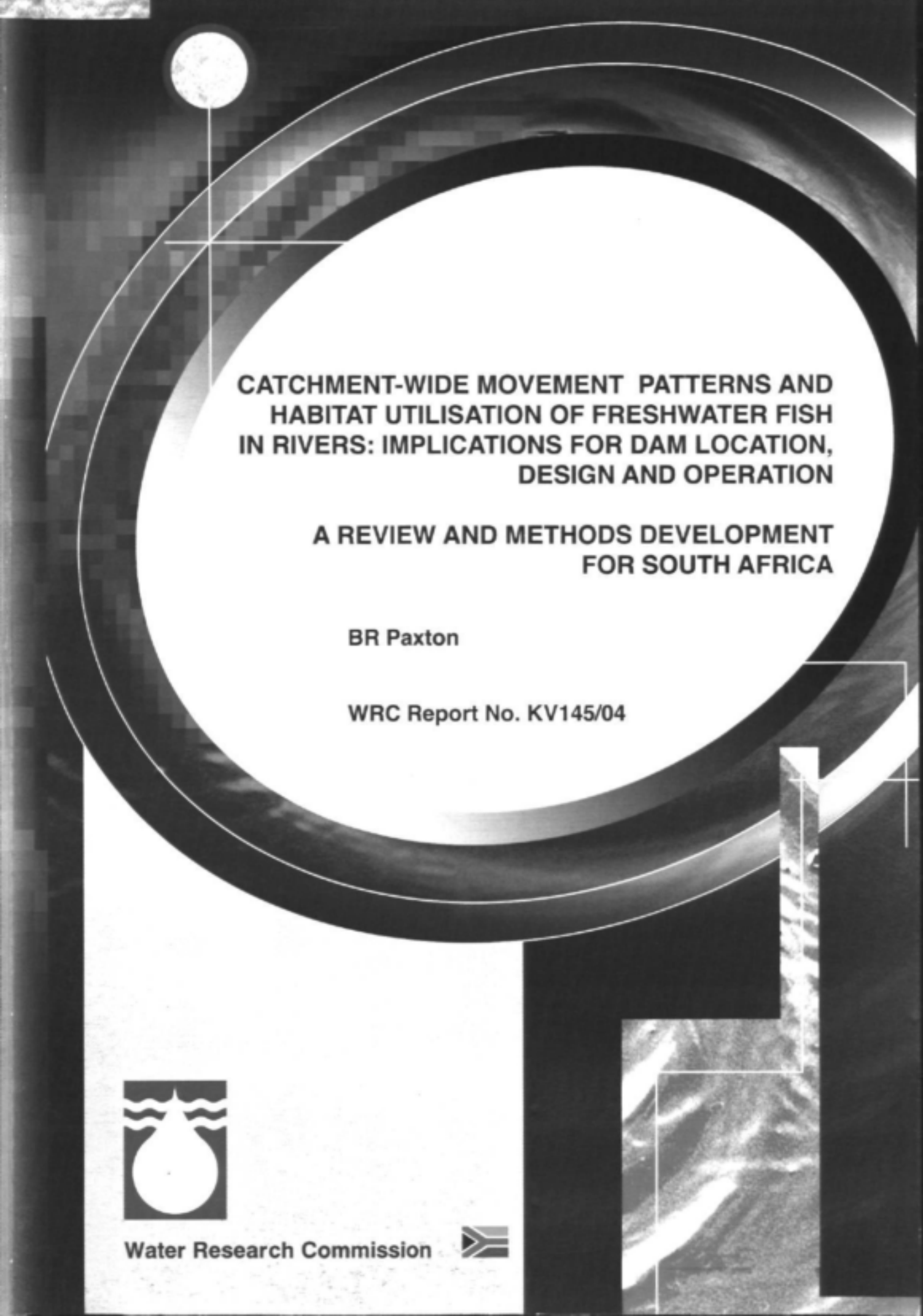

CATCHMENT-WIDE MOVEMENT PATTERNS AND HABITAT UTILISATION OF FRESHWATER FISH IN RIVERS: IMPLICATIONS FOR DAM LOCATION, DESIGN AND OPERATION

A REVIEW AND METHODS DEVELOPMENT FOR SOUTH AFRICA

BR Paxton

WRC Report No. KV145/04

Water Research Commission

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By

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EXECUTIVE SUMMARY

PART A: LITERATURE REVIEW

CHAPTER 1: BACKGROUND TO THE STUDY

The primary objective of this study was to initiate an investigation into the effects of river fragmentation and flow regulation on the spatial behaviour and habitat utilisation of freshwater fish species at the scale of the catchment, and to report on the implications for dam location, operation and design.

CHAPTER 2: INTRODUCTION

The effects of river fragmentation and flow regulation on freshwater fish populations locally and internationally are reviewed. Most studies were found to focus on anadromous salmonids in European and North American rivers. Studies conducted in the USA, Great Britian, Australia, as well as Africa and China are, however, beginning to show that non-salmonid species are undergoing similar demographic declines as a consequence of reduced passage and habitat degradation arising from water resource development. In South Africa, despite an extensive water resource infrastructure to meet the country's growing water needs, little is known about the flow and passage requirements of native fish species. The need for empirical studies to address the spatial behaviours of local freshwater fish – particularly in relation to the importance of this behaviour for recruitment.

CHAPTER 3: HABITAT UTILISATION AND THE SPATIAL BEHAVIOUR OF FRESHWATER FISH

Chapter 3 examines habitat utilisation and fish movement as two parts of a single, interrelated topic. The importance of founding sustainable management practices on a sound conceptual understanding of the biophysical interactions in river ecosystems is discussed. In particular, the issue of scale and the hierarchical structure of habitat in lotic ecosystems is emphasised. Geomorphological and hydrological variability in relation to the habitat and passage requirements of fish species needs to be examined at a range of scales from the microhabitat to the landscape or catchment – catchment-scale variability is particularly important for species which are highly mobile. The *habitat template* is introduced as a model for conceptualising the linkages between the biotic and abiotic components of river ecosystems and to understand the functional significance of fish movement and habitat utilisation. In order to maximize survival, different fish species have evolved a range of spatial behaviours associated with different life stages. The spatial behaviour of freshwater fish is discussed in relation to ontogenetic habitat shifts and seasonal movements.

CHAPTER 4: THE CONSEQUENCES OF RIVER FRAGMENTATION AND FLOW REGULATION FOR FRESHWATER FISH

Chapter 4 deals with the ways in which human intervention has, and continues to, modify the spatial behaviour of fish, and how this impacts fish recruitment. The chapter deals with river fragmentation and flow regulation as two of the most important impacts of dams on freshwater fish. Flow regulation in the Orange River and its effects on freshwater fish populations is presented as a South African case study.

CHAPTER 5: IMPLICATIONS FOR DAM LOCATION, DESIGN AND OPERATION

Three phases of the dam development cycle, with respect to the management of freshwater fish communities, are addressed in this chapter: (1) dam location, (2) dam design and (3) dam operation. The location of a dam needs to be considered in relation to ecologically significant landscape- or catchment-scale features of river systems, specifically the longitudinal changes along the length of the river and the position of functional habitat units (habitats which are critical to the survival of fish populations). Factors which need to be accounted for during the dam design phase include: the design of fishways to facilitate fish passage, and the design of release mechanisms to regulate water temperature and quality below the reservoir. The importance of designing fishways taking into account swimming ability and passage requirements of target species is emphasised. During the operational phase of the dam development cycle, the management of flows which give rise to geomorphological and ecological changes in the river channel downstream of the dam following its construction need to be considered. Species-specific methods of determining environmental flows are compared with more holistic methods.

CHAPTER 6: MANAGING FRESHWATER FISH POPULATIONS IN REGULATED RIVERS – CONCLUDING REMARKS

The discussion in Chapter six regarding the sustainable management of freshwater fish populations can be summarised by the following remarks:

(i) Managing fish populations in rivers affected by regulation and fragmentation requires an holistic approach – i.e. managing for all aspects of fish ecology, including utilisation.

(ii) Species should be targeted for research into life history strategies. This is based on the supposition that ecosystems should not be managed on the basis of 'average' conditions – a few well-founded facts are better than a large number of speculations.

(iii) Critical habitats (or functional habitat units) of a range of species should be identified and described over a range of spatial and temporal scales.

(iv) Vulnerable life stages (e.g. migration, spawning, growth and development) should be identified for each species and linked to the environmental requirements for each stage.

PART B: RESEARCH AND METHODS DEVELOPMENT

CHAPTER 7: RESEARCH AND METHODS DEVELOPMENT IN SOUTH AFRICA

In this chapter specific information requirements of managing freshwater fish populations in systems subject to flow regulation are listed. These are summarised below.

Environmental baseline data

- *Habitat distribution*: catchment-wide analysis of the distribution of critical habitat.
- *Hydrological analysis*: historical analysis of hydrological conditions in the catchment and hydrological modelling.

Fish distribution and abundance

- *Fish distribution*: patterns of distribution and abundance of exotic and indigenous fish species and age-classes, upstream and downstream of the dam site.
- *Exotic species*: patterns of distribution and abundance of exotic species and potential for range extensions.

Ecological profile of affected species

- *Life history profiles*: age-length relationships, age at first maturity, age-specific fecundity and diet, physiological tolerances to water quality conditions.
- *Temperature*: temperature requirements of fish for critical periods, i.e. gonad development, spawning, egg incubation, larval development.
- *Physical habitat description*: geomorphological and hydraulic meso- and microhabitat descriptions of egg, larval, juvenile and adult habitat for the affected species.

Spatial dynamics of affected species

- *Migration*: timing and extent of seasonal migrations in relation to prevailing hydrological and temperature conditions during the year, information on hydraulic requirements of fish species for passage.
- *Dispersal of young*: timing and extent of active or passive dispersal of larvae and juveniles.
- *Existing instream structures*: assessment of the location of existing natural and artificial obstacles to movement in the catchment.

Methods for researching fish movement and habitat utilisation are reviewed, including: variations in population density based on catch per unit effort (*cpue*); mark-recapture studies; fishway counts; passive integrated transponders (PIT); telemetry and genetic studies. A combination of telemetry and genetic studies is suggested as the most effective way of acquiring information on the catchment-scale dynamics of freshwater fish populations.

PART C: PILOT STUDY: OLIFANTS-DORING RIVERS FISH SURVEY

CHAPTER 8: CHANGES IN THE CATCHMENT-WIDE DISTRIBUTION OF THREE THREATENED CYPRINIDS ENDEMIC TO THE OLIFANTS AND DORING RIVERS, WESTERN CAPE

This chapter presents the findings of four surveys conducted between February 2001 and December 2002 which examined the distribution of three cyprinids the Clanwilliam yellowfish *Labeobarbus capensis*, the sawfin *Barbus serra*, and Clanwilliam sandfish *Labeo seeberi*, endemic to the Olifants and Doring Rivers, Western Cape. In the Olifants River, the Clanwilliam Dam and Bulshoek Barrage have inundated a total of 30 km of river, and obstructed access to a further 140 km of upstream lotic (running water) habitat. The modified flow conditions downstream and immediately upstream of the dams have increased the proportion of lentic (standing water) conditions and have provided optimal conditions for the proliferation of bass, bluegill sunfish and tilapia. Regulation by the Bulshoek Barrage, the level of which is controlled by releases from the Clanwilliam Dam, also appears to have changed the geomorphological characteristics of the downstream reaches. The absence of flushing flows downstream of the impoundments has also changed sediment dynamics downstream and contributed to the degradation of spawning habitat. The distribution of fish in the two sub-catchments is discussed in relation to these changes.

TABLE OF CONTENTS

EXECUTIVE SUMMARY i
TABLE OF CONTENTS v
LIST OF FIGURES viii
1. BACKGROUND TO THE STUDY 1
1.1 OBJECTIVES AND TERMS OF REFERENCE 1
1.2 DATES OF THE STUDY 2

PART A: LITERATURE REVIEW

2. INTRODUCTION 3
2.1 FLOW REGULATION AND RIVER FRAGMENTATION: A GLOBAL PERSPECTIVE 3
2.2 THE SOUTHERN AFRICAN CONTEXT 4

3. HABITAT UTILISATION AND THE SPATIAL BEHAVIOUR OF FRESHWATER FISH 8
3.1 THE SPATIAL AND TEMPORAL SCALING OF LOTIC SYSTEMS 8
3.1.1. The physical habitat template 9
3.2 THE SPATIAL DYNAMICS OF FRESHWATER FISH POPULATIONS 10
3.2.1. Movements related to ontogenetic habitat shifts 12
3.2.1.1. Dispersal of eggs and larvae 12
3.2.1.2. Juvenile and sub-adult movements 13
3.2.2. Seasonal movements 14
3.2.2.1. Spawning and over-wintering migrations 14
3.2.2.2. Environmental cues 16
3.2.3. Case Study: Fish migration in the Letaba and Elands Rivers (Meyer 1974) 17
3.3 APPROPRIATE SCALES OF STUDY AND MANAGEMENT 19

4. THE CONSEQUENCES OF RIVER FRAGMENTATION AND FLOW REGULATION FOR FRESHWATER FISH 22
4.1 RIVER FRAGMENATION 22
4.2 FLOW REGULATION 24
4.2.1. Case Study: Flow regulation in the Orange River (Allanson and Jackson 1983) 25

5. IMPLICATIONS FOR DAM LOCATION, DESIGN AND OPERATION 27
5.1 DAM LOCATION 27
5.2 DAM DESIGN 28
5.3 DAM OPERATION 30

6. MANAGING FRESHWATER FISH POPULATIONS IN REGULATED RIVERS – CONCLUDING REMARKS 32

PART B: RESEARCH AND METHODS DEVELOPMENT

7. RESEARCH AND METHODS DEVELOPMENT IN SOUTH AFRICA 36
7.1 INFORMATION REQUIRED FOR MANAGING FISH POPULATIONS AFFECTED BY DAMS 36
7.2 RESEARCH METHODS FOR STUDYING FISH MOVEMENT AND HABITAT UTILISATION 37
7.2.1. Variations in density and catch per unit effort *cpue* 38
7.2.2. Mark-recapture studies 38
7.2.3. Fishway counts 40
7.2.4. Passive Integrated Transponders (PIT) 40
7.2.5. Telemetry 41
7.2.6. Genetic studies 42

PART C: PILOT STUDY: OLIFANTS-DORING RIVERS FISH SURVEY

8. CHANGES IN THE CATCHMENT-WIDE DISTRIBUTION OF THREE THREATENDED CYPRINIDS ENDEMIC TO THE OLIFANTS AND DORING RIVERS, WESTERN CAPE 43
8.1 INTRODUCTION 43
8.2 STUDY AREA 46
8.3 METHODS 47
8.4 RESULTS 48
8.4.1. Distribution 49
8.4.2. Spawning and reproductive development 52
8.5 DISCUSSION 52
8.5.1. Abundance and distribution 52
8.5.2. Spawning and environmental cues 53

8.5.3. Migration and dispersal 55
8.5.4. Conclusion 57

9. LITERATURE CITED 59

LIST OF FIGURES

Figure 3.1 Number of fish caught in the Elands River fyke weir (adapted from Meyer 1974) 18
Figure 8.1 Map of the Olifants Doring Rivers showing the study area 46
Figure 8.2 Map of the Olifants and Doring Rivers showing the distribution records for the Clanwilliam yellowfish *L. capensis* 49
Figure 8.3 Map of the Olifants and Doring Rivers showing the distribution records for the sawfin *B. serra* 50
Figure 8.4 Map of the Olifants and Doring Rivers showing the distribution records for the sandfish *L. seeberi* 51

1. BACKGROUND TO THE STUDY

1.1 OBJECTIVES AND TERMS OF REFERENCE

In terms of the agreement between the University of Cape Town and the Water Research Commission (K8/485/2), the primary objective of this report, consisting of a literature review and a report on methods development, was to examine the effects of river fragmentation and flow regulation on the spatial behaviour and habitat utilisation of freshwater fish species in South Africa at the scale of the catchment, and to report on the implications for dam location, operation and design. The present report forms part of a pilot study to ascertain the feasibility of investigating the spatial behaviour of fish in local river systems. The pilot study was to address these issues in the context of a biodiversity 'hotspot' in the Western Cape where the numbers and range of three fish species endemic to the Olifants and Doring Rivers system have declined over the last 70+ years as a consequence of water resource development and invasion by non-native fish species. All three species are currently listed by the IUCN, i.e. the Clanwilliam yellowfish *Labeobarbus capensis* (vulnerable VU A1ce), the sawfin *Barbus serra* (endangered EN B1 +2abde, C1), and Clanwilliam sandfish *Labeo seeberi* (critically endangered CR A1ace). It was intended that the study follow on from surveys commissioned by the Department of Water Affairs and Forestry and Department of Agriculture which began in 2001 (Paxton *et al.* 2002) and which aimed to address the deficiencies in our knowledge and understanding of the spatial behaviour and ecological requirements of these species. The surveys were commissioned out of concern that the Melkboom Dam, proposed for development on the lower Doring River (DWAF 2002), would further impact the populations in these reaches.

While the initial objectives of the project have been retained, the scope was broadened when it became evident that, due to the interrelatedness of river flow, fish passage and habitat utilisation in the life history of freshwater fish, a synthesis of the available information on the topic was needed, and stemming from this, an integrated or holistic approach to solving management problems relating to fish populations in catchments subject to anthropogenic disturbance. Complicating issues are that very little is known about the migratory behaviour of local freshwater fish species and a large proportion these species may not be migratory in the strictest use of the term. 'Migration' is only one form of a range of spatial behaviours that are affected by modified flow and passage conditions. In addition, the impacts of river fragmentation and flow regulation need to be addressed at multiple spatial and temporal scales, i.e. from microhabitat to catchment, and from daily to decadal time intervals. A theoretical examination of the way physical habitat in rivers is structured at a landscape scale was therefore included to address the functional significance of fish movement and habitat utilisation. It was felt that covering a broader range of topics would set the stage for a more detailed examination of these topics in future studies.

This report has as its basis the fundamental premise that managing freshwater fish in the absence of empirically derived information on the ecological requirements of all life stages is unjustifiable and unsustainable in the long term. A call has therefore been made for more empirical studies to be conducted on local freshwater fish in order to increase confidence in the predictions of ecological models and Environmental Flow Assessments (EFAs), as well as in the effectiveness of fish passage facilities.

1.2 DATES OF THE STUDY

The study took place between 31 March 2002 and 01 April 2003. The dates of the fieldtrips undertaken during the course of the study are listed below.

15-27 Sep 2002: A survey was conducted of the lower Doring River from Doringbos to the confluence of the Olifants River to identify spawning sites and assess the topography of this reach, and its suitability for tracking fish by means of radio telemetry.

03-08 Dec 2002: A survey of the upper Olifants River and sites not visited during previous surveys because of access problems was conducted. The primary goal of this survey was to extend information on fish distribution in the catchment.

5-18 Feb 2003 Mr Paxton took part in a collaborative research project between the South African Institute for Aquatic Biodiversity (SAIAB) and the Norwegian Institute for Nature Research (NINA) to track spotted grunter *Pomadasys commersonnii* in the Fish River estuary by means of acoustic telemetry.

PART A: LITERATURE REVIEW

2. INTRODUCTION

2.1 FLOW REGULATION AND RIVER FRAGMENTATION: A GLOBAL PERSPECTIVE

A study commissioned by the Pilot Analysis of Global Ecosystems (PAGE; Revenga *et al*. 2000) that assessed 227 major river basins on five continents revealed that 60% were affected by regulation of flow for hydropower or irrigation purposes and fragmentation of river corridors by dams. Strongly affected rivers (i.e. rivers with less than one quarter of their main channel unaffected by dams and with at least one dam on the largest tributary) accounted for as much as 90 % of the total water volume of the rivers analysed (Nilsson *et al*. cited in Revenga *et al*. 2000). These human interventions have resulted in major changes to the structural and functional components of river ecosystems and their fish communities (Ligon *et al*. 1995; Marmulla 2001). Together with invasion by introduced species and degraded water quality conditions, river regulation and fragmentation by dams is believed to be responsible for over 20 % of the world's freshwater fish species having become extinct, threatened or endangered in the last few decades (Revenga *et al*. 2000).

Research into the effects of regulation and fragmentation on the migration and reproduction of freshwater fish species has focussed largely on anadromous[1] salmonids in European (e.g. Ikonen 1984; Linlokken 1993; Rivinoja *et al.* 2001) and North American rivers (e.g. Andrews 1983; Dauble *et al*. 2001). These fish form the basis of valuable commercial fisheries, and are particularly susceptible to migration barriers (Baras and Lucas 2001). In the Columbia and Snake Rivers, for example, only 13% and 58% respectively of the mainstems of these rivers are still considered riverine – the remaining sections are impounded or heavily regulated by hydropower schemes. As much as 70% of the riverine habitat in the Snake River is inaccessible to Pacific salmon (*Oncorhynchus* spp.) as a result of the Hells Canyon Dam (Dauble *et al*. 2001). As a consequence, annual returns of salmon in these rivers have decreased from 10 – 16 million fish to 2.5 million despite attempts to facilitate upstream and downstream passage by means of fishways, barges and trucks (Ward *et al*. 1997; Williams 1998). Dam breaching is now considered the only way to restore populations (Blumm *et al*. 1998).

More recently, awareness has grown that the impacts of fragmentation and regulation extend to non-salmonid species in other parts of the world (Baras and Lucas 2001; Walker and Thoms 1993), and scientific attention is now shifting toward examining the impacts of water resource development on these groups. In Australia, catches of Murray cod *Maccullochella peeli* have declined in the River Murray with the expansion of flow regulation between the 1950s and 1990s, and the elimination or attenuation of floods by dams in this river has been implicated in the decline of many other native Australian fish that are dependent on floods for spawning and larval rearing. The Murray River now has the lowest

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[1] Migratory fish which spawn in freshwater ecosystems, but need to return to the ocean for growth and development.

commercial fish yield per kilometer of floodplain of any of the world's major rivers (Walker and Thoms 1993). In Great Britain, lowland rivers have undergone extensive regulation, and populations of many sport fishes other than salmonids have become drastically reduced or locally extinct (Copp 1990). Other evidence for the detrimental effects of river regulation and fragmentation on non-salmonid riverine fish species comes from the Colorado River, where extensive water resource development, including 40 major dams and 11 hydropower plants, have blocked migration routes, destroyed habitat, inhibited spawning, and thereby reduced the range and abundance of Colorado pikeminnow *Ptychocheilus lucius*, humpback chub *Gila cypha*, razorback sucker *Xyrauchen texanus* and bonytail chub *Gila elegans*. Recovery programmes are now concentrated on the remaining self-sustaining populations in the Colorado's upper basin (Nesler *et al*. 1988; Ryden 2000, Webb 2001). Elsewhere in the world, the proliferation of hydropower schemes in China has had severe consequences for many of the country's freshwater fish. Below the Fuchunjiang Dam, the Chinese shad *Macrura reevesii*, an anadromous species, became extinct because the hydrological conditions necessary for its spawning were rarely met (Zhong and Power 1996). Since the completion of the Gezhouba Dam on the Yangtze River in 1981, spawning by the Chinese paddlefish *Psephurus gladius* has become severely curtailed and only 3-10 adult paddlefishes per year have been found below the dam (Zhong and Power 1996).

Studies from African freshwater ecosystems have shown that the effects of river regulation extend to river-floodplain systems as well. The highly productive fisheries of river-floodplain systems play an important part in the rural economies of many developing countries in Africa, yielding up to 143 $\text{kgha}^{-1}\text{year}^{-1}$ (Welcomme 1985). The response of African river fish populations to impoundment is variable. Generally, riverine species tend to be replaced by fish species which are more adapted to the new reservoir conditions. For example, prior to impoundment the Niger River supported floodplain fisheries which included mormyrids, citharinids and distichodontids. Since construction of the Kainji Dam, catches of commercially important mormyrids declined but cichlid, cyprinid and bagrid catches increased (Balogun and Ibuen, *cited in* Jackson and Marmulla 2001). While a new reservoir may present different fishery opportunities upstream of the dam, there is generally a significant reduction in yield from floodplains downstream of the dam. This has been recorded for the Kainji Dam, the Akosombo Dam on the Volta River and the Cohora Bassa Dam on the Zambezi River (Bernacsek 1984 and references thererin).

2.2 THE SOUTHERN AFRICAN CONTEXT

The general scarcity of water in South Africa has meant that flow regulation and river fragmentation are as much features of rivers in this country as they are of rivers elsewhere in the world. Several climatic factors contribute to water scarcity in this region. On the whole South Africa is a semi-arid country, with a mean annual precipitation (MAP: 496 mm) of approximately half the world average, and with only a small proportion of the MAP (8.6%) being converted to mean annual runoff as a result of high evaporative loss (Alexander 1985). Water resources are unevenly distributed over the surface of the country: there is a steep longitudinal gradient from the moist sub-tropical east coast to the semi-arid west, and variations produced by differences in local physiography are evident within this general pattern (Shulze *et al.* 2001). Temporal availability is characterised by a strong seasonality and high intra- and inter-annual variability. Two major weather systems determine seasonality in the country: low pressure systems over the interior produce rain during the summer months, whereas in the south and south-western region a Mediterranean climate prevails, with frontal systems bringing rain in winter. In this region, low discharges coincide with high temperatures, in contrast to the summer-rainfall areas of the interior and east, where low discharges coincide with low temperatures. Inter-annual variability in river flow is reflected by a high coefficient of variation (C_V: 1.14) compared to the mean global average for arid zones of 0.99 (Alexander 1985). Much of this hydrological variability appears to be related to El Nino-Southern Oscillation (ENSO) phases (Jury 2003). Recurrent droughts and floods are therefore a feature of the South African climate. These variations in climatic conditions have important consequences for the ecology of the fish fauna and the management of water resources in each region.

The need to meet increasing domestic, agricultural and industrial demand has necessitated the development of an extensive national water storage, abstraction and transfer infrastructure. Approximately 43% of the total mean annual runoff (MAR) in South Africa is lost to rivers as a consequence of human activity – 20 % is abstracted, 8 % is lost to evaporation from storage or conveyance systems, and a further 6 % is lost to land-use activities (DWAF 2002). Up to 60% of the total water volume abstracted is used for irrigation. There are currently 3969 registered dams in South Africa which have walls over 5 m high and capacities exceeding 50 000 m^3 (Jan Nortje, Dams Safety Office, Pretoria, South Africa *pers comm.*), and the National Water Resource Strategy (DWAF 2002) has identified another 16 major dams or dam-related development projects proposed for completion before 2025. All large- and medium-sized rivers in South Africa are already impounded (Davies and Day 1998) and many pass through two or more dams before reaching the sea (Alexander 1985). The number of unregistered farm dams and weirs in the country is unknown, but is estimated to exceed 100 000 (Jan Nortje, Dams Safety Office, Pretoria, South Africa *pers comm.*). Approximately 780 gauging weirs have been built by the Hydrology Directorate of the Department of Water Affairs and Forestry (DWAF). All these structures, to a greater or less degree, alter downstream hydrological, sediment and temperature regimes as well as physico-chemical conditions, ultimately impacting on freshwater fish populations by changing habitat and restricting passage.

That many of South Africa's native freshwater fish populations are undergoing a demographic decline (Skelton 2002), is perhaps best reflected by the fact that, of the 97 fish species occurring in South Africa, 30 % have been listed by the IUCN as threatened (Skelton 2002; Skelton and Cowan 1999). This decline is likely to be due to a number of factors acting synergistically, including water pollution, habitat degradation and the introduction of exotic fish species. Flow regulation and river fragmentation are likely to have played major roles in reducing recruitment, by obstructing fish passage, degrading instream habitat, and facilitating invasion by introduced fish (De Moor 1996).

With notable exceptions, there have been few studies in South Africa that have examined the consequences of river fragmentation and flow regulation on native fish populations, or the mechanisms by which these factors have affected recruitment. Several studies have addressed the problem of regulation (e.g. Cambray 1984; Jackson 1989), and attempts have been made to understand the relationship between the flow and temperature conditions in rivers and – reproduction (Allanson and Jackson 1983; Cambray *et al*. 1997; King *et al*. 1998) – community dynamics (Merron *et al*. 1993) – and habitat (Gore *et al*. 1991; Weeks *et al*. 1996; Pollard 2000).

Effective management protocols for freshwater fish need to be based on a scientific understanding of the relationship between biological and environmental parameters, particularly those factors which govern spawning and migratory behaviour. In many cases, knowledge of the relationship between the hydrological regime and the life-histories of South Africa's indigenous fish fauna is totally lacking, or inferred on the basis of limited information gleaned from short-term surveys and/or generalisations derived from studies conducted elsewhere in the world. The causal links between river regulation, fragmentation and the demographic decline of freshwater fish populations in South Africa are therefore obscure. One area in particular that has been neglected in research is the role that movement and migration play in sustaining native populations. Some attention has been given to the subject by Meyer (1974), who showed that fish species in the Letaba and Elands Rivers undertake coordinated movements along the river at certain times of the year. However, their extent, function, and the environmental cues which triggered them, were not determined. There is clearly, therefore, a need to introduce consideration of migration in management of freshwater fish populations in this country – particularly in relation to the importance of this behaviour for recruitment. This was recently highlighted by Bok (2001) who reviewed the effectiveness of fishways in South Africa. Bok (2001), emphasised the importance of continued monitoring of existing fishways in the country, hydraulic testing and swimming trials on native fish species, and of understanding the timing of migrations in relation to the hydrological regime of rivers in the different eco-regions.

This information is particularly important with regards to the larger fish species, which may depend on more extensive movements for feeding, spawning, dispersal and colonisation, and are therefore likely to be more vulnerable to river fragmentation (Bok 2001). Cyprinids (in South Africa the *Barbus*, *Labeobarbus* and *Labeo* genera) are an abundant and ecologically important component of many freshwater fish communities both nationally and internationally, yet relatively little is understood about their habitat and passage requirements compared with salmonids (Lucas and Batley 1996). The lack of scientific studies on the movement of cyprinids has been supported by the assumption, and reinforced by legislation in some countries such as the U.K., that ‘non-salmonids’ are ‘non-migratory’ (Baras and Lucas 2001). Perceptions are changing however, and it is becoming increasingly evident that information on the movement of non-salmonid families is required in order that appropriate management techniques be applied to these groups as well. In the following chapters therefore, habitat utilisation and its relation to the spatial behaviour and general life history of freshwater fish species is reviewed, the potential impacts of dams on these processes is discussed, and future research needs and methods aimed at guiding and providing input to management protocols are suggested.

3. HABITAT UTILISATION AND THE SPATIAL BEHAVIOUR OF FRESHWATER FISH

3.1 THE SPATIAL AND TEMPORAL SCALING OF LOTIC SYSTEMS

Decisions regarding the sustainable management of river ecosystems should be well founded in a sound conceptual understanding of ecological processes in order that major biophysical interactions can be taken account of in management actions (Stanford *et al.* 1996). The dynamics of biological populations in response to the spatial and temporal heterogeneity of their environment is a fundamental theme in terrestrial, marine and freshwater ecology (Levin 1992; Raffaelli *et al.* 1992), and studies have shown that there are strong associations between the structure of physical habitat and the occurrence of fish species and size classes (Schlosser 1991). A number of principles, concepts and models derived from empirical studies have been used by ecologists to provide input to management and conservation initiatives. This section, therefore, reviews conceptual frameworks relevant to understanding habitat scale and structure in river systems and how this affects the distributions and utilisation of habitat by freshwater fish.

Identifying the appropriate scale at which to study physical habitat has emerged as an important theme in studies of freshwater biological communities (Fausch and Young 1995; Kocik and Paola Ferreri 1998). Frissel *et al.* (1986) have suggested that the spatial, abiotic components of river systems are structured hierarchically into successively smaller nested units ranging in scale from the watershed to the stream segment, reach, pool-riffle sequence, and microhabitat. This model has since been adapted for South African rivers by Rowntree and Wadeson (1999) and proposed as a classification system for the geomorphological components of South African river systems (DWAF 1999). The six nested units in this model correspond to Frissel *et al.*'s (1986) original classification, i.e. the catchment, zone, segment, reach, morphological unit and hydraulic biotope.

Overlayed on the landform features of rivers are the hydrological and sedimenat regimes and their local hydraulic manifestations, which shape these features. Thus Hildrew and Giller (1992) introduced a temporal dimension to Frissel *et al.*'s (1986) hierarchical model by linking it to the spatio-temporal scaling of fluvial landscapes described by Salo (1990). In this model, fluvial processes acting over a range spatio-temporal scales create a hierarchy of landforms which have corresponding persistence times related to the frequency of disturbance events. Landforms at the catchment scale (kilometres) may be shaped by processes such as climate change and plate tectonics, which operate on scales of geological eras. Reach characteristics (tens of metres) are be shaped by disturbance events with a recurrence period of decades, whereas microhabitat conditions (centimeters to meters) may be controlled by hourly, monthly or seasonal variations in flow (Rowntree and Wadeson 1999). In the spatial dimension, each level in the hierarchy imposes boundary conditions on the level below it. For example, catchment-scale features such as climate, gradient, geology, soils and vegetation cover, influence runoff and sediment production, which control morphology at the reach scale and therefore habitat for the biota (Rowntree and Wadeson 1999).

Of the many important theoretical frameworks which have been used to conceptualise river functioning and guide river management, the River Continuum Concept (the RCC, Vannote *et al.* 1980), has perhaps been one of the most pervasive (e.g. Davies and Day 1998). The RCC addresses downstream changes in the production, loading, transport, utilisation and storage of organic matter, which provides the energy and nutrient base for river ecosystems and fish communities. It emphasises the importance of taking the longitudinal continuity of river systems into consideration, as well as ecosystem process and structure. Although the longitudinal profiles of rivers differ considerably as a result of local variations in geology, the classic profile of a river is concave in shape, with steep headwaters and low gradient lowland reaches (Rowntree and Wadeson 1999). In general therefore, decreasing gradients and downstream increases in discharge, as well as changes in nutrient and sediment production, give rise to a continuum of changes in the physical and chemical characteristics of rivers from headwater to lowland reaches (Vannote *et al.* 1980). The upper reaches of rivers (mountain headwall and mountain stream zones) are characterised by bedrock and boulder-bed channels with step pool morphology, waterfalls, rapids and pools; in the middle reaches (foothills and transitional zones) channel morphology is characterised by mixed alluvial (sand, cobble and boulder) channels with pool-rapid and pool-riffle sequences; and a meandering sand bed channel with floodplains and reduced pool-riffle frequency (Schlosser 1991) characterises lowland rivers (Rowntree and Wadeson 1999).

3.1.1. The physical habitat template

Ecologists have recognised that the hydrological, geomorphological and chemical components of river systems discussed above, represent a suite of selective processes which comprise the habitat template, and upon which the life-history strategies of the biota, through evolutionary mechanisms, have been superimposed (Southwood 1988; Townsend and Hildrew 1994). Biological responses to the spatial and temporal scaling of physical landforms and processes (i.e. Frissel *et al.*'s hierarchical model) can be identified as well, i.e. spatial and temporal variability in the abiotic environment can be linked to the distribution of species and size classes in catchments, as well as to ontogenetic[2] habitat shifts. Abiotic variability which is experienced over the lifetime of an individual gives rise to seasonal movements, and patterns of colonisation and extinction can be linked to changes in meta-population processes.

The spatial distribution of age classes can be explained in terms of the habitat needs required by different life stages. Physical habitat conditions which are optimal for spawning and egg incubation will seldom be

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[2] Relating to the history of growth and development of an individual organism.

optimal for growth and feeding. Studies have demonstrated age/size-related habitat selectivity in fish species (e.g. Rincón *et al*. 1992). In general, juvenile fish display a preference for shallow lateral habitat, whereas large fish display a preference for deeper habitat. Several selective factors are believed to have given rise to this preference. Smaller fish that are vulnerable to predation from aquatic piscivores seek out shallow water, whereas larger fish seek out deeper water where they are less vulnerable to terrestrial piscivores such as herons (Schlosser 1991). In addition, the relatively higher concentrations of prey of suitable size for smaller fish occur in warmer shallow water, where productivity is higher, and this makes littoral areas ideal feeding grounds for early life stages (Humphries *et al*. 1999). The low-velocity slackwaters provide smaller fish with hydraulic cover. Thus differential habitat requirements for different life stages and fish sizes, combined with lateral and longitudinal heterogeneity in habitat conditions in the river, mean that fish must move between habitats in order to maximise fitness and survival (Fausch and Young 1995).

Spatial and temporal variation in physical habitat conditions affect the evolution of life history strategies and give rise to characteristic fish assemblages in river systems. For example, Poff and Allan (1995) investigated the relationship between fish assemblage structure, and the temporal (hydrological) variability in major rivers around the world. They found that hydrologically variable streams characterised by a high coefficient of variation of daily flows and a moderate frequency of spates were associated with species which had generalised life history strategies, whereas hydrologically stable streams, characterised by a high predictability of daily flows and stable baseflows were associated with specialists. Any change in the physical habitat template can therefore be expected to produce changes in the abundances and composition of freshwater fish assemblages.

3.2 THE SPATIAL DYNAMICS OF FRESHWATER FISH POPULATIONS

In this section, fish movement is introduced as an important biological link between habitat elements (Kocik and Paola Ferreri 1998), and as an adaptive response to enhance growth, survival and abundance in an environment where resources are patchily distributed (Harden Jones 1968, Northcote 1978). Since habitat use is a dynamic rather than static process, i.e. the habitat requirements of fish changing according to the time of the day, year and life stage of the fish, habitat use and fish movement is discussed here as a single inter-related topic.

As previously emphasised, the timing and extent of movements undertaken by diadromous[3] fish species such as salmon have been well researched (e.g. Andrews 1983; Ikonen 1984; Linløkken 1993; Dauble *et al*. 2001), whereas the movement patterns of other groups resident in rivers systems are much less well

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[3] Fishes which, during the lifespan of an individual, make regular migrations between freshwater and marine ecosystems (includes both anadromous and catadromous species).

known (Fausch and Young 1995; Baras and Lucas 2001). Although many fish species display some form of movement between habitat types at different times of the year, not all species can be classified as migratory. Landsborough Thompson (cited in Harden Jones 1968), identified three major forms of spatial behaviour: (1) local movements confined to a single geographical area; (2) dispersals, which are more extensive and entail an expansion from an identifiable area and; (3) true migrations, in which organisms move between widely separated geographical regions. Northcote (1978) defines true migration as 'movements resulting in an alternation between two or more separate habitats (i.e. a movement away from one habitat followed eventually by a return again) occurring with regular periodicity (usually seasonal or annual, but certainly within the lifespan of an individual) and involving a large fraction of the population'.

Migratory fish species tend to be larger, with delayed maturation and a relatively faster growth rate, than more resident species (Roff 1988). Migratory fish also tend to be more numerous than non-migratory fish species. The evolution of larger size and greater numbers has probably been both a cause of migration, i.e. the need for covering greater distances as a result of the local depletion of food resources by numerous large fish, and a consequence of migration, i.e. increased access to greater food resources enabling faster growth and greater numbers (Roff 1988). This combination of factors gives many migratory fishes (particularly diadromous fishes) their high commercial or subsistence value (Harden Jones 1968).

Potamodromy[4] has evolved where migration has conferred an adaptive advantage to species which complete their life history entirely within freshwater ecosystems. However, individuals or populations within a species may show considerable variation along a continuum from residency to potamodromy. The boundary between species which are 'migratory' or 'resident' is therefore not always that clear. Baras and Lucas (2001) have suggested that this may be especially pronounced in highly variable temperate environments where either one of the strategies have not been subjected to a definite selection pressure and that both residency and migration may therefore be adopted by different sectors of a population. They suggest, however, that chronic human disturbances may shift the species in favour of one strategy or the other.

The term 'migration' is used in this report to denote any form of active movement which is synchronised and undertaken by a large fraction of a population between one location and another. In this respect, local movements related to foraging activity, passive dispersal of eggs or larvae, or random wandering do not constitute migratory behaviour. Nevertheless, the adaptive significance of these secondary movements

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[4] From 'potamodromous' – migratory fishes which complete all life history phases within freshwater ecosystems (e.g. most cyprinids).

should not be viewed as being any less relevant to the persistence of freshwater fish populations and their management than true migrations. These secondary movements are therefore included in this discussion.

The discussion below has been organised on the basis of movements which fall into the category of ontogenetic habitat shifts, and those which occur on a seasonal basis. Longer-term changes in fish distribution related to processes of emigration and immigration are dealt with briefly in Section 4.1 in the discussion on river fragmentation. Ontogenetic (developmental) habitat shifts are the result of differential habitat selection by fish in response to changes in the morphology, physiology and dietary requirements of different life stages (Hartmann 1983; Mark *et al.* 1989). These movements are undertaken only once during an organism's life. Seasonal movements occur periodically and relate to the need for specific habitat conditions at different times of the year.

3.2.1. Movements related to ontogenetic habitat shifts

3.2.1.1. Dispersal of eggs and larvae

During their earliest life stages, fish undergo a series of largely passive dispersals through river systems. Dispersal of these early life stages may not, however, be entirely random, but may be controlled to some degree by reproductive strategies, including the nature and placement of eggs as well as the behavioural response of larvae to flow. The distance which eggs disperse, and the microhabitat preferences of larvae between species, is variable. Eggs that are laid in gravel, or that are adhesive, may be retained for longer in the adult spawning area before the larvae hatch. Upon 'swim-up', the larvae are carried downstream to nursery habitat. The eggs of Dace *Leuciscus leuciscus*, for example, are adhesive and negatively buoyant and will remain attached to the gravel substratum, even during heavy spates (Mills 1981). The eggs of the Clanwilliam yellowfish *Labeobarbus capensis* in the Olifants River, South Africa are non-adhesive and laid in the interstitial spaces between cobble and gravel-bed riffles. After hatching the larvae may be carried by flow downstream into pools up to a kilometre from the spawning beds, where the larvae accumulate in shallow areas with low current speeds (Cambray *et al.* 1997). Other reproductive guilds have semi-buoyant, non-adhesive eggs which float in the current, and develop as they are dispersed downstream (e.g. plains minnow *Hybognathus placitus*, Durham and Wilde 2001). The eggs and/or larvae of these species may disperse for a considerable distance downstream before the larvae settle in nursery habitats. The eggs of the golden perch *Macquaria ambigua* in the Murray River, Australia, are semi-buoyant and are carried passively by the current for seven days until the larvae are able to maintain themselves against the current. Migration in this species appears to have evolved as a mechanism to minimise the danger of eggs being carried into the sea, and Reynolds (1983) estimated that eggs would need to be spawned approximately 500 km upstream to prevent this happening.

During their early life stages, riverine fish are especially vulnerable to flow conditions (Robinson *et al.* 1998). The behavioural response of larvae to flow conditions, i.e. their orientation to the current, determines where they will settle and how well they will survive adverse environmental conditions. Meffe (1984) investigated the response of the larvae of two species of poeciliid stream fish with similar morphologies, but that evolved in rivers subject to different hydrological disturbance regimes. The Sonoran topminnow *Poeciliopsis occidentalis* is native to streams in the arid American Southwest that are subject to regular flash floods, whereas the mosquitofish *Gambusia affinis* evolved in the less flood-prone mesic, central and eastern United States. *G. affinis* has been introduced into native *P. occidentalis* streams. Following a large scouring flood, Meffe (1984) found that mosquitofish populations had been reduced by over 98%, whereas topminnow populations were merely displaced approximately 200 m downstream. Laboratory experiments in artificial flumes confirmed that the mosquitofish oriented toward the current more slowly, and were therefore displaced more frequently, than topminnow. This study demonstrated the importance of flow in mediating the interactions between a native and introduced species – an important consideration in South African rivers where water abstraction is believed to have aided invasions by introduced fish.

Once the larvae disperse, they will settle in a habitat which favours their growth and development. A number of studies have shown that shallow littoral areas are important habitat for the larval and post-larval life stages. Backwaters formed by sand bars, or side channels along the margin of the main river channel (e.g. cyprinids, Cambray *et al.* 1997 and castomids, Archer *et al.* 2000), floodplains (e.g. cyprinids Copp 1992), the inlet of tributaries (e.g. castomids Robinson *et al.* 1998), or the littoral areas in lakes e.g. (Halvorsen *et al.* 1997) are a few examples of the kinds of habitat which have been described for these early life stages. These areas provide hydraulic refuge when swimming performance is limited and larvae and juveniles are vulnerable to aquatic predation. They also provide productive feeding grounds and appropriately sized prey (Humphries *et al.* 1999). The period of time spent in these nursery areas varies from species to species and may be anything from hours, days or weeks to months or years (Northcote 1978).

3.2.1.2. Juvenile and sub-adult movements

Once fish have grown beyond a certain age/size in nursery areas, they will move further from the bank to areas with deeper, faster flowing waters. This may be accompanied by a diet shift to feeding on drift (Rincón *et al.* 1992). The movement may be local, i.e. within the same river reach, or juveniles or sub-adults may undertake a feeding migration covering much greater distances to more productive feeding grounds. This may entail a gradual dispersal of individuals from the nursery grounds with foraging along the way (e.g. grayling, Northcote 1978), or it may take the form of a well-timed synchronised migration by a large number of individuals (e.g. the seaward migration of salmon smolts, for example, Wootton 1983).

Pink salmon *Oncorhynchus gorbuscha* and chum salmon *Oncorhynchus keta* move to the sea shortly after emerging from their spawning beds. However, for other salmonids, the period of freshwater residence before seaward migration may vary between one and six years (Harden Jones 1968). While most studies have shown that juvenile salmon migrate to more productive habitat downstream, Erkinaro *et al*. (1998) report substantial migrations by juvenile Atlantic salmon *Salmo salar* from spawning grounds in the mainstem of the Teno River, Finland into tributaries. The Grayling *Thymallus thymallus* have been found to undertake two *upstream* migrations in the Glomma River, Norway (Linløkken 1993). The first peak, in May, is a spawning migration, while the second peak, in June-July is a feeding migration undertaken by smaller fish presumed to have originated from recruitment areas downstream.

Elliott (1985) used variation in population densities to study the spatial distribution of brown trout *Salmo trutta* in a Lake District stream, by sampling at selected sites over a period of 18 years. An index of dispersion (a ratio of sample variance to mean) was used to describe life-stage specific changes in the spatial distribution of trout parr between 0+ and 2+ years. Three major behavioural movements could be identified, beginning with a transition from a clumped to regular distribution by fry to reduce competition and maximise the use of food and space. A second behavioural movement was identified as a refuge-seeking migration, as 0+ parr moved from shallow, fast-flowing water to deeper pools during the first winter of their lives. The third behavioural movement was believed to be associated with the emigration of young smolt out of their natal stream to the sea and estuary to feed.

The movements of non-salmonid fish have only recently received scientific investigation, and these studies have focussed primarily on seasonal migrations of adult fish (e.g. Lucas and Batley 1996). Information on the spatial behaviour of juvenile non-salmonid fish is therefore limited. Upstream movement by large numbers of juvenile golden perch *Macquaria ambigua* through the Torrumbarry Weir on the Murray River, Australia, reported by Mallen-Cooper *et al*. (cited in Humphries *et al*. 1999), were assumed to be related to recolonisation from downstream rearing habitat.

3.2.2. Seasonal movements

3.2.2.1. Spawning and over-wintering migrations

While movements related to ontogenetic changes in habitat use may occur only once during an organism's life, seasonal movements between spawning, feeding and over-wintering habitats occur periodically. Spawning migrations enable fish to optimise reproductive success by coordinating the arrival of potential mates in the correct physiological condition at sites with appropriate physico-chemical habitat conditions (Northcote 1978). They therefore tend to be more ordered and better synchronised than feeding migrations. They ensure that, in a patchy environment, sites with suitable physical conditions for spawning (e.g. substrate) are optimally used during a period of the year when the prevailing flow, temperature and trophic conditions at spawning sites will maximise egg and larval survival (*sensu* Cushing 1990). Shallow riffles with high-velocity flow are used by many species of potamodromous fish. The higher concentration and rate of oxygen delivery in these areas relative to other habitat types result from increased turbulence and the entrainment of air bubbles near the surface and make them ideal environments for incubating fish eggs (Soulsby *et al*. 2001). Because of their elevated topography in relation to the rest of the channel, riffles also accumulate organic matter which provides food for invertebrates living in the interstices between the bed material (Brussock and Brown 1991). These invertebrates, which are most plentiful in spring and summer, provide a ready source of nutrition for the developing fry over this period. Riffles occur with greater frequency in the middle and upper reaches of rivers, whereas the more productive lower reaches, where riffles are fewer, are more suitable for the growth and feeding of adults. The habitats suitable for each of the above activities are therefore both spatially and seasonally separated and fish need to move between these areas in order to successfully complete their life history.

Semelparous[5] fish species will undertake a single spawning migration to the rivers of their origin. A typical example of this are the extensive, well-timed spawning migrations undertaken by adult salmon from the sea to the rivers of their birth. Iteroparous fish species[6], which alternate between over-wintering, feeding and spawnings sites, may undertake several migrations during their lifetimes. The Hilsa shad *Tenualosa ilisha* for example, unusual for tropical regions in that it is anadromous, undertakes spawning migrations of up to 1200 km in river systems of the Indian subcontinent during the monsoon floods (Rahman 2002). After they have spawned, they return to the sea until the next season (Dahle *et al*. 1997).

The timing of spawning and migration is important in regions where there is marked seasonality. High mortalities may result if conditions at the spawning sites are unsuitable (e.g. unusual flows or temperatures). For example, Humphries *et al*. (1999) reported that spawning by certain fish species in the Murray-Darling River occurs as flows subside during the low-flow season. They suggest that this has evolved to coincide with optimal conditions for larvae and juvenile feeding. The warmer temperatures increased residence time of water in pools and reduced water volumes during the low-flow period favour production and concentration of zooplankton. As a consequence of this, high spring flows have been found to cause poor year classes of golden perch *Macquaria ambigua* and silver perch *Nemadactylus macropterus* in the Murray River. Because of the importance of synchronising spawning events, external

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[5] Production of all offspring on a single occasion during the lifespan of an individual.
[6] Production off offspring on several successive occasions during the lifespan of an individual.

environmental cues (specifically, water temperature, flow and photoperiod) may trigger physiological or behavioural patterns which initiate spawning migrations and spawning events.

3.2.2.2. Environmental cues

Modde and Irving (1998) suggest that while environmental cues may not directly affect reproduction, they are important for initiating migrations and therefore the ability of fish to form spawning aggregations. One of the few studies which provides conclusive evidence that riverine Cyprinids depend on seasonal spawning migrations was conducted by Lucas and Batley (1996) in the River Nidd (a tributary of the Yorkshire Ouse in England), who tracked a total of 31 adult barbel *Barbus barbus* between June 1993 and September 1994 using radio telemetry. They found that barbel moved significant distances (between 2 and 20 km), with some fish utilising both the Nidd and the Ouse rivers at different times of the year. During spring (the period of highest temperatures and lowest flows) following an upstream movement, the fish congregated in shallow, fast flowing, gravel-bed riffles for spawning. Females showed a net downstream movement following spawning, but during autumn there was a net downstream movement by both males and females which was found to be associated with flood events. This resulted in a step-like pattern of downstream movement by individual fish. The downstream movement was presumed to a be either an active or passive displacement by adult fish to refuge areas in the lower river. A return migration from the mouth of the River Nidd was positively correlated with increasing day length and temperatures in spring, but negatively correlated with mean monthly flow. The reason for upstream movement from the lower Nidd and Ouse appeared to be because these reaches have relatively few suitable spawning grounds.

In southwestern Spain, the migration of three cyprinids: the Iberian barbel *Barbus sclateri*, Iberian nase *Chondrostoma polylepis willkommii* and mirror carp *Cyprinus carpio* var. *specularis* from the Bornos Reservoir on the Guadalete River, were found to be correlated with water temperature. Rodriguez-Ruiz and Granado-Lorencio (1992) found that migrations began when water temperatures reached 12-14 °C.

The Colorado pikeminnow *Ptychocheilus lucius*, is an endangered piscivorous cyprinid which is endemic to the Colorado River basin. Colorado pikeminnow spawn in a 50 km segment of the Yampa River and a 14.5 km segment of the Green River. Some fish have been found to make a 100-350 km round-trip to use these spawning grounds. (Nesler *et al*. 1988 and references therein). Nesler *et al*. 1988 demonstrated that spawning by Colorado pikeminnow is cued by peak flow events in early summer. Also endemic to the Colorado River basin, the razoback sucker *Xyrauchen texanus* (Castomidae) has been shown to move downstream following spawning and after the onset of high flow conditions in the Green River, a tributary of the Colorado River (Modde and Irving 1998). Natural hydrographic and thermal regimes, rather than uniform stimuli like photoperiod, appeared to initiate migratory behaviour.

3.2.3. Case Study: Fish migration in the Letaba and Elands Rivers (Meyer 1974)

One of the most extensive studies on freshwater fish migration in South Africa was undertaken by Meyer (1974) on the Letaba and Elands Rivers in what was then the Transvaal. Over 80 000 fish belonging to 28 different species (primarily *Labeo* and *Barbus* spp.) were sampled from a two-way fyke weir on the Elands River between 1970 and 1973, and an additional 5600 were sampled from a fish ladder on the Letaba River below the 13 m high Engelhard Dam between 1972 and 1973. Meyer used the numbers of fish caught in the weir and fish ladder over a three-year period as an indication of seasonal variations in fish activity.

For the purposes of this review, data taken from Meyer's study for 21 fish species were used to compile the graphics shown in Figure 3.2. The number of fish of each species caught in each month was expressed as a proportion of the total number of fish caught over the entire study period in the Elands River fyke weir. These percentages were then summed for each month. Figure 3.2A and B represent the combined distribution of fish activity for all the fish caught in the Elands River fyke weir without the undue influence of numerically dominant species. Superimposed on Figure 3.2A is the mean monthly naturalised flow record of the Groot Letaba River (Gauge B8H017, 1979 – 1988) in millions of cubic metres per month giving an approximate indication of the runoff regime of the study area. Figure 3.2B shows mean daily temperatures for each month from Letaba (Station No. 0682141A2, 1961-1990) superimposed on the same histogram of fish activity. The Groot Letaba River exhibits a typical summer-rainfall seasonality with flows increasing from November, reaching a maximum in February and declining from March to June. Temperatures start increasing in August reaching a maximum in January before declining to a minimum in June. Very little to no fish activity is evident during winter (June – August), when temperatures and flow are low. A marked increase in fish activity commences at the beginning of spring (September), prior to the onset of the highest flows, and increases to a maximum in November. Activity was lower during summer, the period of highest flows and temperatures. A second peak of activity was evident in March, as flows start declining in autumn, whereafter activity levels decline through April and May, tracking declining flow and temperature conditions. An examination of the patterns of movement of individual fish shows that most fish show peak activities in November. Although these data gives some indication of how the seasonality of temperature and flow might influence fish activity, they cannot reveal within-month and inter-annual variability or the function of these migrations in relation to the life history of species.

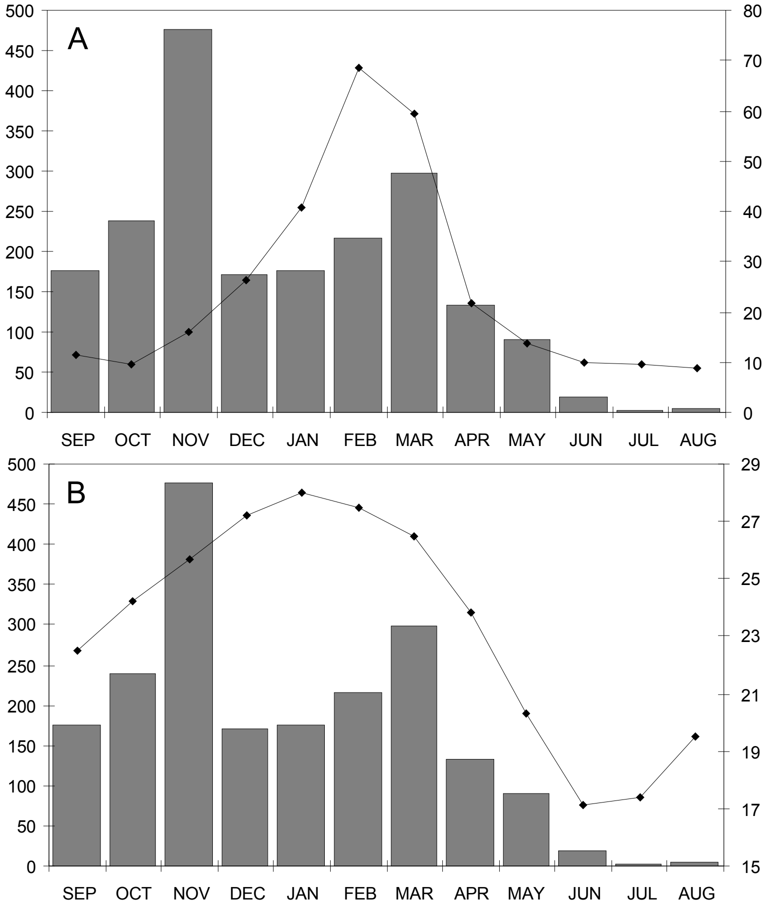

Figure 3.1 Figures 3.2 A and B show the number of fish caught of each species in each month expressed as a proportion of the total number of fish caught over the entire study period in the Elands River fyke weir during Meyer's (1974) study. These percentages are summed for each month. Superimposed on Figure 3.2A is the mean monthly naturalised flow record of the Groot Letaba River (Gauge B8H017, 1979 – 1988) in millions of cubic metres per month. Figure 3.2B shows mean daily temperatures for each month from Letaba (Station No. 0682141A2, 1961-1990) superimposed on the same histogram of fish activity.

Although sexually active *Labeo* and *Barbus* were present, the length distributions provided by Meyer suggested that a large proportion of the fish which were migrating were young fish (*Labeo cylindricus* between 40-100 mm comprised 77.7% of the catch and 31.2% of *Labeo molybinus* were between 40-100 mm). Meyer suggested that these migrations were 'first instinctive breeding migrations'. The studies reviewed so far in this report, however, suggest that the reasons for migration are complex and that the observed movements may be anything from early dispersals to refuge seeking migrations into feeding or nursery areas.

Cambray (1990) pointed out that the migrations of juvenile moggel *Labeo umbratus*, smallscale redfin minnow *Pseudobarbus asper*, and Mozambique tilapia *Oreochromis mossambicus* and chubbyhead barb *Barbus anoplus* observed in the Gamtoos River, Eastern Cape, were probably opportunistic feeding migrations which had evolved as an adaptive response to rapidly exploit a temporarily rich food source in the dynamic and fluctuating hydrological conditions of this river. However, as in Meyer's study, the presence of late life stages among the migrating fish suggested that an additional function of these migrations may be to promote recolonisation of new habitat following the reconnection of previously isolated pools after the dry season. The adaptive significance of fish migration in South Africa may therefore be strongly linked, not only to reproductive imperatives, but also to dispersal and recolonisation in a variable environment.

3.3 APPROPRIATE SCALES OF STUDY AND MANAGEMENT

Habitat studies in freshwater ecology have focussed largely on explaining the responses of fish populations to environmental variability at a local, site-specific, i.e. microhabitat scale (e.g. Moyle and Baltz 1985; Valdez *et al.* 1990; Hatfield and Bruce 2000). However, freshwater fish inhabit a patchy landscape (Pringle *et al.* 1988) and exhibit seasonal, ontogenetic or longer-term shifts in distribution in response to hydrological and geomorphological variability at multiple scales (Wiley *et al.* 1997). Broad mesohabitat or catchment-wide analyses of river habitat are therefore as important for understanding the dynamics of freshwater fish populations as are microhabitat studies. Studies of microhabitat, using point measurements of physical habitat variables to describe habitat suitability, have been driven primarily by the need for determining the instream flow requirements for the biota (e.g. the Instream Flow Incremental Methodology, IFIM, Bovee 1982). However, integrating local ecological perspectives with much broader landscape or catchment-scale perspectives and taking into account processes which operate over the entire geographic range of the species, is becoming increasingly recognised as important for fish conservation and management purposes (Schlosser 1991; Allan *et al.* 1997; Richards *et al.* 1997; Wiley *et al.* 1997; Jewitt and Gorgens 2000).

This was highlighted in a study by Reimers (1973), who found that – although adult fall chinook salmon *Oncorhynchus tshawytscha* in the Sixes River, Oregon, depended on large-scale migrations between the tributaries, mainstem and ocean, up to 60 – 70% of all spawning activity took place in a 4 – 5 km stretch of a single tributary. Similarly, in the Colorado River, the Colorado pike minnow *Ptychocheilus lucius* migrates 100-350 km to use spawning grounds on the Yampa and Green Rivers (Nesler *et al.* 1988). It is clear that the significance of these reaches for reproduction cannot be understood on the basis of microhabitat or reach-scale studies alone.

Broader catchment-scale views of river systems have also been recognised as relevant to river health. In a study of a river in south-eastern Michigan, Allan *et al.* (1997) found that half of the variance of the fish Index of Biotic Integrity (IBI, an index of biological integrity developed for North American Rivers, Karr 1991) was explained by agricultural land use. Using local ground surveys along a 150 m stream reach, aerial photograph measurements from 1500 m stream segments, and Geographical Information System (GIS) analyses of riparian and catchment-wide land use for the region upstream of a site, Allan *et al.*

(1997) found that catchment-wide land use was more important than either local or riparian land use for explaining the distribution of the biota.

In South Africa, scale issues, physical habitat heterogeneity, and the view of the catchment as a basic management unit, have received much attention, and formed an important component of the conceptual basis for models developed for the management of rivers in the Kruger National Park (Jewitt *et al*. 1998; Jewitt and Görgens 2000). The BLINK (Abiotic-Biotic Link) model integrated a hydrology model with three qualitative rule-based models for geomorphology, vegetation and fish. As part of the input to this model, Weeks *et al*. (1996) examined the distribution and abundance of fishes in the Sabie-Sand system, identified target species which would be representative of zones, reaches and macrohabitats, and described the microhabitat requirements (water velocity, depth and cover) of these species by means of habitat suitability curves. The changing patterns of fish abundance in both normal and extreme seasons were described and these data then formed the basis of input to a predictive model. The model provided catchment managers and planners with a means of assessing the response of the aquatic ecosystem to alternative flow manipulation scenarios (Jewitt and Görgens 2000).

Weeks *et al*. (1996) used the IFIM point abundance approach (using an electrofisher) suggested by Bovee (1982) and developed for use in this country by King and Tharme (1993) to describe fish habitat. For predicting responses of fishes to changes in flow and channel conditions, a geomorphological map of each study reach (10-100 m^2) was translated into a habitat availability and this was related to the habitat suitability curves derived for individual species. The model accounts primarily for changes in juveniles, since these were most targeted during Weeks *et al*.'s (1996) study. Microhabitat was therefore the most appropriate scale of study. For older, or larger fish, or fish that depend on movement between widely separated habitat types, a broader, mesohabitat scale description of habitat may be equally important.

Kocik and Paola Ferreri (1998) proposed the concept of natural production units, or 'functional habitat units' (FHUs) which they define as 'natural partitions (strata) within river systems that contain the necessary habitat elements to support all life stages through the life stage of interest'. The appropriate scale for studying the spatial dynamics of fish populations in lotic systems is therefore defined by the boundaries of the FHU. These boundaries depend on the spatial arrangement of habitat elements in the landscape, the life stage of interest (egg, larvae, juvenile, adult), the dispersal capabilities of each life stage, and by filters (natural or artificial barriers to movement). Thus, they suggested that the appropriate scale expands with age/size, from egg (sub-metre), to juvenile (mesohabitat, sub-basin) and global (adults). The appropriate scale for study and management of freshwater fish populations therefore depends largely on the degree of movement exhibited by the species, as well as the life stage of interest.

While modelling abiotic and biotic processes at multiple scales may not be feasible, and is in any event not the subject of the current report, it is re-emphasised here that ecological studies need to address habitat use at multiple spatial and temporal scales, and predictions need to be integrated over several life stages. The scale of the study needs to be set at the level of variability which is believed by the researcher to be ecologically relevant to the species and life stage of interest. Failure to do so may bias the results of the study, reduce confidence in the predictions designed to aid managers and planners in assessing alternative flow and development scenarios, and ultimately compromise the ability of the target species to grow, survive and reproduce.

4. THE CONSEQUENCES OF RIVER FRAGMENTATION AND FLOW REGULATION FOR FRESHWATER FISH

4.1 RIVER FRAGMENTATION

Fish movements in rivers are especially vulnerable to human modification since rivers are linear systems and are therefore easily obstructed (Schlosser and Angermeier 1995). One of the most deleterious impacts of dams on fish diversity, fish stocks and fisheries is that they obstruct upstream and downstream movements. As Section 3.2 emphasised, these movements coincide with critical stages in the life history of fish species. Thus the long term viability of fish populations is compromised when rivers are fragmented by instream barriers which limit the dispersal of eggs, larvae (Agostinho *et al*. 2002) and juveniles (Raymond 1979), obstruct or delay upstream and downstream migrations by adults (Baras and Lucas 2001), and interfere with patterns of colonisation and extinction that encompass longer-term natural variations in spatial distributions (Schlosser and Angermeier 1995).

While the impact of dams in obstructing upstream spawning migrations is widely recognised, the role that dams play in obstructing the downstream dispersal of young has been largely ignored in planning, despite the fact that their impact on fish populations may be as critical, or more critical, than their role in impeding the upstream migration of adult fish (Quirós 1988 and Clay 1995, cited in Agostinho *et al.* 2002). Larvae spawned upstream of a dam may drift into reservoir waters where they may encounter unfavourable physico-chemical conditions (temperature, water quality, velocity) as well as intense predation. Since colonisation of downstream reaches frequently depends on larval and/or juvenile dispersal from upstream natal habitat, recruitment of fish populations downstream of dams may be significantly curtailed. The eggs and larvae of potamodromous fish in the Plata River, Brazil migrate passively with the current as they develop, before they take up residence in lagoons and bays tens of kilometres downstream of the areas where they were spawned (this is in contrast to salmonids which migrate downstream at much large sizes; Agostinho *et al*. 2002). If the larvae are washed into dams, however, they are exposed to low velocities and high-transparency conditions that make them especially vulnerable to predation. Agostinho *et al*. (2002) suggested that the larvae would be decimated by the abundant foraging fish that occur in dam reservoirs. Those reaching the dam wall would then face additional mortality from damage in turbines or spillways.

The role that dams play in obstructing upstream spawning migrations is more widely recognised and researched. A steady decline in stocks of migratory species has followed the construction of dams on all continents (Marmulla 2001). Depending on their size, design and location, dams as impediments to movement may present:

- a total obstruction (permanently insurmountable for all individuals in a species);
- partial obstruction (surmountable for some individuals, but may cause damage, exhaustion or delay);
- or temporary obstruction (passable under suitable hydrological/temperature conditions) (Larinier 2000).

It is less widely appreciated that even low structures such as farm dams, culverts and weirs may present obstructions to certain species or size classes at critical times of the year. Whether or not temporary obstructions (i.e. structures that are passable only under suitable hydrological/temperature conditions) are surmountable depends on the hydraulic and water-quality conditions at the base of the weir at the time of migration, as well as the swimming and leaping ability of the fish (Larinier 2001). Because of the quantity of these smaller structures in river systems, their combined impact may as great, if not greater than that of large dams. Understanding the impact of temporary structures requires a knowledge of the function and timing of fish migrations, the age structure of the fish undertaking the migrations, and the hydraulic conditions in the reaches downstream of the weir over the critical period. For example, the River Nidd is an important tributary of the Ouse River for lithophilous cyprinids (barbel *Barbus barbus*, dace *Leuciscus leuciscus* and gudgeon *Gobio gobio* L.) (Lucas and Frear 1997). Following construction of a flat-V flow gauging weir with a height difference of 0.4 m, angling catch rates of cyprinids upstream of the weir declined. A subsidiary weir was built downstream of the gauging weir to increase the elevation of the tailwater, but no improvements in angling catches were recorded. To understand why, Lucas and Frear (1997) tracked fish using radio telemetry upstream and downstream of the two weirs. They showed, firstly, that only 40 % of the tagged fish successfully negotiated the weir and, secondly, that the net rate of upstream movement by those that were able to negotiate the weir was significantly reduced, resulting in a delay of several weeks.

River fragmentation also affects longer-term, catchment-wide patterns of colonisation and extinction at the level of the metapopulation. In fish species with restricted distributions these patterns may ultimately affect the survival of the species as whole. The dynamic spatial organisation of freshwater fish populations at the scale of the landscape or catchment has only recently received attention (Grossman *et al.* 1995; Schlosser and Angermeier 1995; Jager *et al.* 2001). A metapopulation may be defined as a set of hierarchically structured local populations which are patchily distributed in a heterogeneous landscape, and which are linked by infrequent exchanges of a limited number of individuals (Schlosser and Angermeier 1995; Begon *et al.* 1996; Jager *et al.* 2001). The metapopulation persists as a result of a balance between colonisation and extinction between local populations, even though these local populations may be unstable (Begon *et al.* 1996). Fragmentation of river systems by artificial barriers increases the incidence of localised extinctions, resulting in gaps in previously contiguous populations, and also reduces the possibility of re-colonisation from other areas.

4.2 FLOW REGULATION

Flow provides the basic habitat necessary for fish survival in rivers. Flow also affects the geomorphological structure, and therefore critical habitats such as egg larval or spawning habitat. It provides important behavioural or physiological cues for gonad development, migration or spawning events, and its variability mediates relationships between species in a community. Flow regulation may also reduce fish passage, since flows downstream of the dam may be insufficient for fish to overcome natural or artificial geomorphological or hydraulic barriers (Baras and Lucas 2001).

Flow regulation downstream of a dam reduces the overall volume of water in the river, and all but the highest flows may be withheld. As demand for water increases, overtopping becomes less frequent, with the result that flows in many rivers are entirely dependent on reservoir releases. The reduction in volume of water in the river diminishes the absolute quantity of instream habitat and therefore the overall capacity of the river to support fish populations (Newcombe 1981). Water is stored during the high-flow period and released downstream for irrigation during the low-flow period, resulting in a reversal of natural dry and wet season flows. Thus the inter-annual and seasonal variability is reduced and the magnitude, frequency and timing of floods are reset to meet irrigation or hydropower demands. Flow- and temperature-related cues which trigger the maturation of gonads, or synchronise spawning so that reproduction coincides with favourable environmental conditions (Bye 1984; Cushing 1990), are eliminated or attenuated. Thus spawning either fails to occur or occurs less frequently. Flow regulation also impacts reproduction and fish productivity in river-floodplain systems. In these systems fish undertake lateral migrations onto seasonally inundated floodplains that provide near optimal conditions for feeding, reproduction and growth (Bayley 1995). By suppressing the flood cycle, dams change the timing of the flood pulse and reduce the duration and aerial extent of floodplain inundation.

The storage of sediments by impoundments and the attenuation of floods alter sediment dynamics and therefore the geomorphology of downstream reaches. Specific physical-habitat types within the river that are critical for egg incubation and the development of young become inundated upstream of the dam (Copp 1992; Montgomery *et al.* 1996; Dauble and Geist 2000), while downstream, the quality of these habitats is degraded as a result of hydrological, geomorphological and thermal changes associated with flow regulation (Andrews 1983; Bernacsek 2001). The successful incubation of eggs depends on correct temperatures and delivery of oxygen and nutrients through intragravellar flow. In the absence of flushing flows, riffles accumulate sediment, which reduces the interstitial habitat available for, and the delivery of oxygen and nutrients to, developing eggs. Fine sediment concentrations, resulting in reduced intragravellar flows in experimental riffles, reduce egg survival in salmonids (Reiser and White 1990), while the release of hypolimnetic flows is detrimental to embryonic development (Hamman 1982 *cited in*

Robinson *et al.* 1998) and post embryonic growth (Black and Bulkley 1985 *cited in* Robinson *et al.* 1998).

In addition to degrading spawning habitat, flow regulation also affects the suitability of larval habitat as well as the active or passive dispersal of larvae in river reaches. Because of their poor swimming ability, larvae are largely dependent for their distribution on hydraulic conditions in the river (Robinson *et al.* 1998). Shallow littoral habitat is especially important for successful development and predator avoidance in river channels (Schiemer and Spindler 1989; Copp 1992; Rincón *et al.* 1992). Flow regulation downstream of a dam results in destabilisation of lateral nursery habitat and the transport of larvae into unfavourable habitat (Scheidegger and Bain 1995). For example, regulation by the Glen Canyon Dam has reduced larval survival of several threatened fish species (cyprinids and catostomids) native to the Colorado River (Robinson *et al.* 1998). Before impoundment, reproduction coincided with decreasing flows in tributaries. These baseflow conditions ponded areas at the mouth of tributaries, which provided nursery habitat for fish larvae. Flows released from the Glen Canyon Dam during the larval rearing period now flush larvae from ponded areas at the mouth of the Little Colorado River into the mainstem of the Colorado River, which is on average 9 ºC cooler. Larvae either die from thermal shock, become lethargic and vulnerable to high flows or predation, or are flushed from lateral nursery habitats by irregular fluctutations in discharge (Robinson *et al.* 1998) .

4.2.1. Case Study: flow regulation in the Orange River (Allanson and Jackson 1983)

Considerable changes to the geomorphological and ecological components of Orange River ecosystems have occurred as a result of regulation by the Gariep and Vanderkloof Dams. These changes have been linked to manipulation of the hydrological regime which has altered the magnitude, timing and frequency of natural river flows. The number of small to medium floods (3000 m^3s^{-1}) has diminished and maximum floods (31 000 m^3s^{-1}) have been reduced to 35 % of their original magnitude (WCD 2000). The Orange River lies in the summer rainfall region of the country and under natural conditions, only 25% of the annual runoff occurred in winter – the remainder (75%) was distributed between spring and early winter (October to May). Since the construction of the Gariep and Vanderkloof Dams, 54% of the flows occur in summer and 45% in winter (Cambray 1984) when hydropower demand is highest. As a consequence, where the river near the present day Gariep Dam was reduced to a series of isolated pools during winter, the river now flows continuously (Allanson and Jackson 1983). The stabilisation of flows has resulted in a reduction in the inter-annual and seasonal hydrological variability. Reduction in the magnitude of major flood events has resulted in geomorphological changes, whereas the loss of small flood events is believed to have eliminated the spawning cues that stimulate fish to breed (WCD 2000). Temperatures have been stabilised for 130-180 km downstream of Vanderkloof Dam and average monthly maximum temperatures have been reduced by up to 7 ºC in spring and early summer (Pitchford and Visser 1975 cited in Tómasson *et al.* 1985). Rapid fluctuations in flow as a result of hydropower production are likely to destabilise shallow marginal areas important for the reproduction of many fish species (Cambray 1984). In addition, as a consequence of the stabilisation of river flows, reedbeds (primarily *Phragmites australis*) have expanded from none, under pre-impoundment conditions, to 41 000 h following impoundment (Chutter *et al*. cited in WCD 2000). This may be an additional factor impacting the availability of shallow lateral habitat required as nursery areas by young fish.

Allanson and Jackson (1983) investigated the consequences of flow regulation for the reproduction, growth, dispersal and mortality of freshwater fish populations between the Vanderkloof and Gariep Dams on the Orange River (see above) through quarterly sampling over a period of five years between 1978 and 1983. Although largemouth yellowfish *Barbus kimberleyensis* were not found in large numbers, smallmouth yellowfish *Barbus aeneus* were abundant in the Vanderkloof Dam. The chubbyhead barb *Barbus anoplus* was also found in abundance, although the numbers of rock catfish *Austroglanis sclateri*, which are more dependent on lotic habitat than the former species, had declined and isolated populations had become restricted to tributary rivers. Several other species including two *Labeos* (the Orange River labeo *Labeo capensis* and the Moggel *Labeo umbratus*) were also examined.

Regulation by the Gariep Dam was found to have significant biological consequences for the populations of yellowfish in the Vanderkloof Dam further downstream (Allanson and Jackson 1983). Following a migration from the Vanderkloof Dam to the lotic reaches between this dam and the Gariep, both species spawn in gravel-bed riffles – the entire population of yellowfish in the Vanderkloof Dam was believed to depend on recruitment from this region. Largemouth and smallmouth yellowfish spawn during the first floods of early spring. However, Allanson and Jackson (1983) suggested that since impoundment, continuous flows from the Gariep Dam mean that spawning events are triggered primarily by temperature.

Regulation has lowered the summer temperature maxima (during the spawning period) and increased the winter minima. The intakes of the turbines in the Gariep Dam are situated at a mean sea level of ~1220 m. Warm releases required for fish spawning, therefore, occur only if lake levels drop to this height, and increasing volumes of epilimnetic water are released downstream of the dam. Largemouth yellowfish, which spawn between four and six weeks after smallmouth yellowfish and need higher temperatures, are particularly susceptible to hypolimentic releases, a factor which is believed to explain their relative scarcity in the downstream reaches (they were found to be ten times rarer than the smallmouth yellowfish in the reaches between the Vanderkloof and Gariep Dams). Hypolimentic releases during summer result in late spawning and a weakened year-class (5% the strength of a strong year-class, Tómasson *et al.* 1985). Year-class strength was also believed to affected by rapid fluctuations in water levels downstream of the dam, which result in the stranding of eggs, larvae and adults.

5. IMPLICATIONS FOR DAM LOCATION, DESIGN AND OPERATION

Bernacesk (2001) identified six major phases in the dam development cycle: (1) the dam identification phase – which includes identification of a dam site and type and its potential yield; (2) dam design phase – the preparation of detailed dam site studies and alternative dam designs; (3) dam project appraisal - the examination and evaluation of a proposed project; (4) dam construction; (5) dam operation – the pattern of storage or release of water for electricity, agricultural or domestic supply and finally; (6) dam decommissioning. Three phases of this cycle, with respect to the management of freshwater fish communities, are addressed below: (1) dam location (identification), (2) dam design and (3) dam operation.

5.1. DAM LOCATION

This phase of the dam-project cycle includes the identification of a dam site, which involves an assessment of catchment hydrology, the hydraulic parameters of proposed sites, reservoir morphometry and the potential yield for irrigation, hydropower or water supply (Bernascek 2001). The proposed sites for the dam should be considered in relation to ecologically significant landscape- or catchment-scale features of the river system, i.e. the physical habitat template, as well as the dynamics of the system as a whole in terms of the downstream transport of nutrients and energy as outlined by the RCC (see Section 3.1). Because physical, chemical and biological characteristics vary along a continuum from the headwaters to the lower reaches of a river, the siting of a dam along its longitudinal profile will have different consequences for the biota (Ward and Stanford 1983a). Changes in sediment and nutrient input and transport need to be accounted for in terms of their significance to ecosystem structure and function. For example, by obstructing the transport of detritus, a headwater dam will reduce the ratio of coarse particulate matter to fine particulate matter (CPOM/FPOM), which may affect the trophic relationships downstream, whereas a dam in the lower reaches will have little effect on detrital size ratios (Ward and Stanford 1983a). However, these impacts are case-specific, since numerous other factors that affect ecosystem dynamics may cause individual systems to deviate from the classical notion of the river continuum. Thus detailed physical, chemical and biological studies need to be carried out before the impacts of alternative locations can be assessed.

The potential impacts of a dam in terms of its inundation of upstream, or degradation of downstream, habitats, and access to these habitats, should be addressed before a suitable location can be identified. An assessment of the habitat requirements of resident fish species and the distribution of habitats in the river system being considered for development should be undertaken in conjunction with the acquisition of baseline data on the distribution of fish communities and populations. For example, if all functional habitat units (*sensu* Kocik and Paola Ferreri 1998) are represented in the reaches upstream of a reservoir, then fish populations could be sustained here, despite losses to genetic diversity over time. However, if any important functional habitat unit is missing from these reaches (for example, if there is sufficient spawning habitat, but limited nursery or feeding habitat), then fish populations will suffer declines in recruitment. Similarly, downstream of the dam, feeding habitat for adults may be plentiful in productive lowland reaches, but access to spawning habitat such as cobble-bed riffles in the middle reaches could be eliminated.

Fragmentation effects of flow regulation as a result of reduced water depth, and therefore connectivity between reaches downstream of dams, is likely to be most critical in foothill and transition zones as a consequence of the higher width to depth ratios which are found here (Rowntree and Wadeson 1999). If the negative affects of a dam cannot be avoided, then the potential for refuge areas which can support viable populations in the remainder of the catchment needs to be considered. An assessment of functional habitat units in proposed aquatic protected areas should therefore be undertaken. In this respect, decisions need to be guided by an understanding of metapopulation dynamics. For example, if the identified refuge areas provide only marginal habitat for the species being considered, i.e. if local populations in the refuge areas suffer frequent extinctions as a result of natural disturbance – and therefore depend to large extent on recruitment from source populations – then these refuge populations will not be sustainable.

5.2. DAM DESIGN

There are two important factors that need to be accounted for during the dam design phase in terms of the impact on fish populations: the design of fishways to facilitate fish passage, and the design of release mechanisms to regulate water temperature and quality downstream of the reservoir. Fishways, fish passes and fish ladders are all terms used to describe facilities that allow the passage of fish species past an instream obstruction in a river (Bell 1986). Research on fish passage requirements related to the construction of fishways is a complex and specialised topic that has been comprehensively dealt with by Bok (2001) for South African Rivers and is not dealt with in detail here. The limitations of fish passage facilities need to be recognised, however, and alternative management strategies need to be developed in cases where it is impossible to provide fish passage.

Fishway technology is well advanced in the USA and Europe where rivers support important commercial and recreational migratory fish species, including salmonids and clupeids. Francfort *et al*. (cited in Larinier 2000) examined the costs and benefits of 16 case studies around the USA. Only six of the case studies, including two fish lifts, were found to be successful in increasing the upstream passage of fish (Cada cited in Larinier 2000). In cases where there was limited knowledge of fish passage requirements, and species- and site-specific criteria for fish passage design were not implemented, limited success was achieved. In Japan, fish passes designed for ayu (*Plecoglossus altivelus*) were found to be ineffective because they were based on European designs that proved suitable only for large ayu (Nakamura *et al*. 1991). In South America, fish migrate upstream at the beginning of the annual floods in spring in search of spawning areas. Borghetti *et al*. (1994) carried out a study of the effectiveness of a fish ladder on the Itaipu Dam on the Parana River in Brazil where a decrease in the population of migratory fish downstream of the dam had been observed. The fish ladder was selective with respect to fish size with only fish under 1 m in length able to pass. Linløkken (1993) showed that the efficiency of fishways on the Glomma River in Norway was very poor - only a very small proportion of the populations of grayling *Thymallus thymallus* (0.7%) and brown trout *Salmo trutta* (0.4 - 1.1%) were able to utilise them. One of the main problems in fishway design is the attraction flow: in the Glomma River fish, were attracted to turbine flows rather than fishway flow when discharge from the fishway was much lower than discharge from the turbines. A similar problem was experienced in Norway, where Rivinoja *et al*. (2001) found that only 26% of Atlantic salmon *Salmo salar* found the fish ladder on the River Umeälven since a large proportion had been attracted away from it by the discharge from dam turbines.

Fishway technology in South Africa is, as yet, undeveloped and while the importance of fish passage has been recognised, and a number of fishways have been built around the country, their designs have not been based on the swimming ability and passage requirements of local species, and there have been no monitoring surveys that could provide an indication of their effectiveness (Bok 2001). Where it is practical and feasible, the construction of fishways in South Africa should be considered a priority, especially considering that a large number of existing smaller instream obstacles such as farm dams and gauging weirs are likely to significantly the affect the migration and dispersal of local fish populations.

Bok (2001) emphasized the importance of acquiring data on the migratory behaviour and swimming ability of indigenous fish, and to integrate these data with an investigation into the hydraulic characteristics of various fishway designs in order to develop fish passage facilities that will meet local requirements. Where dams are too high, however, or where the success of fish fishways may be limited, or prove to be too expensive, an integrated approach to the management of fish populations at the catchment scale will need to be adopted, taking into consideration the viability of the populations in the undisturbed parts of the catchment according to the assessments outlined in Section 4.3. One possibility might be to identify priority conservation areas in the remainder of the catchment where it would be feasible to restore connectivity, thereby offsetting the impacts of existing or proposed developments.

The second important factor to consider during the design phase is the effect of temperature on downstream fish communities. The thermal stratification of dam reservoirs and the build up of a thermocline can have significant effects on these communities. The depth of withdrawal of water from reservoirs dictates the levels of dissolved gases, nutrients, tubidity and toxic or oxygen-demanding material (Miranda 2001). Downstream releases of cold, oxygen-depleted, hypolimnetic water from dams inhibits spawning by adult fish (Cambray *et al.* 1997), as well as the embryonic development, swimming performance, growth and survival of the early life stages (Clarkson and Childs 2000). Multi-level discharges are therefore advisable for dam projects where thermal effects on riverine fish species are predicted to be significant. The design of these release mechanisms involves a close collaboration between engineers and ecologists with a detailed knowledge of the thermal requirements of the affected fish populations.

5.3. DAM OPERATION

This section deals primarily with the management of flows that give rise to geomorphological and ecological changes in the river channel downstream of the dam following its construction. The release of environmental flows from dams to mimic the natural flow regimes of rivers for the benefit of downstream ecosystems has become a focus of river conservation and restoration around the world (King *et al.* 2000). Methodologies such as the IFIM (Bovee and Milhous 1978), BBM (King *et al.* 2000) and DRIFT (King *et al.* 2003) have, and are being developed to facilitate the transformation of scientific expertise and information into flows to be released from dams to meet human water demands while minimising the impacts to downstream ecosystems. These methodologies are informed and guided by the paradigm of the 'natural flow regime' (Poff *et al.* 1997). The fundamental tenet of this paradigm is that the ecological integrity of river ecosystems depends on the dynamic nature of river flow. Translating the natural flow paradigm into management objectives involves separating the complexity of natural flow regimes into meaningful categories. The DRIFT methodology discriminates two main, and several sub-categories of flow (see Table 5.1): (1) *low flows*, which are daily flows between high-flow peaks, further divided into wet-season and dry-season flows; and (2) *high flows*, which are peak flows and are sub-divided into four size classes of intra-annual floods, and four flood magnitudes with return periods of 2, 5, 10 and 20 years. These flow categories are associated with a number of generic functions; for example, low flows define the seasonality of rivers and the amount of habitat available to instream biota, smaller high flows are associated with fish spawning and flushing sediment from spawning gravels, whereas larger floods inundate floodplains and maintain the major geomorphological features of the river channel (Brown and King 2000).

Each flow category can be further described in terms of five ecologically relevant properties (Poff *et al.* 1997): (1) the *magnitude* of discharge at any time interval; (2) the *frequency* of occurrence of a flow at any given magnitude over a specified time interval; (3) the *duration* of any specified flow condition; (4) the *timing* or *predictability* of flows at a given magnitude; and (5) the *rate of change* or *flashiness* of flow conditions. The properties of each flow category will depend on the regional characteristics of the river. Essentially, flow categories and their associated properties provide a means of describing the hydrological template upon which the life histories of the biota are superimposed (*sensu* Southwood 1988 discussed in

Table 5.1 Flow components identified by the DRIFT methodology and their importance to ecosystem functioning (adapted from Brown and King 2000).

Flow	Description	Ecological significance
Lowflows	the normal flow in the river outside of floods	Defines the basic seasonality a rivers – its dry and wet season, whether it flows all year or dries out for part of it. The different magnitudes of lowflow in the dry and wet seasons create more or less wetted habitat and different hydraulic and chemical conditions, which directly influence what the balance of species will be in any season.
Inter-annual floods	small floods that occur several times within a year.	Small pulses of higher flow, freshes are usually of most ecological importance in the dry season. Smaller floods stimulate spawning in fish, flush out poor quality water, mobilise sandy sediments, and contribute to flow variability. They re-set a wide spectrum of conditions in the river, triggering and synchronising activities as varied as upstream migration of fish and germination of riparian seedlings.
Inter-annual floods	floods that occur less often than once a year.	Scouring floods which dictate the form of the channel. They mobilise sediments and deposit silt, nutrients and seeds on floodplains. They inundate backwater areas, and trigger the emergence of flying adults of aquatic insects, which provide food for fish, frogs and birds. They maintain moisture levels in the banks, which support trees and shrubs, inundate floodplains, and scour estuaries thereby maintaining the link with the sea.

Section 3.1.1). The challenge that faces ecologists is to quantify flows that have been identified as ecologically relevant in terms of the categories and the properties outlined above. For fish species, this means including flows to maintain the correct hydraulic and geomorphological conditions for all species and life stages (egg, larvae, juvenile and adult) at appropriate times during the year. In the United States, the IFIM (Bovee and Milhous 1978) became the favoured methodology used to determine these biotic-abiotic links. By describing the physical-habitat preferences of target species in terms of selected environmental variables such as depth, velocity and substrate, and linking these to the availability of habitat modelled at different discharges, the IFIM procedure enabled river ecologists to quantify how habitat changed as flow changed. This method, which is data-intensive and species-specific, however, was found to be inadequate for addressing flow requirements of the broader ecosystem which are important for maintaining other, process-related habitat features, as well as ecosystem services (Poff *et al.* 1997). Another problem of species-specific methods such as the IFIM is that, providing optimal conditions for one species can create sub-optimal conditions for others (Sparks 1995). For example, in any given river system, there may be several reproductive guilds of fish (e.g. lithopilic, rheopholic, psammophilic), each requiring specific habitat conditions for spawning. These reproductive guilds may then have specific trophic requirements and depend on different flows for reproductive cues and maintenance of habitat or passage. In natural river systems, intra- and inter-annual variability mediates relationships between species and maintains high levels of diversity (Ward and Stanford 1983b). Variability is therefore another essential parameter that needs to be quantified and included in all EFA methods.

6. MANAGING FRESHWATER FISH POPULATIONS – CONCLUDING REMARKS

So far this report has examined the impacts of dams primarily from two perspectives, (1) the effect of fragmentation and (2); the downstream effects of river regulation, on the habitat, passage and spawning requirements of freshwater fish. While methods for assessing the effects of ecological changes downstream of a dam are well advanced in this country (e.g. DRIFT King *et al*. 2003), research aimed at providing input to these methods is lacking. For example, few studies have attempted to define and quantify critical habitat (i.e. functional habitat units) for native species, nor are there currently techniques available to evaluate the consequences of reduced connectivity between habitats. Only once the importance of critical habitats is recognised and understood, and the extent and timing of fish movement between them are described, will it be possible to put in place the appropriate management and legislative mechanisms necessary to prevent further declines in native fish populations.

It has been suggested that the complexity of rivers makes the task of managing systems subject to fragmentation and regulation – taking into account the requirements of all biophysical processes and species – exceedingly difficult, if not impossible (Sparks 1995; Poff *et al*. 1997). This has presented a major challenge to the development of both species-specific methods (e.g. IFIM, Bovee 1982), and holistic EFA methods that are designed to incorporate all biological, physical, as well as social components of river ecosystems into the EFA process (e.g. DRIFT King *et al*. 2003). Scientists and managers should therefore recognise the shortcomings of management and acknowledge the function that inherent intra- as well as inter-annual variability at a multiplicity of scales has played in maintaining high levels of diversity in natural systems (Poff *et al*. 1997). Recognising the shortcomings of managing degraded systems, scientists and managers should identify specific objectives which are both desirable and achievable – desirable in the sense that they reflect the interests of the majority of stakeholders, and achievable in sense they are within the scope of scientific investigation, given budgetary and manpower constraints.

In terms of fish movement, while connectivity cannot be wholly restored in most systems, a basic understanding of the spatial dynamics of freshwater fish in a catchment may go a long way towards providing guidelines for rehabilitating key river reaches that have the potential to support viable fish populations. For South Africa’s freshwater fish species, this may mean prioritising research aimed at determining the flow, habitat and passage requirements at species and populations that are threatened or subject to exploitation by subsistence or commercial fisheries. Although ‘targeting’ species has fallen into disfavour in terms of management objectives, understanding the life histories of individual organisms frequently, is the only way to increase confidence in the predictions of science and the success of management actions.

Despite the complexity of natural systems, there is considerable scope for bridging the gaps in our knowledge of the relationships between physical disturbance and ecological process. In some contrast to the statements made above regarding the impossibility of managing river systems therefore, Miranda (2001) argues that environmentalists often fail to acknowledge that variability in ecosystems may also mean that they may be more 'forgiving' than they are generally given credit for. If this is the case, then management does indeed have an important role to play in mediating the relationship between society and natural ecosystems.

The response of an organism to any particular anthropogenic disturbance exists along a continuum of change from mild to severe – the latitude of this continuum defines how 'forgiving' a certain organism or ecosystem component might be. To simplify the task of managing complex ecosystems and species it is necessary to identify actions that will have the most leverage. In the life history of any fish species, there may be periods when populations are susceptible to certain critical limiting environmental factors that govern the viability of populations more so than other factors. Management actions will have the most chance of success if these 'windows of vulnerability' (both spatial and temporal) can be identified together with the limiting factors. In general, mortality rates in fish populations are much higher in younger fish (Wootton 1990).

For example, in the Colorado River, the biggest bottleneck in the life cycle of endangered fish species is between from when the eggs are fertilised until the young recruit into adult populations (Dale Ryden, Biologist, U.S. Fish and Wildlife Service, Colorado *pers. comm.*). If river flows have not been adequate to flush sediments from cobble substrata, then eggs fail to reach the interstitial spaces between the substratum where they can safely develop into juveniles. A second window of vulnerability is the period after the larvae swim up out of the gravel and drift until they find a suitable low-velocity habitat further downstream to develop into juveniles. If the flows are not high enough to inundate marginal areas, the larvae drift into Lake Powell where they are preyed on by non-native predators. Limiting environmental factors in the former cases therefore include: sufficient flows to flush sediment from cobble substrata, and flows that inundate floodplain areas. Other limiting factors may be: the presence of natural or artificial barriers in the path of important migrations, hydraulic conditions in the river at the time of migration, and temperatures or flows that could serve as a behavioural or physiological cues.

These critical phases need to be defined more clearly and their tolerance ranges quantified for individual species – an 'average' condition will not ensure maximum diversity under modified conditions. The reason for this is that ecological processes are frequently non-linear – as Poff *et al.* (1997) have pointed out: 'half the peak discharge will not move half of the sediment, half of the migrational-motivational flow will not motivate half of the fish, and half of an overbank flow will not inundate half of the floodplain'.

The objective of managing fish populations should be to ensure that, in river systems subject to disturbance, there will be sufficient numbers of fish to maintain genetic diversity and demographic stability and buffer against catastrophic loss (Nesler 2000). Section 5 in this report focussed on what can be done to mitigate specific impacts of various phases of the dam development cycle. However, it is emphasised that effective management of fish populations requires a holistic approach in catchments where it is impossible to mitigate the impacts of water-resource developments – i.e. management objectives should be identified, and an assessment should be made as to whether populations can sustain further development. An alternative approach to providing fish passage facilities where these are not feasible or too expensive may therefore be to assess what the capacity of the remainder of the system is to buffer against the extinction of a vulnerable species, or the collapse of a valuable fisheries resource.

In a recent review of river research in South Africa, Breen *et al.* (2003) call for rivers to be viewed as complex 'production systems' and that, in order for us to manage them in a sustainable fashion, it is necessary to establish the requirements for water to sustain the production process. In a similar fashion, and in the context of freshwater fish and fisheries management, this report has presented a model of rivers that suggests that they can be viewed as a series of hierarchically nested production units, with some units being more critical to fish production – and more susceptible to modification – than others. The capacity of a river system to support fish production depends on the quantity and quality of critical production units (referred to by Kocik and Paola Ferreri 1998 as Functional Habitat Units or FHUs) (determined largely by hydrological and sediment dynamics); the connectivity between production units, (determined by natural and artificial barriers as well as river flow); as well as environmental cues (temperature and/or flow) that may trigger behavioural or physiological responses. In order to rehabilitate rivers as fish production systems, it is therefore necessary to be able to identify and describe critical production units, and understand how the components and processes in river systems are transformed through regulation and fragmentation. However, rivers should be managed not only to maintain high levels of 'fish production', however, but also to maintain diverse communities. Understanding the requirements of the species which comprise that community is therefore a prerequisite for sound biodiversity management. The United States Congress has recognised the importance of fish habitat to the productivity and sustainability of fisheries, and in 1996 added the Magnuson-Stevens Fishery Conservation and Management Act to federal law, which requires fishery management plans to describe Essential Fish Habitat (EFH), i.e. the flow and substratum necessary for spawning, breeding, feeding and growth to maturity of the fish being managed, and to define the threats to that habitat from both fishing and non-fishing activities. Sound research is needed to back up these management plans.

In conjunction with the identification and description of functional habitat units for a range of species' life stages of key ecological or social importance, key criteria for evaluating the sustainability and recovery of fish populations should include: an assessment of the number of populations in a catchment, their distribution, abundance and age structure, the compilation of life history profiles.

In summary

Based on the discussion above, suggestions for research and management guidelines can be summarised as follows:

(v) Managing fish populations in rivers affected by regulation and fragmentation requires an holistic approach – i.e. managing for all aspects of fish ecology, including utilisation.

(vi) Species should be targeted for research into life history strategies. This is based on the supposition that ecosystems should not be managed on the basis of 'average' conditions – a few well-founded facts are better than a large number of speculations.

(vii) Critical habitats (or functional habitat units) of a range of species should be identified and described over a range of spatial and temporal scales.

(viii) Vulnerable life stages (e.g. migration, spawning, growth and development) should be identified for each species and linked to the environmental requirements for each stage.

Suggestions as to how this can be achieved are discussed in more detail in the following chapter.

PART B: RESEARCH AND METHODS DEVELOPMENT

7. RESEARCH AND METHODS DEVELOPMENT IN SOUTH AFRICA

7.1. INFORMATION REQUIRED FOR MANAGING FRESHWATER FISH POPULATIONS AFFECTED BY DAMS

Empirical information on landscape-scale habitat utilisation by various life stages, as well as their flow and passage requirements, is needed to effectively manage freshwater fish populations in systems subject to river fragmentation flow regulation. Ideally, it is suggested that the following key information be available for compiling an integrated management framework for fish populations affected by water resource development:

Environmental baseline data

- *Habitat distribution*: catchment-wide analysis of the distribution of habitat (spawning, feeding, nursery) identified as critical by the ecological profile of selected species and compiled from a desktop reach analysis, followed by ground-truthing at selected sites.
- *Hydrological analysis*: historical analysis of hydrological conditions in the catchment and hydrological modelling.

Fish distribution and abundance

- *Fish distribution*: baseline data on existing and historical patterns of distribution and abundance of both exotic and indigenous fish species and age-classes upstream and downstream of the dam site, compiled from historical distribution records and monitoring surveys. However, as Weeks *et al.* (1996) pointed out, pre-impoundment baseline information on the distribution and abundance of species should account for spatial and temporal variability, i.e. zonal, intra- and inter-annual variations in assemblage structure and distribution need to be described.
- *Exotic species*: patterns of distribution and abundance of exotic species and potential for range extensions following habitat modification and flow regulation.

Ecological profile of affected species

- *Life history profiles*: age-length relationships, age at first maturity, age-specific fecundity and diet, physiological tolerances to water quality conditions.
- *Temperature*: temperature requirements of fish for critical periods, i.e. gonad development, spawning, egg incubation, larval development.
- *Physical habitat description*: geomorphological and hydraulic meso- and microhabitat descriptions of egg, larval, juvenile and adult habitat for the affected species.

Spatial dynamics of affected species

- *Migration*: timing and extent of seasonal migrations by adults of species dependent on longitudinal or lateral movements in relation to prevailing hydrological and temperature conditions during the year, information on hydraulic requirements of fish species for passage.
- *Dispersal of young*: timing and extent of active or passive dispersal of larvae and juveniles;
- *Existing instream structures*: assessment of the location of existing natural and artificial obstacles to movement in the catchment.

Research findings should feed into policy formulation and legislation to protect native fish populations and the aquatic habitat which supports them. Presently in South Africa, the paucity of empirical studies on the ecological requirements of fish species means that confidence in the predictions of EIAs and ecological Reserve Determinations is low. Data collected over several years are essential for understanding historical trends of fish populations and relating these to the environmental variability of river systems. In conjunction with long term monitoring surveys, essential research areas for fish populations in South African rivers include: (1) the timing of fish migrations in relation to the hydrological profile of ecoregions, (2); the application of catchment-scale management principles which involve an understanding of metapopulation dynamics, source and sink concepts, and the role of functional habitat units in explaining fish distribution (3); describing and quantifying functional habitat units more precisely, taking into account the requirements of all life stages (4); 'limiting factors', whether they be particular flow, habitat or temperature requirements need to be identified and defined for vulnerable life stages.

7.2. RESEARCH METHODS FOR STUDYING FISH MOVEMENT AND HABITAT UTILISATION

Studying the spatial dynamics of fish populations is one of the most effective ways of providing insights into the habitat use, environmental cues and other ecological requirements of freshwater fish (Lucas and Baras 2000). A variety of techniques is available for studying the use of space by fish, yielding information that varies with regard to accuracy, as well as spatial and temporal resolution. Advances in technology over the last few decades have yielded valuable insights into fish movement, but they have not been widely applied to species with limited commercial value due to their cost and the limited expertise available. In South Africa, the need for accounting for the impact of water-resource development has only recently been recognised by environmental legislation (Bok 2001). Techniques to study the movement of freshwater fish in South Africa are therefore undeveloped and information on fish movements has been based on opportunistic observation or, in more systematic studies, on fishways counts (e.g. Meyer 1974). Lucas and Baras (2000) provide a review of a variety of state-of-the-art methods for studying the spatial behaviour of fish including telemetry, automatic fish counters and hydroacoustics, as well as more traditional methods such as mark-recapture. This brief review examines these more traditional approaches, but presents telemetry as the most appropriate way forward for studying the passage and habitat requirements of native fish species over the medium-term.

7.2.1. Variations in population density and catch per unit effort (*cpue*)

Method The most basic technique for studying the spatial behaviour of fish is to study variations in the spatial distribution of fish over a period of time. A number of sites is sampled on a regular basis and variations in catch statistics (absolute estimates of abundance, or catch per unit effort, *cpue*) are used to infer emigration and immigration. Birth and mortality rates need to be estimated if there are long intervals between sampling events (Baras and Lucas 2001).

Advantages Variations in fish distribution and abundance are useful for long term studies aimed at linking population and community dynamics with site-specific as well as landscape scale heterogeneity. For example, in Michigan streams, long term (20+ years) temporal variations in population densities of brown trout were found to be associated with a number of site-specific mechanisms including variation in habitat quality, climate, competition, predation and fishing pressure (Nuhfer and Alexander 1993; Clark and Nuhfer 1995 – both cited in Wiley *et al.* 1997).

Disadvantages Wiley *et al.* 1997 stress the importance of data sets that are both spatially (landscape scale) and temporally extensive: long-term studies (15-20 years, or 10+ generations) are the only way of minimising the risk of incorrectly attributing variations in population densities to landscape factors. Unless extensive data sets are available, these techniques have a low temporal resolution, and capture efficiency (which may vary on a daily, seasonal and site-specific basis) has a significant influence on results (Baras and Lucas 2001).

7.2.2. Mark-recapture studies

Method Mark-recapture studies involve the capture, marking, release and recapture of individuals at selected sites over a period of time. A variety of methods is available for marking fish including, amongst others, mutilation (e.g. fin clipping), dyes, anchor tags, clamp tags, and subcutaneous tags. There are advantages and disadvantages to each tagging method, and the method chosen depends largely on the species of interest. Pilot studies to ascertain retention and mortality rates are therefore essential before mark-recapture studies can commence.

Advantages Apart from providing information on fish movement, mark-recapture studies also provide information on population size, growth and mortality. Mark-recapture studies do not require sophisticated technology and do not have high equipment costs. Failing the availability of more sophisticated techniques for studying fish movement, therefore, mark-recapture programmes may present the only alternative.

Disadvantages A major disadvantage of mark-recapture studies is there low temporal resolution. In order to establish patterns of movement, mark recapture studies require the capture of a large number of individuals at a number of sites, and this limits their applicability to movements that occur over a very limited spatial extent, if manpower and time are limited. Estimates of the timing and extent of movements are imprecise and the extent of fish movement has frequently been misinterpreted due to low recapture rates. For example, studies, based on mark-recapture techniques, gave rise to the incorrect assumption that adult resident stream salmonids were largely sedentary. In these studies, fish were captured, marked and recaptured from a defined set of reaches. Individual fish were later recaptured from the same reaches. In 83% of the studies, 50% of the fish recaptured were in their home reach, the rest were assumed to have died or evaded recapture, leading the researchers to incorrectly assume that these species were sedentary (Gowan *et al*. 1994). In Australia, mark-recapture techniques are believed to have over-estimated the extent of fish movement. Reynolds (1983) conducted one of the most comprehensive tagging studies of freshwater fish movement in Australia over a four year period between 1974 and 1978. A total of 9674 common carp *Cyprinus carpio*, 3267 golden perch *Macquaria ambigua*, 307 Murray cod *Maccullochella peeli*, 660 silver perch *Bidyanus bidyanus* and 425 catfish *Tandanus tandanus* were tagged in the Murray River using numbered floy anchor tags. Of the 14 333 fish tagged, 1276 (8.9%) were recaptured and classified according to their size and the distance they had moved. Golden perch were found to cover distances of over 1000 km and on this basis were classified by Reynolds as migratory. However, this conclusion has been recently criticised by Crook and Humphries (in press) who pointed out that, of the 483 recaptures of golden perch, only 11 fish (2%) had covered more than 1000 km, and that over half had moved less than 10 km. Crook and Humphries therefore argue that Reynold's study did not provide enough evidence to conclude whether or not golden perch were migratory.

7.2.3. Fishway counts

Method Fish can be monitored by means of fyke traps set at weirs with fish passage facilities. The numbers, sizes and sex of fish passing through the weir at different times of the year can then be ascertained from captured fish. Fishway counts are most effective if fish have been implanted with PIT tags (see 7.2.4 below). A flatbed antenna can then be placed at the entrance to the weir and the passage of individuals monitored automatically.

Advantages As Meyer's (1974) study demonstrated, counts of fish at fishways can provide an indication of the timing of fish migration in rivers. Such studies can also provide important information on the age- and sex-structure of the migrating population.

Disadvantages Although fishway counts provide an indication of the timing of fish movement, they do not provide information on its extent, duration and therefore little insight into its function. In addition, movement through weirs, particularly those with poorly designed passage facilities, may be influenced more by the ability of fish to pass the weir at all (i.e. when the weir is overtopped), rather than by natural patterns of movement.

7.2.4. Passive Integrated Transponders (PIT)

Method More recently, Passive Integrated Transponders, or PIT tags have been used at fishways to identify fish passing through the weir. PIT tags are injected either into the abdominal cavity or musculature of a fish and are programmed to transmit individual electronic codes that can be detected by means of an antenna placed near the fishway entrance. Fish injected with the tag that pass through the fishway are automatically recognised by a reader.

Advantages Because tags are passive, i.e. they do not rely on a power source to transmit a signal, they have a potentially infinite lifespan and individual fish can be monitored over many years. An additional advantage is that they do not rely on the recapture of fish for identification.

Disadvantages The range of PIT tags is limited to between 20 – 50 cm and therefore can only be used where receivers can be positioned in close proximity to passing fish, e.g. in a fishway. Some studies have made advances in detecting fish movement across streams up to 8 m wide (Lucas and Baras 2000).

7.2.5. Telemetry

Method Tracking the movement of freshwater fish by means of telemetry involves the remote detection of a fish's position by means of a surgically implanted radio or acoustic transmitter. The transmitter sends out an individually coded signal that can be detected by means of a receiver (either a directional antenna or microphone). The type of telemetry equipment used depends on environmental conditions. Acoustic transmitters are most suitable for studies in estuarine or marine conditions because signal strength is not reduced in deep water and acoustic signals are not susceptible to conductivity. Radio transmitters emit a pulsed signal that is filtered by the receiver unit and converted to a numeric code that allows the investigator to identify individual fish. VHF radio signals are attenuated in deep water or when conductivity increases above 650μS. Radio telemetry is therefore more suitable for tracking fish in freshwater environments. The type of transmitter used depends on the size and weight of the fish, the number of fish to be tracked, the time period over which the fish are to be tracked and the tracking method. Transmitters vary according to size, pulse interval and detection range, all of which determine battery life and therefore the size and weight of the transmitter. Since transmitters should weigh no more than 2% of the weight of the fish, and batteries make up a large proportion of the volume and weight of the transmitter, the performance of a transmitter needs to be traded-off against its weight, e.g. a longer interval between pulses preserves battery life and enables the fish to be tracked over a longer period, but makes it more difficult to track large numbers of fish, or fish that are very mobile. Fish can be tracked from the shore, boat or aircraft by means of a directional antenna or their location can be recorded automatically by means of listening stations (receivers linked to a data-logger) positioned along the length of the river. The location of the fish is then logged as it passes the station.

Advantages Radiotelemetry has the potential to provide information at a high spatial and temporal resolution on the movement and habitat utilisation of individual freshwater fish over the short and medium term (i.e. hourly to several years) and therefore has the potential to provide the most immediate answers to management-related problems. Concepts such as 'restricted movement' (Gerking 1959), which have informed scientific views on many fish groups, are giving way to a more fluid view of the spatial and temporal dynamics of freshwater fish populations as a result of the increased application of this technology (Fausch and Young 1995).

Disadvantages Telemetry equipment is expensive and tracking fish is complicated in difficult terrain which,-may add to the cost of studies.

7.2.6. Genetic studies

Method The use of genetic studies to provide a perspective on historical gene flow patterns is the most effective means of identifying fish populations in river catchments and determining the relationships – and thereby the exchange of migrants – between them. Microsatellite DNA displays a high degree of variation at the same locus, which allows investigators to use the locus as a marker to differentiate between individuals or populations. Although allozyme electrophoresis has been a standard technique for genetic studies on fish populations, the use of microsatellite markers is becoming increasingly popular for differentiating populations, identifying population bottlenecks, estimating migration rates and assigning individuals to populations (Hansen *et al*. 2001).

Advantages In river systems where the connectivity between reaches has been interrupted by dams, microsatellite DNA analysis may shed light on the initial distribution and interchange of individuals between previously contiguous populations. By applying statistical assignment techniques, it may be possible to determine the population of origin of a single fish and thereby to estimate the extent to which a freshwater fish population may utilise a whole river system.

Disadvantages Genetic techniques do not provide sufficient spatial and temporal resolution for addressing seasonal migration patterns or isolating environmental cues. Genetic studies are most useful when applied in conjunction with telemetry studies that can address these more immediate management concerns. Finding suitable polymorphic loci to use as markers requires considerable groundwork research before genetic analysis of microsatellite DNA can begin, if the species has not been worked on before.

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PART C: PILOT STUDY: OLIFANTS-DORING RIVERS FISH SURVEY

8. CHANGES IN THE CATCHMENT-WIDE DISTRIBUTION OF THREE THREATENED CYPRINIDS ENDEMIC TO THE OLIFANTS AND DORING RIVERS, WESTERN CAPE

8.1 INTRODUCTION

River fragmentation and flow regulation by dams and weirs, together with invasion by introduced fish species, have deservedly been acknowledged as amongst the principal threats to freshwater fish biodiversity in South Africa (Skelton *et al*. 1995; De Moor 1996; Skelton 2002). Despite this, research in this country has been slow in responding to the need for examining the mechanisms by which these factors have operated and studies have largely failed to provide the level of ecological detail necessary to guide policy formulation, legislation and management. In many instances therefore, recommendations on the passage and flow requirements of freshwater fish have been based on criteria established for systems and species elsewhere in the world, or on expert opinion. In a region where human demand for freshwater resources has exerted, and will continue to exert, increasing pressure on organisms living in freshwater ecosystems, it is imperative that management and conservation initiatives be guided by locally and empirically derived biological criteria if aquatic science is to remain relevant to management. These biological criteria need to be based on systematic, long-term monitoring programmes, combined with in-depth investigations which are scientifically defensible. While an over-reliance on expert opinion for guiding management is unavoidable in the short term, the sustainability of South Africa's freshwater biodiversity into the future cannot be assured with any level of confidence if this empirical information is not forthcoming.

The impacts that dams have had on freshwater fish populations is not limited to northern hemisphere anadromous salmonids, but extends to many temperate and tropical non-salmonid species as well (Baras and Lucas 2001; Walker and Thoms 1993). Not only have impoundments and hydrological manipulation obstructed fish movement and degraded instream habitat, but they are also likely to have been instrumental in increasing the susceptibility of river systems in this country to invasion by introduced fish species (Gehrke and Harris 2001). Studies elsewhere in the world have shown that hydrological conditions play a major role in mediating species interactions in river systems (Meffe 1984; Larson *et al*. 1995; Fausch *et al*. 2001), and de Moor (1996) has hypothesised that a recent 'second phase' of invasion in South Africa has followed the intensification of water-resource development in the country. Non-native species have therefore been able to invade areas from which they had previously been excluded by environmental resistance. Species assemblages which are susceptible to invasion by introduced species are therefore even more vulnerable if the river systems in which they occur are subject to intensive development. It is this combination of factors that is believed to be responsible for changes in the catchment-wide distribution and recruitment of three large cyprinids endemic to the Olifants and Doring

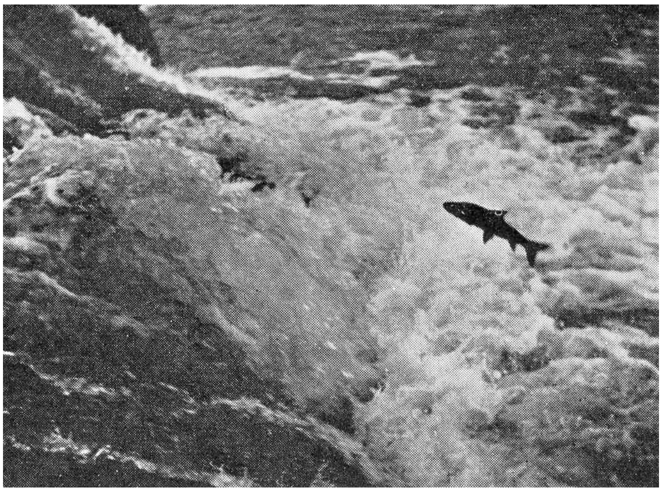


Plate 8.1 A sandfish (*Labeo seeberi*) ascending the Cascades on the Olifants River below the Bulshoek Barrage during a spawning run in the spring of 1950 (Harrison 1963). Sandfish are no believed to longer occur in these reaches.

Rivers in the Western Cape, South Africa: the Clanwilliam yellowfish *Labeobarbus capensis*, the sawfin *Barbus serra*, and Clanwilliam sandfish *Labeo seeberi* (Plate 8.1).

The decline in the numbers and ranges of these cyprinids in, and the complete elimination of the smaller endemic minnows from, the mainstem of the Olifants River over the last seventy years, has been linked to the introduction of largemouth bass *Micropterus salmoides* and smallmouth bass *Micropterus dolomieu* for angling purposes in the 1930s and 40s (Roth 1952; Gaigher 1973), and the construction of the Bulshoek Barrage and Clanwilliam Dam in 1919 and 1932 respectively (Scott 1982). All three species are now IUCN listed: the Clanwilliam yellowfish is vulnerable (VU A1ce), the sawfin is endangered (EN B1 +2abde, C1), and Clanwilliam sandfish is regarded as critically endangered (CR A1ace) (Hilton-Taylor 2000).

The two impoundments have, between them, inundated a total of 30 km, and obstructed access to 140 km, of upstream lotic (running water) habitat. During the first half of the 20th century, large aggregations of Clanwilliam yellowfish, sawfin and sandfish were regularly observed downstream of the Bulshoek Barrage and Clanwilliam Dam during spring – their attempts to reach upstream spawning grounds apparently thwarted by the presence of the dams (Brooks 1950; Harrison 1963; Harrison 1976). The modified flow conditions downstream and immediately upstream of the dams have increased the proportion of lentic (standing water) conditions and provided optimal conditions for the proliferation of bass, bluegill sunfish *Lepomis macrochirus* (introduced as fodder for the bass) and tilapia (*Oreochromis mossambicus* and *Tilapia sparmanii*). Regulation by the Bulshoek Barrage, the level of which is controlled by releases from the Clanwilliam Dam, also appears to have changed the geomorphological characteristics of the downstream reaches. Reduced flows have resulted in the encroachment of riffles and rapids by exotic vegetation and palmiet *Prionium serratum*, and sedimentation has degraded spawning habitat – a note by Harrison to Brooks (1950) pointed out that, by the time of writing, the former cobble-bed riffles downstream of the Clanwilliam Dam and Bulshoek Barrage had become embedded in sand.

Several surveys and scientific studies assessed the status and determined baseline ecological information on the cyprinids: a number of surveys, conducted by Cape Nature Conservation, took place during the

1980s (Scott 1982; Impson 1999); van Rensburg (1966) investigated the timing of reproduction in Clanwilliam yellowfish; Cambray *et al*. (1997) and King *et al*. (1998) studied the temperature and flow requirements of spawning yellowfish, and Gore *et al*. (1991) investigated the habitat requirements of yellowfish and sawfin. However, these studies were inconclusive regarding the environmental cues for migration and spawning and the status of the current populations as well as the extent to which they continue to depend on connectivity between river reaches remains unclear.

A number of sites for dam construction have been proposed in the Olifants and Doring River catchments to meet current water demands and extend irrigated agriculture in the region (Howard 1998). The most recent, at Melkboom on the Doring River, was listed in the National Water Resource Strategy as a priority for development by the Department of Water Affairs and Forestry (DWAF 2002). The construction of a major dam on the relatively undeveloped Doring River, which serves as a refuge for remaining mainstem cyprinid populations, would most certainly be detrimental to these populations.

Studies aimed at understanding the relevant biological criteria necessary for input to management recommendations in the Olifants and Doring Rivers should meet multiple objectives. Firstly, remedial measures aimed at stabilising existing populations should be determined on the basis of an understanding of their ecological requirements, i.e. their passage and flow requirements over a range of seasons should be established and incorporated into the design and operation phases of proposed water-resource developments. Secondly, should remedial measures prove ineffectual (the changes precipitated by the dams on the Olifants River are largely irreversible for instance), the consequences for the erosion of remaining populations will need to be understood. The response of refuge populations to accelerated change depends on the degree to which impacts are localised in catchments and on the degree to which genetic exchange occurs between populations.

The objectives of the ongoing fish surveys in the Olifants and Doring Rivers, of which the present study forms a part, are to assess the status of endemic fish populations in the Olifants and Doring Rivers system and to provide baseline data for an extended research programme into the ecological requirements of *L. capensis*, *L. seeberi* and *B. serra* related specifically to their movements and habitat utilisation at a range of spatial and temporal scales. The status of our knowledge on the distribution of these populations, using historical records and data from surveys for the Water Research Commission, the Department of Water Affairs and Forestry and the Department of Agriculture (Paxton *et al*. 2002), is presented.

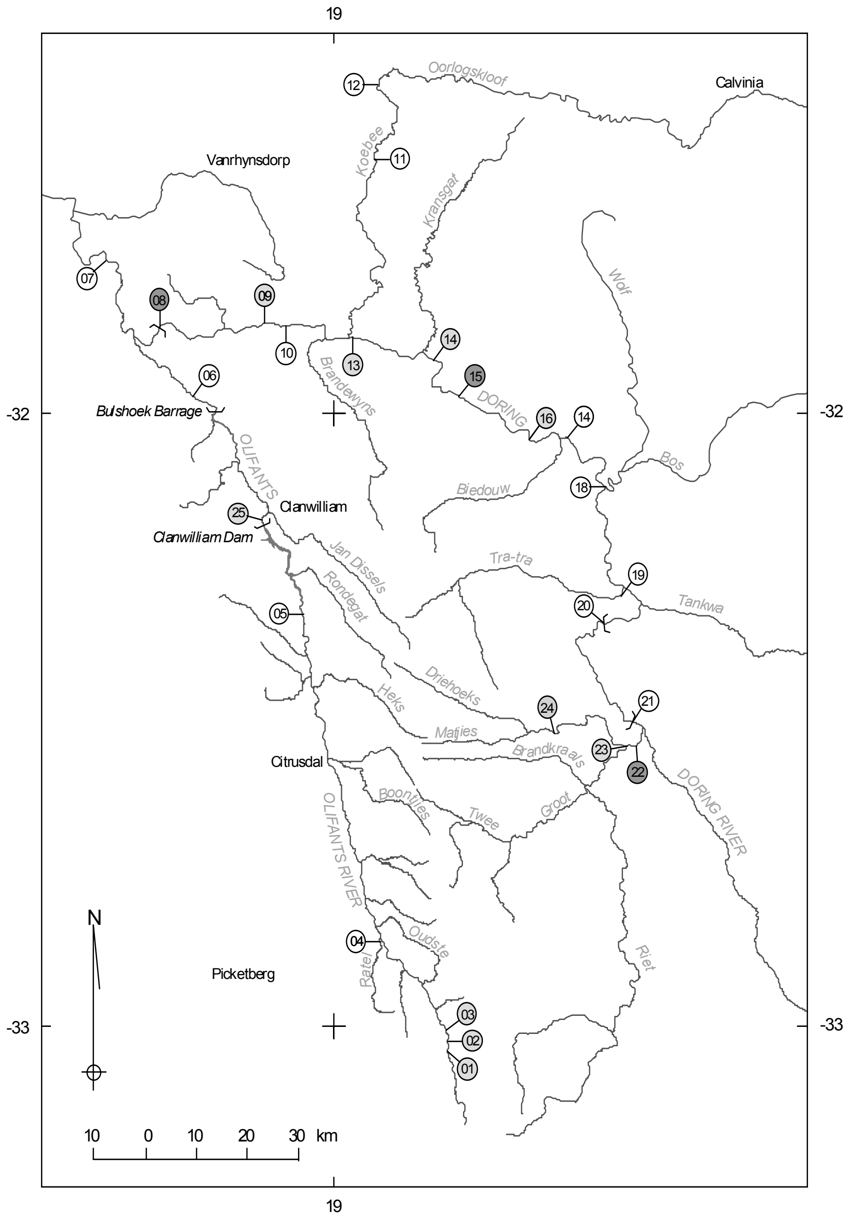


Figure 8.1 Olifants and Doring Rivers showing sites visited during the course of surveys conducted in the catchment in 2001 (unshaded) and 2002 (shaded).

8.2. STUDY AREA

Olifants River – The Olifants River rises on the Agter-Witsenberg plateau and enters a narrow, steep-sided gorge between the Skurweberg and Kouebokkeveld mountains in the Western Cape, South Africa. After emerging from the gorge into the Citrusdal valley, several tributaries contribute runoff from the western flanks of the Cederberg. All these tributaries contribute clear, low conductivity water from the quartzitic sandstones of the Cederberg mountains. However, water contributed from the Doring River as well as return flows from agricultural runoff results in a steep rise in conductivity towards the lower reaches in the vicinity of Klawer (Figure 8.1). The naturalised flow at the confluence of the Doring River is 513 Mm^3y^{-1} and the natural mean runoff (nMAR) of the Olifants River at the estuary is *c*. 1000 Mm^3y^{-1}.

However, intensive abstraction for agriculture in the Olifants River valley (primarily for citrus orchards and vineyards) means that only 54% of the nMAR (*c*. 280 Mm^3y^{-1}) reaches the Doring River confluence.

Doring River – The greatest proportion of the water in the upper Doring River is contributed by runoff from the Skurweberge and Kouebokkeveld mountains. The primary tributary in this region is the Groot River which contributes over 50 % of the runoff in the Doring River measured at the confluence of the Olifants River (*c*. 510 Mm^3y^{-1}). Several major tributaries contribute water from the eastern flanks of the Cederberg mountains including the Tra-tra, Biedouw and Brandewyn Rivers. Of the tributaries which originate in the Karoo, the Koebee, which rises as the Oorlogkloof River draining the northernmost reaches of the catchment from Calvinia, is the largest. This drainage pattern gives rise to the dual nature of the water chemistry in the Doring River: clear, low conductivity water is delivered by the quartzitic sandstones of the Cederberg mountains, whereas turbid, high conductivity water is delivered by the shales and mudstones of the Dwyka Formations and Ecca Group in the Karoo. Highly turbid flows are observed when episodic flooding by the Tankwa River sends pulses of sediment-rich water into the lower Doring River. The upper reaches of the rivers which drain from the Kouebokkeveld are subject to intensive abstraction and impoundment. Although the Doring River mainstem is undammed, there are gauging weirs at Aspoort (E2H002) in the middle reaches, and at Melkboom (E2H003), at the confluence with the Olifants River. In addition, a large (>5 m high) farm dam on the farm Brakfontein has been built in the middle reaches of the Doring River downstream of the Aspoort gauging weir.

8.3. METHODS

Two surveys of the fish populations in the Olifants and Doring Rivers took place between 4-18 February and 13-27 October 2001. A total of 16 sites were sampled on each of these occasions, with most of the sites located on the mainstem of the Doring River – previous surveys had focussed largely on the Olifants River and its tributaries and data on fish distribution in the Doring River was therefore sparse. Sites on the Groot, Tra-tra, Biedouw, Koebee and Oorlogkloof Rivers were also sampled.

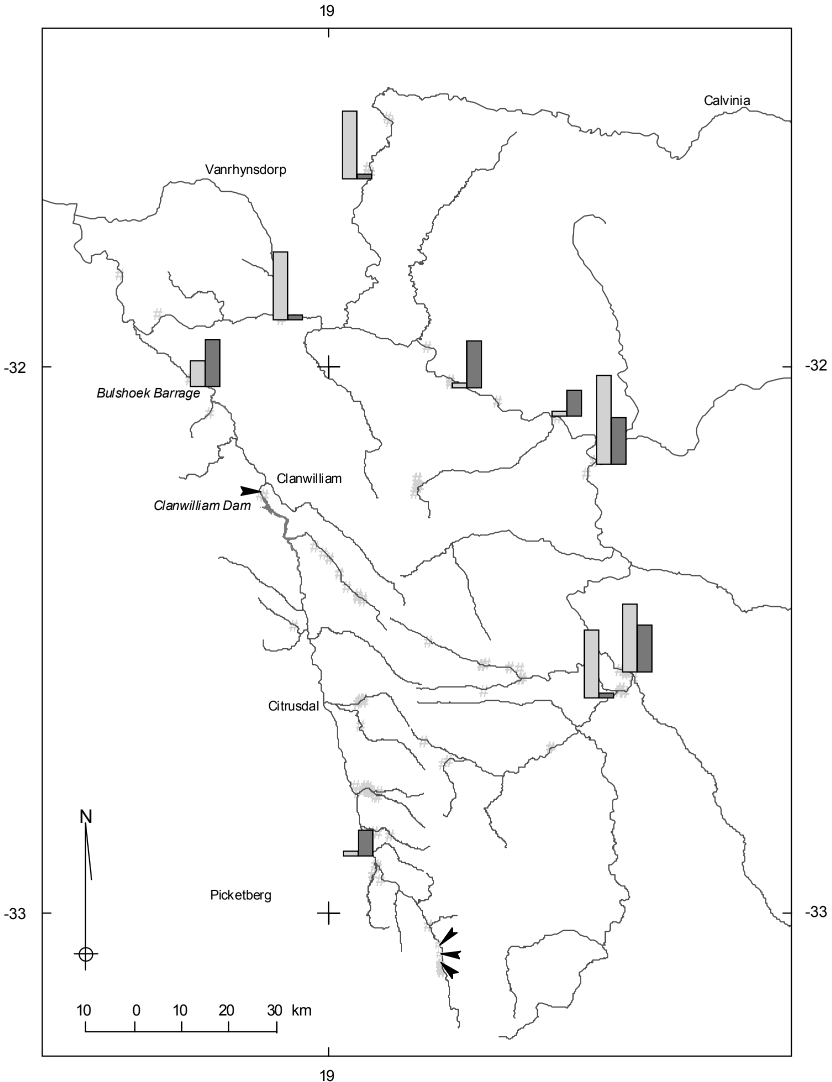
Four gill-nets with mesh sizes of 54 mm, 70 mm, 90 mm and 145 mm were used to sample pools. Each net was 30 m long and 2 m wide, fitted with weighted foot ropes and set in the river for a period of between 2 and 5 hours. The nets were cleared regularly and all indigenous fish were identified, measured live (mm TL), tagged and released. A sub-sample of indigenous fish species and exotic species were kept for biological analysis. Data from gill-net catches expressed as *cpue* were calculated as number of fish $m^{-2}h^{-1}$. In February 2001 an anchovy seine-net (mesh size 12 mm; length 30 m; depth 2 m) fitted with a weighted foot rope and a 2 m deep bag at its midpoint, was used to sample shallow sandy areas. In October, an anchovy seine-net 20 m in length was used. Between one and two seines were conducted per site. The data were expressed as the density of fish m^{-2}, calculated from the surface area of water seined ($\frac{1}{2}\pi r^2$). In order to compare general trends in spatial and temporal distributions, data from gill-net and seine-net catches were expressed as a relative abundance index (RAI). The RAI was calculated by classifying *cpue* values according to a range of values between 0 – 5, based on the highest and lowest values for that method. A box sampler was used to sample shallow riffles for eggs and larvae. The box sampler was placed on the substratum, all rocks removed, and eggs and larvae were washed into the downstream collecting jar. Specimens are currently being held at the Freshwater Research Unit, University of Cape Town.

During September and December 2002, surveys focused on the more inaccessible mainstem reaches of the Doring and Olifants Rivers that were not visited in 2001. The September survey took place between the farm Doringbos and the confluence of the Olifants River – a region that cannot be accessed by vehicle. The aim of this survey was to identify spawning sites and assess the topography of this segment of the river for telemetry studies. The second survey took place during December 2002 from the farm Visgat in the upper reaches of the Olifants River to the farm Boskloof, a distance of approximately 15 km. The focus of this survey was on the Olifants River Gorge which, because of its inaccessibility, could not be sampled during 2001. No sampling equipment of any description could be used. However, clear waters enabled visual surveys to be conducted. Quantitative estimates of abundance were not possible due to limited time.

Distributional data accumulated during the above surveys have been supplemented by historical distribution records dating from 1882 and compiled from the following sources: Cape Nature Conservation (CNC); the Albany Museum; the JLB Smith Institute; FISHBASE (Froese and Pauly 2001) and surveys conducted for the World Wildlife Fund (WWF) by Bills (1999). All historical distribution records and records obtained from the surveys conducted in 2001 and 2002 were entered into a GIS software package (ARCVIEW ©) and are presented in figure 8.2, 8.3 and 8.4 (a more comprehensive and detailed spatial analysis of the historical data is presented by Paxton *et al*. 2002). Land covers for the Western and Northern Cape came from ENPAT produced by the Department of Environmental Affairs and Tourism (DEAT). Rivers were digitised from 1:50 000 topographical maps.

8.4. RESULTS

Historical and present-day distribution records of *L. capensis*, *B. serra* and *L. seeberi* are represented in Figures 8.2 – 8.4. During the course of surveys conducted during 2001, large adult *L. seeberi* (> 350mm) accounted for 77% of the fish caught in the mainstem (320), followed by *L. capensis* (51; 12%) and *B. serra* (40; 10%). In addition, a large number (79 and 227 respectively) of *L. seeberi* and *B. serra* < 350 mm were seined or gill-netted from the Oorlogskloof River, a tributary of the Koebee River. Most fish (72 % *L. capensis*, 87 % *L. seeberi* and 90 % *B. serra*) were caught during February when the Doring River had stopped flowing and fish were concentrated in isolated pools.



● Historical distribution records of *L. capensis* ▯ February 2001 ▮ October 2001

Arrows indicate sites from which larval *L. capensis* were collected in 2002.

Figure 8.2 Olifants and Doring Rivers showing the distribution records for the Clanwilliam yellowfish *L. capensis* compiled from historical records and surveys conducted in 2001 and 2002. Histograms represent the RAIs calculated for the 2001 surveys.

8.4.1. Distribution

Labeobarbus capensis (Figure 8.3) – *L. capensis* has been recorded from most rivers in the catchment, but most frequently from the tributaries of the Olifants River flowing off the western flanks of the Cederberg mountains, particularly the Rondegat, Boskloof and Noordhoeks Rivers. Highest *cpue* (0.031 fish $m^{-2}h^{-1}$) for *L. capensis* was recorded in the middle reaches of the Doring River at the confluence of the Bos River (Site 18 Figure 8.3) during February 2001. A more even distribution of fish through the catchment during October 2001 when the Doring River was flowing is reflected by the much lower Standard Deviation (SD) for this month (SD: 1.4) than for February (SD: 4.9). While high RAIs were calculated for Ou Drif, Koebee and De Mond during February (Sites 10, 11 and 22; Figure 8.2), no *L.*

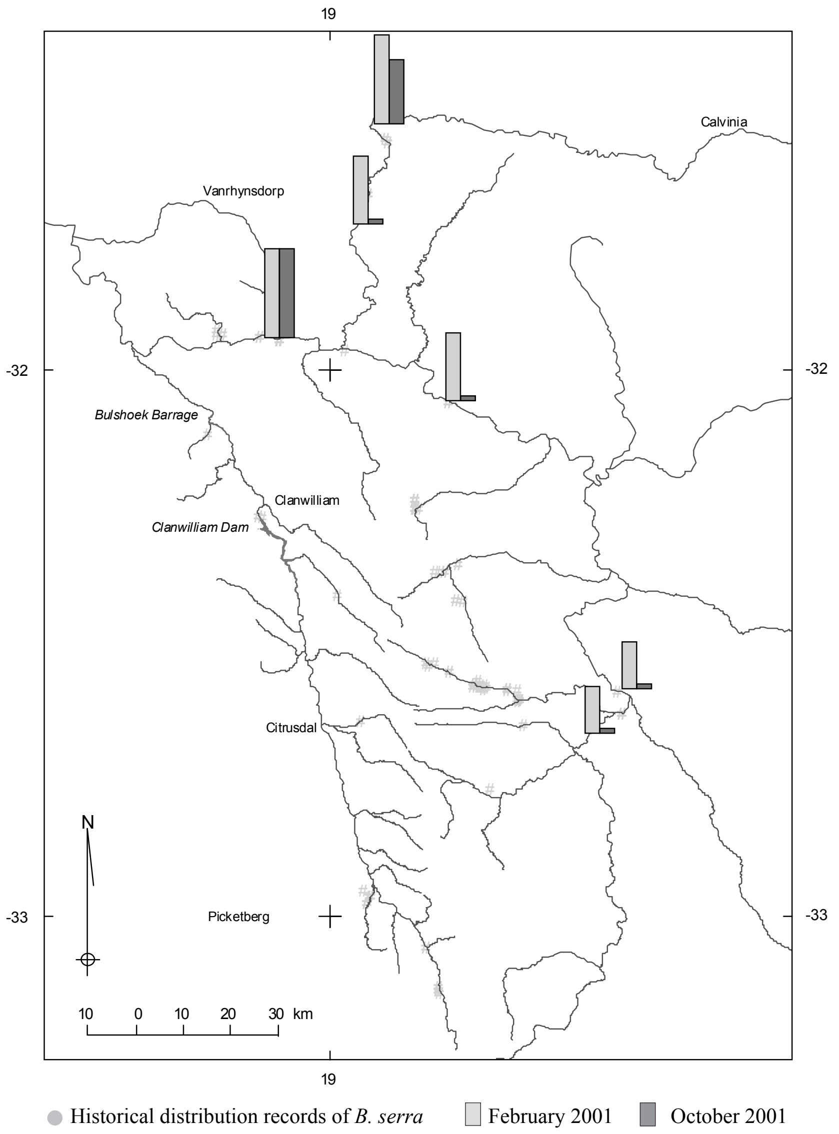
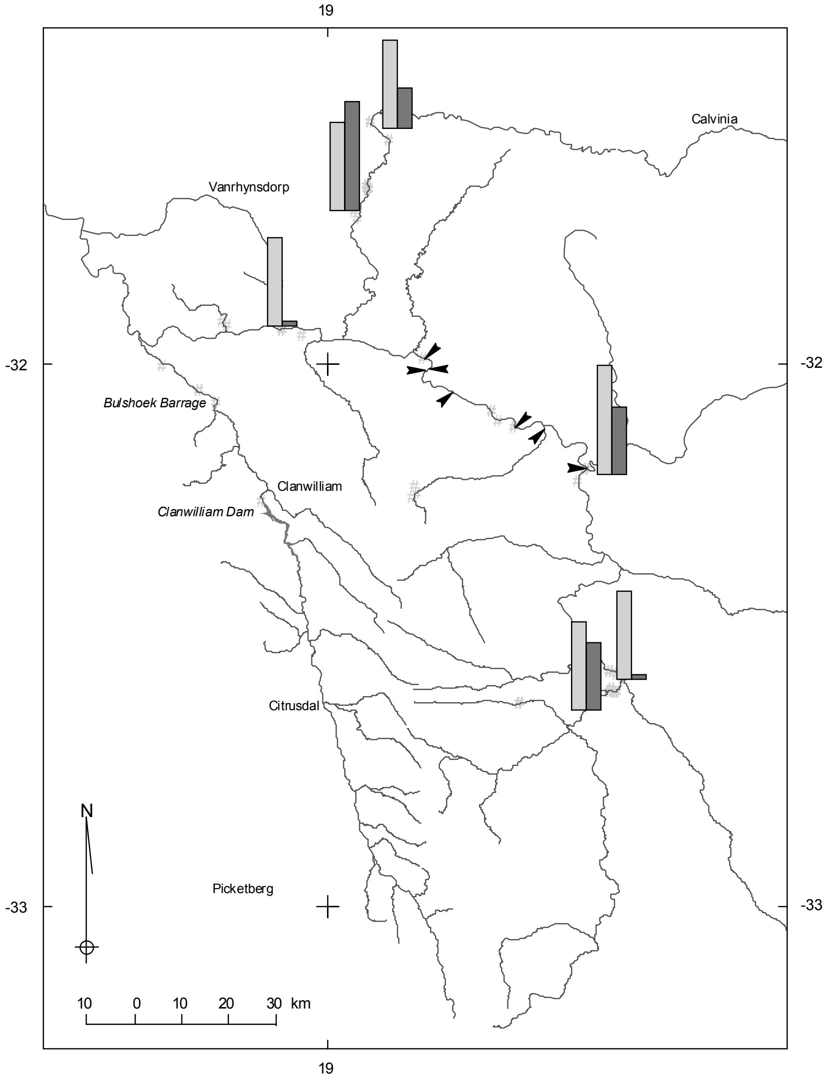


Figure 8.3 Olifants and Doring Rivers showing the distribution records for the sawfin *B. serra* compiled from historical records and surveys conducted in 2001 and 2002. Histograms represent the RAIs calculated for the 2001 surveys.

capensis were recorded from these places in October. The highest RAIs during October were obtained from the middle reaches of the Doring River between the confluence of the Kransgat River and the weir at Aspoort. During October 2002 a dive survey conducted in the uppermost headwaters of the Olifants River revealed large numbers (between 8 and 15 fish per 100 m transect) of adult *L. capensis* at sites 1, 2 and 3 (Figure 8.1). These numbers appeared to be fairly consistent along the 15 km stretch of river. Numerous larvae and juveniles were also observed in the shallows in these reaches. Quantitative estimates of abundance could not be made due to time constraints, however, the concentrations of *L. capensis* in this area are believed to be the greater than anywhere else in the catchment.



● Historical distribution records of *L. seeberi* ☐ February 2001 ■ October 2001

Arrows indicate sites from which larval *L. seeberi* were collected in 2002.

Figure 8.4 Olifants and Doring Rivers showing the distribution records for the sandfish *L. seeberi* compiled from historical records and surveys conducted in 2001 and 2002. Histograms represent the RAIs calculated for the 2001 surveys.

B. serra (Figure 8.3) – While historical records show *B. serra* as occurring in rivers throughout the Olifants-Doring catchment, it has been reported far less frequently than *L. capensis*. *B. serra* has been recorded on a number of occasion in the Ratels River, on the upper Olifants River, and the Driehoeks River, flowing off the eastern flanks of the Cederberg mountains. RAIs calculated for the 2001 surveys suggest that *B. serra* occur throughout the Doring River, but may be more abundant in the river below the confluence of the Koebee River where high *cpue* values were recorded in February and October 2001. Large numbers of *B. serra* <350 mm TL were recorded from the Oorlogskloof River on both sampling occasions – no fish of this size were recorded in the mainstem. A single school of 30-40 adult *B. serra* were observed during a dive transect in the upper Olifants River (Site 2 Figure 8.1) during October 2002.

Labeo seeberi (Figure 8.4) – Historical distribution records of *L. seeberi* suggest that this fish may have the most limited distribution range of all three species, being largely confined to the mainstem of the Doring River. A single *L. seeberi* (Figure 8.4) was recorded in 1958 downstream of the Clanwilliam Dam, the remaining records on the mainstem of the Olifants River downstream of the Bulshoek Barrage date from the early 1980s and are the only records of *L. seeberi* anywhere in the Olifants River catchment, apart from Harrison's (1963) mention of their presence at Keerom in 1938 (Site 4 Figure 8.1). No *L. seeberi* were recorded anywhere in the Olifants River during the 2001 surveys. Large numbers of fish were caught in the Koebee River (Site 11), in the Doring River near the confluence of the Bos River (Site 18) and at De Mond in during both February and October 2001. No fish were recorded from Ou Drif (Site 10) or Aspoort (Site 21) during October 2001, whereas large numbers were caught at these sites in February 2001.

8.4.2. Spawning and reproductive development

During February 2001 gonads in all three species *L. capensis* were in varying stages of development, between I and IV, although no milt or eggs could be stripped from live fish. During October however, *L. capensis* and *B. serra* individuals were in an advanced stage of reproductive development and milt and eggs could be stripped from most individuals. Six *L. seeberi* collected for biological examination from De Mond on the Groot River, the Doring River at the confluence with the Bos River and the Koebee River during October 2001 were all spent (Stage VII).

During a survey of the lower Doring River in October 2002, *L. seeberi* larvae were collected from shallow (<0.015m) littoral habitat below riffles at a number of sites between the confluence of the Biedouw River and the Kransgat River (Figure 8.4). No *L. seeberi* were collected from below the Kransgat River where numerous bass larvae were caught or observed in eddies of bedrock runs between the Kransgat River an the confluence Melkboom (Site 8) on the Doring River. Larvae of *L. capensis* were collected from below the Clanwilliam Dam.

8.5. DISCUSSION

8.5.1. Abundance and distribution

The present investigation substantiates earlier statements that the numbers of endemic cyprinids in the Olifants and Doring Rivers and their tributaries have declined, and that the distribution ranges of these populations have diminished over the last 70 years. Despite the fact that invasive fish species have spread throughout both river systems (Paxton *et al.* 2002), there are greater numbers of endemic fish remaining in the relatively undeveloped Doring than in the Olifants River, suggesting that water-resource development and utilisation have contributed significantly to the decline of the native species in the Olifants River.

The tributaries of the Olifants River, in particular, the Ratels, Noordhoeks and Rondegat Rivers, as well as the mainstem of the Olifants River upstream of the most intensive agricultural development (in the vicinity of Site 4 Figure 8.1) provide partial refuge for breeding populations of Clanwilliam yellowfish and sawfin. Late summer and spring surveys in the Olifants River during 2001, revealed no indigenous juvenile fish, and only one adult Clanwilliam yellowfish at the head of the Citrusdal valley on the farm Keerom (Site 4) where Harrison (1963) had, in 1938, reported large numbers of adult and juvenile yellowfish, sawfin and sandfish. During the 2001 survey, only smallmouth bass and bluegill sunfish were observed in these reaches during dive transects, caught in nets, or angled. Young adult sawfin (200-300 mm TL) were found in the upper Olifants (Sites 1, 2, 3) and Ratels Rivers, as well as the tributaries of the Doring River, notably the Driehoeks and Oorlogskloof Rivers (Site 12). All these sites are above the upper limit of bass invasion (Paxton *et al.* 2002). Low *cpue* values for large adult sawfin in the mainstem of both rivers suggest that this species is particularly rare.

The apparent absence of Clanwilliam sandfish from the Olifants River cannot be accounted for, unless the habitat conditions in this river were initially marginal for this species which favours slow flowing water over a sandy or muddy substratum for feeding (Skelton 1998). These conditions are scarce in the Olifants River, but are prevalent in the Koebee and the lower reaches of the Doring River, particularly downstream of the mouth of the Bos River (Site 18) from which regular inputs of eroded shales and mudstones are contributed from the Karoo. Large numbers of Clanwilliam sandfish were caught here during the 2001 surveys. The higher turbidity in these reaches may also afford larvae and juveniles optical refuge from predation by bass and bluegill sunfish.

8.5.2. Spawning and environmental cues

The only Clanwilliam yellowfish larvae encountered during the 2002 surveys were in a cobble-bed riffle downstream of the Clanwilliam Dam, confirming that spawning by a population between this dam and the Bulshoek Barrage continues to take place. The mainstem and tributaries of the Doring River from and including the Biedouw River, to Doringbos, appear to provide important spawning habitat for Clanwilliam sandfish. Larvae in the mainstem of the Doring River downstream of the confluence of the Biedouw River (Site 14) to the Kransgat River (Site 16) in September 2002, indicated that spawning by this species had occurred within days of the survey. All larvae were approximately the same size (7-10 mm TL), suggesting that the spawning events had been synchronised to some degree, despite the fact that the sites were spread over some 35 km of river.

All larvae were found in slow flowing, shallow littoral habitat (<0.15 m deep) at the base of cobble-bed riffles in the mainstem. The use of littoral areas and slackwaters as nursery habitat by fish larvae during their early stages of development, followed by an ontogenetic habitat shift towards deeper waters as they develop, has been well documented in many other rivers around the world (Schiemer and Spindler 1989; Copp 1992; Rincón *et al*. 1992). In the reaches downstream of the Kransgat River, Clanwilliam sandfish larvae were replaced by bass larvae (*Micropterus* spp.). This may in some way be related to the fact that the sand-bed pools and cobble-bed riffles prevalent downstream of the Biedouw River give way to bedrock pools, rapids and runs in the former region. Bass larvae were found schooling in deeper water (> 0.8 m) in eddies downstream of the rapids in these reaches.

The relationship between flow and spawning of the large endemic fish in the catchment remains unclear. Investigations into the relationship between experimental releases from the Clanwilliam Dam and spawning by Clanwilliam yellowfish populations (King *et al*. 1998) suggested that a minimum temperature of 19 °C was necessary for spawning to take place. Yellowfish moved away from the spawning beds when cold (16 – 18 °C) hypolimnetic baseflows were released. Back-calculation of larval development suggested that spawning had taken place when warm 21 – 23 °C water was spilling over the dam (King *et al*. 1998), however, due to the inability to control for both temperature and flow, findings linking flow to spawning events were inconclusive.

Most South African freshwater fish fauna occur in summer rainfall regions, where spawning appears to be triggered by summer high-flow events (Allanson and Jackson 1983). Rainfall in the Western Cape is driven by frontal systems in winter, with peak flows coinciding with low temperatures. Van Rensburg (1966) found that the gonad mass of Clanwilliam yellowfish began increasing from late winter to early spring (August to September), reaching a peak between early spring and mid summer (October to December), before declining in late summer (January). Thus fish in the Olifants and Doring Rivers, Western Cape, are unique in South Africa in that they spawn at the onset of, as well as during, the low-flow season. From October onwards there are very few peak-flow events, and by December, these would have ceased altogether. It appears unlikely, therefore, that the fish would depend on flow to trigger spawning if the prospect of flow-related cues in the form of spates is negligible.

Contrary to other models which suggest that small spates increase recruitment, (e.g. the ‘flood recruitment model’, Harris and Gehrke 1994; Colorado pikeminnow *Ptychocheitus lucius*, Nesler *et al*. 1988), Humphries *et al*. (1999) report that high spring flows cause poor year classes of golden perch *Macquaria ambigua* and silver perch *Nemadactylus macropterus* in the Murray River. Humphries *et al*. (1999) have proposed the ‘low flow recruitment’ hypothesis to account for this. During the low-flow period, zooplankton production and prey concentrations increase as the temperature rises, water volumes decrease, and the residence time of water in pools increases. They suggest that low flow spawning by certain species has therefore evolved to coincide with optimal conditions for larvae and juvenile feeding. If the magnitude of the flows is too high, or floods are released too frequently, they may reduce recruitment by disrupting littoral food webs and washing larvae from slackwaters. In the absence of a clearer understanding of the role which peak flows play in triggering spawning, and the role which littoral habitat plays in the development of young, the risk of releasing environmental flows to 'trigger spawning', becomes apparent.

Other authors have suggested that the relationship between flow and temperature for triggering spawning may possibly be more complex than was previously thought, particularly for cyprinids. On the basis of extensive research into the migratory and spawning behaviour of Colorado pikeminnow, Nesler *et al.* 1988 propose 'flow cue' hypothesis. In this hypothesis they suggest a complex sequences of environmental cues which ultimately result in successful spawning: increased flow and warmer water temperatures in summer stimulate gonad development and migratory behaviour; olfactory stimuli from water-quality changes and groundwater seepage with which they had been imprinted aid the fish in locating spawning grounds; the fish aggregate in pools near the spawning sites and finally, a spike in the baseline flow provides the cue for ovulation and spawning. Should such a peak in flow not occur, an increase in water temperature to 20-22 °C may provide the stimulus. Nesler *et al.*'s (1988) study therefore supports Northcote's (1984) suggestion that there may be a hierarchy of environmental factors which stimulate migratory and spawning behaviours. It would be unwise to make recommendations on the flow and passage requirements of the endemic fish of the Olifants and Doring Rivers until empirical data on their recruitment patterns, migratory and spawning behaviour (which would provide evidence for or against any one of the above hypotheses) becomes available.

8.5.3. Migration and dispersal

Extremely low numbers of the larger endemic cyprinids below the Bulshoek weir may be explained by the shortage of suitable spawning habitat in these reaches – a situation which is believed to be the result of habitat degradation through flow regulation by the dams and the fact they are no longer able to reach upstream spawning sites. An additional factor which may be contributing towards the elimination of populations in these reaches is that the dams act as barriers to downstream dispersal of larvae and juveniles. Larvae, spawned by upstream populations, occurring either in tributaries or the mainstem, and washed into the dams are likely to suffer severe predation from the predators (mainly bass) which occur in both impoundments in large numbers. Instream habitat in the mainstem of the Olifants River between Citrusdal and the Clanwilliam Dam has been severely degraded by intensive run-of-river abstraction for citrus orchards. These reaches would presumably have served as important recruitment areas for downstream populations.

It is not clear why the predominant size of cyprinids in the upper reaches of tributaries such as the Ratels River (sawfin and Clanwilliam yellowfish), Oorlogskloof River (sawfin and Clanwilliam sandfish), and headwaters of the Olifants River (sawfin and Clanwilliam yellowfish) is <300 mm TL. Fish of this size class were not found in the middle and lower mainstem of both the Olifants and Doring Rivers (the possibility that these patterns may be an artefact of gear selectivity cannot be ruled out, although the fact that the same sampling protocols were applied in both areas makes this unlikely). Four hypotheses are proposed to explain this size-related habitat segregation: (1) adults migrate from the mainstem during spring and spawn in the tributaries, the offspring remain in the headwaters until they reach a certain size threshold (~250 – 300 mm TL), before migrating into the mainstem to feed, grow and reproduce; (2) the populations in the tributaries are largely self-sustaining – there is no migration by large adult fish into the tributary systems and limited downstream dispersal of juveniles and sub-adults, tributary populations are therefore sustained by young or growth-limited adults; (3) juveniles which were spawned in the mainstem or lower tributary reaches migrate into the upper tributary reaches to feed and grow before moving back into the mainstem; (4) any combination of the above scenarios, i.e. tributary populations are supported by young adults and are supplemented by migration into the tributaries by large adults and/or juveniles.

Clanwilliam sandfish are known to spawn in the mainstem of the Doring River as well as the Biedouw River (Paxton *et al.* 2002). In addition, examination of two Clanwilliam sandfish between 200-300 mm TL in the Oorlogskloof River during October 2001 revealed that they were ripe and running (Stage VI). Thus there is some evidence to suggest that (4) above may be the most likely scenario. This still does not explain the absence of a juvenile and sub-adult cohort in the mainstem, however, unless high predation pressure from bass and blue gill sunfish severely curtails recruitment here – especially during the low-flow season when larvae and juveniles in the lower Doring River become concentrated in ever-shrinking pools with large numbers of these predators. The observed size-class distributions may be natural, however. Schlosser (1991) lists several studies that have shown that small fish are found predominantly in shallow upstream or littoral habitats, whereas large fish are found more frequently in downstream, mid-channel habitats. These scenarios will have different implications for water-resource planning and conservation actions. No further confirmation will be forthcoming until specific studies are targeted at understanding patterns of juvenile dispersal and the effects of predation by introduced fish in the mainstem and tributaries of both rivers.

The flow regime of the Doring River from downstream of Aspoort to the confluence with the Olifants River is characterised by extreme seasonal variation, with flow ceasing for approximately five months of the year (December to May). During this time fish populations are restricted to isolated pools of between 100-300 m in length and 1.5-3 m in depth. Once passage becomes possible between the pools after flows recommence in May, the fish are likely to re-disperse through the system. Mediterranean rivers in the south of Portugal exhibit a similar hydrological regime. The biota in these rivers is subjected to alternating lotic and lentic conditions during the year as the river is reduced to a series of isolated pools during low flow periods (Bernado and Alves 1999). Several endemic rheophilous cyprinids, which depend on cobble-bed riffles for spawning occur, in these rivers. Following recharge of the river, the fish recolonise the system from downstream to upstream, or from pools in the same stream, or from third and/or fourth order streams to first and/or second order streams. It appears likely that fish in the Olifants and Doring Rivers undergo similar movements. The lower *cpue* values for all species (x: 0.01), and hence lower densities of fish per pool, recorded during October 2001 when the river was flowing, compared with *cpue* values for February (x: 0.05), supports this assumption. More intensive sampling over several years would be required to determine whether these patterns are a consequence of re-dispersal, or whether directional shifts in the distribution of a large sector of the population are indicative of migratory behaviour.

The exact timing of the movement is unknown. Re-dispersal through the river following reconnection of isolated pools in early winter may be delayed until the spring while the fish wait out the high winter flows in deep pools. Active or passive movement into lower reaches during winter high flows is also conceivable (Northcote 1978). If this does occur there may be a danger of a net downstream displacement of fish populations, as fish washed downstream, or which actively swim over weirs and dams during winter high flows, are unable to regain access to upstream reaches when the these structures become impassable as flows subside in early spring.

There are three artificial structures on the Doring River that are likely to limit movement by fish species between river reaches for a considerable portion of the year: two gauging weirs at Melkboom, near the confluence with the Doring river (E2H003), and at Aspoort (E2H002), and a large farm dam (>5m in height) at Brakfontein (indicated by the dam symbol at site 20 in Figure 8.1). A road culvert downstream of De Mond (Site 22) may also obstruct fish movement during low flows. Whether these structures present complete obstacles to migration depends on the hydrological conditions in the river at the time of migration. It would appear, however, that upstream migration during the spawning period past these structures is unlikely.

8.5.4. Conclusion

The combined impacts of invasion by introduced fish and water-resource development have profoundly changed the populations of endemic fish in the Olifants and Doring Rivers. In the Olifants River recruitment declined as a result of impoundments obstructing access to spawning habitat, while run-of-river abstractions and flow regulation would have depressed the overall capacity of this river to support fish by reducing the absolute volume of water in the river. The lentic conditions immediately upstream, and the modified hydrological regime downstream of the impoundments would have favoured the proliferation of invasive fish, changed sediment dynamics and inundated or degraded critical egg, larval spawning habitat for indigenous fish. While the Doring River appears to have provided some refuge for remaining populations of endemic cyprinids, reports by farmers indicate that numbers have declined significantly in this river as well. Apart from the uppermost reaches of the tributaries, smallmouth bass and bluegill sunfish are present in large numbers throughout the system. While anthropogenic change in the Doring River is not negligible (two gauging weirs, a culvert, the Brakfontein Dam and agricultural activity in the Kouebokkeveld for instance) the impact is not likely to have been as severe as it has been in the Olifants River – access to spawning habitat, certainly for the Clanwilliam sandfish, is still possible. This is unlikely to continue to be the case if a large dam is built in the lower reaches of the Doring River. The impact of the present instream barriers in the Doring River should not be underestimated since they are likely to limit fish movement for a significant, and most likely critical, portion of the year. Fish passage facilities on these structures therefore need to be considered.

Presently there are not enough data to provide accurate and reliable information to guide managers or conservation authorities with regards to the flow or passage requirements of endemic fish populations in this catchment. It is also not possible to predict what the long-term effects of further water-resource developments on these populations might be – further erosion of existing populations would be a certainty, but its extent and severity depends on the nature and location of the development and a more detailed understanding on catchment-scale processes, particularly the relationship between mainstem and tributary populations, the importance of flow and temperature as cues for migration and spawning, and the importance of flows during the reproductive period for larval drift and habitat.

9. LITERATURE CITED

Agostinho, A.A.; Gomes, L.C.; Fernandez, D.R.; and H.I. Suzuki. 2002. Efficiency of fish ladders for neotropical ichthyofauna. *River Research and Applications*. 18. 3: 299-306.

Alexander, W.J.R. 1985. Hydrology of the Southern Hemisphere land masses. *Hydrobiologia*. 125: 75-83.

Allan, J.D.; Erickson, D.L. and J. Fay. 1997. The influence of catchment land use on stream integrity across multiple spatial scales. *Freshwater Biology*. 37: 149-161.

Allanson, B.R. and P.B.N. Jackson. 1983. Limnology and fisheries potential of Lake le Roux. *South African National Scientific Programmes Report No. 77*. 182 p.

Andrews, E.D. 1983. Preservation of aquatic habitat in the Green River, Utah – a regulated sand and gravel-bed river. *American Geophysical Union*. 64 (45): 702.

Archer, E.; Crowl, T. A. and M. Trammell. 2000. Abundance of age-0 native fish species and nursery habitat quality and availability in the San Juan River New Mexico, Colorado, and Utah. State of Utah Department of Natural Resources. Division of Wildlife Resources - Native Aquatic Species. *Publication Number 00-9*.

Baras, E. and M.C. Lucas. 2001. Impacts of man's modifications of river hydrology on the migration of freshwater fishes: a mechanistic perspective. *Ecohydrology and Hydrobiology*. 1 (3): 291-304.

Bayley, P.B. 1995. Understanding large river-floodplain ecosystems. *Bioscience*. 45 (3): 153-158.

Begon, M.; Harper, J.L. and C.R. Townsend. 1996. *Ecology: individuals, populations and communities*. Third Edition. Blackwell Science. 1068 p.

Bell, M.C. 1986. Fisheries handbook of engineering requirements and biological criteria. *Fish Passage Development and Evaluation Programme*. US Army Corps of Engineers. Portland, Oregon. 290 p.

Bernacsek, G.M. 1984. Dam design and operation to optimize fish production in impounded river basins. CIFA Technical Paper No. 11. FAO, Rome. 98 p.

Bernacsek, G.M. 2001. Environmental issues, capacity and information base for management of fisheries affected by dams. *In*: Marmulla, G. Dams, fish and fisheries. Opportunities, challenges and conflict resolution. *FAO Fisheries Technical Paper No. 419*. Rome, FAO. Pp. 139-166.

Bernado, J. M.; Alves, M. H. 1999. New perspectives for ecological flow determination in semi-arid regions: a preliminary approach. *Regulated Rivers: Research and Management*. 15: 221-229.

Bills, R. 1999. Biology and conservation status of the Clanwilliam rock catfish and spotted rock catfish. *WWF Investigational Report No. 60*. 54 p.

Blumm, M.C.; Lucas, L.J.; Miller, D.B.; Rohlf, D.J. and G.H. Spain. 1998. Saving Snake River water and salmon simultaneously: the biological, economic, and legal case for breaching the Lower Snake

River dams, lowering John Day Reservoir, and restoring natural river flows. *Environmental Law*. 28 (4): 997-1054.

Bok, A. 2001. Review of fishways in South Africa: are they effective and what needs to be done to improve fish passage? Anton Bok and Associates. *Water Research Commission Report No. 1270*. Water Research Commission. Pretoria. 27 p.

Borghetti, J.R. Nogueira, V.S.; Borghetti, N.R. & C. Canzi. 1994. The fish ladder at the Itaipu binational hydroelectric complex on the Parana River, Brazil. *Regulated Rivers: Research and Management*. 9: 127-130.

Bovee, K.D. 1982. A Guide to Stream Habitat Analysis Using the Instream Flow Incremental Methodology. U.S. Fish and Wildlife Service. *Instream Flow Information Paper No. 12. FWS/OBS-82/26*. 274 pp.

Bovee, K.D. and R. Milhous. 1978. Hydraulic simulation in instream flow studies: theory and techniques. Ft. Collins (CO): Office of Biolgical Services, US Fish and Wildlife Service. *Instream Flow Information Paper No. 5. FWS/OBS-78/33*.

Breen, C.M.; Cox, D.; Dickens, C.; Mackay, H.; Mander, M.; Roux, D.J.; Turton, A. and E. van Wyk. 2003. Strategic review of river research. *Water Research Commission Report No. 1198/1/03*. Water Research Commission. Pretoria. 116 pp.

Brooks, T.H. 1950. Flypaste fishing on the Olifants River. *Piscator*. 13: 27-32.

Brussock, P.P. & A.V. Brown. 1991. Riffle-pool geomorphology disrupts longitudinal patterns of stream benthos. *Hydrobiologia*. 220: 109-117.

Bye, V. J. 1984. The role of environmental factors in the timing of reproductive cycles. *Fish reproduction: strategies and tactics*. Academic Press. London. 187-205 pp.

Cambray, J. A. 1990. Adaptive significance of a longitudinal migration by juvenile freshwater fish in the Gamtoos River system. *South African Journal of Science*. 20: 148-156.

Cambray, J. A.; King, J. A. and C. Bruwer. 1997. Reproduction behaviour and early development of the Clanwilliam yellowfish (*Barbus capensis*: Cyprinidae), linked to experimental dam releases in the olifants River, South Africa. *Regulated Rivers: Research and Management*. 13: 579-602.

Cambray, J.A. 1984. Fish populations in the middle and lower Orange River, with special reference to the effects of stream regulation. *Journal of the Limnological Society of South Africa*. 10 (2): 37-49.

Clarkson, R.W. and M.R. Childs. 2000. Temperature effects of hypolimnial-release dams on early life stages of Colorado River Basin big-river fishes. *Copeia*. 2: 402-412.

Copp, G.H. 1990. Experimental design in fluvial ichthyology: getting the most for your money. Freshwater Biological Association 58th Annual Report. Ambleside (UK). 68-87pp.

Copp, G.H. 1992. Comparative microhabitat use of cyprinid larvae and juveniles in a lotic floodplain channel. *Environmental Biology of Fish*. 33: 181-193

Crook, D.A. and P. Humphries. (in press). Problems with translating ecological results into messages for management, with an example of fish movement in Australian rivers.

Cushing, D.H. 1990. Plankton production and year class strength in fish populations: an update of the match/mismatch hypothesis. *Advances in Marine Biology*. 26: 249-293

Dahle, G.; Rahman, M. and A.G. Eriksen. 1997. RAPD fingerprinting used for discriminating among three populations of Hilsa shad (Tenualosa ilisha). *Fisheries Research*. 32: 263-269.

Dauble, D.D. and D.R. Geist. 2000. Comparison of mainstem spawning habitats for two populations of fall chinook salmon in the Columbia River Basin. *Regulated Rivers: Research and Management*. 16: 345-361.

Dauble, D.D.; Hanrahan, T.; Geist, D.; Parsely, M.; Sheer, M. and K. Tiffan. 2001. Impacts of the Columbia River hydroelectric system on mainstream riverine processes and salmon habitats. *American Fisheries Society Annual Meeting*. 131: 75. Abstracts from the 131st Annual Meeting of the American Fisheries Society: 2001 - a Fisheries Odyssey, the Journey of Science and Education Continues, Phoenix, Arizona, 19-23 August 2001.

Davies, B.R. and J.A. Day 1998. *Vanishing Waters*. University of Cape Town Press. Cape Town. 487 pp.

De Moor, I.J. 1996. Case studies of the exotic species by four alien fish species (*Cyprinus carpio*, *Micropterus salmoides*, *Oreochromis macrochir* and *O. mossambicus*) of freshwater ecosystems in Southern Africa. *Transactions of the Royal Society of South Africa*. 51 233-255.

Department of Water Affairs and Forestry (DWAF) 2002. *National Water Resource Strategy*. Proposed first edition. Pp. 132.

Department of Water Affairs and Forestry (DWAF). 1999. Resource Directed Measures for Protection of Water Resources. Volume 3: River Ecosystems. Version 1.0, Pretoria. Appendix 2: Stream Classification.

Durham, D.W. and G.R. Wilde. 2001. Influence of stream discharge levels on production of larval fishes in the Canadian River, Texas. *American Fisheries Society Annual Meeting*. 131: 108. Abstracts from the 131st Annual Meeting of the American Fisheries Society: 2001 - a Fisheries Odyssey, the Journey of Science and Education Continues, Phoenix, Arizona, 19-23 August 2001.

Elliot, J.M. 1985. Population dynamics of migratory trout, *Salmo trutta*, ina Lake District stream, 1966-83. and their implications for fisheries management. *Journal of Fish Biology*. 27 (Suppl. A): 35-43.

Erkinaro, J; Julkunen, M. and E. Niemela. 1998. Migration of juvenile Atlantic salmon *Salmo salar* in small tributaries of the subarctic River Teno, northern Finland. *Aquaculture*. 168: 105-119.

Fausch, K.D. and M.K. Young. 1995. Evolutionary Significant Units and movement of resident stream fishes: a cautionary tale. *American Fisheries Society Symposium*. 17: 360-370.

Fausch, K.D.; Taniguchi, Y.; Nakano, S.; Grossman, G.D. and C.R. Townsend. 2001. Flood disturbance regimes influence rainbow trout invasion success among five Holarctic regions. *Ecological Applications*. 11 (5): 1438-1455.

Frissell C.A.; Liss W.J.; Warren C.E. and M.D. Hurley. 1986. A hierarchical framework for stream classification: viewing streams in a watershed context. *Environmental Management* 10: 199 - 214.

Froese, R. and D. Pauly. Editors. 2003. FishBase. World Wide Web electronic publication. www.fishbase.org. version 24. September 2003.

Gaigher, C.M. 1973. *Die status van inheemse vis in die Olifantsrivier*. Cape Department of Nature and Environmental Conservation Report.

Gehrke, P.C. and J.H. Harris. 2001. Regional-scale effects of flow regulation on lowland riverine fish communities in New South Wales, Australia. *Regulated Rivers Research and Management*. 17: 369-391.

Gerking, S.D. 1959. The restricted movement of fish populations. *Biological Review*. 34: 221-242.

Gore, J. A. King J. M.; K. C. D Hamman. 1991. Application of the instream flow incremental methodology to Southern African rivers: protecting endemic fish of the Olifants River. *Water SA*. 17: 225-236.

Gowan, C.M.K.; Young, K.D.; Fausch and S.C. Riley. 1994. Restricted movement in resident stream salmonids: a paradigm lost? *Canadian Journal of Fisheries and Aquatic Sciences*. 51: 2626-2637.

Grossman, G.D.; Hill, J. and J.T. Petty. 1995. Observations on habitat structure, population regulation, and habitat use with respect to Evolutionary Significant Units: a landscape perspective for lotic systems. *American Fisheries Society Symposium*. 17: 381-391.

Halvorsen, M.; Jorgensen, L. and P.-A. Amundsen. 1997. Habitat utilization of juvenile Atlantic salmon (*Salmo salar* L.), brown trout (*Salmo trutta* L.) and Arctic charr (*Salvelinus alpinus* L.) in two lakes in northern Norway. *Ecology of Freshwater Fish*. 6 (2): 67-77.

Hansen, M.M.; Kenchington, E. and E.E. Nielsen. 2001. Assigning individual fish to populations using microsatellite DNA markers. *Fish and Fisheries*. 2. 93-112.

Harden Jones, F.R. 1968. *Fish Migration*. Edward Arnold Publishers. London. 325 p.

Harris, J.H. and P.C. Gehrke. 1994. Modelling the relationship between streamflow and population recruitment to manage freshwater fisheries. *Australian Fisheries*. 6: 28-30.

Harrison, A.C. 1963. The Olifants/Doorn River system and its fishing. *Piscator.* 98: 25-28.

Harrison, A.C. 1976. The early transactions of the Cape Piscatorial Society. Part IV. *Piscator*. 98: 118-123.

Hartmann, J. 1983. Two feeding strategies of young fishes. *Archiv für Hydrobiologie*. 96: 496-509.

Hatfield, T. and J. Bruce. 2000. Predicting Salmonid Habitat-Flow Relationships for Streams from Western North America. *North American Journal of Fisheries Management.* 20 (4): 1005-1015.

Hildrew, A.G. and P.S. Giller. 1992. Patchiness, species interactions and disturbance in the stream benthos. Chap 2. *In*: Giller, P.S.; Hildrew, A.G. and D.G. Raffaelli (eds). *Aquatic biology: scale, pattern and process*.. Blackwell Science. Oxford. Pp. 21-62.

Hilton-Taylor, C. 2000 (Compiler). 2000. IUCN Red List of Threatened Species. IUCN - The World Conservation Union. 61p.

Howard, G. 1998. *Water resources evaluation: hydrology*. Olifants and Doring River Basin Study. Report prepared by BKS (Pty) Ltd in association with Ninham Shand (Pty) Ltd for the Department of Water Affairs and Forestry. *DWAF Report No. PE00/00/0398*.

Humphries, P.; King, A.J. and J.D. Khoen. 1999. Fish, flows and flood plains: links between freshwater fishes and their environment in the Murray-Darling River system, Australia. *Environmental Biology of Fishes*. 56: 129-151.

Ikonen, E. 1984. Migratory fish stocks and fishery management in regulated Finnish rivers flowing into the Baltic Sea. In: Lillehammer, A.;Saltveit, S.J. (eds.). *Regululated Rivers*. Pp. 437-451.

Impson, N.D. 1999. Fish distribution in the Western Cape's upper Doring River and its implications for river management and flyfishing. *Piscator*. 131: 86-92.

Jackson, D.C. and G. Marjulla. 2001. The Influence of dams on river fisheries. *In:* Marmulla, G. (ed.). Dams, fish and fisheries: opportunities, challenges and conflict resolution. *FOA Fisheries Technical Paper No. 419*. Rome. FAO. Pp. 1-44.

Jackson, P. B. N. 1989. Prediction of regulation effects on natural biological rhythms in south-central African freshwater fish. *Regulated Rivers: Research and Management*. 3: 205-220.

Jager, H.I.; Chandler, J.A.; Lepla, K.B. and W. van Winkle. 2001. A theoretical study of river fragmentation by dams and its effect on white sturgeon populations. *Environmental Biology of Fishes*. 60: 347-361.

Jewitt, G.P.W. and A.H.M Görgens. 2000. Scale and model interfaces in the context of integrated water resources management for the rivers of the Kruger National Park. *Water Research Commission. Report No. 627/1/00*. Water Research Commission, Pretoria. 184 pp.

Jewitt, G.P.W.; Heritage, G.L.; Weeks, D.C.; Mackenzie, J.A.; van Niekerk, A.; Görgens, A.H.M.; O'Keeffe, J.; Rogers, K. and H. Horn. 1998. Modelling abiotic-biotic links in the Sabie River. *Water Research Commission Report No. 777/1/98*. Water Research Commission, Pretoria. 157 pp.

Jury, M.R. 2003. The coherent variability of African river flows: composite climate structure and the Atlantic circulation. *Water SA*. 29 (1): 1-10.

Karr, J.R. 1991. Biological integrity: a long-neglected aspect of water resource management. *Ecological Applications*. 1: 66-84.

King, J.M. and R.E. Tharme. 1993. Assessment of the Instream Flow Incremental Methodology and initial development of alternative Instream Flow Methodogies for South Africa. *Water Research Commission Report No. 295/1/94*. Water Research Commission, Pretoria. 590 pp.

King, J.M., Brown, C.A. and Sabet, H. 2003. A scenario-based holistic approach to environmental flow assessments for rivers. *Rivers Research and Application*. 19 (5-6): 619-639.

King, J.M.; Cambray, J. A. and N.D. Impson. 1998. Linked effects of dam-released floods and water temperature on reproduction of the Clanwilliam yellowfish *Barbus capensis*. *Hydrobiologia*. 384: 245-265.

King, J.M.; Tharme, R.E. and M. de Villiers. 2000. Environmental Flow Assessments for Rivers: Manual for the Building Block Methodology. *Water Research Commission Report TT131/00*. Water Research Commission, Pretoria. 339pp.

King, J.M.; Tharme, R.E.; and C.A. Brown. 2000. Definition and Implementation of Instream flows. Prepared for Thematic Review II.1: Dams, ecosystem functions and environmental restoration. *World Commission on Dams Report*. 87 pp.

Kocik, J.F. and C. Paola Ferreri. 1998. Juvenile production variation in salmonids: population dynamics, habitat, and the role of spatial relationships. *Canadian Journal of Aquatic Science*. 55 (Suppl. 1): 191-200.

Larinier, M. 2000. Dams and fish migration. Prepared for Thematic Review II.1: Dams, ecosystem functions and environmental restoration. *World Commission on Dams Report*. 26 pp.

Larinier, M. 2001. Environmental Issues, dams and fish migration. *In*: Marmulla, G. (ed). Dams, fish and fisheries. Opportunities, challenges and conflict resolution. *FAO Fisheries Technical Paper: No. 419*. Rome, FAO. 45-89 pp.

Larson, G.L.; Moore, S.E. and B. Carter. 1995. Ebb and flow of encroachment by non-native rainbow trout in a small stream in the southern Appalachian mountains. *Transactions of the American Fisheries Society*. 124: 613-622.

Levin, R.H. 1992. The problem of pattern and scale in biology. *Ecology*. 73 (6): 1943-1967.

Ligon, F.K.; Dietrich, W.E. and W.J. Trush. 1995. Downstream ecological effects of dams. *Bioscience*. 45 (3): 183-192.

Linløkken, A. 1993. Efficiency of fishways and impact of dams on the migration of grayling and brown trout in the Glomma River system, south-eastern Norway. *Regul. Rivers: Res. Mgmt*. 8: 145-153.

Lucas, M.C. and E. Baras. 2000. Methods for studying spatial behaviour of freshwater fishes in the natural environment. *Fish and Fisheries*. 1(4): 283-316.

Lucas, M.C. and E. Batley. 1996 Seasonal movements and behaviour of adult barbel Barbus barbus, a riverine cyprinid fish: Implications for river management. *Journal of applied ecology*. 33 (6): 1345-1358.

Lucas, M.C. and P.A. Frear. 1997. Effects of a flow-gauging weir on the migratory behaviour of adult barbel, a riverine cyprinid. *Journal of Fish Biology*. 50: 382-396.

Mark, W.; Wieser, W. and C. Hohenauer. 1989. Interactions between developmental processes, growth and food selection in the larvae and juveniles of *Rutilus rutilus* (L.) (Cyprinidae). *Oecologia*. 78: 330-337.

Marmulla, G. (ed). 2001. Dams, fish and fisheries. Opportunities, challenges and conflict resolution. *FAO Fisheries Technical Paper: No. 419*. Rome, FAO. 116 p.

Meffe, G.K. 1984. Effects of abiotic disturbance on coexistence of predator-prey fish species. *Ecology*. 65 (5): 1525-1534.

Merron, G.S.; Bruton, M.N. and P. la Hausse de Lalouviere. 1993. Implications of water release from the Pongolapoort Dam for the fish and fishery of the Phongolo floodplain, Zululand. *South African Journal of Aquatic Science*. 19: 34-39.

Meyer, S.R. 1974. *Die gebruik van vislere in die bestudering van migrasiegewoontes van vis in Transvaalse riviersisteme*. MSc Thesis. Rand Afrikaans University. South Africa.

Mills, C.A. 1981. The Attachment of Dace, *Leuciscus leuciscus* L., Eggs to the Spawning Substratum and the Influence of Changes in Water Current on Their Survival. *Journal of Fish Biology*. 19 (2): 129-134.

Miranda, L.E. 2001. A review of guidance and criteria for managing reservoirs and associated riverine environments to benefit fish and fisheries. *In*: Marmulla, G. (ed). Dams, fish and fisheries. Opportunities, challenges and conflict resolution. *FAO Fisheries Technical Paper: No. 419*. Rome, FAO. 91-137 pp.

Modde, T. and D.B. Irving. 1998. Use of multiple sites and seasonal movement by razorback suckers in the middle Green River, Utah. *North American Journal of Fisheries Management*. 18: 318-326.

Montgomery, D. R.; Buffington, J. M.; Peterson, N. P.; Schuett-Hames, D.; Quinn, T. P. 1996. Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. *Canadian Journal of Fisheries and Aquatic Sciences*. 53 (5): 1061-1070.

Moyle, P.B. and D.M. Baltz. 1985. Microhabitat use by an assemblage of California stream fishes: Developing criteria for instream flow determinations. *Transactions of the American Fisheries Society.* 114 (5): 695-704.

Nakamura, S.; Mizuno, N.; Tamai, N. and R. Ishida. 1991. An investigation of environmental improvements for fish production in developed Japanese rivers. *In*: Colt, J.;White, R.J. (eds.).*American Fisheries Society Symposium*. 10: 32-41. Fisheries Bioengineering Symposium.

Nesler, T.P. 2000. Recovery of the Colorado River endangered fishes. Biological recovery goals and criteria for Colorado pikeminnow, humback chub, razorback sucker and bonytail. A proposal for downlisting and delisting. San Juan River Basin Recovery Implementation Program, US Fish and Wildlife Service, Albuquerque, NM.

Nesler, T.P.; Muth, R.T. and A.F. Wasowicz. 1988. Evidence for baseline flow spikes as spawning cues for Colorado squawfish in the Yampa River, Colorado. *American Fisheries Society Symposium*. 5: 68-79.

Newcombe, C. 1981. A procedure to estimate changes in fish populations caused by changes in stream discharge. *Transactions of the American Fisheries Society*. 110: 382-390.

Northcote, T.G. 1978. Migratory strategies and production in freshwater fishes. In: *The biology of freshwater fish production*. Pp. 326-359. Gerking, S.D. (ed.). Blackwell Scientific Publications. Oxford. 520 pp.

Northcote, T.G. 1984. Mechanisms of fish migration in rivers. *In*: J.D. McCleave, G.P. Arnold, J.J. Dodson and W.H. Neill (eds.). *Mechanisms of migration in fishes*. Plenum Press. New York. Pp. 317-355

Paxton, B.R.; Clark, B.M. and C.A. Brown. 2002. An assessment of the effects of habitat degradation and exotic fish species invasions on the distribution of three endemic cyprinids: *Barbus capensis*, *Barbus serra* and *Labeo seeberi* in the Olifants and Doring Rivers, Western Cape. Report prepared for Department of Water Affairs and Forestry by Southern Waters Ecological Research and Consulting cc. *DWAF Report No. PB E000-00-1302*. 53 pp.

Poff, N.L. and J. David Allan. 1995. Functional organisation of stream fish assemblages in relation to hydrological variability. *Ecology*. 6 (2): 606-627.

Poff, N.L.; Allan J.D.; Bain, M. B.; Karr, J.R.; Prestegaard, K.L.; Richter, B.D.; Sparks, R.E. and C. Stromberg. 1997. The natural flow regime. *Bioscience*. 47 (11): 769-784.

Pollard, S.R. 2000. Defining flow to protect instream biota: a critique of the instream flow incremental methodology and the development of a hierarchical habitat-based approach, using the pennant-tailed catlet, *Chiloglanis anoterus* in the Marite River, South Africa. PhD Thesis. University of Cape Town. Cape Town. South Africa.

Pringle, C.M.; Naiman, R.J.; Bretschko, G.; Karr, J.R.; Oswood, M.W.; Webster, J.R.; Welcomme, R.L. and M.J. Winterbourn. 1988. Patch dynamics in lotic systems: the stream as a mosaic. *Journal of the North American Benthological Society*. 7 (4): 503-524.

Raffaelli, D.G.; Hildrew, A.G. and P.S. Giller. 1992. Scale, pattern and process in aquatic ecosystems: concluding remarks. Chap 21. Pp. 601-606. In: *Aquatic biology: scale, pattern and process*. Giller, P.S.; Hildrew, A.G. and D.G. Raffaelli (eds). Blackwell Science. Oxford.

Rahman, M. 2002. *The Story of The Hilsa Shad*. virtualbangladesh.com/ilish.html.

Raymond, H.L. 1979. Effects of dams and impoundments on migrations of juvenile chinook salmon and steelhead from the Snake River, 1966 to 1975. *Transactions of the American Fisheries Society.* 108 (6): 505-529.

Reimers, P.E. 1973. The length of residence of juvenile fall chinook salmon in the Sixes River, Oregon. *Research Reports of the Fish Commission of Oregon*. 4 (2). Portland.

Reiser, D.W. and R.G. White. 1990. Effects of streamflow reduction on chinook salmon egg incubation and fry quality. *Rivers*. 1 (2): 110-118.

Revenga, C.; Brunner, J.; Henniger, N.; Kassem, K. and R. Payne. 2000. Pilot analysis of global ecosystems (PAGE): freshwater systems. World Resources Institute. Washington D.C. 65 p.

Reynolds, L.F. 1983. Migration patterns of five fish species in the Murray-Darling River system. *Australian Journal of Marine and Freshwater Research*. 34 (6): 857-871.

Richards, C.; Haro, R.J.; Johnson, L.B. and G.E. Host. 1997. Catchment and reach-scale properties as indicators of macroinvertebrate species traits. *Freshwater Biology*. 37: 219-230.

Rincón, P.A.; Barrachina, P.; Bernat, Y. 1992. Microhabitat use by 0+ juvenile cyprinids during summer in a Mediterranean river. *Archiv für Hydrobiologie*. 125 (3): 323-337.

Rivinoja, P.; McKinnell, S. and H. Lundqvist. 2001. Hindrances to upstream migration of Atlantic salmon (*Salmo salar*) in a northern Swedish river caused by a hydroelectric power-station. *Regul. Rivers: Res. Mgmt*. 17: 101-115.

Robinson, A.T.; Clarkson, R.W. and R.E. Forrest. 1998. Dispersal of larval fishes in a regulated river tributary. *Transactions of the American Fisheries Society*. 127: 772-786.

Rodriguez-Ruiz, A. and C. Granado-Lorencio. 1992. Spawning period and migration of three species of cyprinids in a stream with Mediterranean regimen (SW Spain). *Journal of fish biology*. 41 (4): 545-556.

Roff, D.A. 1988. The evolution of migration and some life history parameters in marine fishes. *Environmental Biology of Fishes*. 22 (2): 133-146.

Roth, D. 1952. A remarkable bag of smallmouth bass from the Olifants River, Clanwilliam. *Piscator*. 6: 68.

Rowntree, K.M. and R.A. Wadeson. 1999. A hierarchical geomorphological model for the classification of selected South African Rivers. *Water Research Commission Report*. No. 497/1/99. Water Research Commission. Pretoria. 334 pp.

Ryden, D.W. 2000. *Adult fish community monitoring on the San Juan River, 1991-1997*. Final Report. San Juan River Basin Recovery Implementation Program. United States Fish and Wildlife Service. Albuquerque, NM. 269 pp.

Salo, J. 1990. External processes influencing origin and maintenance of inland water-land ecotones. In: *The Ecology and Management of Aquatic-Terrestrial Ecotones*. R.J. Naiman and H. Décamps (eds.). Man and the Biosphere Series Vol. 4. UNESCO. Parthenon Publishing. France.

Scheidegger, K.J. and M.B. Bain. 1995. Larval fish distribution and microhabitat use in free-flowing and regulated rivers. *Copeia*. 1: 125-135.

Schiemer, F. and T. Spindler. 1989. Endangered fish species of the Danube River in Austria. *Regulated Rivers: Research and Management*. 4 (4): 397-407.

Schlosser, I.J. 1991. Stream fish biology: a landscape perspective. *Bioscience*. 41: 704-712.

Schlosser, I.J. and P.L. Angermeier. 1995. Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and the implications for conservation. *American Fisheries Society Symposium*. 17: 392-401.

Schulze, R.; Meigh, J.; Horan, M. 2001. Present and potential future vulnerability of eastern and southern Africa's hydrology and water resources. *South African Journal of Science*. 97: 150-160.

Scott, H.A. 1982. The Olifants System - unique habitat for rare Cape fishes Cape Department of Nature and Environmental Conservation. *Cape Conservation Series 2*.

Skelton, P. H. 1998. Our most threatened fish - the Clanwilliam sandfish, *Labeo seeberi*. South African Fishkeeping and Aquarium News. 3: 32.

Skelton, P. H. Cambray J. A.; Lombard, A.; Benn, G. A. 1995. Patterns of distribution and conservation status of freshwater fishes in South Africa. *African Journal of Zoology*. 30: 71-81.

Skelton, P.H. 2002. An overview of the challenges of conserving freshwater fishes in South Africa. *In*: Collares-Pereira, M.J.; Cowx, I.G. and M.M. Coelho (eds.). *Conservation of freshwater fishes: options for the future*. Blackwell Science. 21-236 pp.

Skelton, P.H. and G.I. Cowan. 1999. Fish. In: *Biota of South African Wetlands in relating to the Ramsar Convention*. Chap 7. Cowan, G.I. (ed.) Pp. 51-56.

Soulsby, C.; Malcolm, L.A. and A.F. Youngson. 2001. Hydrochemistry of the hyporheic zone in salmon reproduction gravels: a preliminary assessment in a degraded stream. *Regulated Rivers: Research and Management*. 17: 561-665.

Southwood, T.R.E. 1988. Tactics, strategies and templets. *Oikos*. 52 (1): 3-18.

Sparks, R.E. 1995. Need for ecosystem management of large rivers and their floodplains. *Bioscience*. 45 (3): 168-182.

Stanford, J.A.; Ward, J.V.; Liss, W.J.; Frissel, C.A.; Williams, R.N.; Lichatowich, J.A. and C.C. Coutant. 1996. A general protocol for restoration of regulated rivers. *Regulated Rivers: Research and Management*. 12: 391-413.

Tómasson, T.; Bruton, M.N. and K.C.D. Hamman. 1985. The demography and management of large cyprinids in a reservoir on the Orange River, South Africa. *Fisheries Research*. 3 (4): 279-308.

Townsend, C.R. and A.G. Hildrew. 1994. Species traits in relation to habitat templet for river systems. *Freshwater Biology*. 31: 265-275.

Valdez, R.A. and Holden, P.B. Hardy, T.B. 1990. Habitat suitability index curves for humpback chub of the Upper Colorado River Basin. *Rivers*. 1 (1): 31-42.

van Rensburg, K.J. 1966 *Die vis van die Olifantsrivier (Weskus) met speciale verwysing na die geelvis Barbus capensis en saagvis Barbus serra* Dept. Natuurbewaring, Prov. Admin., Kaap die Gooie Hoop.

Vannote, R.L.; Minshall, G.W.; Cummins, K.W.; Sedell, J.R. and C.E. Cushing. 1980. The River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Science*. 37: 130-137.

Walker, K.F. and M.C. Thoms. 1993. Environmental effects of flow regulation on the lower River Murray, Australia. *Regulated Rivers: Research and Management*. 8: 103-119.

Ward, D.L.; Boyce, R.R.; Young, F.R.; Olney, F.E. 1997. A review and assessment of transportation studies for juvenile chinook salmon in the Snake River. *North American Journal of Fisheries Management*. 17 (3): 652-662.

Ward, J.V. & Stanford, J.A. 1983a. The serial discontinuity concept of lotic ecosystems. *In*: . Fontaine, T.D. and S.M. Bartell (eds.). *Dynamics of Lotic Ecosystems*. Ann Arbor Science. Pp. 30-42.

Ward, J.V. and J.A. Stanford. 1983b. The intermediate-disturbance hypothesis: an explanation for biotic diversity patterns in lotic ecosystems. *In*: Fontaine, T.D. and S.M. Bartell (eds.). *Dynamics of lotic ecosystems*. Ann Arbor Science: 347-356.

Webb, R.H. 2001. The Colorado River: an overview of historical changes in riverine and aquatic habitat. *American Fisheries Society Annual Meeting*; Vol. 131, pp. 131-132. Abstracts from the 131st Annual Meeting of the American Fisheries Society: 2001 - a Fisheries Odyssey, the Journey of Science and Education Continues, Phoenix, Arizona, 19-23 August 2001.

Weeks, D.C.; O'Keeffe, J.H.; Fourie, A. and B.R. Davies. 1996. A pre-impoundment study of the Sabie-Sand River system, Mpumalanga with special reference to predicted impacts on the Kruger National Park. Vol. 1. *Water Research Commission Report No. 294/1/96*. 261 p.

Welcomme, R.L. 1985. River Fisheries. FAO Fish. Tech. Pap. No. 262. FAO, Rome. 330 p.

Wiley, M.J.; Kohler, S.L. and P.W. Seelbach. 1997. Reconciling landscape and local views of aquatic communities: lessons from Michigan trout streams. *Freshwater Biology*. 37: 133-148.

Williams, J.G. 1998. Fish passage in the Columbia River, USA and its tributaries: problems and solutions. In: *Fish Migration and Fish Bypasses*. Jungwirth, M.; Schmutz, S.; Weiss, S. (eds.). Fishing News Books. Pp. 180-192.

Wootton, R.J. 1990. *The ecology of teleost fishes*. T.J. Press. Cornwall. 404 pp.

World Commission on Dams (WCD). 2000. *Orange River Development Project, South Africa*. Case study prepared as an input to the World Commission on Dams. Cape Town. www.dams.org.

Zhong, Y. and G. Power. 1996. Environmental impacts of hydroelectric projects on fish resources in China. *Regulated Rivers: Research and Management*. 17: 81-98.

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Prioritization of South African Estuaries based on their potential importance to estuarine-associated fish species

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The National Water Act of 1998 ensures that estuaries are regarded as a water resource, and are therefore subject to legislation regarding water resources. Consequently, the monitoring of estuarine water quality and quantity is important to maintain a desired level of structure and function within an aquatic ecosystem. Because biological communities are regarded as an integral component of the estuarine water resource, the prioritization of potential conservation areas are often necessary for the successful determination of aquatic reserve sites. This exercise, referred to as the 'Fish Importance Rating' (FIR), aims to prioritize South African estuaries in terms of their importance to estuarine-associated fish species. The FIR complements similar procedures undertaken for botanical and waterbird communities.

The FIR is based on a scoring system of seven criteria that are considered to reflect the importance of estuaries to estuarine-associated ichthyofauna. Scores are allocated to criteria, where factors that influence the estuarine fish community positively are allocated higher scores than those that influence fish communities negatively. Allocated scores within each criterion are subjected to various weighing factors, after which the products are added to generate a fish-based estuarine hierarchy.

This prioritization exercise presents a ranking of South African estuarine systems based on their importance to estuarine-associated fish species, and aims to facilitate the identification of South African estuaries with a high conservation priority, by placing all South African systems in a regional and national context.

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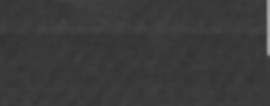

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