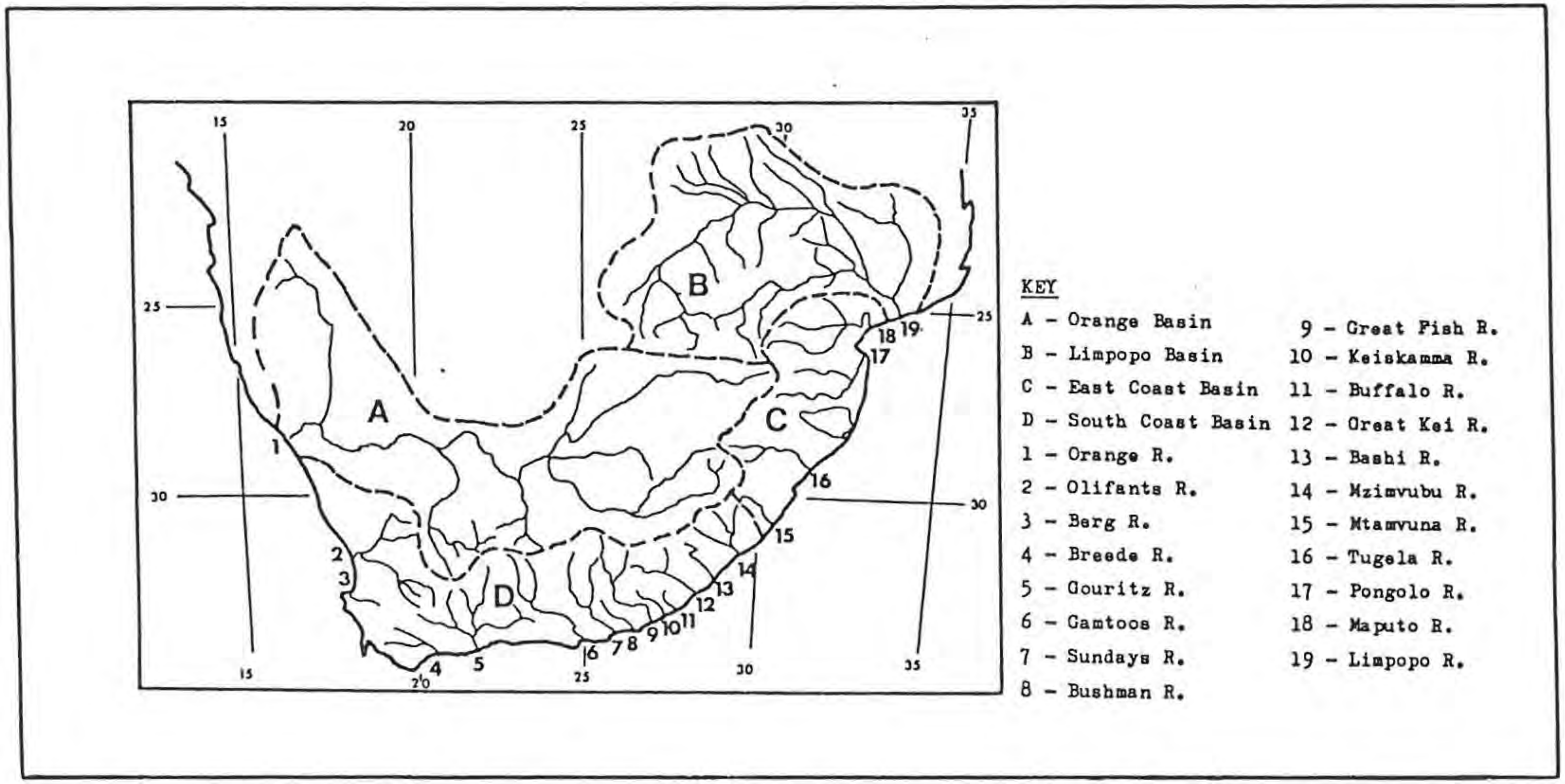


Figure 5: Map of southern Africa showing the major drainage basins and rivers in the region.

Table 5: Numbers of indigenous fishes and catchment area of southern African Rivers.

River system	Number of indigenous species	Catchment area (km^2)	Reference
Orange	15	974 000	Skelton, 1983
Olifants	10	18 793	Skelton, 1983
Berg	4	15 730	Skelton, 1983
Breede	3	9 561	Skelton, 1983
Gouritz	7	28 257	Jubb, 1967
Gamtoos	10	21 307	Jubb, 1967
Sundays	8	12 973	Jubb, 1967
Bushmans	7	3 106	Jubb, 1967
Great Fish	11	18 793	This Study
Keiskamma	7	4 947	Jubb, 1967
Great Kei	7	12 730	Jubb, 1967
Mtamvuna	7	885	Skelton, 1983
Tugela	18	17 978	Skelton, 1983
Limpopo	62	51 290	Skelton, 1983

1983). Endemism is considered to be reflective of the number of vicariant events which have isolated ancestral fish faunal stocks, leading to their genetical segregation (Hocutt, pers. comm.).

In general, most South African drainages are subjected to severe seasonal natural fluctuations in water quantity and quality. This natural phenomenon has certainly precipitated formation of a unique faunal assemblage of species resilient to these fluctuations. Hocutt (1984) contends that it is normal to consider that an unstable environment is conducive to colonization by r-strategist species; however, it is best to consider this generalisation in terms of an artificial situation, i.e. one impacted by man where recovery takes place. Naturally unstable environments promote development of resistant faunas and are less susceptible to invasion by exotic fauna. However, when the exotic species is an ecological equivalent or sibling to the indigenous form(s), then the potential success of an invasion is enhanced. Thus, ecological equivalents or phylogenetically-related exotics, which have similar ecological requirements and thresholds, are likely to pose more of a threat to an indigenous fauna than introduction of "foreign" species (Hocutt, 1984).

2.2 THE GREAT FISH RIVER DRAINAGE

The Great Fish River heads up against the Orange River to the south of the Haasfonteine Mountains and is part of the south coastal drainage of southern Africa (Fig. 6); it eventually flows into the Indian Ocean at Great Fish River Point (33° 28'S and 27° 10'E). The river is approximately 400 km in length and has a catchment area of 18793 km^2 (Midgley & Pitman, 1969) which drains mostly arid Karoo areas with the result that the upper tributaries flow only after regional storms. Prior to the

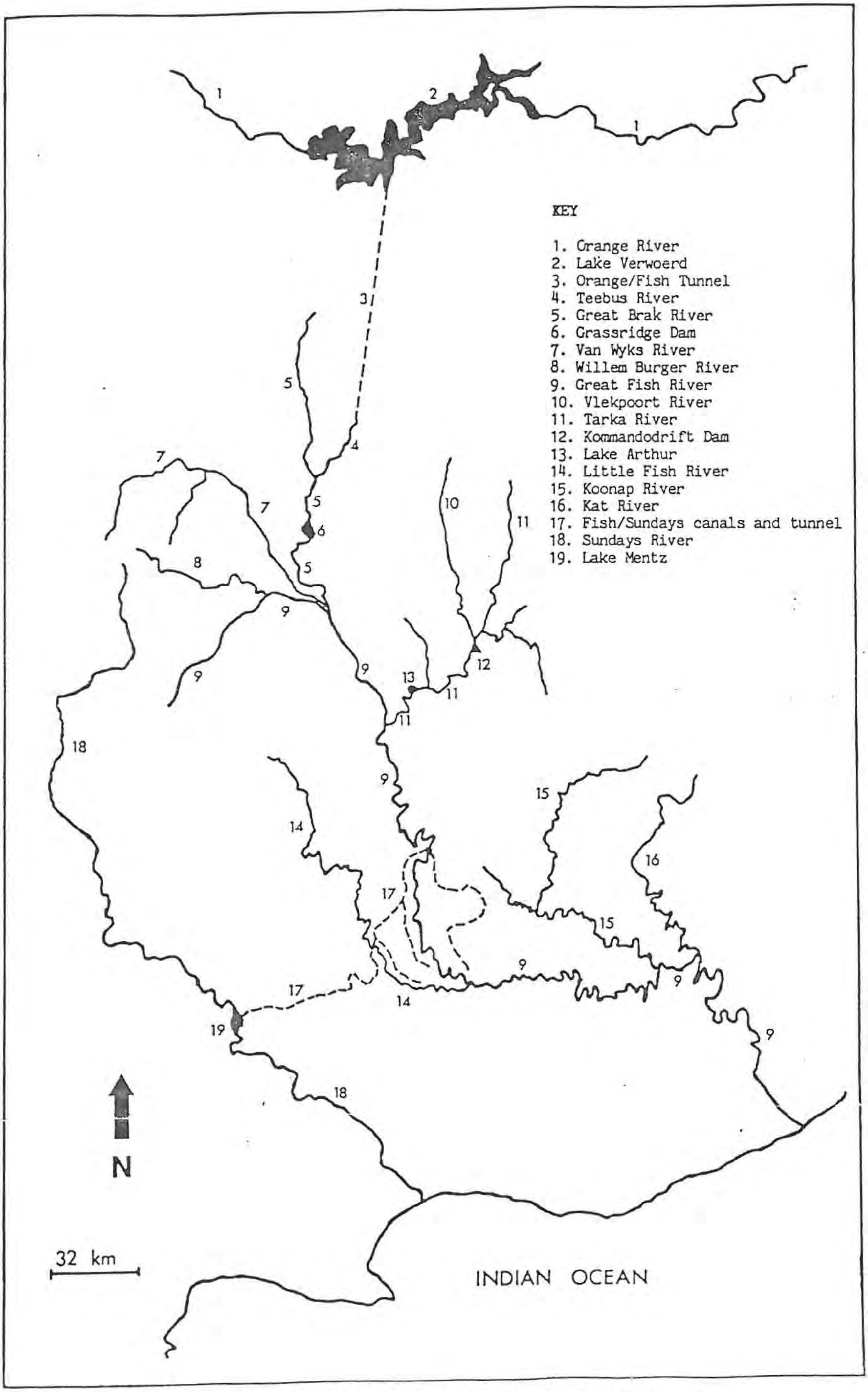


Figure 6: The Great Fish River Catchment, South Africa

construction of the Orange/Fish Tunnel in 1975, flow in the mainstem also was intermittent. The majority of the catchment area receives 250 to 500 mm rain per annum with some areas receiving as little as 125 mm. However, two tributaries, the Koonap and the Kat rivers, are exceptions since they drain the Suurberg Mountains which receive 500 to 1000 mm rain per annum (Scott et al., 1972) and usually flow perennially.

There are two large irrigation reservoirs on the mainstem of the drainage from the Orange/Fish Tunnel to the sea: Grassridge Dam on the Great Brak River (31° 45'S and 25° 28'E) and Elandsdrift Dam (32° 30'S and 25° 40' E) on the Great Fish River. Two other major reservoirs are located on the Tarka River tributary: Kommandodrift Dam (32° 05'S and 26° 02'E) and Lake Arthur (32° 10'S and 25° 25'E). In addition to these, there are numerous small weirs scattered irregularly down the length of the drainage. The majority are heavily silted (more silt than water) and water storage capacity is minimal.

As part of the Orange River Project (ORP), a tunnel connecting the Great Fish River to the Orange River was commissioned in May 1975 and constructed to allow large scale irrigated farming of the Great Fish and Sundays River drainages (Fig. 6). The tunnel extends 82.45 km beneath the Suurberg Plateau (Cambray and Jubb, 1977) with the intake located at Oviston on Lake Verwoerd (25° 45'S and 30° 40'E) and the outlet at Teebus in the lower drainage of the Teebus River (25° 42'S and 31°27'E), a tributary of the Great Fish River. Usually there is a substantial flow of water passing through the tunnel and as a result the once seasonal flowing regime of the Great Fish River has, since the construction of the tunnel, been converted to a permanently flowing pattern. Water flow is controlled at the Teebus outlet facility by six "pepper-pot" valves (a reference to their shape) which can be raised and lowered to effectively control the amount of water entering the river. Flow is governed by irrigation requirements below the tunnel and can vary from 0 - 45 m^3/sec. The "pepper-pot" valves are not wholly effective and a small amount of leakage occurs, especially when the system is not in operation.

The Orange River drains the Karoo region of central southern Africa from its headwaters in the Drakensberg to the south Atlantic Ocean, encompassing a catchment area of over 974000 km^2 (Midgley & Pitman, 1969). Water flow is substantial, seasonal and highly variable with annual variations ranging from 17 to 267% of the mean (before water regulation in 1970) (Kriel, 1972).

A major feature of Orange River water and consequently Great Fish River water is its turbidity. Tomasson (1983) found that the silt load in Lake Le Roux, as measured by secchi disc, varied from 10 to 160 cm. Lake Le Roux, however, is about 35 km down river from Lake Verwoerd in which 90% of the suspended sediment is deposited. The Orange River carries an average 0.6% sediment load (Kriel, 1972).

Although the Orange/Fish Tunnel presents a severe hazard to fishes that enter it, the tunnel itself has no mechanisms specifically designed to prevent fish translocation. A more detailed account of the hazards to fish found in the tunnel is presented in Chapter IV.

2.3 Sampling Sites

In March 1983 seventeen sites (Fig. 6b) were intensively sampled in the drainage of the Great Fish River to ascertain the general distribution of species in the system. The aim of this survey was to substantiate the final distributional data made

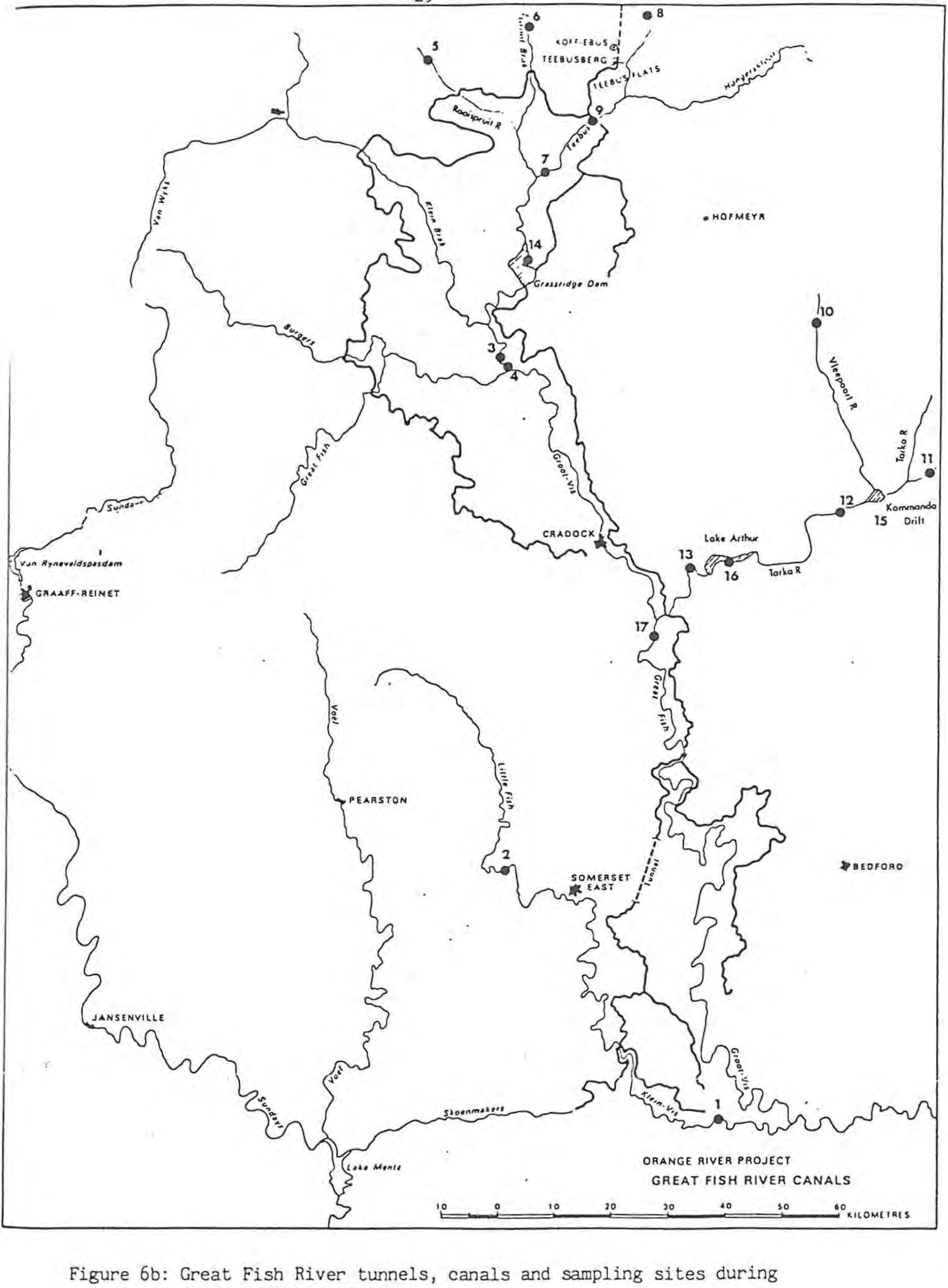


Figure 6b: Great Fish River tunnels, canals and sampling sites during course of this study.

available by the Department of Environment and Nature Conservation. After the March 1983 survey the number of sites was reduced to four (May 1983) and subsequently to two (June 1983), namely stations 7 and 9 (Fig. 6).

Site 7 is located approximately 30 km downstream of the Orange/Fish Tunnel outlet facility (31° 35'S and 25° 29'E) on the Teebus River before the confluence with the Great Brak River. The substrate consists of gravel, mud, sand and small quantities of concrete below a secondary road bridge. The site is a true riverine region with a characteristic substantial water flow and few backwater areas. There is little aquatic vegetation, that which is present is in the form of small quantities of algae growing on shallow rocks.

Site 9 is situated at the Orange/Fish Tunnel discharge (31° 30'S and 25° 30'E). The site is characterised by heavily grassed and reeded banks with little aquatic algae, the substrate is approximately 50% concrete, the remainder is rocky grading into mud in backwater regions. Water flow is mostly rapid but calm backwater areas are present. During periods of tunnel shut-down the site remains inundated with water but becomes a pool with an increased water residence time.

CHAPTER III

THE DISTRIBUTION OF ENDEMIC AND INVASIVE FISH SPECIES IN THE GREAT FISH RIVER (WITH EMPHASIS ON THE ORANGE-FISH TUNNEL)

3.1 Introduction

This chapter examines the literature available on the distribution of fish species in the Great Fish River. These findings are supplemented with the data from recent surveys and provides a more lucid picture concerning the temporal arrival and distribution as well as spatial distribution of the fishes in the system.

3.2 The Distribution of Indigenous Great Fish River Fishes

Little published information is available on the ichthyofauna of the Great Fish River prior to 1977. Scott et al. (1972) undertook extensive studies on the limnology of both the Sundays and Great Fish rivers but no data on fish were recorded. The first fish surveys of the river were carried out from October 1973 to February 1979 (Cambray, 1976; Cambray et al., 1977; Cambray & Hahndiek, 1979) in order to obtain a preliminary assessment of the impact of the opening of the Orange-Fish Tunnel on the river. All surveys conducted on the Great Fish River drainage are summarised in Table 6, these data combine both data collected during the course of this study and data gathered by the Department of Environment and Nature Conservation. Nature Conservation surveys were concentrated exclusively in Grassridge Dam (Fig. 6) where only Labeo umbratus, Cyprinus carpio and Barbus anoplus were found prior to the opening of the tunnel. The reasons for this concentration of fishing effort are twofold, (1) the Orange/Fish Tunnel drains

Table 6: Combined field excursions from this study and the Department for the Environment and Nature Conservation to the Great Fish River Drainage. Only data from species relevant to the discussion are presented. * - Numbers of specimens collected unavailable. & - Samples collected by the Department of Environment and Nature Conservation. à - Samples collected for this study. All values shown are real numbers of individuals.

FIELD YEAR	TRIP MONTH	SPECIES *L. umbratus*	*C. carpio*	*B. aeneus*	*L. capensis*	*C. gariepinus*	*G. sclateri*	SITE
1973	October	119						& Grassridge Dam (14)
1974	January	61						
	April	8						
	June	2	29					
	August	12	3					
	October							
	December	18	1					
1975	January	40	2					
	March	83	5					
	May	861	55					
	July	248	28					
	September	78	5					
	November	265	10					
1976	January	198						
	March	15	1					
	May	10	1					
	June	1	23					& Lake Arthur (16)
	July	196	32	1				& Grassridge Dam (14)
	November		196					& Lake Arthur (16)
1977	February	3660	1853	7	7			& Grassridge Dam (14)
1978	February	8611	3358	1	2	2		
	October	2	3					& Kap River
1979	February	3076	4486		1	3		& Grassridge Dam (14)
1980	March		255					& Kommandodrift Dam (15)
1981	January		510					
	February	36	8					& Little Fish River (2)
	July	84						& Koonap River (15 Fig. 6)
	September	20	1					
	September	207	2					& Kat River (16 Fig. 6)
	September	10	6					& Tyefu Dam

Table 6 Continued

FIELD TRIP		SPECIES						
YEAR	MONTH	*L. umbratus*	*C. carpio*	*B. aeneus*	*L. capensis*	*C. gariepinus*	*G. sclateri*	SITE
1982	February	639	5					& Double drift
	March	147	15			2		& Elandsdrift Dam (Point C)
	September	343	3					& Doubledrift
	September	66	12			1		& Bekkerskraal
	September	94	10			1		& Elandsdrift Dam (Point C)
	September	1						& Cradock (Point B)
1983	March	42	111					à/& Lake Arthur (16)
	March	230	35	*	1	1		à/& Grassridge Dam (14)
	March	10						à Little Fish River (2)
	March			9				à Teebus River (7)
	March				6	1		à Tunnel Outlet (9)
	March		2					à/& Tarka River (12,13)
	March	4	1					
	March	31						& The Forte
	May				2			à Tunnel Outlet (9)
	May	*		61	219	9	4	à Tunnel Outlet (9)
	May			24				à Teebus River (7)
	June			64				
	June	41		1	1			& Cradock (Point B)
	June					1		à Tunnel Outlet (9)
	August							
	August			1				
	August	51						à Mortimer (17)
	August		4		2			à Tunnel Outlet (9)
	August			20				à Teebus River (7)
	October				18			à Tunnel Outlet (9)
	October		1	14				à Teebus River (7)
	November	44	15					& Elandsdrift Dam (Point C)
	December			20		2		à Teebus River (7)
	December				4			à Tunnel Outlet (9)
1984	February			15	11	13		
	February			20		2		à Teebus River (7)
	June	87	26	14				& Elandsdrift Dam (Point C)
	October				20			à Tunnel Outlet (9)

virtually directly into Grassridge Dam (Figure 6), and (2) fishing in the main channel of the river is extremely difficult and it is impossible to fish with large seines and full series of gill nets in the river environment. Table 7 lists the ichthyofauna of the Great Fish River and indicates the distribution of fish, whether they have restricted ranges and if they are exotic or indigenous.

3.3 The Distribution of Exotic Fish of the Great Fish River

In February 1977 the first two of four translocated species were caught, *Barbus aeneus* and *Labeo capensis*. These were followed by a third in February 1978, *Clarias gariepinus*. Unfortunately, sampling of the impoundment was suspended in 1979 and it was not until May 1983 when the fourth translocated species, *Gephyroglanis sclateri*, was recorded by Laurenson & Hocutt (1984). It is also quite likely that *L. umbratus*, *C. carpio* and *B. anoplus* have also been translocated, however, this has been impossible to ascertain as they are found in both systems.

Figure 6b shows the lowest recorded limits of the distribution of the four main invasive species (*B. aeneus*, *C. gariepinus*, *G. sclateri* and *L. capensis*) in the Great Fish River. Ten of the 26 (38%) recorded species from the system are exotic, and 5 of these are present as a direct result of the Orange-Fish Tunnel: *B. aeneus*, *L. capensis*, *L. umbratus*, *C. gariepinus*, and *G. sclateri*. The five other exotic species in the system are: *Lepomis macrochirus*, *Micropterus salmoides*, *Tilapia sparrmanii*, *Salmo gairdneri* and *S. trutta*.

3.3.1 *Barbus aeneus*

Barbus aeneus (= *B. holubi*, see Hocutt & Skelton 1983) has a preference for flowing

Table 7: Fishes of the Great Fish River.

SPECIES	PLACE	STATUS	RANGE
Anabantidae			
Sandelia bainsii	Koonap, Kat R.	N	R
Anguillidae			
Anguilla bengalensis labeata	Widespread	N	
Anguilla bicolor bicolor	Estuarine	N	R
Anguilla marmorata	Widespread	N	
Anguilla mossambica	Widespread	N	
Bagridae			
Gepheroglanis sclateri	Tunnel	E	R
Centrarchidae			
Lepomis macrochirus		E	
Micropterus salmoides	Kat, Fish R.	E	
Clariidae			
Clarias gariepinus	Widespread	E	W
Clupeidae			
Gilchristella aestuarius	River mouth	N	
Cichlidae			
Oreochromis mossambica	?		
Tilapia sparrmanii	Fish R.	E	
Cyprinidae			
Barbus aeneus	Teebus R.	E	
Barbus anoplus	Widespread	N & E	W
Barbus pallidus	Cap R.	N	R
Cyprinis carpio	Widespread	E	W
Labeo capensis	Teebus R.	E	
Labeo umbratus	Widespread	N & E	W
Gobiidae			
Glossogobius tenuiformis	?		
Mugilidae			
Liza richardsoni	Lower regions	N	R
Mugil cephalus	Lower regions	N	R
Myxus capensis	Lower reions	N	R
Salmonidae			
Salmo gairdneri	?	E	
Salmo trutta	?	E	

N - Indigenous to the system.
E - Exotic to the system.
W - Widespread in the drainage.
R - Range restricted.
? - Suspected in the system but not recorded.

water and is often found in significant numbers in such habitats in the Vaal (Mulder, 1973a) and Orange (Tomasson 1983) rivers. Tomasson (1983) also found it abundant in impounded waters. This species was first recorded in the Great Fish River drainage in Grassridge Dam in 1976 (Cambray *et al.*, 1977; Cambray & Hahndiek, 1979) and has since then dispersed further to Elandsdrift Dam (Table 6). *Barbus aeneus* is relatively rare in Grassridge and Elandsdrift Dams and is more common in flowing water upstream of Grassridge Dam (Table 6 and Figure 6b). During the surveys conducted for the purposes of this study only 14 specimens were collected from Elandsdrift Dam, the majority of them substantially larger than previous specimens captured (Table 8). At least one individual had well developed gonads (Chapter V).

Specimens were captured in a gill net series during the draining of the impoundment and the species is not abundant. They are, nevertheless, of breeding size (Table 8) and indicate that *B. aeneus* is successfully, but slowly, extending its distribution down the length of the drainage.

Barbus aeneus has been actively introduced in many areas (Chapter V) but has not been reported as being introduced into the Great Fish River drainage. The oldest specimen collected was five plus years (Chapter V) and supports the hypothesis that *B. aeneus* did enter the drainage through the Orange/Fish Tunnel.

Although *B. aeneus* has been the most successful of species to adapt to lacustrine conditions in Lake Le Roux (Eccles, 1983) it is predominantly riverine (Tomasson, 1983). This species should be monitored in future to determine whether it is having or will have any detrimental effects on the indigenous fauna of the Great Fish River drainage.

Table 8: Specimens of Barbus aeneus captured at Elandsdrift Dam during June 1984.

LENGTH (mm)	WEIGHT (g)	SEX
210	126	M
187	77	?
227	145	M
237	155	F
237	153	F
222	134	F
235	160	M
243	169	M
210	129	F
227	141	M
235	157	F
270	234	M
355	583	F
311	336	F

3.3.2 Labeo capensis

L. capensis was first recorded in the tunnel valve chambers in 1975 and by 1977 specimens were being collected in Grassridge Dam (Cambray & Jubb, 1977). In June 1983 a single specimen was collected in the river at Cradock (Figure 6b). No further down stream dispersal has occurred since 1977 and abundance of the species is still low in Grassridge Dam. It is readily caught in flowing water upstream where few L. umbratus are found. The oldest specimen of L. capensis collected was six plus years (Chapter V). This lends further support to the hypothesis that this species gained access to the Great Fish River drainage via the Orange/Fish Tunnel.

Labeo capensis is a large, river species like B. aeneus but occurs to a lesser extent in lentic conditions in the Orange and Vaal rivers (Mulder, 1973b). The closely related L. umbratus in the Great Fish River is common in riverine habitats below Grassridge Dam although they have a preference for lentic conditions and are more common in secondary tributaries of large rivers (Skelton, 1984). Cambray & Jubb (1977) suggested that competition between L. capensis and L. umbratus was likely to develop in the Great Fish River, however there is no evidence to support this in Fish River presently. The absence of L. capensis below Grassridge Dam suggests that the dam acts as an environmental buffer to L. capensis dispersal. This may be a result of competitive pressures from L. umbratus, the unfavourable lentic environment or some other variable. This is an interesting problem and warrants further research.

3.3.3 Labeo umbratus

This species is indigenous to both the Orange and Fish River systems, but evidence suggests that it has also managed to survive passage through the tunnel. This conclusion is based on (1) the observation that the tunnel opens into an area that has been isolated from upstream migration since 1963 by an approximately 10m high weir (located at sampling site 7, figure 6) and (2) that periodic dessication of this region was a fairly common occurrence until the opening of the tunnel in 1975. Discussion with farmers on rainfall and water levels in the region supports this argument. It is considered a safe assumption that if L. umbratus ever occurred upstream of this weir that since its construction, this species was extirpated by drought conditions by the time of the commissioning of the tunnel in 1975. Current surveys show that the species occurs above the weir which is likely due to introduction via the tunnel.

3.3.4 Clarias gariepinus

The sharptooth catfish was first recorded in Grassridge Dam in 1976 and has since spread throughout the main channel of Orange River water flow from the tunnel to the sea (Fig. 6b)(Cambray, 1976; Cambray et al., 1977; Cambray et al., 1979). Specimens in excess of 1 kg occur in most areas. Although dispersal has been rapid and widespread it nevertheless appears that the species only occurs in small numbers throughout the Great Fish River. R. Jubb (Pers. Comm.), however, believes that this species may have been introduced into the Great Fish River prior to construction of the tunnel; such an hypothesis may explain the wider distribution than exhibited by the other species considered here. No specimens were collected that were older than five plus years (Chapter V) and the hypothesis remains questioned.

3.3.5 Gephyroglanis sclateri

The rock catfish was first recorded from the Great Fish River in 1983 (Laurenson &

Hocutt, 1984). Only only 4 specimens have so far been collected, all at the tunnel outlet (Table 9, Fig. 6b). Further intensive sampling throughout the drainage for this species has failed to determine its status. The species prefers rocky substrate, riffle areas (P. Skelton, Pers. Comm.) and is notoriously difficult to sample in turbid waters. Its occurrence in the Great Fish River is enigmatic in that by June 1975 it had virtually disappeared from collections in Lake Verwoerd (Hamman, 1980); this, however, is most likely a sampling artifact. Ageing of the largest of the four specimens (Chapter V) furthers the enigma; the fish was four plus years of age when collected in 1983. Thus, the species either was translocated early in 1975 and is now established in the drainage, or has since been translocated. The rarity of G. sclateri in Lake Verwoerd ensures that the chances of entering the tunnel, let alone surviving translocation via the tunnel are extremely remote.

3.3.6 Barbus anoplus

Similar to L. umbratus, a parallel argument for the introduction of Barbus anoplus into the Great Fisn River from the Orange River can be put forward. This small minnow is also indigenous to both drainages. It is therefore speculative whether specimens collected in the Teebus River are indigenous or are of exotic origin and likely introduced via the tunnel. Unlike L. umbratus, B. anoplus is a very resilient species to harsh Karoo conditions (Hocutt & Skelton, 1983), thus it can neither be speculated as to the extent of its extirpation above Grassridge Dam under pre-1975 drought conditions, nor assumed that its occurrence in Teebus River is a result of the tunnel (see section 3.3.3).

3.3.7 Cyprinus carpio

This species is widely distributed throughout the Great Fish and Orange River

Table 9: Fork length (mm) and weight (g) of the four *Gephyroglanis sclateri* captured at the Orange-Fish Tunnel outlet.

FORK LENGTH (mm)	WEIGHT (g)
119	20.3
165	56.1
220	145.3
235	165.6

drainages as a result of active introductions by man. It is impossible to determine whether the species has traversed the tunnel although it is highly likely that it has, considering the hardiness of the species. It is abundant in most Great Fish River impoundments and relatively common in riverine areas.

3.3.8 Other Exotics

A number of other exotics also occur in the Great Fish River drainage. However, their presence has little to do with the contruction of the tunnel. Of particular note are trout (Salmo gairdneri), bluegill (Lepomis macrochirus) and large mouth black bass (Micropterus salmoides). These species have been introduced for angling purposes by fishing clubs and anglers and they were not examined in detail during the course of this study (Table 7).

3.3.9 Possible Future Translocations

Table 10 is a checklist of the fishes from the Orange River according to Hamman (1980) and is divided into those species found commonly in Lake Verwoerd and those found in the Orange River drainage. Of the species found in Lake Verwoerd only three have not been recorded in the tunnel outlet regions of the Great Fish River system, Barbus kimberleyensis, Salmo gairdneri and Salmo trutta. In the drainage of the Orange River though, the list of species is longer and amounts to an additional six (Table 9). Further surveys to monitor the Great Fish River should be undertaken to record if and when the remaining species are translocated.

It is unlikely that any species, other than B. kimberleyensis, will successfully invade the Great Fish River at this stage. The two species of salmonids which are

Table 10: Fishes from the Orange River, N - Native to the system, E - Exotic to the system (Adapted from Hamman, 1961).

SPECIES	STATUS
LAKE VERWOERD	
Cyprinidae	
Barbus aeneus	N
Barbus anoplus	N
Barbus kimberleyensis	N
Labeo capensis	N
Labeo umbratus	N
Cyprinis carpio	E
Bagridae	
Gephyroglanis sclateri	N
Clariidae	
Clarias gariepinus	N
Salmonidae	
Salmo gairdneri	E
Salmo trutta	E
NOT IN LAKE VERWOERD	
Cichlidae	
Pseudocrenilabris philander	N
Tilapia sparrmanii	N
Cyprinidae	
Barbus hospes	N
Barbus pallidus	N
Barbus paludinosus	N
Carassius auratus	E
Barbus trimaculatis	N
Neobola brevianalis	N

present in Lake Verwoerd are there as a result of seasonal stocking (Hamman, 1981) and the chances of successful translocation must be seriously questioned on the basis of arguments presented in Chapter IV. Barbus kimberleyensis is still, however, present in significant numbers in Lake Verwoerd, more so than G. sclateri (which has translocated) (Hamman, 1980), but as yet has not been recorded in the Great Fish River system. Future surveys to monitor the status of this species are desirable.

3.3.10 Summary

It has been shown that the exotic species introduced into the Great Fish River via the Orange/Fish Tunnel have restricted ranges, which do not appear to be expanding with the exception of B. aeneus. This conclusion is based on observations made during the course of this project and those of the Department of Environment and Nature Conservation dating back to 1973 (64 sites). Only two exotic species are found thoughout the drainage, C. carpio and C. gariepinus. The presence of neither of these two species in the system can conclusively be attributed to the functioning of the Orange/Fish Tunnel. However, this does not preclude them from entering the drainage in this manner as evidenced by the large number of immature C. gariepinus taken at the tunnel outlet by seine and rotenone collections.

The literature concerning the Great Fish River is not extensive and the species composition of the drainage prior to the construction of the tunnel is not well documented. However, to date, no known species have been extirpated from the drainage and present surveys indicate that this pattern will continue if the range and abundance of exotic species remains in the present state. However, it is likely that the range of C. gariepinus will expand as a result of the species hardiness.

The distribution of *B. aeneus* has been shown to be increasing in the Great Fish River system. The restricted range of *L. capensis* is speculatively attributed to the presence of Grassridge Dam (Fig 6b) which acts as an environmental barrier preventing further downstream migration of this species.

Further introductions of species by the Orange/Fish Tunnel appear remote at this stage. The remaining species in Lake Verwoerd that can reasonably be expected to translocate in time is *B. kimberleyensis*.

CHAPTER IV

SURVIVAL AND MORTALITY OF FISHES IN THE ORANGE/FISH TUNNEL

4.1 Introduction

Any life history stage of a fish species may potentially pass through the tunnel, but to successfully do so it must negotiate a number of severe obstacles. The tunnel has a diameter of 5.33 m and a gradient of 1:2000. The intake (Plate 1) is guarded by a grid of verticle bars (Plate 2) which prevents debris larger than 6.5 cm from entering the tunnel. The flow of water through the tunnel is controlled by six so-called "pepper-pot" valves arranged in parallel at the tunnel outlet. These valves are cylindrical with a series of 7.8 cm diameter holes through which water is channelled and directed against concrete walls of the valve chambers, the valves dissipate the excess energy of the water (Cambray & Jubb, 1977).

The rigours of such a journey undoubtedly prevent most adult fish from passing through the tunnel when it is in full operation, but larvae and eggs may readily survive hazards of this kind (Robbins & Mathur, 1976; Mathur & Heisey, 1980; Patterson & Smith, 1982). Fish, after passing through the intake grid (Plate 2) encounter baffles which are designed to break the water flow and considerable injury can result. Throughout the tunnel there are similar mechanisms accomplishing the same purpose (Pike, Chief Engineer, Verwoerd Dam: Pers. Comm.) and further injury may result. The most hazardous experience all fish, irrespective of age, are faced with when traversing the tunnel is passing through the "pepper-pot" valves under pressure. Fish enter the valves under a 70 m static head pressure (Cambray & Jubb, 1977) and are passed through the valve ports and sprayed against the concrete walls

Plate 1: The intake tower of the Orange/Fish Tunnel located at Oviston on Lake Verwoerd.

Plate 2: The intake grids of the Orange/Fish Tunnel located at Oviston on Lake Verwoerd. The distance between each verticle bar is 65mm, the grid prevents large objects from entering the tunnel while it is in operation.

of the valve chambers. These can be avoided, however, when the tunnel is drained for inspection and the "pepper-pot" valves are bypassed.

Bearing in mind the severe hazards to fish posed by the tunnel, an experiment to determine the survival and mortality of fishes passing through the tunnel was designed and undertaken. Three species were examined, Cyprinis carpio, Clarias gariepinus and Labeo umbratus; the selection of species was governed by the availability of specimens at the collection site (Grassridge Dam, Fig. 6).

4.2 Methods

On the 2-5th December 1983 fish were collected using a 100 m anchovy mesh bag seine net at Grassridge Dam (Fig. 6). Specimens were measured (fork length (FL) for L. umbratus and C. carpio and total length (TL) for C. gariepinus) and placed in a holding pond after tagging (Plate 3). Tags were inserted using a Floytag Mark II tag gun (FD 67 Floy Tags) and placed slightly posterior and inferior to the leading edge of the dorsal fin. The tags were firmly pulled to ensure that they were secure.

The holding pond was approximately 3 m in diameter and 0.7 m in depth, water was continually changed by means of a pump and siffoning pipes (Plate 3). To avoid large diurnal variations in temperature water was pumped from a depth of about 1 m. A certain amount of mortality was expected during collection, handling and tagging. To avoid experimental error where mortality occurred as a result of these experiences, all specimens were held in the holding tank for 12 hours prior to transportation. All deaths prior to transport were noted.

Tagged specimens were transported 100 km to the Orange/Fish Tunnel intake (Plate 1)

Plate 3: The holding pond at Grassridge Dam in which tagged fishes were placed prior to transportation to the Orange/Fish Tunnel intake.

in three "44-gallon-drums" with a constant flow of oxygen passing through the water (Plate 4). Deaths during this phase were recorded.

All surviving specimens were released into the first surge vent of the tunnel located approximately 1 km from the intake tower (Plate 4) ensuring that all tagged fish entered the tunnel. This would not have been the case had they been released at the intake tower.

The length frequency distribution of all tagged and released fishes is shown in figure 7. Fishes ranged in length (combined total and fork length values) from 60 mm to 335 mm with the majority ranging up to 145 mm. C. gariepinus (Fig. 8) comprised the majority of the larger fish released having a mean TL of 208.8 mm, the smallest catfish released was 145 mm TL. A wide range of L. umbratus specimens (110 mm to 340 mm FL) were released but due to high mortality small numbers were used (mean FL was 176.2 mm)(Fig. 8). The largest group of released fishes constituted the carp, C. carpio, FL of these fishes ranged from 60 to 240 mm. The majority of fishes were below 170 mm FL (mean FL 114.6 mm)(Fig. 9).

Simultaneously, 215 markers were released (Plate 5), these would theoretically travel at current speed through the tunnel. The markers were numbered, self addressed table tennis balls filled with water to achieve neutral buoyancy. They were expected to travel at the velocity of the water in the tunnel and provide a method of determining when the released fishes would emerge. In addition, the markers would not actively avoid capture as might fishes and it was suspected that a greater recovery rate would be attained. Any recoveries of markers would be related to recoveries of tagged fish and a relationship (if present) established. If a relationship occurs between tagged fish and marker recoveries this would prove

Plate 4: The first surge vent of the Orange/Fish Tunnel located at Oviston. Tagged fishes and markers were released into the tunnel at this point. The fish transportation trailer made available by the Cape Nature Conservation is also shown in the photograph.

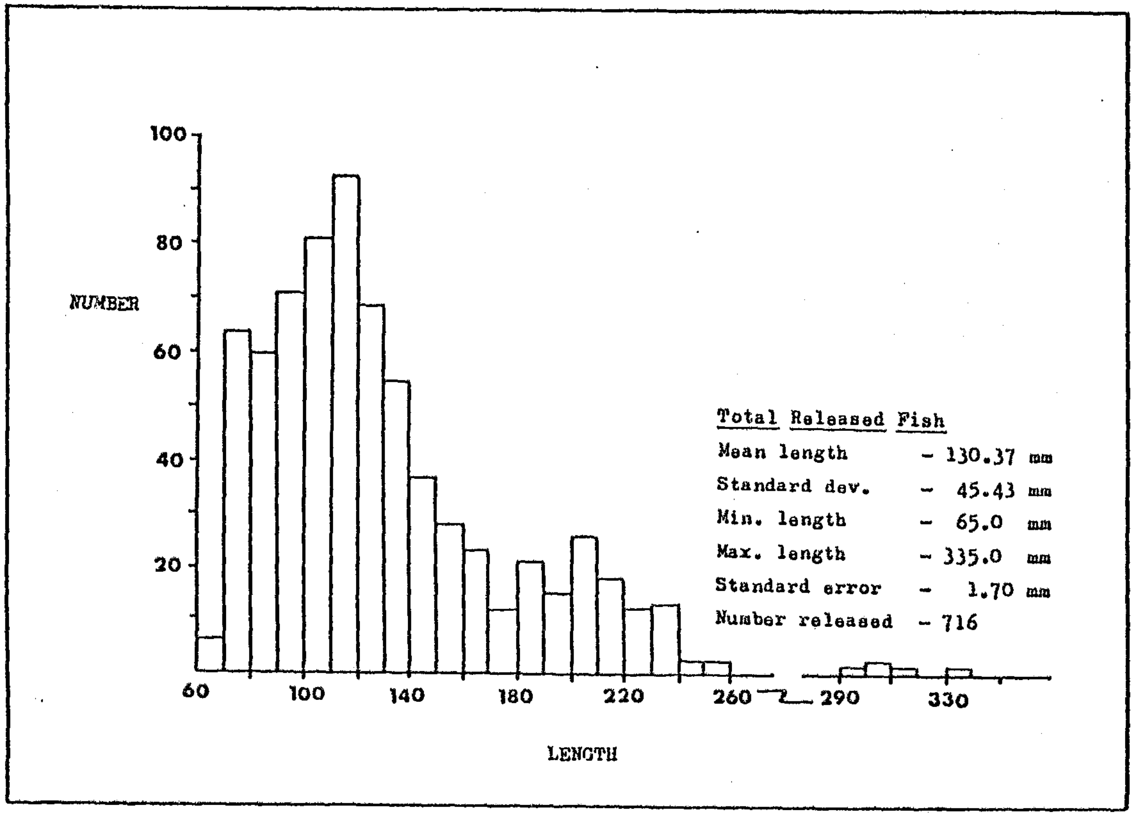
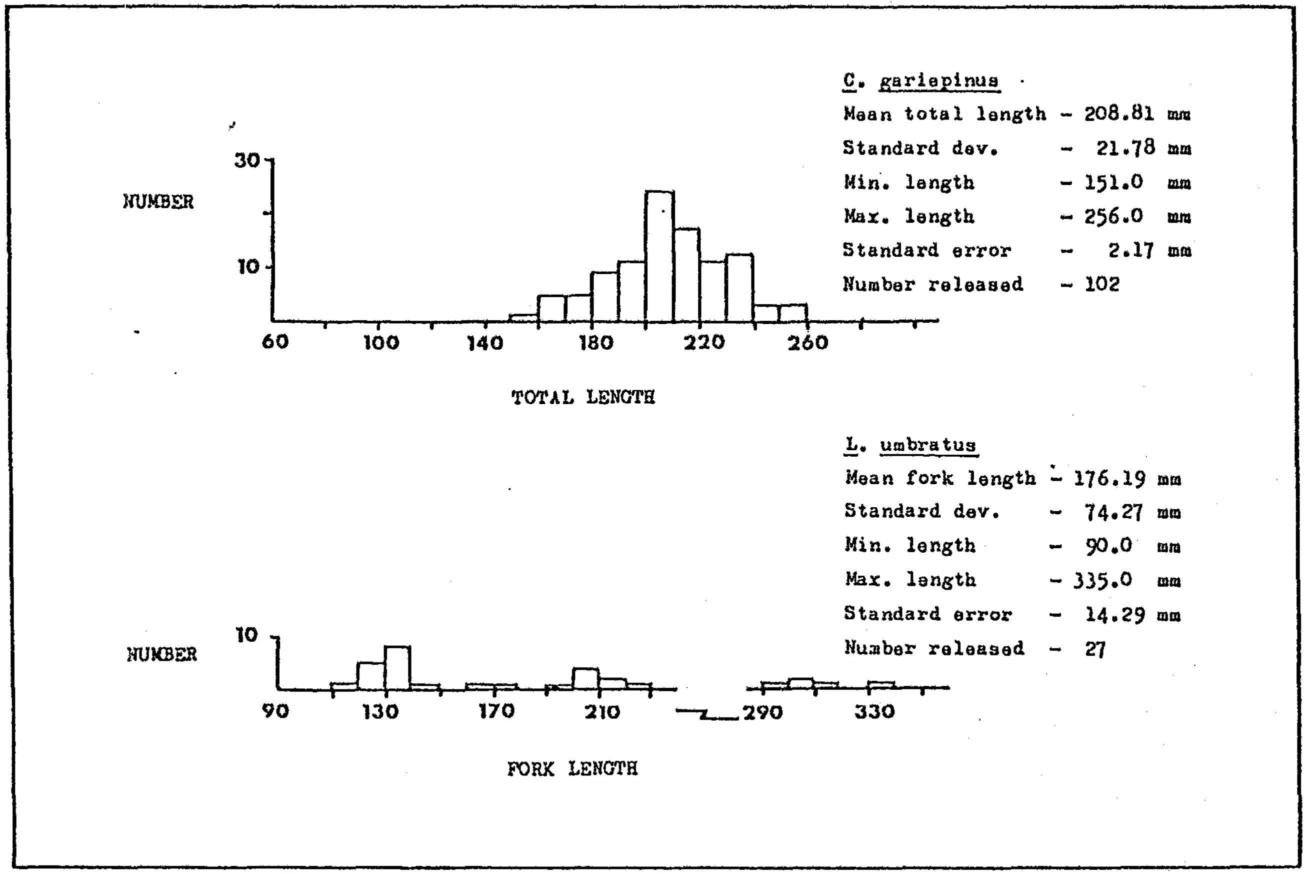


Figure 7: Length/frequency histogram of all species tagged and released into the Orange/Fish Tunnel.



C. gariepinus
Mean total length - 208.81 mm
Standard dev. - 21.78 mm
Min. length - 151.0 mm
Max. length - 256.0 mm
Standard error - 2.17 mm
Number released - 102

L. umbratus
Mean fork length - 176.19 mm
Standard dev. - 74.27 mm
Min. length - 90.0 mm
Max. length - 335.0 mm
Standard error - 14.29 mm
Number released - 27

Figure 8: Length/frequency histogram of all Clarias gariepinus and Labeo umbratus tagged and released into the Orange/Fish Tunnel.

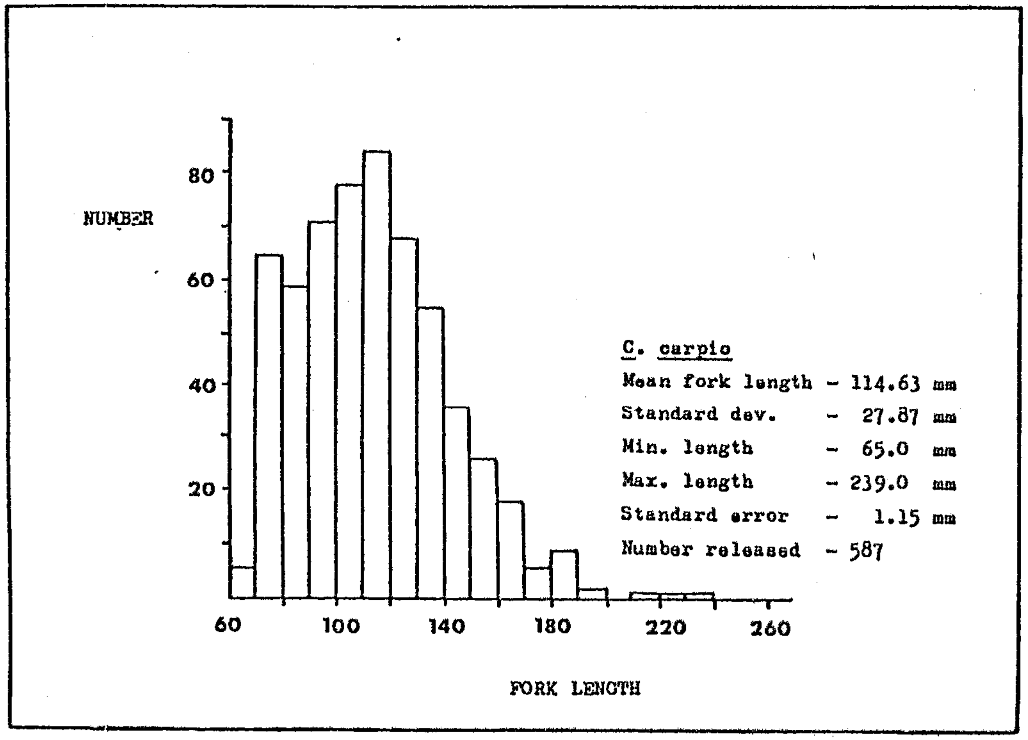


Figure 9: Fork length/frequency histogram of all *Cyprinus carpio* tagged and released into the Orange/Fish Tunnel.

Plate 5: Table tennis ball markers placed in the Orange/Fish Tunnel at the first surge vent (Plate 4), each ball was addressed and filled with water to achieve neutral buoyancy.

invaluable in subsequent studies of this type, particularly where survival estimates are required. The major advantage attained from the technique would be the removal of the necessity of handling and tagging fishes with their associated difficulties.

The outlet facility was fished from the 6-12 December 1983 with 5 gill nets (2 X 30 mm, 45 mm, 47 mm, 86 mm mesh sizes)(Fig. 10) and the main canal was completely blocked by an anchovy mesh bag seine (Plate 6).

4.3 Results

A total of 786 fishes were tagged (Table 11), and 716 of these were released into the intake region of the tunnel. Low mortality in handling, tagging and transport was achieved with C. gariepinus and C. carpio which comprised the bulk of the tagged specimens. A low percentage of lost tags was noted prior to the release (Table 11).

During the five day recovery operation conducted from the 5th to the 9th of December 1983 no tagged fish were recaptured (Table 12). In subsequent excursions there were likewise nil returns. Two L. capensis and one C. gariepinus were captured during the operation but showed no signs of injury due to tagging. A total of 26 (8.3% of the total released) markers were recovered all at the tunnel outlet approximately 8 months after the initial marker and tag releases.

4.4 Discussion

Mark and recapture programs on fishes have an extensive literature (Goldner et al., 1972; Bayliff, 1979; Gunnes & Refstie, 1980; Koch & Schoonbee, 1980; Hankin, 1982;

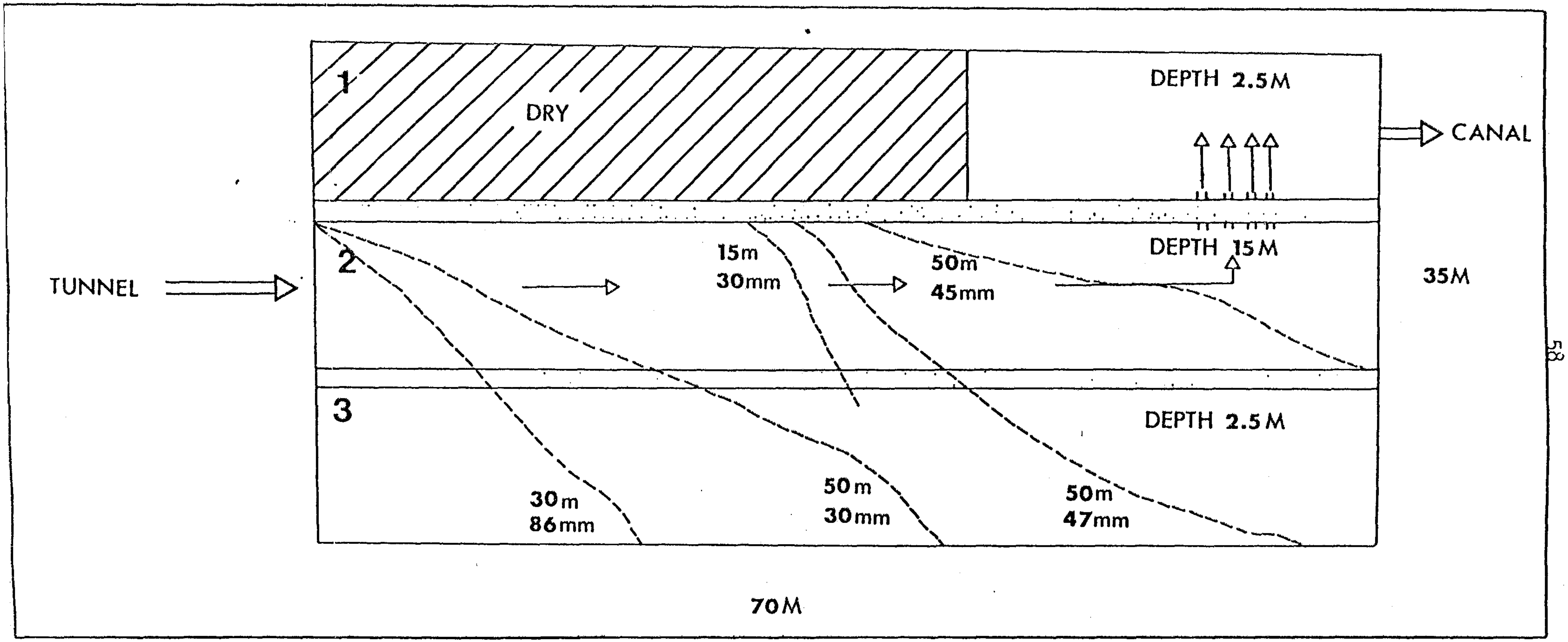


Figure 10: Discharge embayment of Orange/Fish River Tunnel, essentially partitioned into three longitudinal compartments (1,2,3). Dotted lines indicate the position forthe gill nets set in the embayment (length of net in metres (m), mesh size in millimeters (mm)). Arrows indicate direction of water flow. Compartments 1 and 3 essentially were for overflow only.

Plate 6: The Orange/Fish Tunnel outlet facility located at Teebus on the Teebus River. Note the gill net in the foreground.

Table 11 : Mortality of fishes during handling, tagging and transportation. The figure in brackets is the real number of fishes released and the remaining figure is the percentage of all fishes of that species.

	HANDLING/ TAGGING DEATH	TRANSPORT DEATH	LOST TAG	TOTAL ALIVE	TOTAL
C. gariepinus	0.9% (1)	1.9% (2)	0.9% (1)	96.3% (102)	100% (106)
C. carpio	2.9% (17)	1.2% (7)	0.7% (4)	95.2% (587)	100% (615)
L. umbratus	40.0% (26)	16.9% (11)	1.5% (1)	41.6% (27)	100% (65)

Table 12: The captures of fishes at the Orange/Fish Tunnel outlet.

DATE	TIME	SOURCE	FISHES RETURNED
6/12/83	1630	seine	nil
	1815	seine	nil
	1845	gill net	nil
7/12/83	0816	30 mm gill net	1 L. capensis (not tagged)
	1030	gill net	nil
	1030	seine	nil
8/12/83	0645	seine	nil
	0745	gill net	nil
	1445	seine	nil
	1500	gill net	1 C. gariepinus (not tagged)
	1600	seine	1 L. capensis (not tagged) gilled while swimming up stream.
6/2/84		seine	B. anoplus (not tagged)
		gill net	B. aeneus (not tagged)
			L. capensis (not tagged)
			C. gariepinus (not tagged)
7/2/84		seine	B. anoplus (not tagged)
		rotenone	L. capensis (not tagged)
		gill net	C. gariepinus (not tagged)
8/2/84		gill net	L. capensis (not tagged)
-/2/84			markers recovered
20/9/84		cast net	nil
1/10/84		seine	L. capensis (not tagged)
		gill net	C. carpio (not tagged)

Thorson & Lacy, 1982; Tranquilli & Childers, 1982) to mention a few. The methodology for treating these results has also been thoroughly examined (Everhart & Youngs, 1981) and standard mathematical models are available.

Since there were no recaptured fishes in this experiment the available models are at the moment irrelevant. It remains to explain the absence of recaptured individuals to which end a number of arguments can be developed:

1. The fishing techniques at the tunnel outlet facility were inadequate and resulted in total escapement.
2. At the time of discontinuation of fishing activities, no fish had traversed the entire length of the tunnel.
3. And/or no fish survived the hazards of tunnel passage.

It is evident that all the above factors may have contributed to the lack of recapture of marked specimens, however, it is my opinion that the second of the three arguments is the more likely. Fishing activities at the outlet were extensive and involved a series of gill nets as well as a total blocking of the canal by an anchovy mesh bag seine, still, fishes may have escaped. Water entering the tunnel at the intake takes approximately 24 hours to travel the entire length of the tunnel (Spruit, Chief Engineer, Teebus: Pers. Comm.), this may not necesarily be the case with fish. Fish are mobile creatures on the most part and may swim with or against the prevailing current, they are therefore more likely to arrive at the outlet over a time period far different from the expected 24 hours. Furthermore, as the tunnel has many surge vents down its length (one every 12 kms) there are many places where a fish might find refuge from the current, they could therefore spend an indefinite time within the tunnel (bearing available nutritive resources etc. in mind). To compound the factors already mentioned, although the species utilised in the experiment were predominantly benthic fishes, there is no way that a researcher can say with absolute certainty that the specimens did in fact enter the the flowing region of the tunnel. Fishes may have remained within the sheltered region of of the surge vent (where they were initially released) for an uncertain period of time.

The final argument, i.e. no fish survived the hazards of the tunnel, may equally be true as the "pepper-pot" valves are a major stumbling block to fish movement. However this argument relies on the fact that tagged individuals actually reached the valves in the first place.

A compromise view is indicated in this situation. Some fishes did (1) traverse the length of the tunnel, (2) survive passage through the valves and, (3) escaped recapture at the outlet. But the majority of specimens were still within the confines of the tunnel when the recovery work was concluded and would probably have moved through the tunnel over an extented period of time.

The results of this experiment are inconclusive as there are far too many uncontrolled variables influencing the results. Surveys have conclusively shown that _B. aeneus_, _C. gariepinus_ and _L. capensis_ have found their way into the Fish River system (Cambray, 1976; Cambray _et al._, 1977; Cambray & Jubb, 1977; Cambray & Hahndiek, 1979; and this survey). The question to be answered then is at which life history stages do these species successfully negotiate the tunnel when it is in full operation. The "pepper-pot" valves have many series of ports with a diameter of 7.8 cm (each), therfore, to escape extensive injury a fish must have a diameter of less than 7.8 cm. Clearly this restricts the maximum size of a surviving fish.

During the normal operation of the tunnel all water and accompanying objects must pass through the "pepper-pot" valves. However, during periodic tunnel operational shut-down and drainage for inspection, the "pepper-pot" valves are bypassed removing by far the most dangerous part of the translocation process. It is these shut-down periods that allow the majority of fishes to successfully pass through the tunnel. Cambray & Jubb (1977) stated as much when reporting on the dispersal of fishes via the Orange/Fish Tunnel. The recovery of 8.3% of the markers released attests to this. No markers were recovered during the initial recovery phase of the operation in December 1983. However, subsequent recoveries, after a tunnel shut-down and drainage (July 1984) indicate clearly that this shut-down period is the most significant phase in the translocation process and it is during this period that the majority of fishes pass into the Great Fish River. Since no tagged fishes were recovered it is conjecture to relate recovery of markers to fish mortality and the validity of using markers to estimate mortality remains unanswered.

Much literature has been published on the survival of eggs, larvae and juvenile fishes when passing through hydro-electric turbines and various types of pumps (Jubb, 1976; Robbins & Mathur, 1976; Mathur & Heisey, 1980; Patterson & Smith, 1982). Thus, there is no reason why egg to juvenille stages of B. aeneus, C. gariepinus, L. capensis and other species present in Lake Verwoerd cannot pass through the hazards of the Orange/Fish Tunnel. Quantification of this process is difficult and warrants further research. Further tagging operations should be conducted when the tunnel is drained for inspection since passage of fish is clearly divisible into two levels, (1) during normal tunnel operation where fish must pass through the "pepper-pot" valves, and (2) during tunnel shut-down periods when the "pepper-pot" valves are bypassed.

4.5 Summary

The central argument of this experiment, i.e. to quantify fish survival and mortality when passing through the Orange/Fish Tunnel remains largely unanswered. The failure to recapture any marked fishes, rather than illucidating the situation, produced more questions than answers. No unquestionable concrete statements, in terms of the goals of the experiment (i.e. the quantification of the translocation process) can be inferred from these data, although the questions that should be asked are quite clear:

1) Are eggs, larvae and small fish passing through the Orange/Fish at all times, whether in operation or shut-down ?
2) What is the maximum size fish that can pass through the tunnel during normal operation and shut-down ?
3) Which of these life history stages are significantly successful at surviving the passage ?

and 4) How long can an individual fish survive within the confines of the tunnel ?

Mark and recapture operations are clearly difficult and have a remote chance of success in the short term, the variables which must be considered when examining the results are numerous and mostly uncontrollable.

CHAPTER V

AGE, GROWTH, CONDITION AND REPRODUCTION OF FISH SPECIES IN THE GREAT FISH RIVER SYSTEM

5.1 Introduction

The purpose of this chapter is to demonstrate the variations found in age, growth, condition and reproduction between populations of Labeo capensis and Barbus aeneus in Lake Verwoerd and the Great Fish River. An evaluation of how effectively these species are surviving in the newly invaded Great Fish River environment is central to determining how successful the invasion has been. This requires direct comparisons between age and growth studies from many areas but particularly with work carried out in Lake Verwoerd and Lake Le Roux as it is from the area of these impoundments that the exotics were introduced. Age, growth and condition data for Labeo umbratus, Clarias gariepinus and Gephyroglanis sclateri were also collected and an evaluation of these data is presented. Considerable work has been done on B. aeneus and L. capensis but according to Tomasson (1983) the majority of the material has flaws in experimental design and thus are considered inaccurate. These papers are reviewed in this chapter and their short-comings discussed.

5.2 Methods

Sampling was carried out on a two monthly basis (Fig. 11) using a variety of catching techniques. The low catchability of L. capensis and B. aeneus required the use of many techniques and precluded any form of standardisation in terms of selectivity.

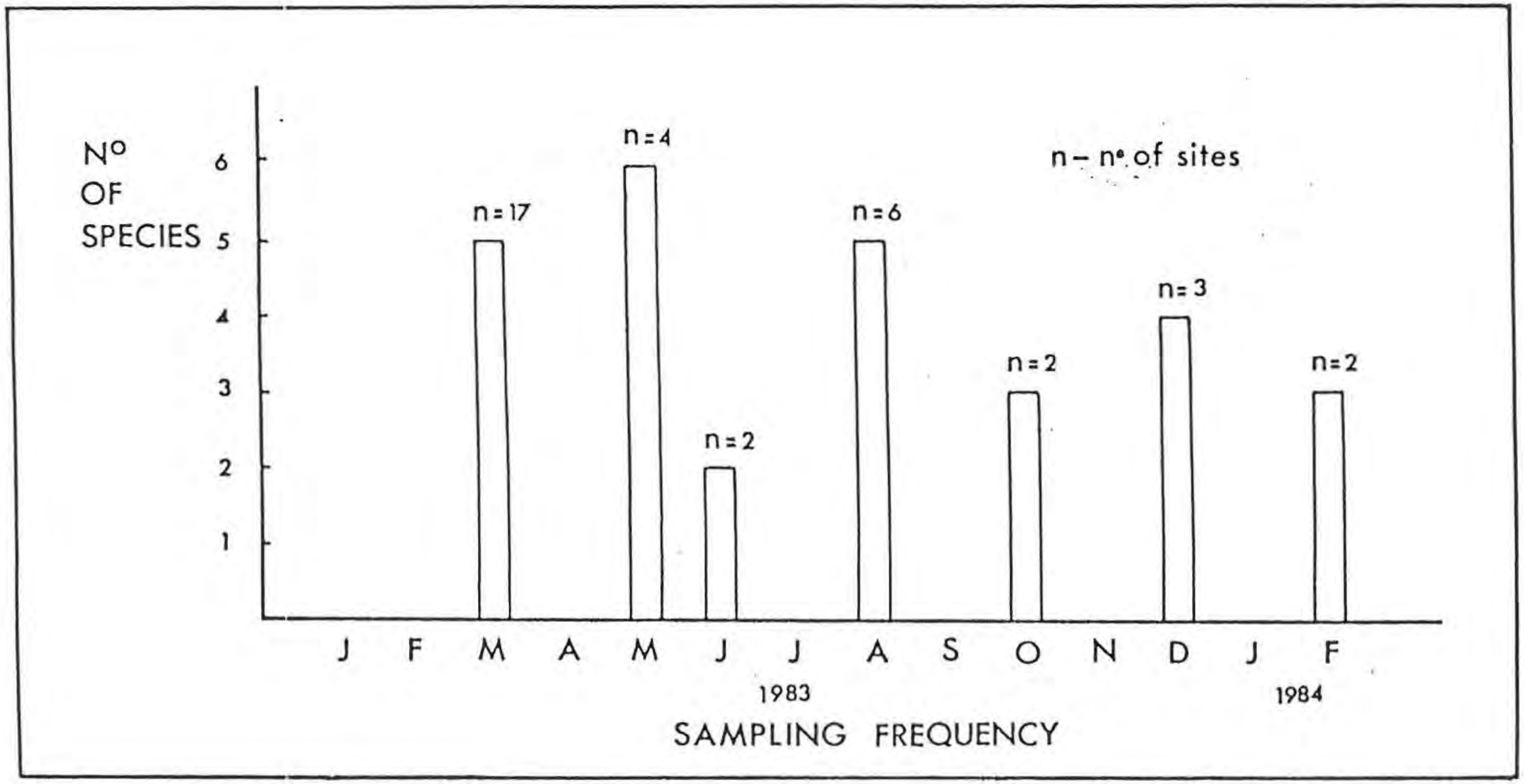


Figure 11: The sampling frequency and number of species captured during the duration of field activities from January 1983 to February 1984.

Rotenone was used on several occasions but only found to be successful during the field work of May 1983 and February 1984. Gill nets were used throughout the study period (30, 45, 47 and 86mm stretched meshes) and were generally set over-night. The most freqently used gear was a 3m by 1.5m anchovy mesh seine. The versatility and effectiveness of this gear in difficult riverine conditions was of great value. Electrofishing using a Lucas-Scholtz electrofisher (constructed in the laboratory) was attempted in December 1983 but due to high turbidity the technique was found to be only marginally successful.

After capture fishes were preserved in 10% formalin and transported to the laboratory. On arrival the fishes were identified, weighed (g) and measured (FL in mm). The lapillus otoliths were dissected from specimens as in cyprinids, these are the largest of the three otoliths (Hecht, 1979) and a sample of scales were taken from between the dorsal fin and the lateral line as recommended by Tomasson (1983).

Otoliths were viewed under a dissecting microscope in methyl salicylate B.P. and scales in a microfiche reader. The majority of scales collected were regenerated and were therefore unreadable and scale reading was eventually discontinued. Growth checks on the otoliths were counted and measured under a microscope using an eyepiece micrometer. Where the growth checks on the otoliths were obscure, the otolith was ground down using 600 grade carborundum paper. This improved visibility of the checks. Backcalculations of length were made following Lee (1920) and Fraser (1916) (Bagenal & Tesch, 1978; Everhart & Youngs, 1981).

$$L' = C + S'/S(L - C)$$

Where L'=backcalculated length, C=correction factor, S'=measured distances to otolith checks, and S=otolith radius

The correction factor (C) is calculated from regressing fish length with otolith radius and is the y-intercept value (Everhart & Youngs, 1981).

Condition factors for B. aeneus and L. capensis were calculated from all available data and are presented in Figure 12. The condition factors followed in this thesis are twofold, the first is based on Tomasson's (1983). Condition factor (K) was defined as:

$$K = \text{Observed weight}/\text{Backcalculated weight}$$

The quotent approximates one, however, when the observed weight is larger than the backcalculated weight, K increases in value (and vice verca). Practically, the condition factor is highly variable even within a single population and may vary within one particular length interval or between different length intervals. In addition, fish populations frequently show variations in condition during reproductive phases, fullness of the alimentary canal and in some species there are permanent sex differences (Weatherley, 1972). Weatherley's (1972) recommendation that condition data for the same age groups not be combined due to possible data bias was followed even though sample sizes were prohibitively small in some cases (Fig. 12). Sex differentiated condition factors could not be calculated as it was impossible to sex most specimens due to their immaturity.

The second measure of condition was used to evaluate the condition of entire species populations. To this end, the length/weight relationship was used:

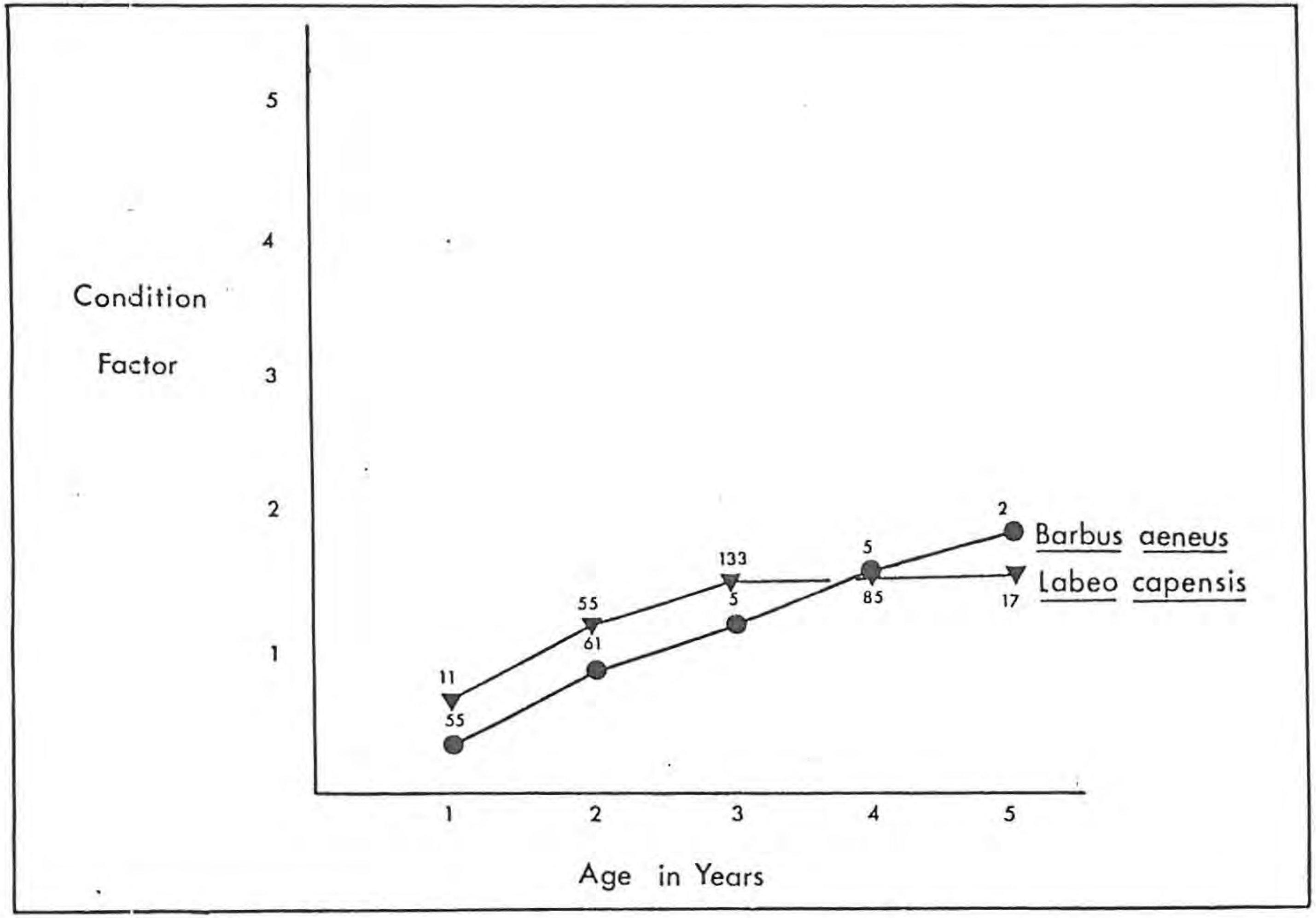


Figure 12: Relative condition factors for Barbus aeneus and Labeo capensis at age collected from the Great Fish River.

$$\text{Weight} = a\ \text{Length}^{b}$$

Where a and b are constants. The logarithm (to the base ten) of this equation is,

$$\text{Log Weight} = b\ \text{Log Length} + a,$$

which is the equation for a straight line. The constant b is the slope of the line and as slope increases positively in value, so the weight at length increases. Therefore the exponent b is indicative of greater weight at a particular length if it is larger in any one population. The exponent then is an effective method of comparing the condition of various populations of a species, the higher the exponent, the better the condition.

All data were entered onto the Rhodes University CDC mainframe computer and processed using M77 Fortran programs and the Statistical Package for the Social Sciences (SPSS)(Nie et al., 1975).

5.3 Results and Discussion

5.3.1 Validation of Check Formation

It is important to examine the environment in which species are captured to validate hen annuli are formed during the year. This has been a major downfall of age and rowth studies in southern Africa (Tomasson, 1983). Growth checks are formed uring periods of environmental stress or during reproductive phases (Lagler et l., 1977) and are laid down on most "hard" parts of the fishes body (e.g. vertebrae, ales, otoliths)(Everhart & Youngs, 1981).

On otoliths, growth rings are distinguished into two distinct zones, the hyaline (translucent) zone and the opaque (not transparent) zone (Hecht, Head of Dept. Ichth., Rhodes Uni.: pers comm.). The hyaline zone is characteristic of rapid growth whereas the opaque zone is characteristic of slow growth (Willoughby & Tweddle, 1978; Tomasson, 1983). These growth checks can, depending on the prevalent environment, be laid down once, twice or at variable times and numbers during the year, particularly in unstable environments (e.g. the Great Fish River), and it is important to show when these occur (Tomasson, 1983).

Validation of annuli formation can be done in a number of ways by combining environmental data with observed data from specimens. Tomasson (1983) used annual increments in growth to show when the greatest growth period during the year occurred, he also related these data to known environmental stress (turbidity). A second method of achieving this is to examine the margin of the otolith (or any hard structure known to lay down growth checks) and determine whether this margin is hyaline or opaque. Since a hyaline zone represents increased rate of growth, the phase that the margin is observed to be in can be related to the date of capture and the growing season may be determined (Hecht, Head Dept. Ichth., Rhodes Uni.: pers. comm.). This may then be related to the prevailing environmental conditions. This second method is the procedure followed in this study.

igure 13 plots the percentage hyaline margins in each sample of fishes against time f year. The percentage hyaline margin increases towards the summer months and is ow over winter. The growing season for the years 1983 to 1984 was clearly the mmer months for both L. capensis and B. aeneus.

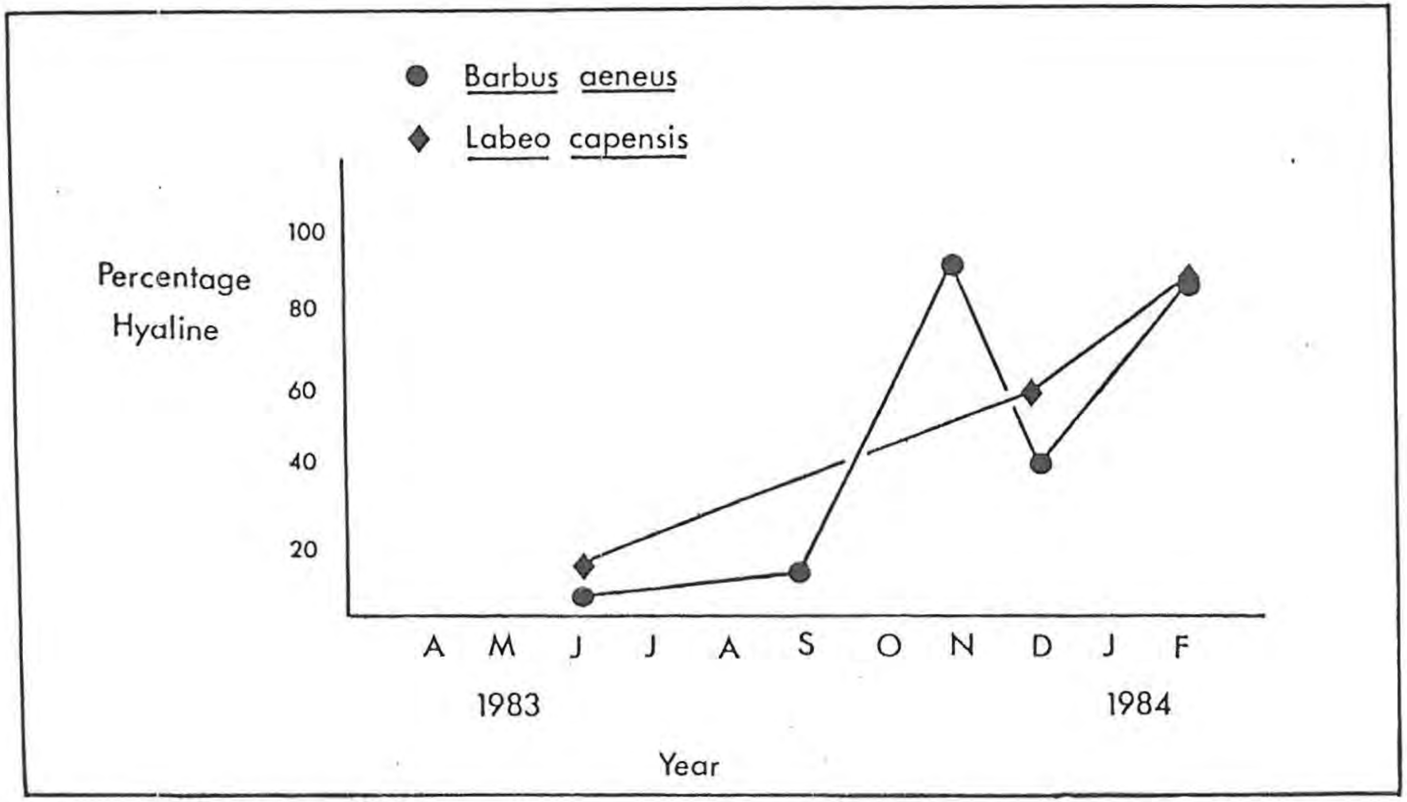


Figure 13: The percentage hyaline margins of otoliths in samples of fishes collected during the course of this study plotted against date of capture.

To extrapolate these data back four to five years annual environmental variables must be correlated to the observed seasonal growing pattern. Figure 14 shows the flow rate of water passing through the Orange/Fish Tunnel from 1978 to December 1983. These data are far from complete as comprehensive records have only recently been collected by engineers at the facility (P. Spruit, Chief Engineer, Orange/Fish Tunnel, Teebus: pers comm.). No real pattern is evident in these data (probably a function of their incompleteness), although in the winter seasons of 1982, 1983 and 1984 there was a marked reduction in water flow.

No temperature data are available in the Great Fish River, nevertheless, some comments may be made. Personal observations have shown that water temperature drops considerably during winter, sufficiently so that rotenone collections were considered impractical and did not work on several occasions. M. King (Dept. Env. & Nat. Cons.: pers. comm.) measured water temperature in Elandsdrift Dam during June 1984 (a single measurement) and found the temperature to be 10°C. It is a reasonable assumption that riverine water temperatures are lower in winter and higher in summer.

Although no attempts have been made to measure turbidity in the Great Fish River, it has been measured in the Orange River and by extension these values are applicable to the Great Fish River. Keulder (1979) measured sediment load during wet (summer) and dry (winter) periods on the Orange River and found that sediment (i.e. turbidity) is considerably higher during the summer months. This is not particularly surprising as the Orange River usually floods annually causing severe erosion in its headwaters in the Drakensberg (Keulder, 1979; Tomasson, 1983). A seasonal increase in turbidity over summer therefore occurs in the Great Fish River.

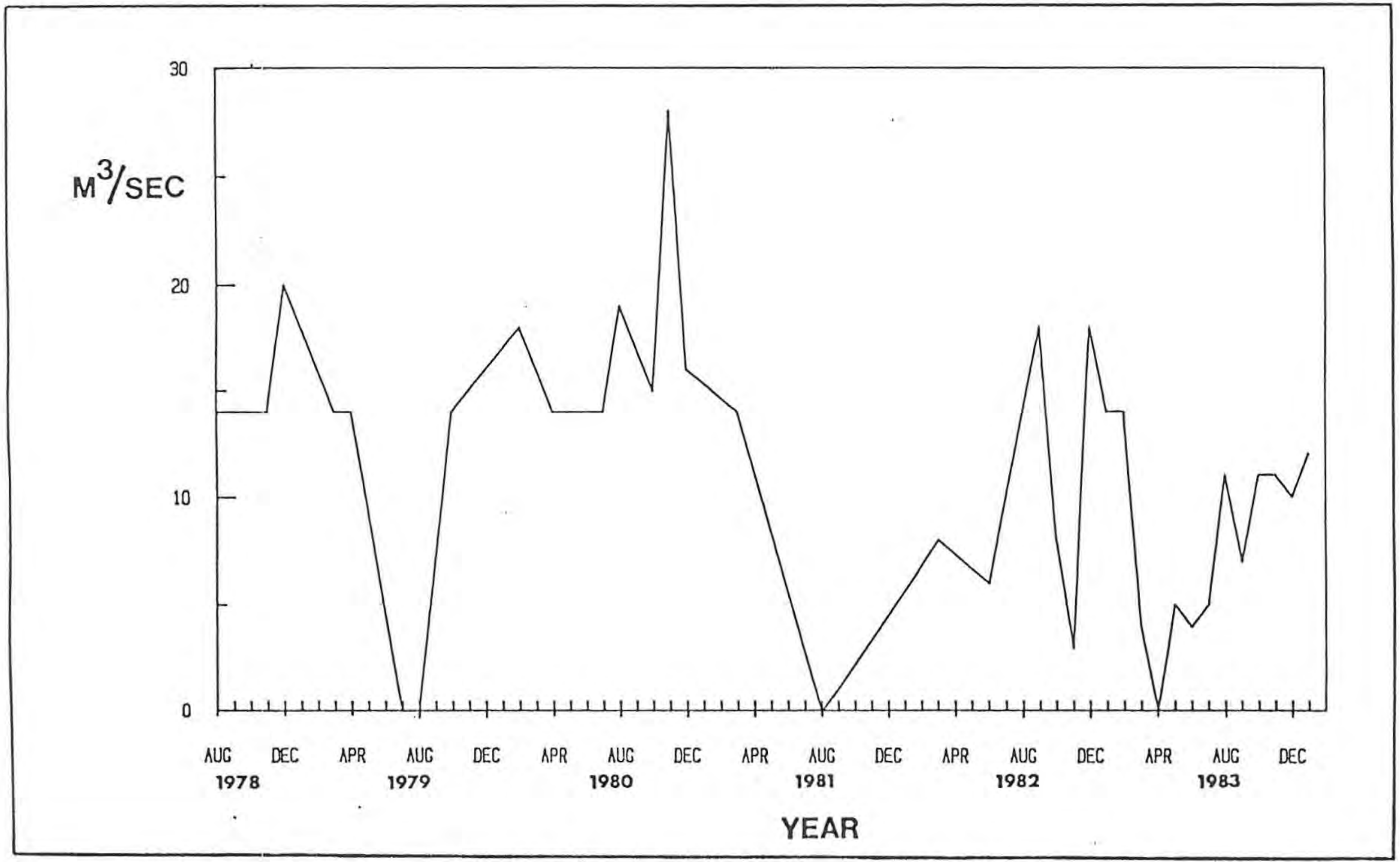


Figure 14: Flow rate (m^3/sec) of water passing through the Orange/Fish Tunnel from August 1978 to January 1984 obtained from the Teebus outlet facilities. The data are not complete as proper recordings of flow rate have not routinely been kept until fairly recently.

Tomasson (1983) found that turbidity severely influenced age and growth of large cyprinids in Lake Le Roux and was the basis for many of his conclusions concerning management. Turbidity clearly increases in summer in the Great Fish River but apparently does not affect growth of either B. aeneus or L. capensis. If turbidity was having a marked detrimental effect on growth then the percentage hyaline margins of otoliths in these species should be reduced when turbidity is high, but this was found not to be the case (Fig. 13). In fact, the reverse is true. Eccles (1983) noted that B. aeneus feeds on invertebrates during the early stages of its life and at 30cm begins changing to larger prey items. Tomasson (1983) found that the high turbidity had minimal effect on growth of B. aeneus until the species was forced to change its diet from benthic invertebrates to benthic algae and angiosperm material. No specimens greater than 30cm were collected in the study of the Great Fish River, therefore, it can be assumed the turbidity does not play a significant role in determining frequency of annuli formation.

The only apparently consistant factor developing between percentage hyaline zones formed at various times of the year and the environment, is temperature and to a lesser extent, water flow. Both of these variables exert their influence during the winter and it is highly likely that these factors, particularly temperature, dictate fish growth in the Great Fish River drainage.

The percentage of unreadable otoliths in the samples can greatly bias the results of any age and growth study (Tomasson, 1983). Barbus aeneus otoliths were 9.8% unreadable, L. capensis 10.0% and L. umbratus 15.7%. The percentage of unreadable scales was not unduly high and the results are not considered biased in this area.

5.3.2 Ageing of Barbus aeneus and Labeo capensis

The age and growth of L. capensis has been extensively studied in South Africa over the past ten years. Mulder (1973b) examined the species in the Vaal River, Bloemhof (1974) in Lake Hardap, Koch (1975) in Barberspan, Baird (1976) in the Caledon River, Hamman (1981) in Lake Verwoerd and Tomasson (1983) in Lake Le Roux. Tomasson (1983) levelled a fair criticism at all of these studies when he noted that the authors, without exception, failed to validate the freqency of annuli formation. In doing so they have assumed a constant environment where checks are formed annually and as shown by Tomasson (1983) and Merron & Tomasson (1984) in Lake Le Roux, this is not necesarily the case.

Table 13 compares the age and growth of L. capensis from all the above mentioned studies. The results compare favourably with each other and has led Tomasson (1983) to regard them with scepticism since he states that the populations come from a variety of environments and hence should show greater variability in growth rates. This may be the case but is not a strong argument, particularly as the reverse may be true, i.e. the species do show the variability of growth which is a reflection of the environment in which they were collected. It is conceivable that the environments examined have highly similar "climates", the exception to the rule may be Lake Le Roux. Nevertheless, the opinions of Tomasson (1983) are accepted in this thesis and the results of all authors with the exception of Tomasson (1983) are regarded with caution.

All previous studies have concentrated on determining age through the examination of annuli on scales. This presents problems of resorption as well as those of scale regeneration and can lead to severe misinterpretations. Ten to 15% of Hamman's (1981) scale samples were unreadable. The percentage of unreadable scales was not presented in other papers.

Table 13: Length at age of Labeo capensis from backcalculated lengths from scales, sources of the information are listed.

SEX \ AGE	1	2	3	4	5	6	7	8	9	10	11	12	13	SOURCE
Male	52	97	143	184	234	274	311	343	368					Caledon R.
Female	52	97	144	185	238	280	320	353	381					(Baird, 1976)
Total	52	115	174	225	273	310	354	380	396					Lake Hardap (Bloemhof, 1974)
Male	75	115	155	205	236	277	317							Lake Verwoerd
Female	78	119	163	210	225	301	344	362	391	427				(Hammon, 1981)
Male	69	107	146	180	210	250								Barberspan
Female	71	107	154	193	232	293	331	345						(Koch, 1975)
Male	90	145	197	251	304	338	372							Vaal R.
Female	87	139	195	249	302	363	377	398						(Mulder, 1973)
Male	56	93	137	181	246	265	296	324	341	357	370	375	378	Lake Le Roux
Female	60	97	142	198	243	289	326	356	376	398	418	430	439	(Tomasson, (1983)
Total	114	137	160	183	207	248								This Study

Similar to L. capensis, B. aeneus has also received considerable attention by researchers (Goldner, 1967; Mulder, 1971; Straub & Combrinck, 1973a,b,c; Koch, 1975; Hamman, 1981; Tomasson, 1983), but the age of this species has been more accurately documented through reservoir stocking and recapture. Le Roux (1963) discussed the introduction of 50 fingerlings into a 3 hectare pond. The fish reached an average length of 30 cm in 2 1/2 years and 40 cm in 5 1/2 years. Twelve years later 74 % of the original stock were recaptured as a result of the pond drying up and were found to have an average length of 53 cm (1.8 to 3.6 kg).

In March 1972, Skelton (1972) collected three B. aeneus of 8+ years in Settlers Dam (approximately 90 hectares) averaging 51 cm and 2 kg. Eighty fingerlings were released in the impoundment in 1964.

In May 1953, 200 fingerlings were released into a 95 hectare reservoir on the Gouritz River. By January 1959, at the age of 6+ years a sample of 13 of these fishes ranged from 50 to 56 cm (2.1 to 3.1 kg). Louw (1970) recaptured five yellowfish in the impoundment 11 years later and the length ranged from 50 to 67 cm. All specimens from this site (with one exception) were found to be extremely deep bodied with the largest individual weighing 5.5 kg (57 cm). In 11 years B. aeneus in this reservoir grew little in length but gained tremendously in weight.

From these data Tomasson (1983) concludes (a) that B. aeneus has an initial rapid growth in length which is offset by rapid growth of weight in later years of life, and (b) because of this change in pattern of growth (i.e. length to weight) older fishes are difficult, if not impossible, to age. This is a direct result of scales growing in proportion to fish length and not weight.

The more conventional method of ageing by analysing check formation on scales of B. aeneus has proved to be as incomplete as that shown for L. capensis. With the exception of Tomasson (1983) and to a lesser extent Straub & Combrinck (1973c) the assumption that check formation occurs annually has not been validated.

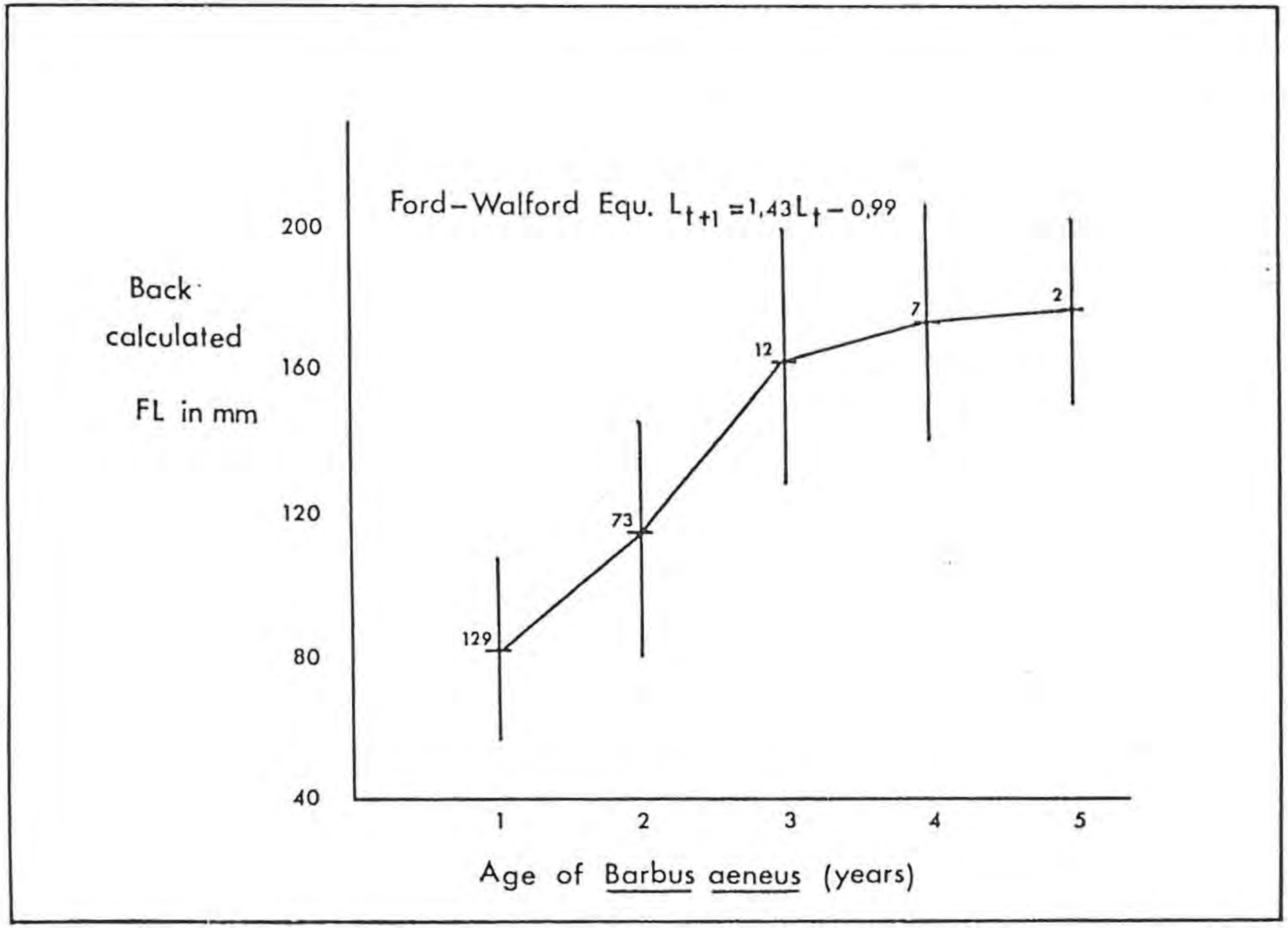
Hamman (1981) found that females grew faster than males during the first four years in Lake Verwoerd (Table 14), however, 50 to 60 % of his scale samples were unreadable and this may have biased his results (Tomasson, 1983). Mulder (1971) noted no substantial disparity between male and female growth rates from the Vaal River. Further, he found that in some Barbus species an annulus may not be formed in the first year of growth. No further attempts were made to validate the results. In Lake Boskop, Koch (1975) showed that females grow substantially faster than males in the first 8 years of life, but again, the frequency of annuli formation was not validated. Tomasson (1983) found that females grew marginally faster up until 11+ years of life in Lake Le Roux, frequency of annuli formation was validated in this study. The results of all the discussed studies are presented in Table 14.

5.3.3 Age and Growth of Barbus aeneus

Figure 15 shows the backcalculated lengths at age of B. aeneus. The results are regarded as reliable only for ages 1, 2 and 3 as sample sizes are questionable thereafter. The oldest fishes collected from the drainage were 5+ years. In the first year the species has an average backcalculated length of 80mm (FL). The length is greater than values obtained in Lake Verwoerd (Hamman, 1981), Lake Le Roux (Tomasson, 1983) and Lake Boskop (Koch, 1975). However, it is less than backcalculated lengths in the first year obtained from the Vaal River (Mulder, 1973) and Barberspan (Straub & Combrinck, 1973)(Table 14). In the subsequent two years

Table 14: Lengths at age of <u>Barbus aeneus</u> from backalculated lengths from scales, sources of information are listed.

AGE SEX	1	2	3	4	5	6	7	8	9	10	11	12	SOURCE
Male	67	108	156	203	256	303	340	372					Lake Verwoerd (Hamman, 1981)
Female	61	113	166	223	276	322	364	391	416				
Male	68	112	151	189	219	248	261	267					Lake Boskop (Koch, 1975)
Female	75	118	153	198	242	293	339	349					
Male	95	151	205	258	311	359	395						Vaal R. (Mulder, 1973)
Female	94	146	198	251	301	351	390	432	474	501			
Total	91	131	191	224	256	288	311	361	394	400	462		Barberspan (Straub & Combrinck, 1973)
Male	67	115	166	215	259	292	323	338	364	380	397	428	Lake Le Roux (Tomasson, 1983)
Female	66	116	173	225	269	305	335	363	379	398	403		
Total	80	114	162	173	176								This Study



. Figure 15: The backcalculated lengths at age of *Barbus aeneus* collected during 1983/84 in the Great Fish River.

where reliable information is available the data are more compatible with Tomasson (1983), Hamman (1981) and Koch's (1975) work.

Data collected for B. aeneus do not fit the von Betalanffy growth model (Fig. 15) as the slope of the Ford-Walford equation (obtained by regressing length at age against length at age plus 1) is not less than one (Everhart & Youngs, 1981; Weatherley, 1972) (Fig. 15). Quick & Bruton (1983) found that Clarias gariepinus data from Lake Le Roux were not compatible with the von Bertalanffy model. Tomasson (1983) expresses some misgivings about the use of the von Bertalanffy model to validate the accuracy of age and growth studies. All studies on B. aeneus to date have shown that the species growth is compatible with this model. The data available in this study covers only the first three years of growth at which stage the species is not sexually mature (Figure 15) and still shows rapid growth with no calculable asymptotic length (L_∞)(Hecht, Head Dept. Ichthy., Rhodes Uni.: pers. comm.; Everhart & Youngs, 1981; Weatherley, 1972). It is therefore probable that these data are not compatible with the von Bertalanffy growth model as a true picture of the growth of the species in the Great Fish River after the first three years is unknown.

The growth of B. aeneus during the first three years is very similar to Lake Verwoerd (Hamman, 1981) and Lake Le Roux (Tomasson, 1983) populations and is good by comparative standards. However, the data differ significantly only from B. aeneus growth in the Vaal River (Mulder, 1973a) and Barberspan (Straub & Combrinck, 1973a,b,c) where, if the data are to be considered reliable, growth is substantially faster in the second and third years. This species is growing well in the Great Fish River.

5.3.4 Age and Growth of Labeo capensis

Statistically reliable data for age and growth of L. capensis wereobtained for the first five years of life (Fig. 16). One individual of 6+ years was collected. These data differ significantly from all other age and growth studies on this species (Table 13). In the first year L. capensis in the Great Fish River reaches an average length of 114mm TL, which is substantially faster than other studies have indicated (Table 13). Lake Verwoerd (Hamman, 1981), Barberspan (Koch, 1975) and Lake Hardap (Bloemhof, 1974) populations of the species reach 114mm TL in their second year. In the second year, Great Fish River populations only grow a further 23mm to 137mm FL and by the third year (160mm FL) their lengths are not greatly different from other studies. This downward trend continues until the fifth year where Fish River populations of the species are considerably smaller than all other populations (Table 13).

As with B. aeneus these data are also not compatible with the von Bertalanffy model of fish growth (Fig. 16) as the slope of the Ford-Walford equation is greater than one and the range of data available does not permit the calculation of the species asymptotic length (L_∞). This is understandable when considering the size at sexual maturity of the species (Table 15). Labeo capensis approaches sexual maturity at about 200mm which, in the case of Great Fish River populations of the species is at an age of five years. Only a small number of five year old L. capensis were collected during this survey and, therefore, the true behaviour of age and growth of this species is cannot be accurately assessed after fives years of age.

Labeo capensis has an initial rapid growth rate in the first year which is substantially faster than shown by other studies. Annual increments thereafter

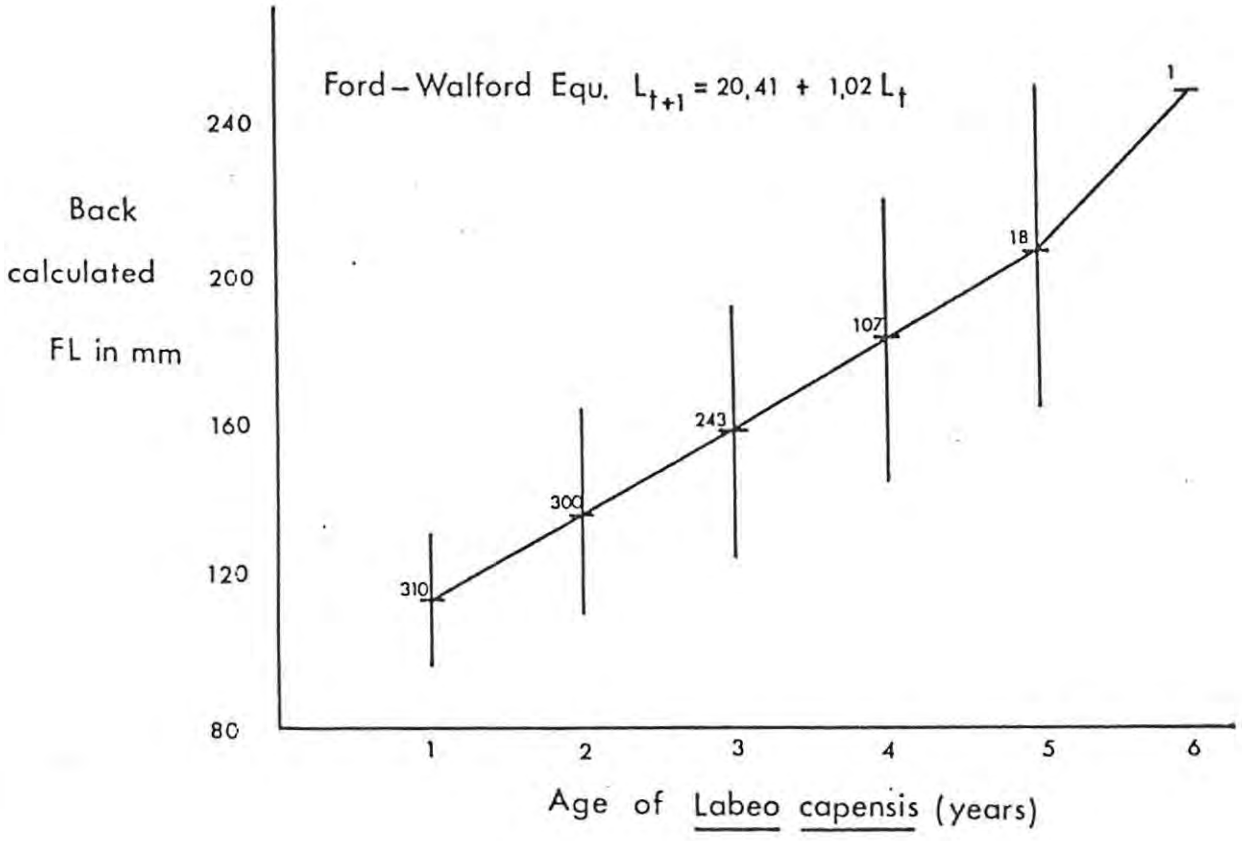


Figure 16: The backcalculated lengths at age of Labeo capensis collected during 1983/84 in the Great Fish River.

Table 15: Length (FL) in mm at sexual maturity for B. aeneus and L. capensis, sources of information are listed.

B. AENEUS		L. CAPENSIS		SOURCE
MALE	FEMALE	MALE	FEMALE	
		160	200	Caledon R. (Baird, 1976)
200	250	260	320	Barberspan (Goldner, 1967)
200	240	220	240	Vaal R. (Groenewald, 1975)
210	310	220	290	Lake Verwoerd (Hammon, 1981)
280	340	260	310	Vaal R. (Mulder, 1971)
300		330	370	Lake Le Roux (Tomasson, 1983)
240		280	350	Lake Le Roux (Tomasson, 1983)

are small and by the fifth year the species is considerably smaller than other populations (Table 13, Figure 16). Initially growth is good but rapidly declines as the fish gets older. The overall performance of this species in the Great Fish River in terms of growth is bad.

5.3.5 Age and Growth of Clarias gariepinus, Labeo umbratus and Gephyroglanis sclateri

The age and growth of Clarias gariepinus, Gephyroglanis sclateri and Labeo umbratus from the Great Fish River were only superficially examined due to small sample sizes. No attempt was made to validate the assumption that growth checks are formed annually. It was assumed, however, that since this pattern has been demonstrated in both L. capensis and B. aeneus that it occurs with other species in the drainage. Merron & Tomasson (1984) noted annual formation of annuli in Lake le Roux populations of L. umbratus and Quick & Bruton (1983) demonstrated similar behaviour in check formation with C. gariepinus from the same impoundment.

5.3.5.1 Clarias gariepinus

Table 16 compares the backcalculated lengths at age of the sharptooth catfish from Lake Le Roux (Quick & Bruton, 1983), Lake Sibaya (Bruton & Allanson, 1980), the Transvaal (Van der Waal & Schoonbee, 1975) and Lake Verwoerd (Hamman, 1981) with data collected during the course of this study. The sample size used to obtain the backcalculated values for Great Fish River populations was extremely small (n = 5) and hence the results should be viewed cautiously.

Clarias gariepinus grows considerably slower in the Fish River on the basis of

Table 16: Backcalculated lengths at age for Clarias gariepinus, sources listed.

AGE	1	2	3	4	5	6	7	8	9	10	SOURCE
Males	213	321	413	520	683	808	903	964			
Females	204	313	402	503	632	760	848	897			Quick & Bruton
Total	209	316	410	517	769	835	897	951			(1984) Lake Le Roux
Males	240	399	517	575	629	659	695	726			
Females	240	406	512	608	639	648					Bruton & Allanson
Total	240	371	494	545	615	652	697				(1980) Lake Sibaya
Males	272	407	571	686	810	960	1010	1128	1200	1210	
Females	269	407	554	649	809	938	999	1045	1010	1210	Hamman (1981)
Total	269	407	562	617	810	946	1005	1087	1105	1210	Lake Verwoerd
Males	426	477	544	628	723	775	835	1005			Van Der Waal &
Females	414	464	526	604	688	728		960	1065	1105	Schoonbee (1975)
											Transvaal
Total	121	167	339	380							This study

available information and although this is consistant with data from L. umbratus and B. aeneus age and growth it is well below the length at age obtained from other populations (Table 16). Van der Waal & Schoonbee's (1975) work in the Transvaal is seriously questioned here. It is extremely unlikely that C. gariepinus grows to over 400mm in its first year. Particularly as the species in the Transvaal shows smaller annual increments than found elsewhere, with the exception of this study. Growth of C. gariepinus in the Great Fish River is poor and the species does not appear to be performing (in terms of growth) well in the drainage.

5.3.5.2 Labeo umbratus

Table 17 compares the age and growth of Labeo umbratus from the Vaal River (Mulder, 1973b), Lake Le Roux (Merron & Tomasson, 1984) and Lake Verwoerd (Hamman, 1981). Sample sizes were larger than those obtained for C. gariepinus and the data are considered more reliable. Growth of this species was found to be considerably slower in the Great Fish River as compared to that in other water bodies. The species grows to 42mm in its first year. By contrast, L. umbratus grows to 85mm in its first year in Lake Le Roux (Merron & Tomasson, 1984). Both Mulder's (1973b) and Hamman's (1981) work show that the species obtains much greater lengths in its first year (with regard to backcalculated lengths at ages). The discrepancies in length at age continue up to the limit of the data, Fish River populations are on average significantly smaller than Vaal River, Lake Le Roux and Lake Verwoerd populations.

Comparisons of backcalculated data from this study to lengths at age calculated from von Bertalanffy equations show a similar trend. However, Mulder's (1973b) work in the Vaal River shows a considerable difference between backcalculated length and empirical length at age 1. Mulder's (1973b) empirical length for the first year

Table 17: Backcalculated lengths at age for *Labeo umbratus*, sources listed. von B. - values calculated from von Bertalanffy equations.

AGE	1	2	3	4	5	6	7	8	SOURCE
Males	146	229	294	339	382	395			
Females	141	253	297	334	408	414	431	460	
Total	142	236	293	337	402	404	425	445	Hamman (1981)
von B.	146	224	287	338	379				Lake Verwoerd
Males	104	197	293	370	408	455			
Females	109	200	294	356	434	473			
Total	107	199	294	360	430	467			Mulder (1973b)
von B.	87	212	308	380	435	477			Vaal River
Total	85	165	235	306	356	387	404	414	Merron & Tomasson (1984) Lake Le Roux
Total	42	125	213	281	339				This study

matches closer to Merron & Tomasson's (1984) than his own. However, the sizes between length at age from this study and that carried out in the Vaal River still remains significant without a major change in pattern. Labeo umbratus, as with virtually all other species of fishes in the Great Fish River, is not growing well in the system.

5.3.5.3 Gephyroglanis sclateri

Since only four specimens of Gephyroglanis sclateri were collected during this study the results are mostly ambiguous. However, one important piece of information was obtained from these data. The largest specimen captured (235mm FL, 166g) was superficially aged and found to have four annuli present on its otoliths. The ageing was not accurate though and the fish may have been older (Laurenson & Hocutt, 1984). These data are interesting in that the species had virtually disappeared from gill net catches in Lake Verwoerd by 1975 (Hamman, 1981). The ramifications of this are dealt with in chapter III and in Laurenson & Hocutt (1984).

5.3.6 Trends Occurring in Fish Production in the Great Fish River

Chapman (1978), in a review on production in fish populations noted a trend of higher production in lentic habitats as opposed to that of lotic systems. Similarly, this trend was discussed by Burgis & Dunn (1978) who examined the River Thames in England, Lake George in Uganda and Loch Leven in Scotland. This basic premise has shown itself to be present in the Great Fish River to a fairly large degree. All species examined have been shown to be growing at a lesser rate when compared to populations from impounded environments. All studies in riverine environments examined so far in this thesis, other than the present study, follow a similar pattern obtained in the impoundments, i.e. fish production is equivalent in lotic and impounded systems. The basic premises of these studies have been questioned and criticised, using the same criteria presented earlier in this chapter criticising studies on B. aeneus and L. capensis (Tomasson, 1983). That is, time of annulus formation has not been validated (Merron & Tomasson, 1984). The results from these works are not, therefore, considered accurate.

5.3.7 Condition

Relative condition as calculated following Tomasson (1983) required the use of length/weight relationships for the prediction of expected weights. The size range of fishes used in preparing these relationships was small and it is likely that errors in this phase of calculations are reflected in the relative condition calculations. Relative condition between populations was evaluated by comparing the exponents of the length/weight equations.

The length/weight equations for all L. capensis from this study are presented in Table 18. The relationships differ markedly from other studies of the species.

Using Lake Le Roux data to calculate expected weights and comparing these data with expected weights of Great Fish River populations we note that for L. capensis expected weight with increasing length drops markedly by comparison (Table 19). Initially Fish River populations are significantly heavier but by the fifth year the discrepancies between weights from various populations is small. This pattern continues in Lake Verwoerd where Hamman (1981) noted the same described trend. Using the overall condition factor (the exponent of the length/weight relationship), the condition of Fish River populations of L. capensis is

Table 18 : The constant values from length/weight relationships from the Vaal River, Lake Le Roux and Lake Verwoerd for Labeo capensis. The equation is of the form: $W=aL^b$ W=Weight, L=Length

SEX	EXPONENT (b)	CONSTANT (a)	SOURCE
Total	2.051	0.00219	This Study
Total	3.241	0.000038	Tomasson (1983) Lake Le Roux
Male	3.0638	0.00125	Hamman (1981) Lake Verwoerd
Female	3.0651	0.00122	
Total	2.9816	0.00059	Mulder (1973) Vaal River

Table 19 : Mass in grams calculated using length/weight relationships from data collected in the Great Fish River, Lake Le Roux and Lake Verwoerd. Data from Tomasson (1983) and Hamman (1981).

	BARBUS AENEUS				LABEO CAPENSIS			
AGE	THIS STUDY	TOMASSON	HAMMAN		THIS STUDY	TOMASSON	HAMMAN	
			M	F			M	F
1	7.1	6.6	7.2	8.1	36.2	18.0	21.6	21.2
2	20.4	19.1	20.9	22.0	52.8	32.3	38.0	37.2
3	58.6	55.6	60.6	62.4	72.6	52.4	60.0	58.7
4	70.4	67.0	71.7	73.1	95.7	82.4	92.2	90.3
5	74.8	71.2	76.8	78.2	123.2	121.8	134.5	131.8

significantly lower than other populations and the species is not in good condition in the drainage as compared to all other populations (Table 18).

The pattern emerging is consistent with the age and growth data presented in the previous section. Labeo capensis was shown to have a decreasing rate of growth which is reflected in a lower weight at length.

The relative conditon factors for L. capensis using Tomasson's (1983) method show an overall increase in the first three years, thereafter condition appears to tail off and a decline sets in (Figure 12). This correlates with the observed reduced growth rates (section 5.3.4) and lower value of the exponent of the species length/weight relationship (Fig. 18).

These data lend credence to the conclusions drawn earlier in this Chapter, i.e. L. capensis is not effectively surviving in the Great Fish River and has not established a population. The presence of the species in the drainage is very likely as a result of continued "stocking" of juvenilles from Lake Verwoerd by the Orange/Fish Tunnel.

Barbus aeneus, on the other hand, has a slowly increasing relative condition (Tomasson's (1983) method) as the species age increases (Figure 12). Sample sizes for 3, 4 and 5 year old fish are, however, relatively small and the results should be viewed cautiously. The increase in relative condition over ages 1 and 2 is seen as real and the remaining changes in condition of age groups is considered nominal (Table 20). The results are consistent with age and growth as well as length/weight data on the species and are considered reliable in this context.

Table 20 : The constant values from length/weight relationships from Lake Le Roux and Lake Verwoerd for *Barbus aeneus*. The equation is of the form: $W=aL^b$ W=Weight, L=Length

SEX	EXPONENT (b)	CONSTANT (a)	SOURCE
Total	3.009	0.000013	This Study
Total	3.039	0.0000106	Tomasson (1983) Lake Le Roux
Male Female	2.9874 2.9266	0.000146 0.000177	Hamman (1981) Lake Verwoerd

Condition comparisons for Barbus aeneus between populations is comparatively good. In the Great Fish River B. aeneus is in good condition and does not lend support to the argument that lentic conditions are more productive than impounded habitats (Chapman, 1978; Dunn & Burgis, 1978). These data are further supported by age and growth results which show the species growing as well as other populations.

Sample sizes for Clarias gariepinus and Labeo umbratus were too small to calculate condition factors according to Tomasson (1983). However, the exponent value is of some use in comparing populations of these species. Table 21 lists the length/weight relationships for L. umbratus from a variety of habitats. Data obtained from this study indicates a nominally equivalent condition with regard to other populations. Only Mulder's (1973) data from the Vaal River follows the lentic/lotic arguments presented earlier in this chapter (see section 5.3.6). Labeo umbratus, on the basis of these data, is in good condition in the Great Fish River drainage and does not seem to be suffering as yet from the presence of exotic species.

Clarias gariepinus length/weight data are shown in Table 22. The sample size in the case was exceedingly small (n = 9) and the data cannot be considered conclusive. No conclusions can therefore be validly drawn from these data.

5.3.8 Reproduction

The majority of fishes, both B. aeneus and L. capensis, collected in the Great Fish River drainage were below breeding size. Gonads were highly reduced and specimens in the most part could not be sexed. Only one breeding condition B. aeneus was collected and no breeding condition L. capensis were sampled. This is likely a

Table 21 : The constant values from length/weight relationships from the Vaal River, Lake Le Roux and Lake Verwoerd for Labeo umbratus. The equation is of the form: $W=aL^b$ W=Weight, L=Length

SEX	EXPONENT (b)	CONSTANT (a)	SOURCE
Total	3.10	0.00000783	This Study
Male Female	3.203 3.204	0.0000035 0.0000038	Merron & Tomasson (1983) Lake Le Roux
Male Female	3.0244 3.0324	0.00126 0.00122	Hamman (1981) Lake Verwoerd
Total	2.9116	0.0016	Mulder (1973) Vaal River

Table 22 : The constant values from length/weight relationships from a variety of studies for the catfish, *Clarias gariepinus*. The equation is of the form: $W=aL^b$ W=Weight, L=Length

SEX	EXPONENT (b)	CONSTANT (a)	SOURCE
Total	1.99	0.0017	This Study
Male Female	3.2548 3.2548	0.00028 0.0028	Hamman (1981) Lake Verwoerd
Male Female	2.699 2.705	0.00004 0.00004	Bruton & Allanson (1980) Lake Sibaya
Total	3.136	0.00045	Willoughby & Tweddle (1978) Shire Valley
Total	3.2284	0.0000016	Quick & Bruton (1983) Lake Le Roux

sampling problem and not a direct reflection of the state of the fish populations, particularly with regard to *B. aeneus*. A small number of large *C. gariepinus* with well developed gonads were collected thoughout the drainage system. Juveniles of *B. aeneus*, *L. capensis* and *C. gariepinus* were collected only at the tunnel outlet.

From these data it can be concluded that the invasive species (with the exception of *B. aeneus* and *C. gariepinus*) are not reproducing in the Great Fish River. They have therefore not established themselves in the drainage system.

5.3.9 Feeding

A qualitative examination of the gut contents of *Barbus aeneus*, *Clarias gariepinus*, *Labeo capensis* and *L. umbratus* was undertaken with a view to obtaining superficial data on overlapping diets. This would not demonstrate competition *per se*, but would show any overlaps of dietary items (i.e. feeding niches) of the species.

The diet of *C. gariepinus* in the Great Fish River can be divided into two stages. In younger fishes invertebrates play an important role (insects, crustaceans, invertebrate larvae). In larger fishes, the diet becomes more piscivorous and the species consumes *Labeo* species and *Cyprinis carpio*.

As an invasive species feeding on indigenous *Labeo umbratus* it may be having an effect on the system. However, data indicates that the species is not numerous in the drainage (Chapter III) and in addition, *Labeo umbratus* is only a portion of its diet. The effect of this species on indigenous ichthyofauna can therefore be regarded as mostly superficial.

Generally Barbus aeneus was found to be consuming mostly invertebrates and invertebrate larvae. The bulk of the stomachs examined also contained quantities of grit and sand. Much of the diet is probably collected from the substrate which accounts for the presence of detritus in the gut. Eccles (1983) found this in younger smallmouth yellowfish from Lake Le Roux.

The species is mostly confined to the lotic regions of the upper river where an overlap of diet occurs with young C. gariepinus. There is a small overlap with the diet of L. umbratus (next section), however, due to variations in distribution (Chapter III) their diets do not coincide.

All specimens of L. capensis and L. umbratus were found to be feeding on the bottom by ingesting large quantities of mud and presumable absorbing nutrition from the micro-organisms in the substrate. There is an indirect overlap in diet between the invasive L. capensis and the indigenous L. umbratus. Personal observations of extensive mud banks in the Great Fish River drainage suggests that this nutritive resource is unlikely to be a limiting factor and therefore there is likely to be little or no competition. In addition, the present distribution of these species (Chapter III) overlaps only marginally. Labeo capensis is not having any real effect as yet on the indigenous ichthyofauna of the Great Fish River system.

The diets of all species superficially overlap in certain areas throughout the Great Fish River drainage. Particularly with regard to L. capensis and L. umbratus. Clarias gariepinus is widespread but not numerous and preys on indigenous species to a small extent, but as the overall number of the species is low, no real effect is noted on indigenous ichthyofauna at the present time.

The major operating force in the Great Fish River, especially with regard to B. aeneus, L. capensis and L. umbratus is distinct habitat preferences (Chapter III). The indigenous Labeo prefers quiet backwaters, secondary tributaries and impoundments (Skelton, 1984), B. aeneus and L. capensis are more common in lotic regions but have distinct dietary differences. Clarias gariepinus does not follow the trend and is found in all habitats but is not common.

5.3.10 Summary

This chapter has demonstrated that in terms of relative condition B. aeneus is performing (i.e. effectively surviving as a whole) well in the Great Fish River drainage. This conclusion is further substantiated by the age and growth data presented earlier in the chapter as well as the observed increase in distribution of the species (Chapter III). In terms of feeding, the species is utilising the same resources as young C. gariepinus but does not have dietary requirements coincidental with indigenous ichthyofauna. Data concerning reproduction conflict with the above assesment, however, the absence of any specimens sampled with developed gonads is attributed to a sampling artifact.

Clarias gariepinus is also performing fairly well in the drainage in that it is widespread and successfully breeding (i.e. established). Age, growth and condition data do not support this conclusion but this is probably a result of the small sample size used in preparing the results. The species is feeding on similar resources to other invasive biota when young and preying on indigenous species as it increases in age, this is not a major problem as yet since the species is not numerous in the drainage.

Labeo capensis by contrast is not performing well in the drainage as demonstrated by (1) its restricted distribution (2) its decreasing relative condition with increasing age, and (3) the behaviour of the species length/weight relationship. Condition by comparison to populations from different drainages is low although younger fishes (1 plus) appear to perform better in the Fish River system. There is a direct overlap of dietary items between L. capensis and L. umbratus, however, competition is remote in that (1) food material is unlikely to be limiting, and (2) habitat preferences have a marked effect on the relative distributions of these species. This species is not established in the drainage.

The indigenous L. umbratus has been shown to be in good condition in the drainage and age and growth data show that growth is comparable to other populations of the species. There is observed overlap in diet between L. umbratus and L. capensis, however, as discussed above this is not considered as detrimental to the population. Labeo umbratus is amongst the prey items of C. gariepinus but this also is not damaging to the population (above).

Of the exotics, although no breeding specimens of L. capensis and only one breeding condition B. aeneus have been collected in the drainage, reproduction is likely to be occuring, especially in B. aeneus, albeit at a reduced rate. The absence of any sampled breeding fishes is very likely a sampling artifact. C. gariepinus is breeding in the Great Fish River system.

CHAPTER VI

CONCLUSIONS AND RECOMMENDATIONS

6.1 Introduction

"Theoretical descriptions of population growth, control and decline are useful only when considering individual ecosystems or species. The highly variable nature of species and environments nullifies attempts to simplify behavioural characteristics into a predictive framework, and as such, each case must be individually examined and evaluated. Invasive species are opportunistic and the form that exploitation will take is dependant on intrinsic and extrinsic environmental and species characteristics." (Conclusion to Chapter I).

6.2 The Great Fish River Drainage System

6.2.1 The Environment

Prior to 1975 the Great Fish River was subject to periodic flooding and dessication with the drainage frequently split into a series of discrete pools. The environment was typically harsh with intermittant pools forming the major habitats. After the opening of the Orange/Fish Tunnel, the upper drainage and lower mainstem were converted into a permanent flowing pattern where there is an abundance of both lotic and impounded habitats and accompanying niches.

From a conservation point of view the system has been heavily impacted by the activities of man (ignoring additions of ichthyofauna) and its present state negates any conservation orientated decisions regarding management even with regard to endangered indigenous fishes (i.e. the native condition no longer exists and the system as it stands now will be better utilised for land use practises such as irrigation rather than conservation of endangered species [Sandelia bainsii] still present in the drainage). Clearly the tunnel has established large areas of permanent lotic habitat susceptible to colonisation. The richness of the environment without regard to resident species has been greatly enhanced, particularly between major reservoirs in lotic regions.

The corollary to the above argument, nevertheless, must also be addressed though. Although the Great Fish River system does not exist in its "native state", the presence of unique fauna is of great potential value (i.e. S. bainsii). In the United States, programmes for the conservation of endangered species have been initiated (C. Hocutt, pers. comm.) and should this become necessary with regard to the Great Fish River, a reversal of the impact of man on the drainage should be seriously considered.

In the present situation, however, in terms of the abiotic characteristics of an ecosystem, the Great Fish River is very susceptible to invasion by exotic species (Discussed in Chapter I, Table 3). The size of the drainage has been increased, the range of habitats has been increased, the environment has been severely disturbed by the activities of man, and available lotic and impounded environments have been widened.

6.2.2 The Species

The increased habitat diversity of the river environment has opened a great many space, feeding and reproductive niches. Irrespective of the species involved, one expects increases in population sizes and distribution. This increase in distribution has been found with Labeo umbratus below Grassridge Dam where the species is readily caught in lotic habitats as well as above Grassridge Dam where both Labeo capensis and Barbus aeneus are currently found in lotic habitats.

With the exception of areas of conflict between native and exotic species in impounded environments, the net effect seems more advantageous to the system than not. Presently no native species are being threatened although this state of affairs may be changing (Chapter III). Even the presence of a piscivorous predator, Clarias gariepinus, does not seem to threaten indigenous ichthyofauna, as yet.

The species composition of the Great Fish River is mostly exotic with a larger percentage of fishes present as a result of deliberate or inadvertent introductions. Fishes such as bass, carp, catfish and tilapia have been present in the drainage for many years and were probably introduced in the above manner. Their presence has not yet been proven deleterious to native fishes (i.e. resulting in extinction of species). It is unreasonable to assume than an undescribed species (P. Skelton, J.L.B. Smith Institute: pers. comm.) has been extirpated by exotic competition from Orange River fishes, particularly considering (a) the lack of historical evidence in favour of such a hypothesis, and (b) the natural harshness of the unaltered drainage.

Labeo capensis is established in the drainage although not common. There is no evidence to support Cambray & Jubb's (1977) contention that there may be interspecific competition between L. capensis and L. umbratus, although this may be proven in future. Labeo capensis occurs in upstream regions above Grassridge Dam where it is speculated that L. umbratus was extirpated by drought prior to the tunnels construction and has not been able to recolonise from Orange River populations. By contrast, L. capensis apparently has not penetrated downstream past Grassridge Dam, probably due to competition from L. umbratus.

Barbus aeneus is similarly not common in the drainage but has been shown to be growing well. The distribution of the species is increasing albeit slowly and there may be an interesting conflict developing between it and L. umbratus in lotic habitats. Should the species distribution spread into the Cap and Kat river tributaries where it will come into direct competition with S. bainsii, then the indigenous species may become threatened. This is not occurring at this stage but may in future.

Clarias gariepinus is established and widespread in the drainage, however, the species is not particularly abundant and is not posing any serious threat as yet. Should this species disperse into the Cap and Kat rivers, then its presence may present a danger to endangered indigenous ichthyofauna.

The biotic characteristics of an ecosystem which make it susceptible to invasion by exotic species (Discussed in Chapter I, Table 3) have been shown to be having an effect in the Great Fish River drainage. The ichthyofauna is naturally depauperate and there are abundant food supplies for fishes in terms of its man impacted state. Equally, there are few piscivorous predators thereby enhancing the survival of translocating fishes. The combination of these factors make the Great Fish River an ideal environment for colonisation by invasive biota.

6.2.3 Colonisation Theory

Direct comparisons of Great Fish River data with theoretical island patterns of colonisation are too simplistic in this case. Island patterns of colonisation are applicable to primarily single species invasions of either established low diversity island communities or uncolonised new environments. In the event of simultaneous multiple species invasions (i.e. Great Fish River) the duration of the usefulness of mathematical colonisation considerations falls away early as a result of extensive environmental resistance in the form of competition from co-invading species. The Great Fish River has many new habitats created by the activities of man, this has enhanced multiple species invasions from the Orange River and the Great Fish River (both intentionally introduced exotics to the Great Fish River and indigenous fauna). It would be surprising indeed if the colonisation and invasion by *C. gariepinus*, *L. capensis* and *B. aeneus* of the system approximated theoretical expectations. The danger of these species to native ichthyofauna of the Great Fish River is, as yet, not of the calibre of *Tilapia aurea* and *T. melantheron* in Florida, U.S.A. (Stauffer, 1984). It is imperative that this system be monitored to prevent further interdrainage transfers of exotic species (e.g. Great Fish River/Kowie River).

6.3 Conclusion

Five species have managed to enter the Great Fish River drainage through the Orange/Fish Tunnel. There is no direct evidence that these introductions are as yet having any deleterious effects on the indigenous species of the drainage. The conclusions reached in this thesis do not condone the deliberate or inadvertent introduction of foreign species into any drainage. The Great Fish River is an example of a system which has been totally exploited by man with little regard to the effects of his impact on the indigenous fauna. Future major interdrainage linkages should be seriously examined during the planning stages with priorities directed to preventing translocation of species.

REFERENCES

AYALA, F.J., TRACEY, M.L., HEDGECOCK, D. & RICHMOND, R.C. (1974). Genetic differentiation during the speciation process in Drosophila. Evolution 28: 576-592.

BAGENAL, T.B. & TESCH, F.W. (1978). Age and growth. In Bagenal, T.B. (Ed.). Methods of Assessment of Fish Production in Fresh Waters. Blackwell Scientific Publications; Oxford, London, Edenburgh, Melbourne.

BAIRD, D.P. (1976). Aspects of the growth and reproduction of Labeo capensis in the Caledon River. Journal of the Limnological Society of southern Africa 2: 25-28.

BAYLIFF, W.H. (1979). Migrations of the yellowfin tuna in the eastern Pacific Ocean as determined from tagging experiments initiated during 1969-1974. Bull. Inter-Am. trop. Tuna Commn. 17(6): 447.

BLOEMHOF, H.J. (1974). 'n Ondersoek na lengte, massa en onderdom van hengelvisse in die Hardapdam S.W.A. Unpublished M.Sc. thesis, Rand Afrikaans University, South Africa.

BRUTON, M. & ALLANSON, B.R. (1980). Growth of Clarias gariepinus in Lake Sibaya, South Africa. J. Fish Biol. 6: 701-715.

BRUTON, M. & MERRON, S. (1984). In prep.

BURGIS, M.J. & DUNN, I.G. (1978). Production in three contrasting ecosystems. In Ecology of Freshwater Fish Production. (Ed. Gerking, S.D.), Blackwell Scientific Publications: Oxford, London, Edinburgh, Melbourne.

CAMBRAY, J.A. (1976). A survey of fishes in Grassridge Dam. Department of Nature and Environmental Conservation (September) pp. 104-113.

CAMBRAY, J.A., HAHNDIEK, S. & HAHNDIEK, Q. (1977). A survey of fishes in the Grassridge Dam. Department of Nature & Environmental Conservation (September) pp. 107-117.

CAMBRAY, J.A. & HAHNDIEK, S. (1979). A survey of fishes in the Grassridge Dam, October 1973 to February 1979. Department of Nature and Environmental Conservation (September) pp. 59-86.

CAMBRAY, J.A. & JUBB, R.A. (1977). Dispersal of fishes via the Orange-Fish tunnel, South Africa. J. Limnol.Soc.sth.Afr. 3 (1): 33-35.

CASWELL, H. (1982). Life history theory and the equilibrium status of populations. Am.Nat. 120 (3): 317-339.

CHAPMAN, D.W. (1966). Food and space as regulators of salmonid population in streams. Am.Nat. 100: 345-357.

CHAPMAN, D.W. (1978). Production in fish populations. In Ecology of Freshwater Fish Production. (Ed. Gerking, S.D.), Blackwell Scientific Publications: Oxford, London, Edinburgh, Melbourne.

COURTENAY, W.R. & MILEY, W.W. (1975). Range expansion and environmental impact of the introduced walking catfish in the United States. Envir.Cons. 2 (2): 145-148.

COURTENAY, W.R. Jr. & ROBINS, C.R. (1975). Exotic organisms: An unsolved complex problem. Biol.Sci. 25 (5): 306-313.

COURTENAY, W.R. Jr. & STAUFFER, J.R. Jr. (1984). Distribution, Biology and Management of Exotic Fishes. John Hopkins Univ. Press, Baltimore M.D. U.S.A.: 446p.

DIAMOND, J.M., BREYTENBACH, J., CHILD, G., COOPER, K.H., FROST, P.G.H., GIVEN, D.E., HEYDORN, A.E.F., MACDONALD, I.A.W., RIBBINK, A.J., ROBINSON, G.A. & SCHEEPERS, J.C. (1982). Implications of island biogeography for ecosystem conservation. In Conservation of ecosystems: Theory and practice. South African National Scientific Programmes Report 61.

CCLES, D.H. (1983). Feeding biology of the smallmouth yellowfish. In

Limnology and fisheries potential of Lake Le Roux. Ed. Allanson, B.R. & Jackson, P.B.N. South African National Scientific programmes Report 77.

EVEREST, F.H. & CHAPMAN, D.W. (1972). Habitat selection and spatial interaction by juvenile chinook salmon and steelhead trout in two Idaho streams. J.Fish.Res.Bd.Can. 29 (1): 91-100.

EVERHART, W.H. & YOUNGS, W.D. (1981). Principles of Fisheries Science. Cornell University Press, Itheca and London.

FAUSCH, K.D. & WHITE, R.J. (1981). Competition between brook trout (Salvelinus fontinalis) and brown trout (Salmo trutta) for positions in a Michigan stream. Can.J.Fish.Aq.Sci. 38 : 1220-1227.

FERRAR, A.A. & KRUGER, F.J. (1983). South African programme for the SCOPE project on the ecology of biological invasions. South African National Scientific Programmes Report 72.

FRASER, C.McL. (1916). Growth of the spring salmon. Trans. Pacif. Fish Soc. Seattle, for 1915: 29-39.

GAUSE, G.F. (1934). The Struggle for Existence. Williams & Wilkins, Baltimore.

GELDENHUYS, N.D. (1973). Growth of the South African maasbanker Trachurus trachurus Linnaeus and age composition of catches, 1950-1971. Sea Fish Branch Invest. Rep. 101: 139-150.

GILL, D.E. (1974). Intrinsic rate of increase, saturation density, and competitive ability. II. The evolution of competitive ability. Amer.Nat. 108 (959): 103-116.

GOLDNER, H.J. (1976). 'n Populasie study van hengelvisse van Loskopdam met verwysing na bevolkingsamestelling in biomassa. Unpublished M.Sc. thesis, Potchefstroom University for Christain Higher Education, South Africa.

GOLDNER, H.J., SCHOONBEE, H.J. & VERMEULEN, J. (1972). Tydskrif vir natuurwetenskappe 'n vergelyking van merk-terugvangskattings-metodes vir visbevolkings in Loskopdam, Oostransvaal. Tydskrif vir Natuurwetenskappe, Junie 1972.

GUNDERSON, D.R. (1980). Using r-K selection theory to predict natural mortality. Can.J.Fish.Aq.Sci. 37: 2266-2271.

GUNNES, K. & REFSTIE, T. (1980). Coldbranding and fin-clipping for marking of salmonids. Aquaculture 19(3): 295-299.

HAIGH, E.A. (1971). Development of Trachurus trachurus (Carangidae), the South African Maasbanker. Ann.S.Afr.Mus. 59 (8): 139-150.

HAMMAN, K.C.D. (1980). Post impoundment trends in the fish populations of Hendrik Verwoerd Dam, South Africa. J.Limnol.Soc.sth.Afr. 6 (2): 101-108.

HAMMAN, K.C.D. (1981). Aspekte van die visbevolkingdinamika van die Hendrik Verwoerddam met verwysing na die ontwikkeling van 'n visserybestuursplan. Ph.D. thesis, Rand Afrikaans University, South Africa.

HANKIN, D.G. (1982). Estimating escapement of pacific salmon: Marking practises to discriminate wild and hatchery fish. Trans. Am. Fish. Soc. 111(3): 286-298.

HARDIN, G. (1960). The competitive exclusion principle. Science 131: 1292-1297.

HECHT, T. (1976). The Biology of Six Major Trawl Species of the Eastern Cape Coast. University of Port Elizabeth, South Africa, Ph.D thesis.

HECHT, T. (1979). The value of otoliths in freshwater fisheries biology. University of the North, Pietersburg. Series A19.

HOCUTT, C.H. (1984). Toward the development of an environmental ethic for exotic fishes, pp 374-386. Courtenay, W.R. Jr., J.R. Stauffer, Jr.(Eds.) *In*: Distribution, biology and management of exotic fishes. Johns Hopkins Univ. Press.

HOCUTT, C.H. & SKELTON, P.H. (1983). Fishes of the Sak River, South Africa with comments on the nomenclature of the smallmouth yellowfish, *Barbus aeneus* (Burchell, 1822). J.L.B. Smith Inst.Ichthyol.Spec.Publ. No. 32: 1-11.

HUBBS, C. (1977). Possible rationale and protocol for faunal supplementations. *Fisheries* *2*(2): 12-14.

HUTCHINSON, G.E. (1958). Concluding Remarks. Cold Springs Harbor Symp. *Quant.Biol.* *22*: 415-427.

JUBB, R.A. (1967). *Freshwater Fishes of Southern Africa.* Balkema, Cape Town.

JUBB, R.A. (1976). Unintentional introduction of fishes via hydro-electric power stations and centrifugal pumps. *Journal of the Limnological Society of southern Africa* *2*: 29-30.

KARLIN, S. (1966). *A First Course in Stochastic Processes.* Academic Press, New York.

KEAST, A. (1978). Trophic and spatial interrelationships in fish species of an Ontario temperate lake. *Env. Biol. Fish* *3*(1): 7-31.

KEULDER, P.C. (1979). Hydrochemistry of the upper Orange River catchment. *Journal of the Limnological Society of southern Africa* *5*: 39-46.

KOCH, B.S. (1975). 'n Vis ekologiese ondersoek van Boskopdam, Wes-Transvaal, met speciale verwysing na diet bevolkingdigheid van *Labeo capensis* en *Labeo umbratus* in verhouding tot die ander hengelvissorte. Unpublished M.Sc. thesis, Rand Afrikaans University, South Africa.

KOCH, B.S. & SCHOONBEE, H.J. (1980). A fish mark-recapture study in Boskop Dam, Western Transvaal. *Water S.A.* *6*(3): 149-155.

KOOPMAN, K.F. (1950). Natural selection for reproductive isolation between Drosophila pseudoobscura and Drosophila persimilis. Evolution 4 : 135-148.

KRIEL, J.P. (1972). The role of the Hendrik Verwoerd Dam in the Orange River Project. The Civil Engineer in South Africa, February 1972.

LACHNER, E.A., C.R. ROBINS & W.R. COURTENAY (1970). Exotic fishes and other organisms introduced into North America. Smithsonian Contribution to Zoology 59.

LAGLER, K.F., BARDACH, J.E., MILLER, R.R. & MAY PASSINO, D.R. (1977). Ichthyology. John Wiley & Sons, New York.

LAURENSON, L.J.B. & HOCUTT, C.H. (1984). The introduction of the rock catfish, Gephyroglanis sclateri, into the Great Fish River via the Orange/Fish Tunnel, South Africa. The Naturalist 28(1): 12-15.

LAURENSON, L.J.B. & HOCUTT, C.H. (In press). Colonisation theory and invasive biota: The Great Fish River, a case history. Env. Monit. Assess.

LEE, R.H. (1920). A review of the methods of age and growth determination by means of scales. Fishery Invest., Lond., Ser.II, 4: 2-32.

LE ROUX, P.J. (1963). Notes on the growth and longevity of the Vaal River yellowfish (Barbus holubi). Fauna and Flora, Pretoria 14: 40-41.

LEWIS, H. (1961). Experimental sympatric populations of Clarkia. Am.Nat. 95 882: 155-168.

LINDSTRÖM, T. & NILSSON, N. (1962). On the competition between whitefish species In: E.D. Le Cren & M.W. Holdgate (eds) The exploitation of natural animal populations Blackwell Scientific Publications, Oxford.

LIVINGSTONE, D.A., ROWLAND, M. & BAILEY, P.E. (1982). On the size of African riverine fish faunas. American Zoologist 22: 361-369.

LOUW, R.J. (1970). Orange River yellowfish in Gouritz River system. Piscator 77: 138-140.

MACARTHUR, R.H. (1972). Geographical Ecology: Patterns in Distribution of Species. Harper & Row, New York.

MATHUR, D. & HEISEY, P.G. (1980). Monitoring of fish in pump storage systems. In: (C.H. Hocutt, J.R., Stauffer Jr., (eds) Biological Monitoring of Fish. Heath & Co. Lexington.

MERRON, G.S. & TOMASSON, T. (1984). Age and growth of Labeo umbratus (Pisces Cyprinidae) in Lake Le Roux on the Orange River, South Africa. In Press.

MIDGLEY, D.C. & PITMAN, W.V. (1969). Surface water resources of South Africa. Hydrological Research Unit Report 2 (69).

MORAN, V.C. & MORAN, P.M. (1982). Alien invasive vascular plants in South African natural and semi-natural environmental bibliography from 1830. South African National Scientific Programmes Report 65.

MULDER, P.F.S. (1971). 'n Ekologiese studie van die hengelvisfauna in die Vaalriviersisteem met speciale verwysing na Barbus kimberleyensis Gilchrist and Thompson. Unpublished Ph.D. thesis, Rand Afrikaans University, South Africa.

MULDER, P.F.S. (1973a). Aspects on the ecology of Barbus Kimberleyensis and Barbus holubi in the Vaal River. Zoologica Africana 8 (1): 1-14.

MULDER, P.F.S. (1973b). Aspects of the ecology of Labeo capensis and Labeo umbratus in the Vaal River. Zoologica Africana 8 (1): 15-24.

NIE, N.H., HULL,C.H., JENKINS, J.G., STEINBRENNER, K. & BENT,D.H. (1975). Statistical Package for the Social Sciences. Mcgraw-Hill, New York.

ODUM, E.P. (1971). Fundamentals of Ecology. W.B. Saunders Company: Philadelphia.

PATERSON, R.L. & SMITH, K.D. (1982). Impact of power plant entrainment of ichthyoplanktonon juvenille recruitment of four fishes in western Lake Erie in 1975-77. J. Great Lakes Res. 8(3): 558-569.

PIANKA, E.R. (1970). On r- and K- Selection. Am.Nat. 104: 592-597.

PIELOU, E.C. (1979). Biogeography. John Wiley & Sons: New York, Chichester, Brisbane, Toronto.

QUICK, A.J.R. & BRUTON, M.N. (1983). Age and growth of *Clarias gariepinus* (Pisces: Clariidae) in the P.K. Le Roux Dam, South Africa. S. Afr. J. Zool. 19(1): 37-45.

RICKLEFS, R.E. (1973). Ecology. Thomas Nelson, London.

ROBBINS, T.W. & MATHUR, D. (1976). The Muddy Run Pumped Storage Project: a case history. Trans.Am.Fish.Soc. 105: 165-172.

SCOTT, H.A. (1982a). Freshwater Fish Management in the Cape - Past and Present. Cape Conservation Series 1.

SCOTT, H.A. (1982b). The Olifants River System - Unique Habitat for Rare Cape Fishes. Cape Conservation Series 2.

SCOTT, K.M.F., ALLANSON, B.R. & CHUTTER, F.M. (1972). Orange River Project working group for ORP Hydrobiology of the Fish and Sundays Rivers. CSIR Research Report 306: 1-61.

SHAFLAND, P.L. & LEWIS, W.M. (1984). Terminology associated with introduced organisms. Fisheries 9(4): 17-18.

SHUSTOV, Y.A., SHUROV, I.L., SMIRNOV, Y.A. (1981). Conditions of existence, behaviour and distribution of young *Salmo salar* in a river. Journal of Ichthyology 20 (1): 119-123.

SIEGFRIED, W.R. & DAVIES, B.R. (1982). Conservation of ecosystems: Theory and Practice. Rep.S.Afr.Nat.Scient.Prog. 61.

SKELTON, P.H. (1972). Smallmouth yellowfish (*Barbus holubi*) in Settlers Dam, Grahamstown. Piscator 84: 27-30.

SKELTON, P.H. (1983). Perspectives on the conservation of threatened fishes in Southern Africa. Naturalist 27 (1): 3-12.

SKELTON, P.H. (1984). Fishes of the Orange River. In Ecology of River Systems. (Ed. Davies, B.R. & Walker, K.), Junk Publishers: The Hague.

STAUFFER, J.R. Jr. (1983). Colonisation theory relative to introduced populations. In Courtenay W.R. Jr. & Stauffer J.R. Jr. (Eds.). Distribution, Biology and Management of Exotic Fishes. John Hopkins Univ. Press, Baltimore, M.D. U.S.A., In Press.

STRAUB, C.C. & COMBRINCK, C. (1973a). Aspects of the age determination of the Vaal River yellowfish Barbus holubi by the scale method. 1. A comparison of scales from different areas of the body as to their suitability for age determination. Wetenskaplike Bydraes van die P.U. vir C.H.O. Reeks B: Natuurwetenskappe 52.

STRAUB, C.C. & COMBRINCK, C. (1973b). Aspects of the age determination of the Vaal River yellowfish Barbus holubi by the scale method. II. The body scale relationship. Wetenskaplike Bydraes van die P.U. vir C.H.O. Reeks B: Natuurwetenskappe 53.

STRAUB, C.C. & COMBRINCK, C. (1973c). Aspects of the age dteremination of the Vaal River yellowfish Barbus holubi by the scale method. III. A comparison of the scale method with the length freqency method of age determination. Wetenskaplike Bydraes van die P.U. vir C.H.O. Reeks B: Natuurwetenskappe 53.

THORSON, T.B. & LACY, E.J. Jr. (1982). Age, growth rate and longevity of Carcharhinus leucas estimated from tagging and vertebral rings. Copeia (1): 110.

TILLMAN, D. (1979). Resources: A graphical-mechanistic approach to competition and predation. Am.Nat. 116 (30): 362-393.

TOMASSON, T. (1983). The Biology and Management considerations of abundant large cyprinids in Lake Le Roux, Orange River, South Africa. Rhodes University Ph.D Thesis, Grahamstown, South Africa.

TRANQUILLI, J.A. & CHILDERS, W.F. (1982). Growth and survival of largemouth bass tagged with floy anchor tags. Nth. Am. J. Fish. Mangmt. 2(2): 184-187.

VAN DER WAAL, B.C.W. & SCHOONBEE, H.J. (1975). Age and growth studies of Clarias gariepinus (Burchell)(Clariidae) in the Transvaal, South Africa. J. Fish Biol. 7: 227-233.

VANNOTE, R.L., MINSHALL, G.W., CUMMINS, K.W., SEDELL, J.R. & CUSHING, C.E. (1980). The river continuum concept. Can. J. Fish. Aquat. Sci. 37: 130-137.

WEATHERLEY, A.H. (1972). Growth and Ecology of Fish Populations. Academic Press, London.

WHITTAKER, R.H., LEVIN, S.A. & ROOT, R.B. (1973). Niche, habitat and ecotope. Am.Nat. 107: 321-338.

WILLOUGHBY, N.G. & TWEDDLE, D. (1978). The ecology of the catfish Clarias gariepinus and Clarias ngamensis in the Shire Valley, Malawi. J. Zool. Lond. 186: 507-534.