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THE INFLUENCE OF HYDRAULICS, HYDROLOGY AND TEMPERATURE ON THE DISTRIBUTION, HABITAT USE AND RECRUITMENT OF THREATENED CYPRINIDS IN A WESTERN CAPE RIVER, SOUTH AFRICA

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Submitted in fulfilment of the requirements for the degree of
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ABSTRACT

This study aims to explore the relationships between river flow and fish ecology in the context of the riverscape model of river ecosystems by examining the seasonal distribution of two endangered fish species, i.e. the Clanwilliam yellowfish and Clanwilliam sawfin, in relation to their physical (structural) and hydraulic habitat requirements at several scales, and to assess the importance temporal changes in flow and temperature in relation to the timing of key life history events and recruitment. From these findings it aims to recommend water management strategies to ensure the persistence of remaining populations, as well as to suggest a way forward for fish habitat studies in South Africa. The study was conducted on the Driehoeks River, a tributary of the Doring River system, which rises in the Cederberg mountains of the Western Cape, South Africa. A 5.9 km segment of this river was selected for the study.

Seasonal variations in the relative abundances and distribution of larval, juvenile and adult sawfin along the longitudinal profile of the study segment were investigated prior to, during and after the spring spawning period (November to January) and these variations were interrogated in terms of the spatial arrangement of physical habitat units within the segment. Dive surveys served to identify the location and extent of critical reproductive and nursery habitats, as well as to characterise the dispersal and/or movement of larval and juvenile fish to nursery habitats following the spawning season.

Habitat Suitability Criteria (HSC) were used to describe the hydraulic (velocity and depth) as well as substratum habitat use by Clanwilliam yellowfish and sawfin. The study included habitats deemed most limiting to fish production, i.e. those used for foraging, early life stages and reproduction. The suitability of a two-dimensional hydraulic modelling programme (River2D) for simulating habitat of the Clanwilliam yellowfish and sawfin was investigated. HSC derived for Clanwilliam yellowfish and sawfin were combined with the simulated depths and velocities generated by River2D and measured substratum particle sizes to produce Combined Suitability Indices (CSIs). To evaluate the consequences of alternative flows on habitat availability, Weighted Usable Area (WUA) – an aggregate of the product of the CSI at each node in the model and the area associated with that node (CSI × surface area) – was then calculated for each species and life stage and for each site over a range of discharges. To test the ability of River2D to accurately predict microposition choice by yellowfish and sawfin, the correspondence between observed fish positions and the spatial distribution of the simulated habitat suitabilities was investigated.

The rate of daily increment deposition on otoliths was validated using known-age larvae reared under laboratory conditions and the early development stages of sawfin eggs and larvae were recorded. Age-length relationships for larval and early juvenile sawfin were then established from wild-caught fish. Younger fish could be aged more accurately than older fish (>20 days) since increment spacing was more compressed in older fish. The results of the aging study were used to investigate the influence of environmental conditions,

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particularly flow and water temperature on the spawning and recruitment patterns of sawfin in the Driehoeks River. This was achieved by back-calculating spawning dates using the age-length models developed in the aging study of random samples of fish collected from the Driehoeks River towards the end of the low-flow season in two consecutive years. Since Clanwilliam yellowfish did not spawn over the study period, it was not possible to include them in the study.

The principle findings were that sawfin require access to a broad range of critical habitat units in a river to complete the different stages of their life cycle. Although sawfin used deeper habitats (> 1.2 m) throughout the year, faster-flowing, shallower habitats (< 1.2 m) were only occupied by fish over the spawning period (November to January). It was established that sawfin are non-guarding, open substratum, lithophilic spawners, selecting riffles and runs with loosely embedded cobble substrata, shallower water (0.13-0.36 m). Current speeds measured in spawning habitats were the highest recorded for this species (0.3-0.8 m s^{-1}). Large differences in habitat use were found between larval, juvenile and adult fish.

Sawfin larvae and juveniles lay down increments on their otoliths at a rate of one per day, and the first visible increment is laid down approximately two days post-fertilisation, or upon hatching. Once they hatch larvae attach themselves to the substratum by means of an adhesive pad. Swim-up occurs after a period of 10-13 days when they are washed into downstream slackwaters. Sawfin spawned over a period of roughly 100 days between November and January. Peak recruitment events were associated with temperature of ~19 °C and continuously rising temperatures over seven days or more.

The HSC derived in this study were compared with Flow Classes currently used to describe fish habitat in South Africa. Several points emerged from this comparison: (1) both sawfin and yellowfish use a much smaller subset of the habitat defined by each Flow Class; (2) there are considerable differences between life-stages as well as differences between behaviours (e.g. feeding *vs* spawning) and (3) connectivity between habitat patches is an important consideration. Flow Classes provide a useful alternative to HSC where these are not available. The risk of applying Flow Classes arbitrarily, however, is that habitat may not be perceived by a fish species in exactly the same way leading to reduced availability or elimination of certain critical categories of habitat. There was a discrepancy between the discharges required for optimal spawning habitat as predicted by River2D and the conditions under which the sawfin actually spawned as suggested by spawning-date distributions. These differences serve to highlight the limitations of hydraulic habitat modelling and the value of hydrological information for identifying flows of ecological importance. An over-reliance on instantaneous measures of habitat is therefore not advised.

By examining the seasonal distribution of sawfin in relation to key habitat units and at a range of scales, as well as the timing of life history events in relation to flow and temperature conditions, this study successfully demonstrates that sawfin depend on certain key components of the annual flow and temperature regime and access to a range different habitats through the year – definable at a range of scales – for their successful reproduction and recruitment. The usefulness and importance of placing flow-ecology relationships in the riverscape context is thereby reinforced.

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This thesis is dedicated to my parents Leith and Lynette Paxton whose support and encouragement through my studies has made this all possible

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CHAPTER 1 Background and motivation

1.1 MOTIVATION

It is estimated that up to 54 percent of the earth's accessible runoff has already been appropriated for human use (Postel *et al*. 1996). The last half century has provided abundant evidence that human activities that alter river flow regimes through water abstraction or in-channel physical structures such as weirs and dams modify downstream river ecosystems in many ways (Ligon *et al*. 1995; Berkamp *et al*. 2000; Revenga *et al*. 2000; Rosenberg *et al*. 2000; Marmulla 2001; Bunn and Arthington 2002; Nilsson *et al*. 2005). One of the mostly heavily impacted components of the ecosystem has proved to be downstream fish communities through the loss of habitat (Walker and Thoms 1993; Zhong and Power 1996); disturbance to the riparian zone (Wichert and Rapport 1998); blocking of upstream-downstream migration routes (Larinier 2000); changes in water quality and temperature through hypolimnetic water releases from dams (Holden and Stalnaker 1975; Friedl and Wüest 2002); and elimination or attenuation of the environmental cues they depend on for spawning and/or migration (Nesler *et al*. 1988; Zhong and Power 1996). Alien fish species, usually introduced for sports angling, have constituted another major threat to river fish communities. In many cases alien fish species have out-competed local fish species for one or more resources, or have become active predators of them. These invasions have frequently been facilitated by habitat modification (Moyle and Light 1996). And the combination of these disturbances has lead to the decline or collapse of fish populations in countless rivers worldwide (Revenga *et al*. 2000).

South Africa is no exception to this trend, and the decline of native fish populations and/or subsistence fisheries has been reported for several of its river basins (e.g. Heeg and Breen 1982; Russell and Rogers 1989; Deacon 1994; Skelton *et al*. 1995; De Moor 1996; Paxton *et al*. 2002). This study focuses on the populations of large migratory fish species of one such basin – the Olifants-Doring River Basin, north of Cape Town – where many of the impacts outlined above are apparent. The study focussed on assessing their present status, their movement and habitat requirements, and possible water management strategies for ensuring their persistence into the future.

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1.2 OVERVIEW OF RESEARCH ON THE LARGE-BODIED CYPRINIDS OF THE OLIFANTS-DORING RIVERS

The Olifants-Doring River system in the south-western Cape is a 'hotspot' of freshwater fish diversity in South Africa and a catchment of national and international biogeographic importance (Skelton *et al*. 1995; Impson 1999). Southern Africa has 25 freshwater fish species listed in the IUCN's Red List and a large proportion of these are endemic to the Cape ichthyofaunal region (Skelton *et al*. 1995). The diversity of indigenous freshwater fish assemblages associated with this region is low, with most systems supporting fewer than six species. The Olifants-Doring River system, with ten indigenous species, is therefore a noteworthy exception. Endemism in this system is unusually high, with eight species, namely six barbine cyprinids and two austroglanidid rock catfishes, endemic to the system itself (Table 1.1). The remaining two species (a cyprinid and galaxiid) have wider distribution ranges.

TABLE 1.1 Freshwater fish species that are: endemic to the Olifants-Doring river system, indigenous to the Western Cape and alien (Skelton 1993; IUCN 2006).

Common name	**Scientific name**	**Family**	**Conservation status**	**Comment**
Clanwilliam sawfin	*Barbus serra*	Cyprinidae	endemic/endangered	large, migratory
Clanwilliam yellowfish	*Labeobarbus capensis*	Cyprinidae	endemic/vulnerable	large, migratory
Clanwilliam sandfish	*Labeo seeberi*	Cyprinidae	endemic/critically endangered	large, migratory
Tweerivier redfin	*Barbus erubescens*	Cyprinidae	endemic/critically endangered	small, non-migratory
Fiery redfin	*Pseudobarbus phlegethon*	Cyprinidae	endemic/endangered	small, non-migratory
Clanwilliam redfin	*Barbus calidus*	Cyprinidae	endemic/endangered	small, non-migratory
Chubby-headed barb	*Barbus anoplus*	Cyprinidae	Indigenous/not threatened	small, indigenous to SA
Clanwilliam rock catfish	*Austroglanis gilli*	Austroglanididae	endemic/vulnerable	small, benthic
Spotted rock catfish	*Austroglanis barnardi*	Austroglanididae	endemic/critically endangered	small, benthic
Cape galaxias	*Galaxias zebratus*	Galaxiidae	indigenous/lower risk/near threatened	indigenous Western Cape
Cape Kurper	*Sandelia capensis*	Anabantidae	translocated within Western Cape	indigenous Western Cape
Bluegill sunfish	*Lepomis macrochirus*	Centrarchidae	alien	predator on indigenous fish
Smallmouth bass	*Micropterus dolomieu*	Centrarchidae	alien	predator on indigenous fish
Spotted bass	*Micropterus punctulatus*	Centrarchidae	alien	predator on indigenous fish
Largemouth bass	*Micropterus salmoides*	Centrarchidae	alien	predator on indigenous fish
Banded tilapia	*Tilapia sparrmanii*	Cichlidae	translocated within South Africa	translocated
Mozambique tilapia	*Oreochromis mossambicus*	Cichlidae	translocated within South Africa	translocated
Brown trout	*Salmo trutta*	Salmonidae	alien	predator on indigenous fish
Rainbow trout	*Oncorhynchus mykiss*	Salmonidae	alien	predator on indigenous fish

This translates to between four and seven endemic species per Quarter Degree Square (QDS), in contrast to the remainder of South Africa where no areas with more than three endemic species per QDS have been identified (Skelton *et al*. 1995). Their national significance notwithstanding, a substantial decline in the number of indigenous fish in this system has been reported by ecologists, sports-fishermen and local farmers in the last half of the twentieth century (Gaigher 1973; Scott 1982; Paxton *et al*. 2002).

The intensification of agricultural activity in the Olifants River catchment, which has resulted in alterations to the flow regime, geomorphological degradation of instream habitat, and the introduction of alien invasive fish species, have all been implicated in the decline (Scott 1982). Clanwilliam Dam and, further downstream, Bulshoek Weir, both on the mainstem of the Olifants River, present impassable obstacles to upstream migrating fish, introduce large expanses of lentic conditions in the river and markedly alter the downstream flow regime. Also implicated in the loss of indigenous species is invasion by alien fish species, most importantly largemouth bass *Micropterus salmoides* and smallmouth bass *Micropterus dolomieu,* both introduced into the catchment for sport fishing in the 1930s and 1940s, and bluegill sunfish *Lepomis macrochirus*, introduced later as fodder for the angling species (Roth 1952; Harrison 1977).

Concern about the status of the endemic freshwater fish species of the river system following the introduction of the exotic species was first expressed by Barnard (1943), who conducted a survey of the Olifants River in 1937 and 1938 for his comprehensive work, '*Revision of the Indigenous Freshwater Fishes of the S.W. Cape Region*'. At that time, largemouth bass were well established in the lower Olifants River downstream of Bulshoek Weir following their introduction to the system in 1933. Attempts to introduce largemouth bass to the river upstream of Clanwilliam Dam had only just begun and so their invasion of the upper Olifants River was at an early stage. Substantial populations of indigenous fish still occurred in this section of the river in 1938, with Harrison (1963) reporting large shoals of Clanwilliam sawfin *Barbus serra* and Clanwilliam

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yellowfish *Labeobarbus capensis*[1] in the vicinity of Keerom on the mainstem of the Olifants, as well as numerous juvenile Clanwilliam sandfish and the smaller indigenous minnows.

In 1943, 50 yearling smallmouth bass were introduced to the Jan Dissels River, a tributary of the Olifants downstream of Clanwilliam Dam and, in 1945, a further 1000 fingerlings were introduced to the upper Olifants River at Keerom (Roth 1952). Four years later (1949) observations by Hoehn (1949) and Harrison (1963), at the same site, reveal that smallmouth bass had become well established. Although shoals of Clanwilliam yellowfish were still in evidence, there were numerous bass in close attendance and a noticeable reduction in the numbers of smaller indigenous fish. By 1960, none of the smaller barbine species could be found between Clanwilliam and Citrusdal and smallmouth bass were present in large numbers (Jubb 1961). Anglers also expressed their concerns about the disappearance of numerous shoals of what had been described as ‘a hundred or more’ Clanwilliam yellowfish making their way upstream during the annual spawning runs (Brooks 1950).

The effects of Bulshoek Weir (constructed in 1919) and Clanwilliam Dam (constructed in 1932) as barriers to migration did not go unnoticed. In September of 1938 ‘thousands’ (Harrison 1977: 123) of Clanwilliam sandfish with Clanwilliam yellowfish were seen massed downstream of Bulshoek Weir during the annual spring spawning run – evidence that their continued migration was being thwarted by the barrages.

Other kinds of habitat degradation were also becoming obvious. Harrison (1963: 28) noted that, between Citrusdal and Clanwilliam, the ‘rocky defiles’ and ‘large pools’ used for spawning by Clanwilliam yellowfish and that had previously been rich in indigenous fish species (Barnard 1945), had been blanketed by white sand (Harrison: comments in Jubb 1961). Harrison (1963) attributed the siltation to soil erosion resulting from farming activity in the upper catchment. Additionally, abnormally low water levels in the dry season, with a probable resultant loss of suitable fish habitat, were noted as early as 1949 when Hoehn (1949) reported that much water from the Thee and Noordhoeks tributaries had been drawn off for irrigation before reaching the mainstem of the Olifants River.

Several other ecological investigations have added to understanding of the fish communities of the system. The first survey of what became a regular sampling programme of the fish in the Olifants River was conducted by van Rensburg (1966), who visited sites between Keerom and Bulshoek Weir monthly between 1963 and 1964. He collected a total of 123 Clanwilliam yellowfish and 410 sawfin over this period, indicating that both species were still relatively abundant at this time. Van Rensburg (1966) found that the mean gonad mass of both sawfin and Clanwilliam yellowfish began increasing from July and peaked in October. Sawfin displayed evidence of a slightly earlier peak in September. By January, however, the gonad mass of both species had declined to pre-July levels. He also estimated age-length relationships for these species and conducted dietary analyses, with his main findings being that both species are omnivorous and that the diet of sawfin comprised mainly of insect larvae (primarily Chironimids: 66%), whereas the major component of the Clanwilliam yellowfish diet consisted of plant material (57%), with the remainder being made up of riffle-dwelling insect larvae (40%).

[1] Common names will be used in the main text throughout the document. The common names of both species are currently preceded by ‘Clanwilliam’. To ensure grammatical efficiency, however, ‘Clanwilliam’ will not be used for sawfin, whereas it will used for Clanwilliam yellowfish in most instances to distinguish this species from other yellowfish species in the country.

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By the early 1970s, declines in the abundance of the indigenous fish were becoming increasingly evident. In 1972 Gaigher (1973) sampled fish at eight sites on the Olifants River. During the course of these surveys, no Clanwilliam yellowfish were netted downstream of Bulshoek Weir and only a few fish were caught in the Bulshoek and Clanwilliam reservoirs. Adult Clanwilliam yellowfish and sawfin were present upstream at Keerom, but Gaigher suggested that there had been no recruitment downstream of Keerom and Citrusdal for a number of years. In addition to the presence of large numbers of alien fish species, however, Gaigher (1973) also noted that water resource developments were playing a role in the decline. Thus he cites obstruction to spawning migrations (combined with the extensive harvesting of the fish over this vulnerable period), sedimentation of spawning sites as a result of erosion in the catchment, water abstraction and the failure of winter rains as additional causal factors. Additional surveys in September 1979, March 1980, January 1981 and March 1982 by Cape Nature Conservation (currently Cape Nature) documented the continued decline of indigenous fish populations into the 1980s (Scott 1982).

Studies undertaken in the early and mid-1990s recorded Clanwilliam yellowfish in the mainstem of the Olifants River, both upstream and downstream of Clanwilliam Dam (King and Tharme 1994), although numbers were low. Gore *et al.* (1991) investigated the applicability of the Physical HABitat SIMulation model (PHABSIM) (Bovee 1986) to describe the availability of hydraulic habitat for several indigenous and exotic fish species in the Olifants River including Clanwilliam yellowfish, sawfin and smallmouth bass. The objective of the study was to determine whether, in the absence of exotic fish species, there would be sufficient hydraulic habitat available for indigenous species to recolonise the mainstem of the river. The findings suggested that there was indeed sufficient habitat available and confirmed the views of van Rensburg (1966) that exotic species were the primary factor responsible for the declines. It should be noted, however, that Gore *et al.*'s (1991) study did not include all life-history stages in the assessment of habitat suitability. In particular, the effects on recruitment levels in the mainstem, loss of cobble-bed riffles to siltation, or the absence of adequate hydraulic habitat over the spawning period, were not evaluated.

To partly address the need for data on spawning requirements, Cambray *et al*. (1997) and King *et al*. (1998), investigated the importance of dry-season pulses for triggering the spawning of Clanwilliam yellowfish downstream of Clanwilliam Dam. They arranged for artificial pulses of high flow to be released from Clanwilliam Dam during the late spring of 1993 and 1994 and monitored the response of fish in the downstream river. Spawning areas were confined to riffle habitat characterised by large boulders and cobble with low embeddedness. Fish were seen to move onto spawning beds after the release of the floods. King *et al*. (1998) hypothesised that the fish are brought into spawning condition by increasing temperatures associated with increases in the photoperiod and that a minimum temperature of 19 °C, coupled to summer freshes, would be required to trigger spawning.

In 2001 a survey of the large-bodied endemic cyprinid populations in the Olifants and Doring Rivers was completed as part of a pre-feasibility study of water-resource development options planned for the lower and middle Doring River (Paxton *et al*. 2002). This provided an opportunity to re-assess the status of mainstem fish populations, particularly in the Doring River, which had last been surveyed by the Albany Museum in 1987 and Cape Nature in 1992 (fish collections databases, South African Institute for Aquatic Biodiversity and Albany Museum). A major finding of the 2001 survey was the extremely low numbers of all size classes of endemic fish and the limited distribution ranges of Clanwilliam yellowfish, sawfin and sandfish, as well as the complete absence of fish less than 200 mm TL, signs that would have suggested recruitment of these

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species in the mainstems of both rivers. In contrast, high abundances of alien fish (notably bluegill sunfish and smallmouth bass) were encountered throughout the mainstems of both rivers.

A follow-up study (PGWC 2004) focussing on the lower Doring and Olifants Rivers confirmed that sandfish and sawfin were probably extinct downstream of Bulshoek Weir and that occurrences of Clanwilliam yellowfish were so few that the presence of viable populations was deemed unlikely. Fish surveys that yielded no indigenous fish, and discussions with local farmers and fishermen, suggested that all three species were probably functionally extinct in the lower 100 km of the Olifants, between its confluence with the Doring and the estuary, although a reasonable number of adults of two of the species (Clanwilliam yellowfish and sawfin) persisted in the uppermost reaches of the Olifants River mainstem. This seems to reinforce the view held that river regulation had contributed significantly to the decline of the populations, either directly through reducing suitability of the aquatic environment or indirectly through enhancing suitable conditions for the invasive species. Similar cases, where the combined effects of invasion and river regulation have led to the decline of a species, have been documented in many river systems around the world (Moyle and Light 1996; Bunn and Arthington 2002).

In summary therefore, these recent surveys confirm that Gaigher (1973) had witnessed the more advanced stages of a trend that has seen the complete elimination of two fish species, i.e. the sawfin and Clanwilliam sandfish, and the decline in numbers of a third, i.e. the Clanwilliam yellowfish, from extensive areas of the Olifants River. Low overall abundances combined with the absence of signs of recruitment, suggest that this trend may be continuing in the Doring River. Further plans for water-resource development of the Olifants-Doring system exist and so, therefore, does the possibility of a further decline, perhaps to extinction, of the three large, migratory endemic species. This is because, despite an extensive national water-development infrastructure, there remains a poor understanding of the direct mechanism by which native fish species in South Africa may be impacted by water-resource developments such as those planned (notable exceptions include: Tómasson *et al*. 1984; Cambray 1991; Gore *et al*. 1991; King and Tharme 1994; Cambray *et al*. 1997; King *et al*. 1998; Pollard 2000). Part of their impact is undoubtedly through manipulations of the flow regime, which could affect the fish *inter alia* by changing migration and spawning cues and blocking migration routes to spawning habitat. Input to decision-makers on potential impacts such as these, and possible mitigatory measures, is now required by the National Water Act of 1998. Predictions regarding the potential impacts of flow modification on freshwater ecosystems in South Africa are provided through Ecological Water Requirement (EWR) assessments. The term EWR in this country is preferred to the more commonly used ‘Environmental Flow Requirements’ (EFR) because ‘flow’ does not include water quality aspects, whereas ‘ecological’ distinguishes it from social impacts (Hirschowitz *et al*. 2007). The Brisbane Declaration on Environmental Flows (Brisbane Declaration on Environmental Flows 2007) as the 'quantity, timing and quality of water flows required to sustain freshwater and estuarine ecosystems and the human livelihoods and well-being that depends on these ecosystems'.

The predictions made in the EWR assessments will only be as good as the data and understanding upon which they are based. For predictions that could mean the difference between survival and extinction of native fish species, a better understanding is needed of the life cycles, habitat requirements and movements of the species and how these are linked to the flow regime, channel geometry and the location of key habitats. In 2002 and 2003 further studies were thus completed on the populations in the mainstems of the two rivers, with the objective of providing management guidelines (Paxton 2004a; Paxton 2004b). These showed that abundances

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in the mainstems were too low to provide sufficient data, and that information on habitats and movement would have to be gleaned from headwater reaches of tributaries where invasion and water regulation were minimal and viable, recruiting populations of the indigenous species still existed.

1.3 CONTEXT AND OBJECTIVES OF THE CURRENT STUDY

The focus of the research therefore shifted to a tributary of the Doring River (the Driehoeks River) that supported viable populations of two of the large-bodied endemic fish species of interest – the Clanwilliam yellowfish and the sawfin. The laboratory and fieldwork for the research reported on in this document began in March 2004 and ended in November 2007 (APPENDIX A.1). The study was conducted on a 5.9 km segment of the Driehoeks River that met all of the criteria for the study: (1) it supported recruiting populations of the two target species; (2) the river was accessible by vehicle along most of its length and was negotiable by dive teams; and (3) although largemouth bass *Micropterus salmoides* occurred there, they were not present in large numbers.

During the course of the study, it was determined that abundances of Clanwilliam yellowfish were much lower than sawfin in the river, no spawning events were observed and no eggs were collected. In addition, the juvenile population was small and none were under 2-3 years of age. Therefore, although hydraulic habitat for Clanwilliam yellowfish juveniles and adults are described and analysed in Chapter 5 and 6, the bulk of the document deals with the distribution, early life history and spawning of sawfin.

As stated in Section 1.1, the motivation for this study was the need for information on the target species that could be used in EWR studies. The problem was addressed using three approaches: (1) examining the seasonal distribution of fish; (2) modelling instream habitat and (3) relating spawning frequency and early life history to the timing of flow events. The three primary objectives, with their respective subsidiary objectives therefore were:

OBJECTIVE 1: Habitat use: seasonal distribution patterns

(i) Ascertain the abundance and distribution sawfin throughout a continuous river segment over the course of the migration and spawning seasons and infer patterns of movement and dispersal by different life stages in order to establish the importance of connectivity between the different habitat patches identified in Objective (2). ***Chapter 4.***

OBJECTIVE 2: Habitat use: hydraulic habitat

(i) Identify, describe and quantify the critical (i.e. spawning, feeding, nursery) hydraulic habitats used by sawfin and Clanwilliam yellowfish in the Driehoeks River. ***Chapter 5***

(ii) Use the information from (i) to develop habitat suitability curves and then test the curves in a two-dimensional hydraulic model of river flow (River2D – derived in a related WRC study K5/1508 "Ecohydraulic Modelling in River Systems"). ***Chapter 6***

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OBJECTIVE 3: Spawning and early life history

(i) Determine age-length relationships for wild caught and captive bred juvenile 0^+ sawfin using daily growth increments on otoliths in order to develop spawning date frequencies for application in Chapter 8. ***Chapter 7***

(ii) Use the spawning date frequencies in Chapter 7 to investigate the timing, duration and frequency of spawning by sawfin and identify potential environmental stimuli (i.e. discharge and/or temperature) that may be required to cue spawning. ***Chapter 8***

The last two objectives address the influence of flow on fish from two somewhat different perspectives; the first (Objective 2) addresses the spatial availability of habitat, while the second (Objective 3) addresses the importance of temporal variation in flow. Objective 2 adopts a habitat simulation approach that has its origins in the Physical HABitat SIMulation (PHABSIM) model (Bovee 1982; Milhous *et al*. 1989) – the modelling component of the Instream Flow Incremental Methodology (IFIM; Bovee 1982).

It may be appropriate at the outset of this study to state that it is not the intention of the current study to endorse the use of habitat simulation approaches for setting environmental flow objectives. Neither is it the intention of this study to present alternative methodologies to those already in use. Rather, by providing quantitative information on fish response to flow, the information presented here is meant as the biological input to the methodologies currently in use in South Africa (e.g. DRIFT; King *et al*. 2004). It is argued in Section 2.3 that habitat simulation, particularly two-dimensional hydraulic models, is one of the most effective means of achieving this. This study therefore is essentially an answer to Arthington *et al*.'s (2003: 58) call that holistic methodologies be improved 'by applying a wider range of quantitative techniques to relate flow alterations to ecological responses and by integrating models that facilitate prediction of the responses of river ecosystems to flow change'.

Habitat simulation approaches have their limitations and a much broader approach has been adopted here following from Gore and Nestler's (1988: 94) assertion that hydraulic habitat simulation studies were never intended as a 'replacement for population studies, a replacement for basic research into the subtleties of fish or benthic ecology, nor a replacement for biological innovation or common sense'. Objectives 1 and 2 therefore address this broader ecological context: fish spawning ecology and early life history, the extent and distribution of critical habitat units and the seasonal distribution of the population.

1.4 LAYOUT OF REPORT

Following this introduction, Chapter 2 provides an overview of the main theoretical concepts relevant to this study. This overview provides an in-depth rationale for the various approaches used in each of Chapters 4-8. The introduction at the beginning of Chapters 4-8 will then revisit some of the issues addressed in Chapter 2, but apply them more specifically to the context of the chapter. Chapter 3 describes the study area. Chapters 4-8 present the body of research as outlined under each of the objectives above. Chapters 4, 5 and 6 address the spatial component of the study, i.e. fish habitat use at intermediate (Chapter 4) and microhabitat (Chapters 5 and 6) scales, whereas Chapter 7 (aging juvenile sawfin) provides the lead-up to Chapter 8. These latter two chapters address the temporal component of the study – the timing of life history events in relation to

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environmental variability. Chapter 9 draws together the main findings of the study and suggests directions for further research and Chapter 10 presents management and conservation recommendations.

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CHAPTER 2 Shifting paradigms: scale, pattern and process in the ecology of river fish

2.1 INTRODUCTION

Informing and underlying each component of the study are a number of theoretical and management frameworks that have provided the methodological bases and rationales for this research. This chapter introduces some of these frameworks and explains how they were used.

The first objective of this study (Section 1.3) addresses the seasonal distribution patterns of sawfin in the Driehoeks River. Thus the focus is on landscape and river segment (intermediate) scale processes that could yield information on interannual patterns of migration and dispersal. Some of the most significant paradigms that have informed research into the spatial dimensions of river fish population dynamics have been Schlosser's (1991) dynamic landscape model of river fish ecology and Fausch *et al.*'s (2002) concept of the 'riverscape'. **Section 2.2** of this chapter introduces Schlosser's model and discusses some of the thinking that has stemmed from it.

The second objective of this study was to define use of hydraulic habitat by sawfin and Clanwilliam yellowfish at the microhabitat scale. Few methodologies have been as pervasive or influential in this regard as habitat simulation approaches, in particular the PHABSIM model (Bovee 1982; Milhous *et al.* 1989). **Section 2.3** of this chapter introduces this methodology, together with other related methodologies that have been applied in South Africa. The section addresses the advantages and disadvantages of habitat simulation approaches to managing river flows and discusses some of the problems that can result from incorrect data collection and misinterpretation.

The third objective of this study was to investigate the temporal aspect of spawning by sawfin, i.e. its timing, duration and frequency, in relation to environmental variability, in particular, river flow and temperature. In **Section 2.4**, some basic concepts regarding fish life history in relation to a river's flow regime are discussed and the key ecological theories that have provided the backdrop for these types of investigations are introduced.

2.2 THE RIVERSCAPE PERSPECTIVE: A FRAMEWORK FOR EXAMINING THE SPATIAL DYNAMICS OF FRESHWATER FISH POPULATIONS

Integrating the principles of landscape ecology (Forman and Godron 1981; Forman 1983) into river ecosystem theory represented a critical juncture in the study and management of river fish populations. Several key papers were responsible for paving the way. The first was Frissel *et al.*'s (1986) application of hierarchy theory to the structure of river systems. Frissel *et al.* suggested that the spatial, abiotic components of river systems can be hierarchically structured into successively smaller nested units ranging in scale from the catchment to segment, reach, morphological unit, and microhabitat. Because the hierarchy is nested, each level is influenced by the level below it and constrained by the level above it. Hildrew and Giller (1992)

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introduced a temporal dimension to this hierarchical model and linked it to the spatio-temporal scaling of fluvial landscapes described by Salo (1990). In their model, fluvial processes acting over a range of spatio-temporal scales create a hierarchy of landforms that have corresponding persistence times related to the frequency of disturbance events. For example, landscape features at the catchment scale (kilometres) may be shaped by processes such as climate change and plate tectonics and operate on scales of geological eras. Reach characteristics (tens of metres) may shaped by disturbance events with a recurrence period of decades, whereas microhabitat conditions (centimetres to meters) may be controlled by hourly, monthly or seasonal variations in flow. Concurrent to the development of these hierarchic models, Pringle *et al*. (1988) proposed a 'patch dynamics' model for river ecosystems, that incorporated many of the concepts from landscape ecology that were being developed at the time. Pringle *et al*. (1988) saw rivers as heterogeneous mosaics of habitat patches and stressed the significance of their arrangement, juxtaposition and connectivity for maintaining ecosystem function.

Identifying appropriate scales of study and management emerged as one of the pivotal issues in the debate surrounding the integration of landscape and aquatic ecology (Wiens 2002). River fish research in the 1980s had begun focussing increasingly at the reach and microhabitat scales (10^2 – 10^{-1} m) in order address the detrimental impacts of flow modification and habitat degradation downstream of dams (Section 2.3). A number of workers (Schlosser 1991; Schlosser 1995; Schlosser and Angermeier 1995; Fausch *et al*. 2002, Durance *et al*. 2006), however, felt that these studies were failing to provide managers with a complete understanding of the response of fish populations to anthropogenic disturbances, because fish population demographics were often affected by processes that were only detectable at much larger scales (Fausch *et al*. 2002). These workers therefore embraced the shift toward landscape ecology with its emphasis on scale-dependent patterns and processes. The proponents of the landscape approach called for studies to focus on larger, intermediate landscape, or river segment scales (10^3-10^5 m) (Fausch *et al*. 2002; Durance *et al*. 2006). It was these scales, they argued, that were critical for the survival of river fish populations and at these scales that land-use practises were impacting fish populations (Schlosser 1995).

Schlosser (1991, 1995) and Schlosser and Angermeier (1995) were among the first to elucidate the linkages between landscape and river fish ecology. It is widely acknowledged that fish habitat use varies according to species (e.g. Roper *et al*. 1994); life stage (Sabo and Orth 1994; Rosenberger and Angermeier 2003) and behaviour, e.g. spawning or feeding (Armstrong *et al*. 2003). Habitat use is therefore a dynamic rather than static process (Schlosser 1991; Heggenes 1996) and the distribution of species and life stages can be linked to the spatial and temporal scaling of physical landforms and processes in catchments (i.e. Frissel *et al*.'s hierarchical model). Schlosser (1991, 1995) and Schlosser and Angermeier's (1995) dynamic landscape model therefore encompassed these considerations and focussed on three interrelated themes: the structural relationships among landscape elements, the functional interactions between them (flows of water, organic matter, nutrients and species) and the changes induced by anthropogenic activities.

By calling attention to the spatial arrangement of different habitat units and the importance of movement and/or dispersal by fish between them, Schlosser (1991) echoed Pringle *et al*.'s (1988) emphasis on connectivity between patches. Apart from being an important biological link between habitat elements, fish movement is also an adaptive response to enhance growth, survival and abundance in an environment where resources are patchily distributed (Harden Jones 1968, Northcote 1978).

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Landsborough Thompson (cited in Harden Jones 1968), identified three major forms of movement: (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. Schlosser's dynamic landscape model of river fish ecology addresses local movements, which are related to foraging activities in habitats favourable to growth, longer distance migrations between feeding habitats and spawning habitats, and migrations between winter or summer refugia from flow or temperature extremes (Figure 2.1).

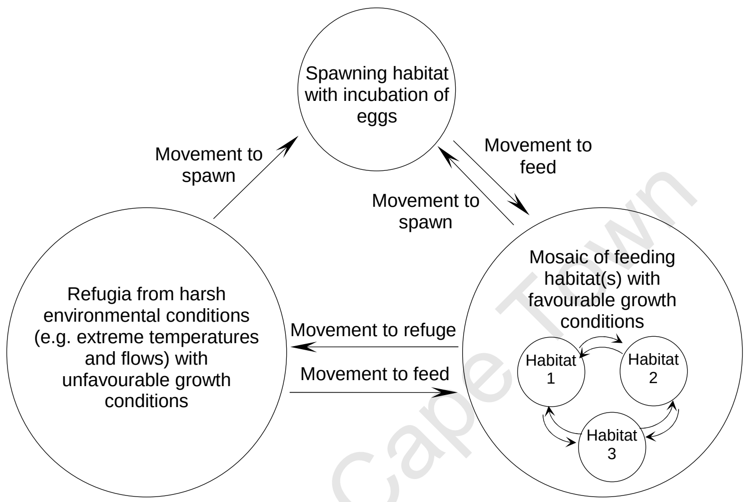

Figure 2.1 Schlosser's dynamic landscape model of river fish ecology (From Schlosser and Angermeier 1995).

Dispersals may entail the active or passive transport of young or adults from rearing habitat (Brown and Armstrong 1985; Reichard *et al*. 2002), or they may entail random wandering. Dispersals therefore influence abundances through immigration and emigration and in certain cases these processes may have greater influence on local population dynamics than environmental variability (Schlosser 1998). Over longer time periods, they play a key role in patterns of colonisation and extinction that are manifest in the dynamics of the metapopulation (Schlosser and Angermeier 1995).

Fausch *et al*. (2002) built on Schlosser's dynamic landscape model and conceived the '*riverscape*' (a term first coined by Ward 1998) as a continuously varying, hierarchically organised and heterogeneous aquatic landscape (after Frissel *et al*. 1986) and suggested approaches for testing the predictions of Schlosser's model. They went on to suggest that critical fish life history events took place at intermediate scales, i.e. the river segment (1-100 km), although ecologists addressed questions at larger spatial scales, and studies were designed around gathering data at small spatial scales (≤ 200 m). Thus Fausch *et al*. (2002) suggested that studies be spatially continuous and georeferenced, and that a multi-scale, nested approach to sampling design be adopted.

Durance *et al*. (2006) addressed many of the concepts discussed thus far and introduced a temporal dimension to Schlosser's model (Figure 2.2). Durance *et al.* suggested scaling river habitats from an organism-centred (in this case river fish) point of view based on Frissel *et al*.'s (1986) nested hierarchy. They proposed that physical habitat heterogeneity at the local Home Range Scale (HRS – Figure 2.2) gives rise to daily movements between feeding areas and temporary refugia (pools or backwaters).

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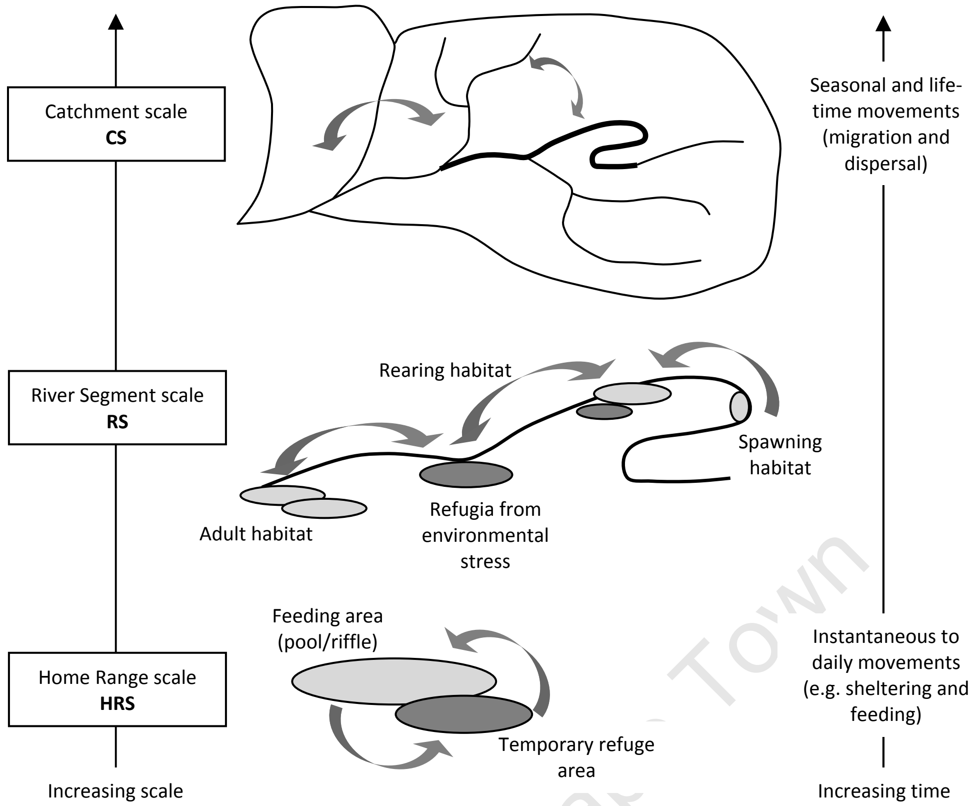

Figure 2.2 Potential fish activities at various stages of their life history across a range of scales as suggested by Frissell *et al*.'s (1986) nested hierarchy. The scales range from the local pool/riffle system (Home Range Scale HRS) to river segment (RS) and catchment (CS). Each level in the hierarchy is of importance to different stages of a fish's life history (from instantaneous and daily movements to seasonal and life time movements) and corresponds to different temporal scales of change (From Durance *et al*. 2006).

At the intermediate River Segment Scale (RS – Figure 2.2), fish actively move, or are dispersed between spawning and nursery areas, adult maintenance habitat and refugia from environmental disturbance (floods or drought). Physical heterogeneity at the Catchment Scale (CS – Figure 2.2) is experienced over the lifetime of an individual and gives rise to seasonal movements. At this scale, patterns of colonisation and extinction (metapopulation processes) also become evident.

Durance *et al*. (2006) made the point that the persistence of any species depends on the availability of all critical habitat units. For instance a species may be absent from a segment or catchment where spawning habitat is favourable, but where feeding habitat is missing. Identifying the scales at which fish respond to habitat heterogeneity is therefore critical for the successful management of fish populations.

The study of river fish habitat and movement in South Africa is in its infancy and most studies have focussed on the microhabitat scale (Section 2.3). The consideration of larger-scale movement and habitat, however, has recently gained prominence with the Department of Water Affairs and Forestry (DWAF) recognising the need for providing fish passage facilities at instream structures such as dams and weirs. Evidence for fish movement, however, has largely been of an anecdotal nature, mostly from observations of movements over weirs (Meyer 1974; Cambray 1990a; Meyer 1974; Kotze *et al*. 1998; Heath *et al*. 2005). With the advent of Geographical Information Systems (GIS) and accompanying advances of geostatistical analysis techniques, together with radio telemetry, the ability to address large-scale processes in river fish ecology is vastly

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improved (Johnson and Gage 1997). In a developing country such as South Africa, however, the cost of telemetry studies is prohibitively expensive and dive surveys offer a viable alternative for inferring fish movements where conditions permit, i.e. in small rivers with low turbidity.

2.2.1 Conclusion

Integrating the principles of landscape ecology into river ecosystems represented an important juncture in the study and management of river fish populations that allowed ecologists to view the river system and the populations it supported in the context of wider catchment and river segment scale patterns and processes. This focused attention on the importance of scale (both spatial and temporal) for understanding these patterns and processes. It also highlighted the importance of habitat patches and connectivity between these patches that enable organisms to respond dynamically to a variable environment.

As demonstrated by the evidence provided in this section, riverscape scale factors such as disturbance, dispersal and habitat patch mosaics may be more important for controlling fish population dynamics at a local scale than biotic or abiotic conditions (Schlosser 1998; Labbe and Fausch 2000). Thus, in this study, before addressing the possible limitations imposed by local-scale (microhabitat) conditions (Section 2.3 and Chapter 5 and 6), it was necessary to examine how populations responded to variability at the river segment scale. Drawing primarily from Fausch *et al*.'s (2002) call for spatially continuous and georeferenced studies at scales larger than the river reach, the current study adopted continuous dive surveys along a whole river segment rather than a pre-selected subset of reaches based on stratified random sampling protocols. A major objective of these dive surveys was to identify and map critical habitat units in the riverscape and to link these to fish distribution through the year (Chapter 4). The dives took place over a six kilometre segment of river, i.e. corresponding to an intermediate River Segment (RS) scale. It was felt that in this way the spatial distribution (the abundance and regularity) of critical habitat units (patches) such as spawning areas, feeding areas and refuge areas – and therefore the scale at which fish were responding to these units – could be mapped more comprehensively than if more traditional sampling approaches were used.

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2.3 QUANTIFYING AND DESCRIBING HYDRAULIC FISH HABITAT AT LOCAL (MICROHABITAT) SCALES

While the previous section focussed on the intermediate- and large-scale processes that affect fish habitat selection, this section deals primarily with the local-scale microhabitat selection. In particular, it focuses on the methods (hydraulic and biological habitat models) that have been applied to solve specific water management issues. The sites selected for the microhabitat investigations in this study were nested within the larger dive segment, partly from necessity (there were no other accessible reaches with viable fish populations) and partly so that the larger-scale processes could be integrated into the findings (Section 3.5 and 3.6).

2.3.1 Instream habitat studies in South African rivers

Since the early 1990s, there has been a growing demand for South African water scientists to provide recommendations for water allocations to sustain freshwater ecosystems. The need for a rapid response to these demands in a data-poor environment led to the development of holistic, whole-ecosystem Ecological

Water Requirement (EWR) methodologies such as the Building Block Methodology (BBM) (King *et al*. 2000) and the Downstream Response to Flow Transformation (DRIFT) methodology (King *et al*. 2003; King *et al*. 2004). These holisitic approaches to river flow management have their origin in a combined workshop of Australian and South African River scientists who recognised the limitations of PHABSIM (Arthington *et al*. 1992). Holistic methodologies allow specialists to evaluate the consequences of alternative flow scenarios when data, manpower or time is limiting (Tharme and King 1998).

Major advances have been made in the refinement of these methodologies and DRIFT has subsequently become recognised widely as one of the foremost in this field (Tharme 2003). However, DRIFT is a multi-criteria decision support system for combining knowledge from a variety of disciplines and using this knowledge to evaluate the outcomes of alternative flow regimes. It relies on a basic understanding of the physical mechanisms that regulate communities of freshwater organisms. This information is often sparse in South African EWR workshops, and specialists must base their predictions of river change on 'best-available-knowledge', 'rule-of-thumb' estimates, or studies of related organisms conducted elsewhere in the world. This means that when there are no empirical studies of how local organisms respond to changes in flow, confidence in the predictions made during the course of these assessments is generally very low. There is therefore an urgent need to invest in fundamental research into the ecology and life history requirements of South Africa's freshwater biota, as well as into the development of quantitative models for predicting the biological outcome of changes in physical habitat as a function of discharge. This is particularly important in high profile river systems with species of outstanding conservation, scientific or socio-economic importance, or where flow recommendations may be contested (Tharme and King 1998).

The most widely applied approach for linking physical habitat to discharge is the PHABSIM model (Bovee 1982; Milhous *et al*. 1989; Tharme 2003). PHABSIM was originally developed by the U.S. Fish and Wildlife Service as the modelling component of the Instream Flow Incremental Methodology (IFIM) (Bovee 1982) and combines empirically derived biological Habitat Suitability Criteria (HSC) with one-dimensional (1-D) hydraulic modelling to compute Weighted Usable Area (WUA) – the wetted area of a river weighted by its suitability as habitat for an organism at a range of discharges.

However, King and Tharme (1994), evaluating the PHABSIM model in the South African context, identified a number of problems with the methodological basis of the model, primarily the manner in which it calculated Weighted Usable Area (WUA) – the total amount of simulated habitat available to the organism. But the main focus of their criticism was its inappropriateness for local conditions because it was deemed species-specific, user-unfriendly and data-intensive (since King and Tharme's study, PHABSIM has undergone numerous revisions, its most recent manifestation being a MS Windows-compatible version with an accompanying manual; Waddle 2001). King and Tharme's (1994) evaluation provided the initial impetus for developing the BBM and later DRIFT. South African geomorphologists and ecologists also abandoned HSC-based methods for describing habitat, adopting instead the physical biotope approach (Newson and Newson 2000). King and Schael (2001) then developed expertise in describing physical biotopes for aquatic macroinvertebrates, proposing an approach based on digitised maps of visually assessed flow-types understood to be of importance to aquatic organisms (hydraulic biotopes). The aerial extent and diversity of these habitats at different levels of flow could then be examined and the response of organisms to this change assessed. This method, which has its origins in Pringle *et al*.'s 1988 patch dynamics and Frissel *et al*.'s

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(1986) view of rivers as being hierarchically organised into spatially-nested units, has been successfully applied in several EWR assessments in South Africa (e.g. Olifants River, Birkhead *et al*. 2005) and in Lesotho on the Orange River (Metsi Consultants 2000).

PHABSIM was evaluated for a second time in South Africa by Pollard (2000) who also proposed using a similar biotope-based approach – the Geomorphological-Biotope Assessment (GBA) – to assess fish habitat – in this case the pennant-tailed catlet *Chiloglanis anoterus* in the Marite River. Pollard concurred with King and Tharme (1994) that the biotope mapping approach may be more appropriate for local conditions. She highlighted the main methodological problems of HSC including, amongst others, the potential bias associated with the under- or over-estimation of habitat availability; problems in the calculation and interpretation of WUA; and the absence of a spatially referenced framework.

Given the subdued reception habitat simulation models (i.e. PHABSIM) linked to biological HSC models received in South Africa, as well as the extensive evaluation and criticism they received in other countries (e.g. Mathur *et al*. 1985; Shirvell 1989; Castleberry *et al*. 1996; Williams 1996; Rosenfeld 2003), the decision to revisit this approach in the present study in order to quantify habitat used by Clanwilliam yellowfish and sawfin warrants some justification.

Perhaps the strongest justification for revisiting HSC methods is that they are quantifiable, precise and repeatable. The many criticisms levelled at PHABSIM (and its associated modules such as HSC) may be more likely due to incorrect application and misinterpretation rather than inherent weaknesses, or – as Brown and King (2003) argued – the criticisms are more symptomatic of extensive use than intrinsic worth. Thus despite continuing criticism and evaluation, habitat simulation models such as PHABSIM – or for that matter comparable models such as the New Zealand River Hydraulic and Habitat Simulation programme (RHYHABSIM, Jowett 1989) – have become increasingly advanced in recent years and the trend towards applying them (often in combination with holistic methodologies) has grown (Tharme 2003). Some of the most significant advances have been made in the refinement of two-dimensional (2-D) hydraulic models (earlier versions of PHABSIM used one-dimensional models). Two-dimensional models are able to incorporate spatial referencing, enabling queries into habitat connectivity, contact zones and juxtaposition of hydraulic conditions (Bovee 1996). They address therefore one of the major weaknesses of earlier habitat models, i.e. the absence of a spatially referenced framework as pointed out by Pollard (2000). Several two dimensional hydraulic models are currently being assessed in South Africa and this study provided the opportunity to test one of these models (River2D).

Some of the criticisms directed at hydraulic simulation models may have arisen as a result of exaggerated perceptions of their capabilities. As already stated in the introduction, Gore and Nestler (1988) assert that PHABSIM was not intended as a 'replacement for population studies, a replacement for basic research into the subtleties of fish or benthic ecology, nor a replacement for biological innovation or common sense'. While various flow-assessment methodologies such as DRIFT (King *et al*. 2003) have advanced rapidly in South Africa, the link between 'modelled' and real river ecosystems in South Africa remains tenuous. To echo Kondolf *et al*.'s (2000) sentiments, it is a poor appreciation for the basic ecology and behaviour of the species of concern, rather than the relative merits of the various models themselves, which requires our attention. King and Tharme (1994) pointed this out over a decade ago and with a few published exceptions

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(notably Cambray *et al*. 1997; King *et al*. 1998 and Pollard 2000) little progress has been made towards understanding the physical processes underpinning the life histories of many of South Africa's native freshwater fish species.

While acknowledging that time, manpower and financial considerations are major constraints to applying HSC-based methods, and that management-oriented research may appear to provide more immediate answers to vexing problems, a lack of insight into the basic ecology and life history of species may compromise the best efforts to maintain and restore freshwater ecosystems. The fact that research cannot respond on the same time-scale as management should not mean that these very necessary and basic investigations should not be carried out in support of present and future management needs.

King and Tharme (1994) emphasised that the limitations of HSC-based studies should not detract from the immense opportunity they offer for learning about how organisms are adapted to flow. They pointed out that these studies remain valuable in their own right, whether or not they are linked to simulation models. With this in mind therefore, HSC methods are revisited in this study and proposed as the most suitable method of studying the hydraulic conditions used by fish in river systems. In the next section some of the weaknesses of the original hydraulic/ecological model as proposed by Bovee (1986) are discussed. The discussion focuses on the biological component of the process – namely the development of HSC – as opposed to hydraulic modelling, which will be described and evaluated in greater detail in Chapters 5 and 6.

2.3.2 Habitat Suitability Criteria (HSC)

Habitat Suitability Criteria (HSC) were developed in order to translate the hydraulic and geomorphological conditions in rivers into indices of habitat quality for fish and macroinvertebrates (Bovee 1986) and to make predictions on how this habitat quality and quantity will change under any given flow scenario when linked to a hydraulic model. Initially developed in the United States (Bovee 1986), they have been applied in Europe (e.g. Gibbins and Acornley 2000; Guay *et al*. 2003; Nykanen and Huusko 2004); and New Zealand (e.g. Hayes and Jowett 1994; Jowett and Richardson 1995); as well as in South Africa (e.g. King and Tharme 1994; Weeks *et al*. 1996; Niehaus *et al*. 1997; Pollard 2000) and Lesotho (Arthington *et al*. 2003b) for a range of aquatic organisms from fish (e.g. Stuber *et al*. 1982) and macroinvertebrates (e.g. Jowett and Richardson 1990), to beavers (Allen 1983) and bullfrogs (Graves and Anderson 1987). In the United States, where HSC models were first developed and have been most extensively applied, the U.S. Fish and Wildlife Service has accumulated a database of 157 HSC models for a range of organisms over the last 30 years ('*Habitat Suitability Index*' 2005).

The fundamental assumption of these models is that organisms will favour, and therefore be associated more frequently, with habitat conditions that promote their survival growth and reproduction (Freeman *et al*. 1997), and that these conditions have definable limits of use (DeGraaf and Bain 1986). They are derived on the basis of instantaneous observations of the location of target species in the field combined with measurements of various physical habitat variables of interest (e.g. depth, velocity, substratum and cover) that are associated with each observation. From this information, frequency distributions of abundances of organisms or individual observations are plotted against a gradient of any habitat variable of interest. The distributions are then smoothed, normalised and expressed as a suitability value between 0 (least favourable) and 1 (optimal) (Bovee 1986). HSC derived in the absence of field observations, i.e. obtained from HSC libraries, from the

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literature, or on the basis of professional experience are referred to as Category I criteria. Category II criteria or 'utilisation functions' are derived from data collected in the field and are simply frequency distributions of observations or abundances of organisms over the range of any habitat variable. However, utilisation functions may be biased by the proportion of the total amount of habitat available in the river. If certain conditions are very common or very rare at the time of observation; either due to the inherent variability of river systems, or to inconsistent discharges in the same river, utilisation functions need to be adjusted. Category III criteria, or 'electivity' functions express habitat suitability as a proportion of the amount of habitat utilised to the amount of habitat available:

$$E = \frac{U}{A}$$

where E is the index of electivity; U is the relative frequency of fish observed in a particular habitat interval and A is the proportion of the total area of that habitat interval (Waddle 2001). It is pointed out that the more commonly used term, 'preference' (P), is not universally accepted since an organism's selection of a habitat may be based on factors such as competition, predation and habitat availability that may differ between rivers and therefore not reflect a true preference (Rosenfeld 2003). The term 'preference' is used here when referring to previous studies that have opted to use this term.

Part of the widespread appeal of HSC lies in their simplicity. However, this simplicity is deceptive and the problems inherent in representing the many species, life stages and behaviours with HSC, and at the same time addressing the dynamic nature of aquatic habitat itself, present perhaps some of the most serious challenges to environmental flow management (Gore and Nestler 1988). Many of the criticisms aimed at HSC stemming from researchers both in South Africa and abroad have centred on these complex issues.

2.3.3 Limitations of Habitat Suitability Criteria

The transferability of HSC refers to their ability to predict habitat quality in one or more rivers different from those in which they were developed. In other words, preference or electivity optima derived for any given species should be the same for all rivers that a species occurs in. However, it has been found that, apart from life-stage and behaviour specific differences, variation of habitat preferences within a species can arise from the practical and methodological difficulties of sampling available habitat (A) in rivers that are themselves diverse and heterogeneous ecosystems exhibiting strong daily and seasonal fluctuations. Under- or over-estimating available habitat due to time, manpower and equipment constraints can therefore substantially bias preference functions.

In South Africa, the sensitivity of electivity functions to available habitat (A) was demonstrated by Pollard (2000) who showed that an adjustment of no more than 4 % to two of the depth classes available to *C. anoterus* in the Marite River, resulted in a major shift in the preference optima (P) for this species from depths of 0.5-0.6 m to depths of between 0.1-0.2 m, thereby suggesting that an inaccurate estimation of A may strongly bias the resulting preferences. Nevertheless, despite this, habitat suitability optima derived for *C. anoterus* by Pollard (2000) concurred with Weeks *et al*.'s (1996) habitat suitability optima for this species suggesting at least some robustness in the method.

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In another instance, Glozier *et al*. (1997) found that the suitability optima of a North American benthic minnow, the longnose dace *Rhinichthys cataractae*, appeared to shift to deeper areas and larger substratum particles when these were more abundant. The implication here is that suitabilities for absent habitat classes cannot be evaluated, or – as Holm *et al*. (2001) point out – when availability (*A*) is zero, preference (*P*) is zero. Thus a reduction or increase in discharge will result in absent habitat classes that will decrease the range of habitats available and those habitats that become unavailable will not be accounted for by the suitability function. In their study of Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, Heggenes and Saltveit (1990) recorded higher water velocities at fish positions in higher flows. Fish are able to adapt to a variety of habitat conditions within defined ranges and the absence of those conditions in the river at the time of sampling means that they cannot be evaluated. Therefore, since most HSC are developed during median flows, the reliability of the predictions is likely to decrease at very low and very high discharges (Gore and Nestler 1988; Heggenes and Saltveit 1990).

Another basic assumption of HSC is that the actual selection of habitat ranges by fish is independent of discharge. However, in a laboratory flume test, Holm *et al*. (2001) found that juvenile Atlantic salmon parr *Salmo salar* used mean water column velocities at the lower end of the available range at high discharge, and at the higher end of the range at low discharge. This appears to imply an interdependence of preference and discharge, i.e. that fish alter their habitat selection under different flow conditions and therefore that individual HSC would need to be developed for a range of discharges. Ibbotson and Dunbar (2002) suggested, however, that the parr in Holm *et al*.'s (2001) were merely restricted by the range of velocities available to them and selected those closest to the preference optima. They suggested that the main problem with linking habitat to biota is that there is no causal link between measured 'preference' and real 'habitat quality' and that a shift in 'preference' with altered discharge may not necessarily imply an adaptive response. They therefore proposed using data pooled from several rivers and over a range discharges. The resulting models may be more general, but also therefore less precise (Hayes and Jowett 1994), and may mask the dynamic nature of habitat use (Pollard 2000).

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The choice of the appropriate habitat variable itself may be another factor that may play a role in the interpretation of habitat preference. In their study of the longnose dace, Glozier *et al*. (1997) found that despite the fact that both their test rivers had similar velocity distributions, the dace occupied higher velocities in one than the other. The longnose dace is a benthic foraging species leading Glozier *et al*. (1997) to suggest that interstitial velocity may have been a more appropriate choice of habitat variable than mean water column velocity as a measure of preferred habitat. Similarly, Pollard's (2000) choice of mean water column velocity to study habitat preferences of the pennant-tailed catlet *C. anoterus*, also a benthic species, may also have given rise to some of the between-site differences in suitability functions that she observed among *C. anoterus*. For this reason, DeGraaf and Bain (1986) suggested that nose velocity be used, in which case benthic species may not be good candidates as indicator species for habitat studies. It should be noted, however, that most two-dimensional hydraulic models only model mean water column velocity and that input to these models has to be made using the appropriate variable (Hayes and Jowett 1994).

Another factor that may affect the transferability of HSC is the mobility of a species or life stage. Nykänen and Huusko (2004) evaluated the habitat preferences of larval European grayling *Thymalus thymalus* and noted that velocity HSC transferred well from the source to destination sites, but that depth and substratum

HSC transferred inconsistently. They found that the grayling larvae were restricted to velocities <0.1 m s^{-1}, leading them to postulate that while the larvae may have had a certain latitude with regard to their selection of depth and substratum conditions, their choice of velocity ranges was most likely limited by their physical capabilities, i.e. their low swimming ability.

Competition and predation affect the transferability of HSC by changing habitat selection between river systems. Harvey (1991) found that the presence of largemouth bass *Micropterus salmoides* not only reduced the abundance of juvenile sunfish *Lepomis* spp., but also that the bass had a significant affect on habitat use by sunfish, inducing them to move to shallower areas when bass were present. Fausch and White (1981) found that competition between brook trout *Salvelinus fontinalis* and brown trout *Salmo trutta* resulted in resting brook trout choosing positions with lower mean focal point velocity, but greater water velocity difference (difference between focal point velocity and the fastest current within 60 cm of the fish) after brown trout were removed from a study reach. HSC may therefore not be transferable between rivers with different levels of predation or competition.

In summary, transferability of HSC may be affected by the variation of available habitat between river systems with widely different habitat conditions or fish communities, within rivers between discharges, by the choice of appropriate species and life-stage as well as by the choice of appropriate habitat variables. The suggestion is that HSC should not be treated as inviolable and that they should not be interpreted without a clear knowledge of their limitations and some knowledge of the ecology, biology and behaviour of the species of concern. Several methods have been developed to test the ability to transfer habitat criteria from source (rivers where the data for HSC where measured) to destination rivers (rivers to which the HSC are being applied); these are discussed in the next section.

2.3.4 Testing transferability of HSC

Bovee (1986) initially proposed the 'abbreviated convergence' method to test the transferability of HSC, which entails visually assessing the agreement between HSC from the source and destination streams. Thomas and Bovee (1993) then went on to develop a more rigorous verification technique that compares predicted habitat suitabilities from the source river with observed fish locations in the destination river. They derived depth, velocity and cover criteria for adult and juvenile rainbow trout *Oncorhynchus mykiss* in the South Platte River, Colorado, and using these curves, computed composite suitabilities in modelled habitat cells of a site on the Cache la Poudre River. They defined a habitat cell as 'optimal' if the suitabilities for depth, velocity and cover were all optimal, i.e. corresponded to the central 50% of observations, and 'suitable' if they corresponded to 95% of observations ('usable' habitat was defined by the limits of optimal and suitable habitat). They hypothesised that (1) suitable cells would be occupied in a significantly higher proportion than unsuitable cells and (2) that optimal cells would be occupied in greater proportion than usable cells. A significant agreement was found between the composite suitabilities and the cells occupied by adult rainbow trout in the destination river enabling them to conclude that the curves were indeed transferable.

Freeman *et al*. (1997) applied a modified version of this test, investigating HSC for a range of species in two Piedmont and Coastal Plain streams in central and south Alabama. However, they only tested the transferability of criteria for 'optimal' habitat, i.e. corresponding to the central 50% of observations, since they assumed that variations in habitat availability would affect the tails of the distributions, i.e. 'suitable' or

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95% of observations, more strongly than the modal range. They tested habitat variables (depth, velocity, substratum and cover) separately to determine whether some variables transferred more consistently than others. Their findings suggested that HSC for target species that showed a stronger preference for shallow, fast-flowing habitats with course substrata transferred better than those for species that preferred deeper, slow-flowing habitats. They therefore proposed that many species (including smallmouth bass and the cyprinids) are habitat generalists, using fast-flowing riffle and run habitats for foraging, but slow-flowing pools for resting (Aadland 1993). They concluded that the habitat criteria developed for these fish are likely to be broader and therefore poorer predictors of habitat requirements than fish with narrower habitat requirements. Freeman *et al*. (1997) suggested that the arrangement of habitat patches, particularly the proximity of habitats to areas of prey production may be better descriptors of habitat quality for these generalist guilds.

2.3.5 Habitat-abundance/biomass relationships

Apart from the practical difficulties imposed by the limited transferability of HSC, a far more fundamental criticism of the method is the assumption that simulated habitat availability (WUA in the case of PHABSIM) is a justifiable predictor of a river's standing stock (abundance or biomass of organisms). Although HSC were never intended to do this (Raleigh *et al*. 1986), this critique has nevertheless generated contentious debate in the literature and prompted a number of studies to test the assumption (Orth and Maughan 1982; Mathur *et al.* 1985; Scott and Shirvell 1987; Gore and Nestler 1988; Capra *et al*. 1995; Nuhfer and Baker 2004). As Orth (1987) has suggested, habitat studies may merely be predictors of fish distribution, not abundance.

Some of the poor correlations between habitat and standing stock are undoubtedly related to the fact that physical habitats in rivers (structural as well as flow environments) are not the only or even necessarily the primary drivers of population dynamics in freshwater systems. Energy sources, water quality, temperature and biotic interactions (competition and predation) also play roles in moderating population numbers (Karr and Dudley 1981 cited in Orth 1987). The failure to take these wider ecosystem level processes into account in habitat models provided the initial impetus in South Africa to develop more holistic EWR methodologies (King and Tharme 1994; Tharme and King 1998; King *et al*. 2003).

A number of studies have aimed at testing the relation between habitat and fish standing stock. Orth and Maughan (1982) tested the relation between usable habitat (WUA) and standing stock of four fish species in Glover Creek, Oklahoma and found significant correlations between usable habitat and the abundance of three of these species during summer. However, Orth and Maughan's study was criticised by Mathur *et al*. (1985) who indicated that the data were highly variable and that linear correlations were poor or absent. Gore and Nestler (1988) suggested that prediction of standing stock from simulated habitat was beyond the capability of IFIM studies. Amongst the reasons they cited for this were those difficulties related to transferability of HSC, as already outlined in Section 2.3.4. However, in addition to these, Gore and Nestler (1988) draw attention to the fact that, in many habitat studies, ecosystems with the simplest biological communities and hydrology (in the U.S.; coldwater communities in systems driven by snowmelt) exhibit the strongest correlations between habitat and standing stock, whereas biologically and hydrologically complex ecosystems exhibit the poorest. Thus, in more hydrologically complex systems, the choice of which component of the flow regime (e.g. mean monthly flow, lowest monthly flow, median flow) to correlate with standing stock is critical.

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One of the more likely explanations for poor correlations between habitat and a river's standing stock is that HSC do not account for the dynamic nature of instream habitat. Daily and seasonal variations in flow suggest that habitat may not always be limiting and that some habitat may be limiting for only part of the time for specific life stages. For example, Stalnaker (1979) found a strong correlation between WUA and standing stock of brown trout *Salmo trutta* during summer when habitat was assumed to be most limiting, and Bovee *et al*. (1994) found that the availability of night-time habitat during summer played an important role in regulating the numbers and sizes of age-0 smallmouth bass *Micropterus dolomieu*. Thus habitat-induced constraints on population abundances may only occur for brief critical periods, which instantaneous measures of habitat (HSC) are unlikely to identify (Orth 1987).

As hydraulic modelling techniques have become more refined, and the importance of incorporating hydrologic time series has been increasingly recognised (Hardy 1998), evidence for links between fish population dynamics and habitat has been mounting. In addition, an increasing number of flow-related studies are focussing on critical habitats during the early life stages of fish and the role of habitat bottlenecks.

Capra *et al*. (1995) found that if available spawning habitat (WUA) for brown trout *Salmo trutta* populations in France was continuously lower than 80% of the optimum for more than 20 days, the relative density of 0^+ recruits was affected the following year. Freeman *et al*. (2001) related four years of hydrological and habitat variability to young-of-the-year fish abundances in regulated and un-regulated reaches of the Tallapoosa River. Using habitat-flow relations generated by PHABSIM to translate discharge through time to habitat through time, they found that the abundance of species that usually spawned during spring declined in the dammed rivers because hydropeaking at the regulated site reduced the persistence of shallow-water habitats (defined as the longest period with habitat continuously above the long-term median). During summer, reduced rainfall limited power generation and curtailed hydropeaking, resulting in the dominance of summer spawning species.

In another study, Capra *et al*. (2003) combined a dynamic model of trout populations with simulated habitat and discharge time series on regulated and unregulated reaches of the river Roizonne, France. They showed that increases of twice the median discharge in the natural reach, and 30 times the median discharge in the regulated reach, were unfavourable for post-emergence brown trout. A major reason for this might have been a reduction in WUA at twice the median discharge that resulted in substantial decreases in hydraulic cover for the young fish (<0.05 m s^{-1}).

These studies (Capra *et al*. 1995; Freeman *et al*. 2001 and Capra *et al*. 2003) thus highlight the importance of accounting for temporal variability as well as critical habitats and life stages. Freeman *et al*.'s (2001) study also demonstrated that flow reversal may be as problematic as low flows in regulated rivers. Heggenes (1996) has called for a dynamic rather than static approach to habitat studies that accounts for the 'sliding spatial niche' response of fish species to variation in habitat availability, e.g. niche shifts in response to changes temperature and light. Thus the integration of hydraulic habitat methods with hydrological records that account for the magnitude, frequency and timing of flows presents perhaps one of the more profitable avenues for further research into the relations between river flow and biota.

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More sophisticated approaches to quantifying fish habitat include mechanistic bioenergetic modelling to link fish habitat with local hydraulics (e.g. Rinóon and. Lobón-cerviá 1993; Braaten 1997; Nislow *et al*. 2000). These techniques involve modelling individual fish energy intake and expenditure in different habitats with different food resources. Given the limited ecological studies on river fish in South Africa it appears unlikely that this method will be appropriate in the foreseeable future, or for promoting in developing-country situations and is therefore not considered further here.

2.3.6 Conclusion

This section has highlighted some of the strengths and limitations of HSC-based methods combined with hydraulic models. Amongst the principal advantages of these methods are their simplicity, and meticulously reviewed track record. Pusey (1998) notes that part of their appeal is that they are perceived by non-biologists and engineers as having a strong quantitative basis. Some of their more significant limitations include the fact that they are data intensive, they rely on instantaneous, static or 'snap shot' representations of habitat use and poor correlations have been found between simulated habitat and standing stock. In many cases, the most limiting factor in the wider application of HSC-based methods is that information on habitat use by most fish species is simply not known (Pusey 1998).

HSC remain the most controversial component of PHABSIM. In a candid admission, twelve experts summed up their divergent views surrounding habitat simulation methods in general and PHABSIM in particular in the following way: "Some of us think that, with modification and careful use, it might produce useful information. Others think it [PHABSIM] should simply be abandoned" (Castleberry *et al*. 1996). However, apart from bioenergetic modelling (see Guensch *et al*. 2001), no other quantitative and repeatable methods have so far been proposed or widely accepted by the scientific community. Castleberry *et al*. (1996) went on to suggest that at the time of writing there was "no scientifically defensible method for defining flow standards". However, as both Kondolf *et al*. (2000) and Castleberry *et al*. (1996) pointed out, all models have limitations and their outputs should not be substitutes for knowledge and experience, good judgement, or critical thinking. This study adopts the latter view; i.e. that HSC-based techniques should not be completely abandoned and that many of the problems can be allayed through careful and qualified application of the methods. Freeman *et al*. (1999) suggested that the uncertainties in developing HSC should be recognised and incorporated into hypotheses to be tested through population monitoring in an adaptive management context. This implies an integration of the temporal dimension into habitat studies, i.e. hydrological indices and habitat time series combined with population monitoring. In addition, habitat studies should not be a substitute for a basic understanding of the biology and ecology of the species of concern.

In an extensive review of the limitations of habitat simulation methods as they have been applied in New Zealand Rivers, Hudson *et al*. (2003) urged scientists to accept the existence of uncertainty and emphasised the importance of understanding river ecosystem processes at multiple scales (not just microhabitat). In Australia, Bunn and Arthington (2002) have called for aquatic science to move into a more manipulative and experimental phase by measuring the response of ecosystems to restored flows (Section 2.4). Also in Australia, Pusey (1998) points at that environmental flow assessments that rely on maintaining a certain amount of habitat are not appropriate unless certain types of microhabitat are known to be of importance ot the biota. All these former reviews warn against an over-reliance on habitat-based approaches for solving flow management problems. As a last word, it must be acknowledged that habitat-based approaches have

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contributed, and continue to contribute, inestimably to our understanding of how fish are adapted to flowing-water environments.

2.4 THE RELATIONSHIP BETWEEN FISH LIFE HISTORIES AND THE FLOW REGIME

Ecologists risk oversimplifying fish-habitat relationships if they apply hydraulic habitat simulation indiscriminately, without regard for the dynamic nature of river flow, or a basic appreciation for fish biology, population dynamics and behaviour (Orth 1987; Capra *et al*. 1995; Heggenes 1996; Hardy 1998). Ideally, habitat simulation studies should include habitat time series in recognition of the fact that the size of a fish population at any given moment is not only contingent upon immediate habitat availability, but also on past habitat conditions (Orth 1987; Stalnaker *et al*. 1989), as well as on factor such as past predation, competition and prey abundance. By addressing only the immediate availability of habitat and not the temporal component of flow, these approaches tend to underplay the role of hydrological variability in regulating ecological processes. Souchon and Capra (2004) have gone as far as to suggest that a frustration with a narrow application of habitat simulation approaches has, in recent years, led to a resurgence in hydrological approaches that enable a more direct link between flows and ecological processes.

Just as the spatial dimension of river habitat is scale dependant, so is the flow regime, i.e. the temporal component of river flow that changes over hourly, daily, seasonal and interannual time scales. Following on from Frissel *et al*.'s (1986) and Hildrew and Giller's (1992) hierarchical view of river systems discussed in Section 2.2, Dollar *et al*. (2007) proposed a time scale-dependent nested hierarchy for organising the flow regime. The two largest-scale hydrological processes occur at paleoclimatic and historical time intervals – the former responding over millennia to long-term climate change, the latter to shorter wet and dry cycles – in South Africa this corresponds to a multi-decadal cycle of around 18 years (Tyson *et al*. 2002; Dollar *et al*. 2007). At the smallest scales and time intervals of hydrological change Dollar *et al*. place channel hydraulics (time-averaged velocity and boundary shear stress) and local fluid mechanics (velocity and turbulence) (these temporal scales were addressed in Section 2.3). Changes at these scales range from almost instantaneous, to hourly, daily and annual time intervals. Intermediate between large and small scale flow processes that occur in rivers is the hydrological regime. The hydrological regime is characterised by discharge events that have return periods of variable and often seasonally predictable cycles ranging from one to one hundred years. This is the scale at which most recorded data are available for river systems and the scale at which most anthropogenic impacts become apparent. It is also the scale that forms the 'habitat template' (*sensu* Southwood 1988) upon which life cycles and life history strategies of living organisms are superimposed (Winemiller and Rose 1992; Lytle and Poff 2004).

Recognising the importance of hydrology for maintaining river ecosystem functioning, Poff *et al*. (1997) proposed the 'Natural Flow Regime' as a conceptual framework for linking river flow to the adaptations of the organisms that inhabit it. The 'Natural Flow Regime' is characterised by five key components of temporal change, i.e. magnitude, frequency, duration, timing and rate of change. Variability in these components creates regional flow patterns: e.g. intermittent flashy, mesic groundwater and winter rain (Poff and Ward 1989; Poff and Ward 1990) that provide the templates for life history adaptations of river organisms. Bunn and Arthington (2002) suggested four basic principles governing the influence of the flow regime on aquatic

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biodiversity: (1) flow is a major determinant of physical habitat in rivers which in turn is a major determinant of biotic composition; (2) various components of flow regime (e.g. timing, seasonality and predictability) shape the life histories of organisms; (3) many river organisms depend on longitudinal and lateral connectivity and (4) natural flow regimes inhibit the success of invasions (Figure 2.3).

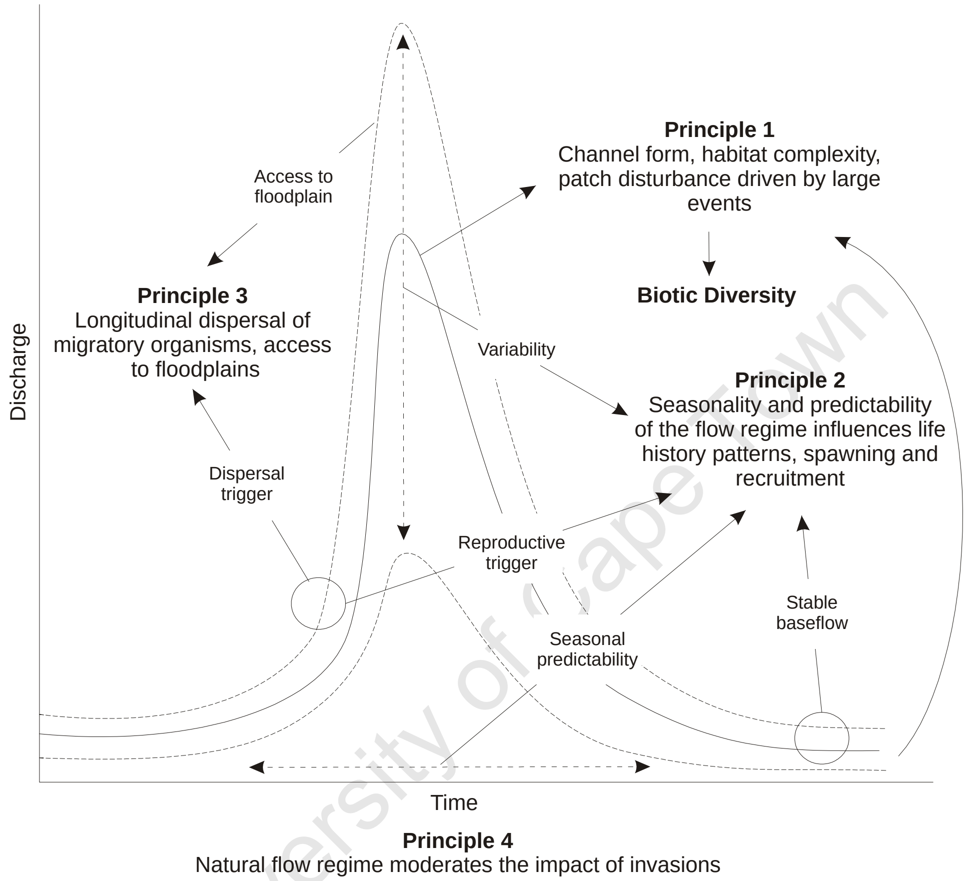

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Figure 2.3 Schematic summarising the influence of the flow regime on aquatic biodiversity based on Bunn and Arthington's (2002) four principles. The solid line represents a hydrograph of a flood and baseflow and the broken lines variability in the magnitude of these flows. Each component of the flow regime, the magnitude, seasonality, predictability, variability is shown to influence a different aspect of importance to aquatic organisms.

The overview discussed here focuses on the second principle: the manner in which the flow regime influences the life cycles and life histories of fish. Many river organisms undergo a sequence of physiological and morphological changes (e.g. egg, larvae, pupa, adult) during the course of their lives that comprise their life cycle. An additional group of attributes, including factors such as maximum age and size, the number of young it produces at any one time, or over the course of its life span, and its frequency of reproduction, constitute an organism's life history characteristics.

The particular combination of attributes it employs – whether it has a short or long life span, a small or large numbers of eggs or reproduces seasonally or aseasonally – can be said to comprise its life history *strategy* (Southwood 1988). In regions where hydrological disturbances of certain magnitudes (i.e. floods or droughts) occur with reasonable frequency and predictability, species have life histories that appear to be adapted to the long-term mean pattern of flows.

In regions where flow regimes are less predictable, life histories may be flexible and poorly synchronised (Winterbourn *et al*. 1981; Baird *et al*. 1987), or species may ‘hedge their bets’, i.e. distribute reproductive effort over a longer time period (Schaffer 1974; Lytle and Poff 2004).

The functional organisation of fish species into guilds based on reproductive and life history traits has yielded important insights into the relation between fish community dynamics and river hydrology. Winemiller and Rose (1992) based their classification of the life history strategies of North American fish on the classical *r*-K life history model of MacArthur and Wilson (1967), but split the *r*-strategists into two groups: opportunistic and periodic. Thus their classification included: (1) *equilibrium strategists* (MacArthur and Wilson’s K-strategists) with parental care, large eggs, inhabiting least disturbed environments and having high juvenile survivorship; (2) *periodic strategists* characterised by delayed maturation, large adult size, high fecundity and a contracted breeding season which inhabit seasonally suitable environments and (3) *opportunistic strategists* that have a small adult body size, short generation time, low fecundity per spawning event and an extended breeding season. This last group inhabits unpredictable environments. Any single species may be a combination of any of these three strategies and may fall anywhere within Winemiller’s (2005) pyramidal adaptive response surface.

Studies aimed at a functional analysis of river fish populations in relation to hydrological variability have been few (Cattanéo *et al*. 2001) because a large amount of biological information about individual species, together with multi-year data-sets on variations in fish abundances, is required. In those studies that have used a functional approach, however, the Winemiller and Rose model has been successful in predicting fish distributions, reproductive behaviour and invasion success in relation to hydrological variability. For example, in the Brazos River, Texas, Zeug and Winemiller (2007) showed that equilibrium strategists were most abundant in off-channel habitats where floods were less frequent; periodic strategists exhibited greatest reproductive activity during spring prior to increasing flows; and opportunistic stategists showed greatest reproductive activity in late spring and summer when flows were highest.

Using a range of adaptive attributes, Olden *et al*. (2006) classified the entire suite of native and non-native fish species in the Colorado River into groups based on the Winemiller and Rose life history model (Winemiller and Rose 1992). They found that the greatest declines in abundance of the native fish species following invasion by exotic fish species as well as flow modification by upstream dams, fell into two groups: (1) species not well adapted to the modified flow regime (i.e. periodic strategists) and (2) species that shared life history traits with the introduced species (suggesting competition for resources with the invaders were responsible for the decline). Conversely, the spread of the non-native fish species was afforded by the creation of 'niche opportunities' affored by the human-induced environment. In the case of the periodic strategists, Olden *et al*. postulated that the decline was due primarily to the alteration of flow from seasonal to non-seasonal conditions.

Fausch *et al*. (2001) showed that brown trout (*Oncorhynchus mykiss*) invasions were most successful where the flow regimes of the invaded rivers matched native flow regimes in their natural geographical range. Recruitment among brown trout populations is favoured by emergence during a declining flow period that reduces the risk of displacement by flooding. Trout were therefore more successful when invading regions

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that had winter flooding and summer low flows coupled with spring emergence. Regions that had spring or summer flooding and low winter flows inhibited trout recruitment.

The more extreme components of the hydrological regime, i.e. floods and droughts, have an important role to play in structuring fish assemblages. Seasonal flooding has been found to be critical for the timing and success of fish production – particularly for tropical floodplain systems (Welcomme 1985; Junk *et al*. 1989; Welcomme and Halls 2001). In temperate rivers, floods provide cues for spawning (e.g. Nestler *et al*. 1988) as well as improve the quality of spawning habitat by scouring sediments from the substratum making available interstitial habitat for lithophilous species (Cattanéo *et al*. 2001). The importance of flooding for fish production is encompassed by the Flood Pulse Concept (Junk *et al*. 1989) (discussed further in Chapter 8).

In arid and semi-arid regions, flow in rivers is less predictable, variability is the norm and droughts are a common occurrence (Walker *et al*. 1995). Droughts result in reduced connectivity and therefore reduced recolonisation, reduced water quality resulting in physiological stress and increased biotic interactions (competition and predation), thereby altering species composition and reducing population densities (Larimore *et al*. 1959; Fausch and Bramblett. 1991; Labbe and Fausch 2000; Lake 2003). Refugia such as deep pools play a critical role in the persistence of fish populations during drought (Magoulick and Kobza 2003).

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2.4.1 Life history studies and the flow regime: the South African context

The southern African region as a whole has amongst the highest interannaual variation in river flow of all the world's arid zone rivers (McMahon 1979), and as already noted, is subject to multi-decadal wet and dry cycles (Tyson *et al*. 2002). Although most rivers are perennial, displaying strong seasonality associated with temperate regions, a large proportion (44 %) of river reaches in South Africa are temporary, i.e. cease flowing for intervals ranging from several months to several years (Davies *et al*. 1993; Uys and O'Keeffe 1997). Given these environmental constraints, one would expect to find fish communities dominated by species with flexible and opportunistic life histories. In fact, rivers on the sub-continent are represented by species that have adopted a wide spectrum of strategies. For example, the chubbyhead barb (*Barbus anoplus*), a small-bodied cyprinid, has one of the widest distributions of any species south of the Limpopo River (Cambray 1983) and is one of the few species to have colonised parts of the arid and semi-arid Karoo. This species has many features that are characteristic of opportunism: small adult body size, short generation time, high fecundity and early maturation (Cambray 1982). In contrast, the Clanwilliam rock catfish (*Austroglanis gilli*) – a threatened species that occurs in the Olifants River of the Western Cape (although relatively small-bodied) has many features in common with equilibrium strategists, i.e. delayed maturation, extended generation time and low fecundity (Mthombeni *et al*. 2008).

The relation between life cycle and life history characteristics of fish species and the hydrological regimes of South Africa has not received much scientific attention. In one study, however, Cambray (1994) compared the reproductive styles of two sister species – the Eastern Cape redfin (*Pseudobarbus afer*) and Smallscale redfin (*P. asper*) – in the Gamtoos River system, Eastern Cape. *P. afer* inhabits perennial mountain streams, whereas *P. asper* is found in the more seasonal, variable and turbid rivers of the Karoo. Cambray (1994) found that although both were seasonal spawners, *P. asper* had a more extended breeding season (6-7 months *vs*. 4-5 months for *P. afer*), a greater number of spawning events per season, smaller egg sizes and greater number of eggs than *P. afer* – all indications that *P. asper* had opted for a more opportunistic life history strategy than *P. afer*.

Over most parts of South Africa, river flow is strongly seasonal. Perennial river flow in the Western Cape region of South Africa is driven by frontal low pressure systems. Peak flows here occur during winter (June to August) and decline through spring and summer. Over the central and eastern parts of the country, summer rainfall is largely driven by convectional thunderstorm activity and peak flows in this region therefore coincide with elevated temperatures. The larger-bodied cyprinids in South Africa, i.e. *Barbus*, *Labeo* and *Labeobarbus* species (the latter two genera being relevant to this study), time their reproductive output with optimal temperatures during spring and summer, as well as the seasonal availability of water (Jackson 1982; Allanson and Jackson 1983; Tomásson *et al*. 1984; Cambray *et al*. 1997; King *et al*. 1998). Thus in the winter rainfall region of the Western Cape, this group spawns when flows are subsiding through spring and early summer months (October to February), whereas in the summer rainfall region, spawning coincides with rising water levels. Their delayed maturation, large adult size, high fecundity and a contracted breeding season means that these cyprinids have a life history strategy commensurate with periodic strategists.

While these general patterns are known from circumstantial evidence, how fish respond to individual flow events and temperature fluctuations has not been well researched. There is some evidence that spawning by large-bodied cyprinids in the summer rainfall regions of the country is triggered by high-flow events (Allanson and Jackson 1983), but studies in the winter rainfall region of the Western Cape of spawning by Clanwilliam yellowfish were inconclusive with respect to the significance of flow (Cambray *et al*. 1997; King *et al*. 1998).

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2.4.2 Conclusion

The fact that fish life history strategies appear to be adapted to long-term hydrological cycles rather than an immediate response to individual flow events, has led some authors to suggest that EWR methodologies should focus more on historical flow characteristics (Lytle and Poff 2004; Zueg and Winemiller 2007). While some knowledge of habitat selection is required to establish causal associations between a particular flow and a population response there are considerable advantages to linking annual flow patterns directly to key events in a fish's life cycle. Studies of the life history strategies of South Africa's fish species have been few and only one of these has examined adaptive responses in the light of the prevailing physical conditions in rivers. Considerable scope therefore exists for future studies to focus on this aspect of indigenous fish ecology.

2.5 IN SUMMARY

The main objective of this overview has been to evaluate some of the conceptual approaches and methodologies that have shaped understanding of how river flow influences freshwater fish population and community dynamics, as well as to provide a background to some of the concepts that have formed the rationale and approach for the current study. The question of scale, both spatial and temporal, has been an abiding theme. Understanding fish population response to flow cannot be understood without understanding their place in the wider catchment context, just as a too narrow focus on micro-scale habitat processes is meaningless without referring to prior habitat conditions, i.e. the response of the population in terms of its relative abundance and size structure to the hydrological regime. An understanding of the life history of fish under consideration, particularly their reproductive style, is critical for understanding how they will respond to flow change. In studies of freshwater fish populations, a multi-scale approach should be adopted. This study has tried to integrate these considerations into its overall design as far as possible by examining patterns of distribution at the intermediate as well as microhabitat scales and by including an investigation into the timing of key early life history events in relation to flow and temperature regimes.

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CHAPTER 3 THE OLIFANTS-DORING RIVERS BASIN AND STUDY AREA

3.1 LOCATION AND PHYSIOGRAPHY OF THE OLIFANTS/DORING RIVER BASIN

The Olifants and Doring Rivers Basin is situated on the west coast of South Africa, centered at around 32º S and 19º E, and covers an area of 56 446 km^2 (Figure 3.1). These river systems straddle two biodiversity hotspots noted for their extraordinary levels of plant endemism – the Cape Floristic Region and the Succulent Karoo. They therefore fall within an ecotonal region that is to some extent reflected in their diverse hydrological and physico-chemical regimes.

3.1.1 The Olifants River

The main river, the Olifants, rises on the Agter-Witsenberg plateau approximately 100 km north-east of Cape Town. The headwaters flow off the eastern flanks of the Witsenberg and western flanks of the Skurweberg mountains. From the Agter-Witsenberg plateau, the river carves a narrow gorge north through the Groot Winterhoek and Skurweberg mountains before widening into the Olifants River Valley a further 25 km downstream at the farm Keerom. The valley, around 2.5 km wide at this point, is flanked by the Kouebokkeveld mountains to the east and the Olifantsrivierberg to the west. Another 30 km downstream of Keerom, and 80 km from the river's source, lies Citrusdal, the first major town in the upper river valley. The south-western portion of the catchment, between Citrusdal and Clanwilliam another 45 km downstream, is intensively cultivated, primarily with citrus orchards. Some of the water for irrigating this region is supplied by Clanwilliam Dam and Bulshoek Weir at 115 and 140 km respectively from the source of the river. The remainder of the water is supplied by run-of-river abstraction from both the mainstem and the tributaries as well as from farm dams. Between Citrusdal and Clanwilliam, several important tributaries enter the Olifants from the western flanks of the Cederberg including the Boontjies, Rondegat and Jan Dissels Rivers. At 160 km the Olifants River is joined on its eastern bank by the Doring River. Downstream of the confluence with the Doring River, the Olifants River becomes a deep, lowland, single-thread entrenched channel and farming activity (mostly vineyards) once more resumes along the banks and for much of the way to the estuary another 90 km downstream.

3.1.2 The Doring River

The Doring River is dry for 150 km from its source in the south of the Ceres Karoo to its confluence with its first major tributary, the Groot River. There are no records of this section of the Doring River ever having flowed. The Groot (fed by the Matjies and Riet rivers) flows from the eastern flanks of the Cederberg and Kouebokkeveld into the Doring, contributing oligotrophic water low in dissolved solids from these drainage regions. From its confluence with the Groot, the Doring River follows a northwards course through the Tankwa Karoo before gradually arcing west into the dolerite-intruded, mesa-and-butte topography characteristic of the Bokkeveld and Ecca Groups and Dwyka Formation sedimentary sequences of the arid south-western Karoo. The Tra-tra and Biedouw Rivers contribute more water from the Cederberg area at 35 and 70 km respectively from the Groot River confluence.

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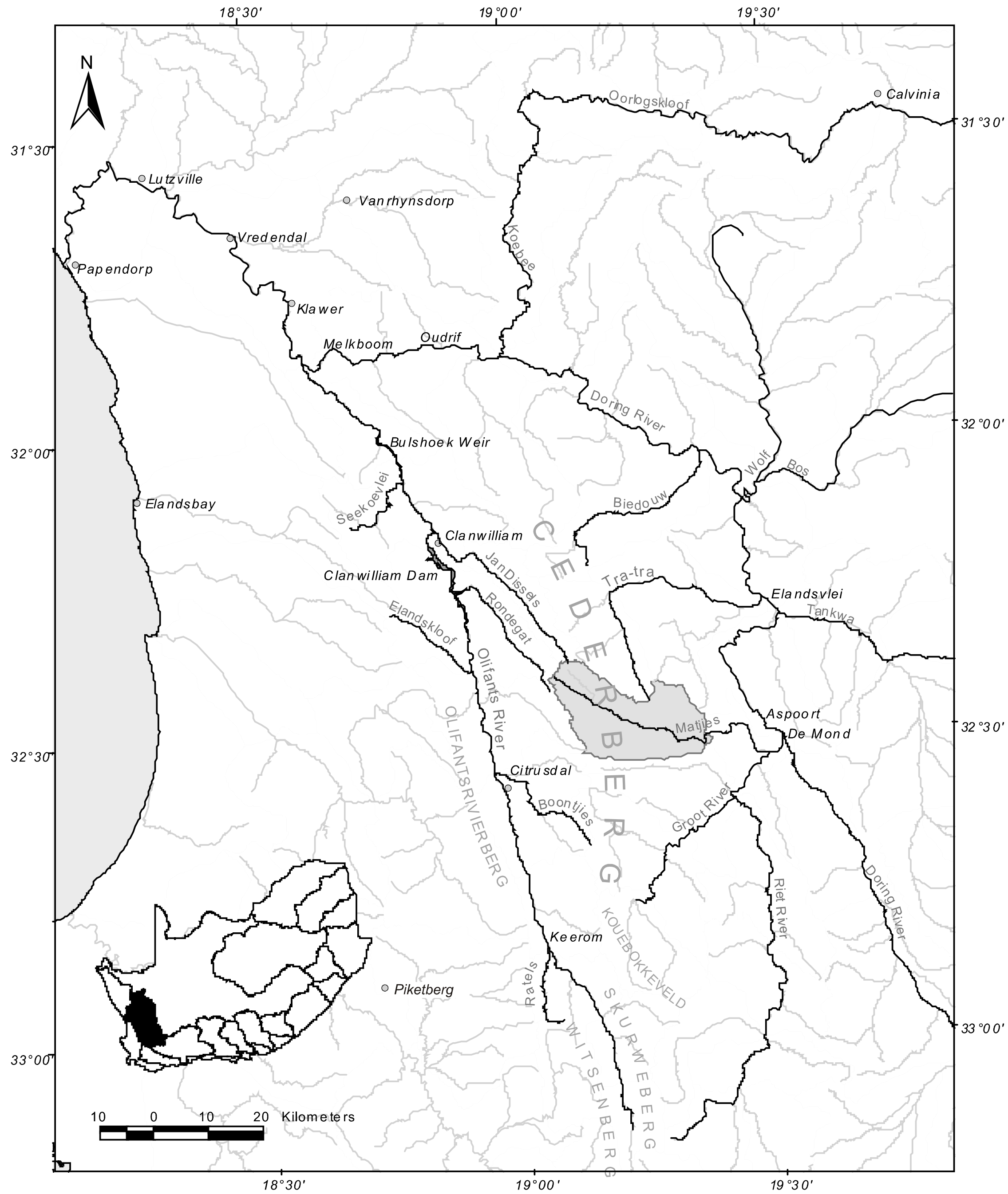

Figure 3.1 The Olifants and Doring Rivers Basin showing the main tributaries, dams and weirs. The shaded area shows catchment E21K (shown in detail in Figure 3.2).

Flow from these systems is augmented by more brackish water from the Tankwa and Bos/Wolf Rivers, which drain the Karoo, and the Koebee and Oorlogskloof rivers, which drain parts of the northernmost reaches of the basin in the vicinity of Calvinia. The Doring River joins the Olifants River near Klawer, roughly 150 km from the confluence of the Groot. Compared with the Olifants River the Doring River remains relatively under-developed. The only major town is Calvinia in the north and agricultural activity is limited to the Kouebokkeveld region to the south where numerous farm dams have been constructed for the irrigation of deciduous fruits and vegetables. Abstraction also takes place at the confluence of the Tankwa and Doring Rivers.

3.2 HYDROLOGY OF THE OLIFANTS AND DORING RIVERS

Discharge in the Olifants River is driven by frontal rains and is therefore seasonal, with high winter flows between May and October and low summer flows between November and April. Mean annual precipitation (MAP) at the headwaters and southern tributaries of the Olifants River varies from *c*. 1400 mm in the south-western corner of the catchment decreasing to *c*. 100 mm in the extreme north (DWAF 2005). A large proportion of the runoff of the Olifants River is derived from its Cederberg tributaries including, amongst others, the Ratels, Boontjies, Rondegat and Jan Dissels Rivers. A considerably smaller component of the runoff is contributed by tributaries rising in the Olifantsrivierberge (e.g. Elandskloof and Seekoevlei Rivers).

The Doring River catchment straddles the boundary between a winter and a non-seasonal rainfall regime, with the MAP varying from *c.* 500 mm near the headwaters to *c.* 100 mm in the northern and eastern regions of the catchment (DWAF 1994). Flows in the western tributaries of the Doring River (e.g. Groot, Tra-tra, Biedouw Rivers) are primarily driven by winter cold fronts, whereas flows from the more northerly areas may be driven by summer thunderstorm activity over the Karoo. Winter baseflows are high along the whole river, but drop off sharply in spring, with river flow ceasing for several months each year since the 1960s. During such times the river may resume flow for brief periods as a result of convectional thunderstorms from the Karoo, but these flows are highly erratic. The perennial Groot River, flowing from the high-rainfall eastern flanks of the Cederberg mountains, contributes approximately 50% of the runoff of the Doring River as measured at its confluence with the Olifants River and is the major influence on water quality and flow.

The total natural mean annual runoff (nMAR) of the Olifants River at the estuary is *c*. 1108 Mm^3, of which 514 Mm^3 is contributed by the Olifants River itself and the remainder by the Doring River (Basson and Rossouw 2003). Present day flows reaching the sea are estimated at 64% of the nMAR (*c*. 708 Mm^3). Clanwilliam Dam (live storage 122 million m^3) releases water downstream on demand to the Bulshoek Weir (live storage 5.7 million m^3) from where it is diverted into a system of irrigation canals that distribute water from the Upper Olifants sub-area to the Lower Olifants. Farm dams supply 35% of the water required for agriculture in the Olifants valley, with Clanwilliam Dam and Bulshoek Weir supplying a further 44% and run-of-river abstractions accounting for an estimated 21% (Basson *et al*. 1998). Flow in the naturally perennial Olifants River upstream of the Clanwilliam Dam in the vicinity of Citrusdal ceases during the late summer when demand for irrigation water is high, thus the duration of the no-flow period in this part of the mainstem has increased from 5% under natural conditions to 45% under present day conditions (Birkhead *et al*. 2005). Under natural conditions dry season low flows > 1 $m^3 s^{-1}$ were exceeded 60% of the time, whereas under present day conditions they are exceeded only 30 % of the time (Birkhead *et al*. 2005). The flood regime in the upper Olifants remains relatively unchanged with Class I to IV floods varying in magnitude between 14.2 and 113.6 $m^3 s^{-1}$, respectively. No water is released from Bulshoek Weir to the lower Olifants River and dry season low flows (estimated at *c*. 0.2 $m^3 s^{-1}$) are the result of a leak in the barrage.

In the Doring River sub-basin, the Kouebokkeveld region that forms the headwaters of the Groot and Riet rivers, is extensively farmed and impounded. Abstraction also takes place from the Tankwa, the Bos and the Koebee Rivers. The Oudebaskraal Dam on the Tankwa River is the largest privately owned farm dam in South Africa although it is seldom full. There are gauging weirs on the Doring at Aspoort and Melkboom. A farm dam of around 5 m in height has been built on the mainstem of the Doring River in the vicinity of the Tankwa River confluence and is the largest instream structure on the river. The extension of the no-flow

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period in the Doring from 45 % under natural conditions to 70 % under present day conditions is the result of abstraction in the Kouebokkeveld region. Class I to IV floods on the Doring River have been estimated at between 35 and 280 $m^3.s^{-1}$ respectively under present day conditions (Birkhead *et al*. 2005).

3.3 WATER QUALITY

The varied geological nature of the Olifants-Doring Basin gives rise to the dual nature of its water chemistry. The resistant quartzitic sandstones of the Table Mountain Group (TMG) of the Cape Fold Belt mountains result in clear, oligotrophic waters of low conductivity in the headwater and foothill reaches of the Olifants (Dallas 1997). At the downstream end of the Olifants River valley, near the town of Klawer, the Cape Fold Belt is replaced by low-lying Vanrhynsdorp Group deposits. This transition, together with its juncture with the Doring River, results in a steep increase in conductivity of the river water downstream (Dallas 1997). The water quality in the tributaries that rise in the Cederberg Mountains is influenced by the quartzitic sandstones of the Table Mountain and Witteberg Groups, and tends to be clear with a low conductivity – pH and conductivity at Keerom in February and October 2001 varied between 6.9 – 7.3 and 22 – 25.2 μS cm^{-1} respectively (Table 3.1).

During periods of high flow from the Karoo tributaries, turbid, saline waters draining the highly erodable shales and mudstones of the Dwyka Formation and Ecca Group enter the Doring River. Waters flowing from these formations exhibit elevated levels of nutrients, pH and conductivity – pH and conductivity in the Keobee River in October 2001 for instance, were 8.08 and 337.7 $\mu S.cm^{-1}$ respectively. Over the summer no-flow period in the Doring River, conductivity levels may increase considerably – conductivities measured in the Doring River at Oudrif and near its confluence with the Olifants River for instance exceeded 1000 μS cm^{-1}.

TABLE 3.1 Water quality in the Olifants and Doring Rivers: temperature (temp, °C), pH, conductivity (cond, μS cm^{-1}) and turbidity (turb, NTU) at sites visited during February and October 2001 surveys (Paxton *et al*. 2002).

		February 2001			October 2001		
River	Site description	Temp. (°C)	pH	Cond. ($\mu S.cm^{-1}$)	Temp. (°C)	pH	Cond. ($\mu S.cm^{-1}$)
Olifants River	Keerom	21.5	7.3	22.0	18.2	6.9	25.2
Olifants River	Olifants River at Clanwilliam	22.2	7.1	386.0	22.1	6.9	86.0
Olifants River	Cascade Pools	25.5	6.5	130.0	20.8	6.9	152.9
Doring River	Aspoort	29.0	7.3		24.7	7.5	90.3
Doring River	Bos confluence	-	-	97.4	23.5	8.0	127.4
Doring River	Biedouw confluence	24.7	8.7	263.8	19.2	7.9	190.4
Doring River	Doringbos	27.8	7.9		19.8	7.8	187.1
Doring River	Oudrif	24.0	8.7	1425.1	19.6	8.0	252.0
Doring River	Olifants confluence	28.2	7.4	1000.4	21.1	8.2	318.2
Groot River	De Mond	27.8	7.6	137.0	21.3	7.2	113.8
Tra-tra	Doring confluence	-	7.6	287.17	22.2	7.5	62.0
Koebee	Koebee River	-	-	-	22.2	8.0	337.8
	Mean	25.7	7.8	537.8	21.0	7.6	195.9

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3.4 SITE SELECTION

For purposes of comparison, it was initially intended that this study include representative reaches in the tributaries and mainstem of the Doring River. A preliminary reconnaissance early in 2004 identified segments of the Driehoeks-Matjies and Groot Rivers, as well as the upper reaches of the Doring River (Quaternary catchments E21K, E21L and E22G) as containing potentially suitable study sites (Figure 3.2).

The Driehoeks River rises in the Cederberg mountains at an altitude of ~1010 m before flowing in an south-easterly direction towards the Doring River. At ~17 km from its source it is joined by a small tributary, the Dwars River, on its right bank and from here, it is named Matjies River. The Matjies River flows into the Groot River, and from there into the mainstem of the Doring River. The whole of the Driehoeks River and parts of the Matjies River are situated in quaternary catchment E21K.

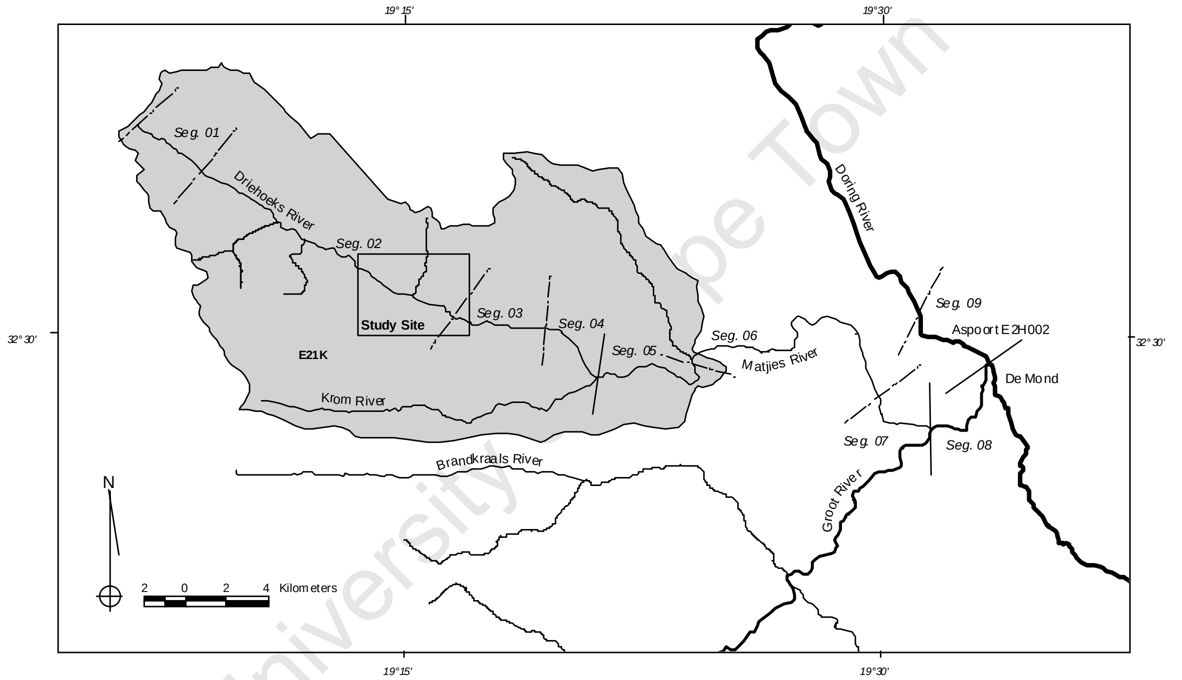

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Figure 3.2 The Driehoeks and Matjies River catchment showing the study area (shaded inset: catchment E21K) and river segments (Seg. 01-09, Figure 3.3) between the headwaters of the Driehoeks River and the mainstem of the Doring River. River segments are based on breaks in mean gradient (broken lines) and the confluence of major tributaries (solid lines) (E2H002 = Aspoort weir). The inset shows the Study Site (Figure 3.4).

The combined Driehoeks-Matjies River system can be partitioned into nine Segments (*Seg.*) on the basis of major breaks in mean river channel gradient, the confluences of major tributaries, and changes in the topography of the river valley (Figure 3.2 and Figure 3.3). The Driehoeks River rises as a series of high-gradient headwater streams (*Seg. 01*) that feed an extensive seepage zone in the upper reaches of *Seg. 02*. For the remainder of *Seg. 02* the river flows over a relatively low gradient upland plateau. From *Seg. 03* the river, now called the Matjies, flows through a steep gorge where the channel comprises a series of deep pools, bedrock steps and waterfalls. Once the river emerges from the gorge in *Seg. 04* the gradient becomes less steep and the valley less confined. Here the river braids through sedges and reedbeds. At Seg. 05, the Matjies River is joined by the Krom and the river once more enters a confined gorge for roughly 25 km with surrounding peaks rising to 900 m amsl.

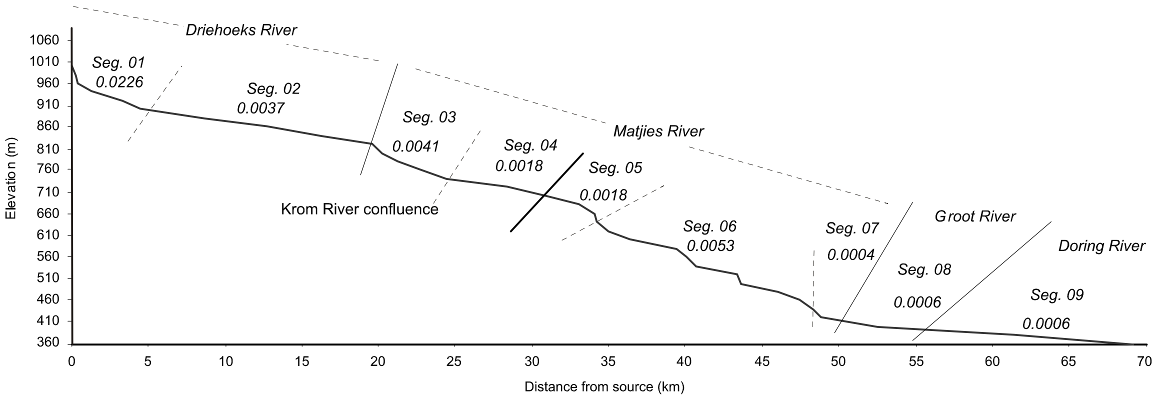

Figure 3.3 Longitudinal profile of the Driehoeks, Matjies, Groot and Doring River from its source to the Doring River. River segments (*Seg. 01-09*) indicate breaks in mean gradient (broken lines) and major confluences (solid lines). The mean gradient over the whole segment is reported beneath the segment number. The study area was located in *Seg. 02*.

This topography characterises *Seg. 06* and *07* as well. Once the Matjies River joins the Groot River at roughly 50 river-km from its source (*Seg. 08*, Figure 3.3) the gradient decreases and remains relatively even (0.006) from the confluence to *Seg. 09*. A DWAF gauging weir (E2H002) is located at Aspoort. Within this region three lengths of river were selected as being potentially suitable for the purposes of the study. These were: *Option 1* the Driehoeks-Matjies Rivers system in *Seg*. 02; *Option 2* the Groot River at De Mond in *Seg*. 08 and *Option 3* the Doring River at Aspoort *Seg*. 09. An initial dive survey in October 2004, however, revealed that the mainstem segments on the Groot (*Option 2*) and Doring Rivers (*Option 3*) were unsuitable due to the very low densities of indigenous species. During the course of this survey that covered most of *Seg*. *09* on the Doring River, only 29 adult Clanwilliam yellowfish were counted – a mean of no more than 5.8 fish.river-km – and a single dead adult sawfin was found. In addition to the low numbers of indigenous fish species, all fish were over 300 mm TL . These preliminary surveys confirmed the findings of earlier surveys, that there had been negligible recruitment of young fish into the adult population in the mainstem reaches for a number of years.

The mainstem reaches were thus rejected as potential sites, and the site selection process focused on the Driehoeks-Matjies River system. Within this system the suitability of river reaches for study purposes was further constrained by the mountainous terrain, the rivers' passage through precipitous gorges from *Seg. 03* to *Seg. 07* (the confluence of the Groot River, Plate 3.1), as well as dense riparian and aquatic vegetation that made access to the river impossible from the banks. Parts of *Seg. 02* were relatively easily accessible by vehicle and a dive survey over 5.9 km of this segment was conducted. In contrast to the conditions in the mainstem – and despite the temperatures in the Driehoeks-Matjies Rivers system being considerably lower than in the Doring and Groot at the time of the initial dive surveys due to the altitudinal difference between the two areas (~12°C as opposed to ~20°C on the Doring) – 117 individual adult fish (56 Clanwilliam yellowfish and 61 sawfin) were counted during the course of the dive. This translated to a mean of 19.7 fish.river-km^{-1}. The 5.9 km segment was therefore selected as the study area.

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Plate 3.1 The confluence of the Matjies with the Groot River at the boundary between *Seg. 07* and *08* (Figure 3.3).

3.5 DRIEHOEKS-MATJIES RIVERS STUDY AREA

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The 5.9 km segment of river that was eventually selected as a suitable location for the study was located in *Seg. 02* and part of *Seg. 03* at an altitudinal range between 800 and 850 *amsl* (Figure 3.3 and 3.4). Although this part of the river was located in the mountain headwater zone, the gradient was gentle (0.004) and the river channel had many features that are more commonly associated with a foothill zone, i.e. a relatively wide macro-channel, alternating riffle-pool-run sequences with fines (sand and silt) dominating the substratum in the slower runs and deeper pools. The channel was mostly straight with few meanders (Figure 3.4). Braided reaches alternated with single-thread alluvial and bedrock runs between 0.3-1.5 m deep. Although the single channel reaches were no more than a meter wide in places, the macro-channel in the braided reaches was up to 120 m wide. In these reaches, a number of interlinked active channels flowed through islands consolidated by sedges and reeds. Twelve pools – reaches that had slow flowing water greater than 1.5 m in depth – were identified within the study area (Figure 3.4). The river banks and bed were largely undisturbed and apart from a causeway 1.5 km upstream from the start of the study segment (passable to adult fish over the study period), there were no major obstacles to fish passage. Limited farming activity was taking place along the upper reaches and oak (*Quercus sp.*) and poplar (*Populus sp.*) had invaded some sections of the river bank. The riparian zone comprised reeds, sedges and shrubs belonging to the Fynbos Biome. For the most part the river was a single-thread channel, interspersed with braided reaches where narrow channels were separated by vegetated islands of predominantly the indigenous rush (*Elegia spp.*) and Cape willow (*Salix capensis*). During spring, the river had a mean width of 6.5 m and mean depth of 1.1 m outside of floods or freshes. Mean discharge over the study period between August 2004 and March 2006 was 0.4 m^3 s^{-1} and water temperatures varied between 5.5 °C in winter to 26 °C in summer. Water conductivity was very low and in December ranged between 24 and 28 μS cm^{-1} and pH was between 5.6 and 6.2.

Four indigenous fish species were known historically to occur in the Driehoeks River (collections database South African Institute for Aquatic Biodiversity, accessed 2006): the sawfin, Clanwilliam yellowfish, fiery redfin (*Pseudobarbus phlegethon*) and Cape Galaxias (*Galaxias* spp). Alien Largemouth bass (*Micropterus salmoides*) were introduced to the river and although they occur throughout the study segment, abundances are low. Fiery redfin appeared to have disappeared from large parts of the river and none were observed during the course of dive surveys – possibly as a result of predation by the bass.

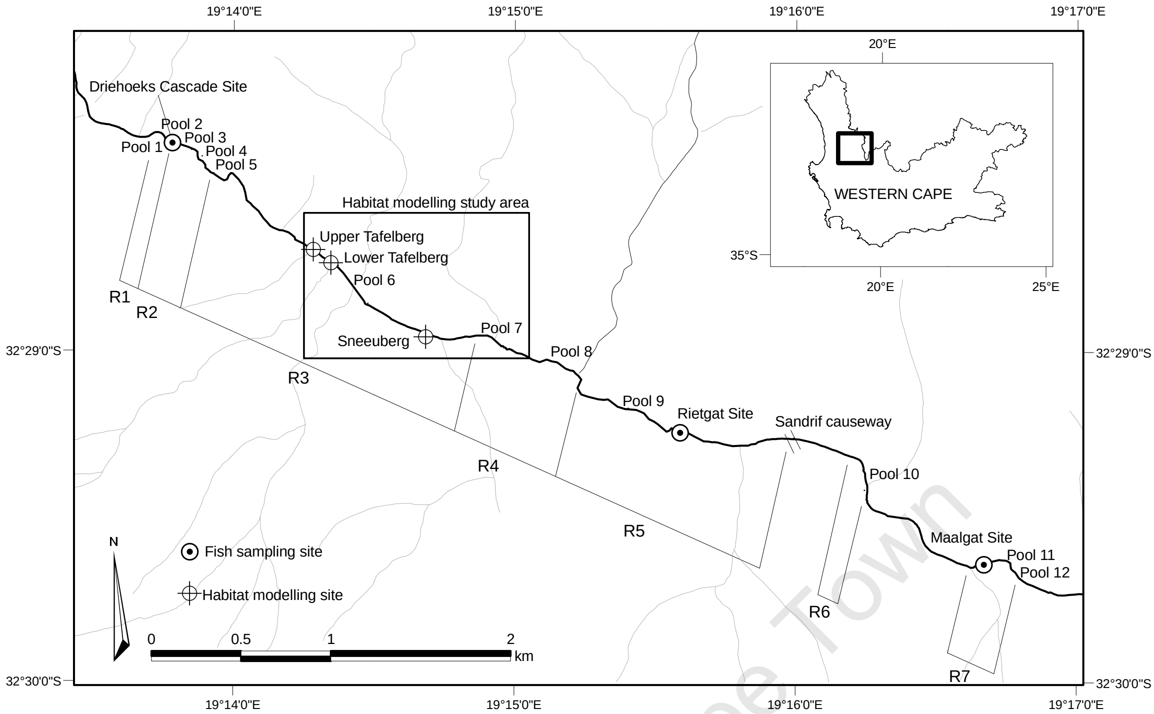

Figure 3.4 Map of the study area showing the Driehoeks River. The direction of the flow is from northwest to southeast. The distance along the river from the beginning of R1 to the end of R7 was 5.9 km. The numbered reaches (R1-R7) relate to the dive surveys conducted in Chapter 4. The box inset shows the region from which data for the development of Habitat Suitability Criteria were derived (Chapter 5). The three modelling sites within this area were: (1) Upper Tafelberg, (2) Lower Tafelberg and (3) Sneeuberg. The sites from which larval and juvenile sawfin were collected for aging studies (Chapter 6) were: Driehoeks Cascade, Rietgat and Maalgat.

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The study area was divided into seven reaches based on the dominant channel type, dominant habitat types and mean depth. The reaches were numbered from upstream (*Reach 1*) to downstream (*Reach 7*) (Figure 3.4). Since the classification of the reaches was primarily for the purposes of the fish distribution surveys, a quantitative description of the habitat in each reach can be found in Chapter 4 (Section 4.3.1). A more qualitative description is provided here. *Reach 1* (Figure 3.4) was the upper limit of the study area. It consisted of a short sequence of deep runs separated by bedrock controls with cascades. *Reach 2* was separated from *Reach 1* by a steep bedrock cascade approximately 3 m in height (Plate 3.2).

Plate 3.2 Driehoeks Cascade forming the boundary between *Reach 1* and *2* (Figure 3.4) Pool 3 is in the immediate foreground

This was considered impassable in an upstream direction to juvenile fish, but adults were observed ascending this cascade over the spawning period. The decision to end the study area in *Reach 1* upstream of the cascade rather than at the cascade was based on the discovery of significant numbers of juvenile sawfin in *Reach 1* – the only other reach in the segment that had juvenile sawfin was *Reach 7* and therefore of significance to the study. *Reach 2* comprised a series of deep pools (Pools 3-5), one of which (Pool 3) was the deepest in the study area (3.5 m). The river banks along *Reach 1* and *2* comprised shrubs, sedges and reeds typical of the Cape Floristic Region, but some oak trees (*Quercus* spp.) were present along the banks of the most downstream end of *Reach 2* (Plate 3.3)

Plate 3.3 Reach 2 (*R2* Figure 3.4) on the Driehoeks River in the Cederberg. Pool 5 is in the immediate foreground

At 1.9 km, *Reach 3* was the longest of the seven reaches since it had the most continuously homogeneous habitat characteristics, i.e. a series of shallow riffle-run sequences with a predominantly sandy substratum in the slower regions and few of the pools or bedrock controls that characterised much of *Reaches 1*, *2* and *7* (Plate 3.4). This reach, together with a short section of *Reach 4* was the focus of the habitat modelling component of the study (Chapters 5 and 6) since most of the spawning activity took place in this reach (box inset, Figure 3.4). The three modelling sites: Upper Tafelberg, Lower Tafelberg and Sneeuberg, were all encompassed within this reach. Some agricultural activity took place on the right bank of *Reach 3* (livestock and vegetables) and oak trees were present along the right bank.

Plate 3.4 A typical riffle-run sequence the Lower Tafelberg site that characterised much of *Reach 03*.

The largest pool in the study area (Pool 8) was located at the start of *Reach 4*, it was 210 m long with a maximum depth of 2.8 m. Although no modelling sites were located in *Reach 4*, data for the development of Habitat Suitability Criteria were collected from the upstream end of the reach (box inset, Figure 3.4). *Reach 5* started at the downstream end of Pool 8. From here the river braided through dense riparian sedges and trees (*Elegia* spp. and *Salix capensis*) for 60 m beyond Pool 6 before opening into a bedrock run. *Reach 5* consisted of a series of shallow sandy runs bordered by an indigenous riparian belt as well as oak and reedbeds. There was only one major pool on this reach (Pool 9), but several meander bend pools of ~1.5 m in depth were scoured out at the upstream end of last shallow run. There was a concrete causeway over the river at the Sandrif (Figure 3.4) and this marked the downstream limit of *Reach 5*. Between the downstream end of *Reach 5* and the upstream limit of *Reach 7*, the river meandered through a series of dense reedbeds that precluded dive surveys. A particularly large pool (Pool 10) between these two reaches was included in the dive surveys (*Reach 6*).

The channel in *Reach 7* was laterally confined by a relatively steep-sided valley and the bedrock-controlled channel was straight and mostly single-thread (Plate 3.5. This reach was dominated by bedrock features and a step-pool morphology with large clasts. The downstream limit of Reach 7 (and therefore the whole study segment) was bounded by a three meter high waterfall (Maalgat) that also marked the beginning of the gorge in *Seg. 03* (Plate 3.5). The downstream end of this waterfall was considered impassable to both adult and juvenile fish moving upstream. The largest pool in Reach 7 (Pool 11) was 54 m long and up to 1.8 m deep.

Plate 3.5 Reach 7 showing the downstream limit of the study area where a steep waterfall followed by a deep pool (left) marked the downstream end of the segment. Pool 11 is visible to the right.

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CHAPTER 4 Spatial and seasonal variations in the distribution and abundance of larval, juvenile and adult sawfin in the Driehoeks River

4.1 INTRODUCTION

As pointed out in Section 2.2, an appreciation for the spatial and temporal patchiness of resources in ecosystems and how these change through time is fundamental to understanding annual and inter-annual shifts in the abundance and distribution of living organisms (Pringle *et al*. 1988; Southwood 1988; Schlosser 1991; Fausch *et al.* 2002). The response of both vertebrates and invertebrates to environmental heterogeneity is dynamic, and the importance of dispersal between one or more core or source habitats (i.e. habitats where birth rates exceed mortality) and (sink habitats i.e. habitats where birth rates are insufficient to balance mortality), has been documented for a number of species and in a variety of ecosystems (Pulliam 1988; Roughgarden 1988; Hanski 1998; Schlosser 1998; Caudill 2003). The availability of, and connectivity between, spawning, nursery and feeding habitats, as well as access to refugia during disturbances such as droughts or floods, are important determinants of the ability of fish populations to persist in any given river segment (Schlosser 1991; Labbe and Fausch 2000; Fausch *et al*. 2002; Magoulick and Kobza 2003). These biological responses to the heterogeneity of the river environment are scale dependent, varying across a range of life stages and activities from daily movement between foraging and resting areas, to seasonal migrations that may cover many hundreds of kilometres (Schlosser and Angermeier 1995; Harvey *et al*. 1999; Durance *et al.* 2006). Crook *et al*. (2001) therefore emphasise the need for scale-dependence in habitat studies.

Despite a broad acknowledgement that intermediate and large-scale processes are as important, if not more so, than local-scale factors in controlling fish population dynamics, a disproportionate number of fish habitat studies have examined processes that occur at the microhabitat or reach scale 10^{-1}-10^{2} m (Labbe and Fausch 2000; Fausch *et al*. 2002; Durance *et al*. 2006). Roper *et al*. (2001), for instance, report that most of what is known about juvenile salmonid distribution comes from studies of reaches <500 m long. Thus, they argue, the selection of a 'representative' reach may not reveal the factors that determine the distribution of fish within a catchment. A small but growing body of research has addressed fish responses to habitat at the landscape or 'riverscape' scale (>10^{3} m), where processes such as disturbance, dispersal and the patch mosaic structure of habitat beyond the reach scale are emphasised over local biotic and abiotic factors in structuring fish populations (e.g. Roper *et al*. 1994; Schlosser 1998; Torgersen *et al.* 1999; Labbe and Fausch 2000; Schaefer and Kerfoot 2004; Mesquita *et al.* 2006). Most of this work has taken place in the northern hemisphere. The spatial dynamics of fish species inhabiting south-temperate rivers that are characterised by strong seasonality, high inter-annual flow variability and frequent drought conditions, are comparatively little known, although some work has been done in Australia (Arthington *et al*. 2005; Balcombe *et al*. 2006; Balcombe *et al*. 2007). These types of rivers are subjected to alternating lotic and lentic conditions during the year, which probably have pronounced effects on the fish populations that inhabit them. During the low-flow period, pools become important refugia, (Schlosser 1982; Magoulick and Kobza 2003) with reduced connectivity between river reaches and a concentration of fish populations in these pool refugia. During the

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wet season, connectivity between pools is re-established and fish are able to recolonise larger parts of the river system (Bernado and Alves 1999). During winter, deep pools are equally important as refugia from high flows (Labbe and Fausch 2000; Muhlfeld and Bennett 2001). These types of processes are believed to be important controlling factors in the seasonal spatial dynamics of the large-bodied endemic cyprinids, including the Clanwilliam yellowfish and sawfin that inhabit the Olifants and Doring Rivers in the Western Cape, where seasonal wetting and drying cycles are prevalent. Prior to their disappearance from mainstem reaches of the Olifants River in the late 20th Century, observers at the time reported seeing large mixed schools of these cyprinids migrating upstream during spring to spawn (Harrison 1977). The reproductive season of these two species coincides with rising temperatures and declining flow in the winter rainfall region of the Western Cape. Studies have subsequently confirmed that these cyprinids are rheophilic spawners, relying on shallow, fast-flowing cobble-bed riffles to deposit eggs during the spring (Cambray *et al*. 1997; King *et al*. 1998, Chapter 5; this study). Thus, in addition to the need for accessing winter and summer refugia, the timely arrival of large numbers of adult fish in suitable habitats at the end of the high-flow period is critical for successful reproduction.

Fausch *et al*. (2002) called for river fish studies to be spatially continuous and georeferenced, and suggested that a multi-scale, nested approach to sampling design be adopted (Section 2.2). Visual census by means of dive surveys has been found to be an effective alternative to electrofishing for estimating the abundance of fish, particularly in small streams where endangered fish occur and therefore where injury, stress or mortality resulting from electrofishing is undesirable (Roper *et al*. 1994; Joyce and Hubert 2003). The primary aim of this component of the study was therefore to query how sawfin in the Driehoeks River respond to heterogeneity at the River Segment scale (Section 2.2). The objectives included: (1) to determine whether there were seasonal variations in the relative abundances and distribution of larval, juvenile and adult sawfin along the longitudinal profile of a six kilometre segment of the Driehoeks River prior to, during and after the spawning period and (2) to establish whether these variations could be explained in terms of the spatial arrangement of physical habitat units within the study segment. The dive surveys also served to identify the location and quantity of critical reproductive and nursery habitats, as well as to characterise the dispersal and/or movement of larval and juvenile fish to nursery habitats following the spawning season. Following from the predictions of Schlosser (1982) and Magoulick and Kobza (2003), pools were expected to be important refugia during the peak of the high flow period and at the end of the low flow period. Prior to the commencement of spawning at the end of the wet season, an upstream or downstream increase in abundance of fish into shallow riffles and runs was expected to be associated with the presence of suitable reproductive habitat. The focus of this chapter is on sawfin since these were the most abundant of the two species in the Driehoeks River.

4.2 METHODS

4.2.1 Study area and sampling regime

Estimates of the relative abundance of fish and description of habitat conditions were obtained by means of dive surveys carried out along the 5.9 km study segment on the Driehoeks River (described in Section 3.5). A total of ten dive surveys covering the entire six kilometre segment was conducted over an 18 month period between October 2004 and March 2006. The exact dates of the dive surveys are reported in APPENDIX A.1.

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In each of the sampling seasons, 2004/5 and 2005/6, two surveys were conducted at the end of high flow season (early and late October), two at the beginning of, and during each of the spawnings season (mid-November and mid-December) and one at the end the two low flow seasons (February/March). Surveys were carried out between 14h00-18h00 when fish were found to be most active and therefore more visible. Except for two reaches that could not be accessed due to extensive reedbeds (between *Reaches 5* and *6* and *Reaches 6* and *7*; Figure 3.4), the dives were continuous throughout the study segment.

4.2.2 Physical habitat description of reaches

A survey of the physical habitat conditions over the entire study segment was undertaken in October 2004, during the course of the initial dive survey. Eighty-seven channel-spanning morphological units (Wadeson 1994; Rowntree and Wadeson 1999) along the longitudinal profile of the river were identified. The maximum depth, width and length of each morphological unit was measured using a measuring tape. Boundaries between individual morphological units were identified using a combination of visually assessed factors including: inflections in channel width, slope and depth as well as the presence of hydraulic controls such as waterfalls, bedrock or boulder steps, cascades or chutes. The geographical coordinates for beginning and end of each morphological unit were recorded using a handheld GPS. The morphological unit, together with its dominant and sub-dominant substratum class, dominant and sub-dominant flow-types and hydraulic biotopes were classified according to the categories suggested by Wadeson (1994) and Rowntree and Wadeson (1999) (Table 4.1).

TABLE 4.1 Definitions of the morphological units, substratum class, flow type and hydraulic biotopes occurring in the study area (from Wadeson 1994 and Rowntree and Wadeson 1999).

MORPHOLOGICAL UNIT	Description
Alluvial Pool	topographical low point caused by scour
Bedrock Pool	deeper flow behind resistant strata
Bedrock Pavement	horizontal area of exposed rock
Cataract	step-like succession of small waterfalls
Step	step-like features formed by large cobbles or boulders
SUBSTRATUM CLASS	
Sand	<2mm
Gravel	2-64 mm
Cobble	64-256 mm
Boulder	256-1000 mm
Bedrock	>1000 mm
FLOW TYPE	
No flow	no water movement
Barely perceptible flow	smooth surface flow, perceptible through floating objects
Smooth boundary turbulent flow	water surface smooth, streaming flow
Rippled surface	transverse ripples across flow direction
Standing waves	undular or broken standing waves
HYDRAULIC BIOTOPE	
Pool	deep, slow flowing
Run	transition between pool and riffle, low relative roughness
Riffle	topographic high points, high relative roughness
Cascade	bed has a stepped structure due to cobble
Chute	water channeled between large bed elements
Waterfall	free-falling flow

The physical characteristics of the 87 habitat units, including the location, length and habitat classification can be found in APPENDIX B.1. In this way a record of the important morphological characteristics and an estimate of the relative dimensions of major channel-spanning features along the length of the entire study segment were obtained.

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4.2.3 *Underwater census*

Hanking (1984) recommended that sample units be equivalent to natural habitat units. Thus each of the 87 morphological units (Section 4.2.2) identified within the study segment corresponded to a sample unit. At the beginning of each morphological unit, the diver entered the river at the most downstream point and began swimming in an upstream direction following the thalweg and maintaining a constant swimming speed. Whenever a fish or school of fish was observed, the species, number and size class (estimated using a calibrated writing slate) were recorded and the location of each fish or school of fish was marked by means of a handheld GPS.

The three size classes were as follows: free-swimming larvae and early juveniles (5-20 mm TL), 0^+ and 1^+ juveniles (21-150 mm TL), and adults (>150 mm TL). For large schools, in situations when it was not possible to chase fish past the counter, the number of fish was estimated by repeated counts and rounded off to the nearest ten. The low diversity of fish species, as well as generally low densities of fish throughout the Driehoeks River facilitated counting. Visibility was constant throughout the study reach, but declined from 4 m in early spring and summer (October-December) to 2-3 m in late summer (March). In all but the deepest and widest pools, the visibility was sufficiently good to see both banks and the bed simultaneously. A single pass of the entire 5.9 km study segment could be completed over three days. In addition to estimating fish abundances, the dive surveys also served to verify the location of spawning sites that were identified on the basis of observed spawning behaviour and the subsequent collection of eggs.

4.2.4 *Fish tagging*

To supplement information from the dive surveys, a mark-recapture programme was undertaken in the study segment between October 2004 and December 2005. Fish were caught using fyke nets that were left in the river overnight and retrieved the following morning. All sawfin > 150 mm TL were marked with soft Visible Implant (VI) Alpha tags (Northwest Marine Technologies, Inc). These tags were implanted into the transparent adipose periocular tissue by means of an injector. The location and number of fish caught and tagged between 2004 and 2005 are listed in Table 4.2. A total of 1346 fish were captured of which 249 were tagged.

TABLE 4.2 Location and number of sawfin caught and proportion tagged in 2004 and 2005.

Year	Month	No.	Tagged	Location
2004	Nov	184	62	Reach 2
	Nov	19	22	Reach 7
	Dec	260	6	Reach 7
2005	Mar	195	21	Reach 7
	Oct	51	46	Reach 4, 6
	Nov	260	92	Reach 3, 4
	Dec	88	0	Reach 2, 3
Total		1346	249	

4.2.5 *Analysis*

The information collected during both the habitat and fish census surveys was imported into a GIS database using the programme ArcGIS 9.1 © (ESRI 2005). Maps of relative fish abundance and distribution were produced for each complete dive survey and the three size classes of interest: larvae, 0^+ and 1^+ juveniles and adult. Dominant flow-types recorded during the course of the habitat surveys were re-classified according to the following categories:

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Slow—no flow, barely perceptible flow
Medium—smooth boundary turbulent
Fast—chute, standing wave, rippled surface

The physical-habitat information was used to consolidate the 87 habitat units into seven river reaches (numbered from upstream to downstream (Reaches 1 – 7, Chapter 3; Figure 3.4). Rather than divide the segment into a number of equal-length reaches that contained a wide range of dissimilar habitat conditions, the segment was divided into reaches that displayed continuity in broadly similar habitat conditions. This meant, however, that the reaches varied considerably in length (~100 and ~1900 m). The reaches were defined on the basis of a wide range of quantitative and qualitative information including: visually assessed breaks in the depth profile of the river, the presence of major obstacles such as causeways, waterfalls or reed beds and the occurrence of similar repeated morphological characteristics, e.g. deep pools, bedrock *vs*. alluvial channels or extensive riffle-run sequences. The GIS database of all the fish locations and abundances recorded during the course of each dive survey was superimposed on a polygon of the morphological units in a GIS software programme (ArcGIS 9.1). Each polygon was assigned a depth, flow and substratum category and the association between different fish size-classes and habitat variables between seasons was then queried using a spatial join. The frequency of occurrence of adult sawfin in each of the three habitat variables in each sample month was calculated, entered into a two-by-two contingency table (rows = months of the year; columns = habitat categories) and tested for significance by means of a Chi-Squared test of independence in Statistica (Statsoft© 2004).

4.3 RESULTS

4.3.1 Reach characteristics

The physical-habitat characteristics of each of the seven reaches are reported in Table 4.3 and those of the morphological units in APPENDIX B.1. *Reach 1*, immediately upstream of a steeply inclined bedrock pavement, was the shortest reach in the study segment (104 m) and consisted of a bedrock-controlled channel with two deep pools (D_{max} 2.5 m – Pools 1 and 2; Figure 3.4) separated by a short series of cascades. *Reach 2* was 306 m in length and began downstream of the bedrock pavement and had the second highest pool volume in the study segment (10 665 m^3 – Pool 3; Figure 3.4). *Reach 2* comprised a series of two deep bedrock pools (D_{max} 2.7 m) separated by short channel-spanning bedrock and cobble bars and terminated in an alluvial pool (Pool 5 – D_{max} 1.7 m). *Reach 3*, the longest (1 877 m) and shallowest ($D_{\bar{x}}$ 0.7 m) reach in the study segment, consisted of a series of long ($L_{\bar{x}}$ 81.6 m) shallow sand-bed runs interspersed by shorter cobble and gravel-bed riffles. Although the macro-channel in *Reach 3* was up to 100 m wide in places, secondary channels only flowed during winter. There were no deep pools in this reach (D_{max} 1.4 m). *Reach 4* had the highest pool volume in the study segment (13 907 m^3) and the largest single pool (200 m in length; D_{max} 2.8 m). For the first 500 m of *Reach 5*, the river consisted of a series of shallow sand-bed runs that braided between reeds and sedges. The remainder of the reach comprised a single channel with relatively shallow ($D_{\bar{x}}$ 0.9 m) sand-bed runs. Between *Reaches 5* and *6* a dense reedbed precluded sampling (Figure 3.4). *Reach 6* comprised a single shallow sand-bed run and a deep pool 150 m in length and 2.6 m in depth.

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TABLE 4.3. Physical habitat characteristics of the seven reaches in the Driehoeks River measured in October 2004. Pool volumes were calculated using the maximum depth, width and length of each pool in the reach that was over 1.5 m deep, summed over the whole reach. The mean channel width ($W_{\bar{x}}$) refers to the active channel at the time of sampling.

	Reach Length (m)	Mean ±SD channel width $W\bar{x}$ (m)	Mean ±SD depth $D\bar{x}$ (m)	Max. depth (Oct) D_{max}	Pool volume (Oct) (m^3)	No. of morph units (N)	Mean ±SD morph unit length $L\bar{x}$ (m)	Dominant, sub-dominant substratum type	Dominant, sub-dominant flow type
Reach 01	104	10.2 ±6.4	1.5 ±1.1	2.5	1 960	3	34.7 ±15.7	bedrock, sand	barely perceptible flow, cascade
Reach 02	306	12.7 ±8.5	1.3 ±1.0	2.7	10 665	5	61.3 ±45.7	sand, bedrock	barely perceptible flow, rippled surface
Reach 03	1 877	8.0 ±4.4	0.7 ±0.3	1.4	0	23	81.6 ±57.4	sand, cobble	rippled surface, smooth boundary turbulent
Reach 04	631	7.6 ±6.2	1.5 ±0.7	2.8	13 907	13	48.6 ±48.7	sand, cobble	barely perceptible flow, rippled surface
Reach 05	1 457	7.2 ±5.6	0.9 ±0.5	2	3 375	25	58.3 ±65.1	sand, cobble	smooth boundary turbulent, barely perceptible flow
Reach 06	186	13.0 ±1.4	1.5 ±1.5	2.6	5 441	3	93.1 ±79.7	sand	barely perceptible flow
Reach 07	310	7.9 ±4.0	1.1 ±0.5	1.9	2 229	13	23.9 ±18.5	bedrock, boulder	rippled surface, smooth boundary turbulent

Downstream of this, another extensive reedbed precluded continuous sampling through to *Reach 7*. *Reach 7* comprised a series of bedrock pools with channel-spanning bedrock bars and pavements. Two pools (the largest was 60 m in length; D_{max} 1.9 m) were located in this final reach that was otherwise characterised by a bedrock and boulder-step morphology. The macro-channel here was confined by steep valley sides. The mean length of habitat units in *Reach 7* was much shorter than in the remainder of the study segment (23.9 ±18.5 m), reflecting greater habitat heterogeneity in this reach and the boulder-step morphology.

4.3.2 Seasonal distribution patterns of sawfin

A cumulative total of 48 km of river was surveyed during the course of the study during which time totals of 4281 adult, 2618 juvenile and 452 larval sawfin were counted. However, there was high variability in the size classes and relative abundances of adult sawfin between reaches and between months of the year.

Adult sawfin—Very few fish were counted at the beginning of the low flow season throughout the whole six kilometer study segment, either during the first dive in October 2004 (61) (Figure 4.1a) or early October 2005 (150) (Figure 4.1b). By mid-October 2004, fish counts had increased substantially (452), but they remained low in mid-October of the following year (218). By mid-November in both years, overall abundances of sawfin were comparable and substantially higher than they were in October (669 and 611 in 2004 and 2005 respectively). By the end of the low flow season in both years (March in Figure 4.1), counts of adult sawfin were lower than in the previous two months (342 in 2005 and 462 in 2006 respectively). Concurrence of abundances between years suggested that the estimates of relative abundance were reasonably precise and that the seasonal trends were consistent between years.

Figures 4.2 (2004/5) and 4.3 (2005/6) show the seasonal distribution and relative abundance of adult sawfin represented by (i) the mean number of fish per km of each reach and (ii) total counts and location of fish along the river channel from October (a) to March (e) (APPENDIX B.3).

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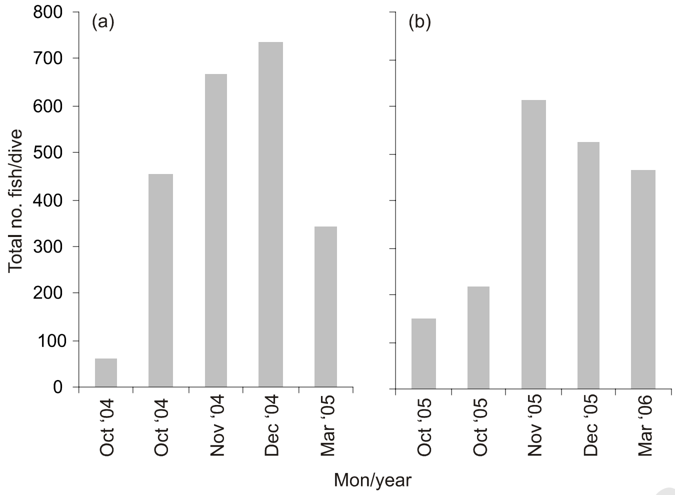

Figure 4.1 Total counts of adult sawfin (*Barbus serra*; >150 mm TL) in the study segment (all reaches) between (a) October 2004 and March 2005 and (b) October 2005 to March 2006.

During early October of both years (Figures 4.2a and 4.3a), all adult sawfin were observed in *Reaches 6*, *7* or the downstream end of *Reach 5*. Although much of *Reach 5* reach was characterised by shallow (<0.3 m) sand-bed runs, sawfin were observed in large schools, holding in the deeper meander-bend scour pools. By late October of both years (Figures 4.2b and 4.3b), increasing numbers of adult sawfin were observed in the shallow intervening runs and deeper pools of *Reaches 4* and *5*. In October 2004 a large shoal of sawfin was observed in the deep pool in *Reach 6* (Figure 4.2b). By November of both years (Figures 4.2c and 4.3c), the upstream limit of fish counts extended to *Reach 2*. In November of both years (Figures 4.2c and 4.3c) the largest proportion of the sawfin population was observed between *Reaches 2* to *4*. The same general pattern was observed during December of both years. By March 2004, although fewer fish were counted in general (Figure 4.1), the distribution of the population through the segment remained similar to the previous two months (Figure 4.2e). In March 2005, an overwhelming proportion of the population was found in the most upstream reach (*Reach 2*).

Spawning sites—In both years, spawning commenced in early to mid-November (Figures 4.2 and 4.3 c and d). Spawning sites were located in the shallow, fast-flowing runs and riffles where sawfin gathered in schools of up to 75 individuals (Plate 4.1). A total of 12 spawning sites was identified, most of these in *Reach 3*. Not all of these sites were occupied simultaneously in the same year, and although some sites were used in both years (notably those in *Reach 3*), others were not. In 2005, spawning fish were found at three of the ten sites identified in 2004 and an additional site was identified in *Reach 2* where sawfin were observed spawning in bedrock potholes.

Larval and juvenile sawfin—Figures 4.4 (2004/5) and 4.5 (2005/6) show the seasonal distribution and relative abundance of larval and juvenile sawfin represented by (i) the mean number of fish per km of each reach and (ii) total counts and location of fish along the river channel from October (a) to March (e) (APPENDIX B.4). As already noted, abundances of juvenile sawfin were very low during October and their distribution restricted to *Reaches 1* and *7* – the only two reaches that were dominated by a bedrock substratum with numerous underwater ledges and large boulders. In *Reach 1*, juvenile sawfin were found during December and March of 2004 and 2005.

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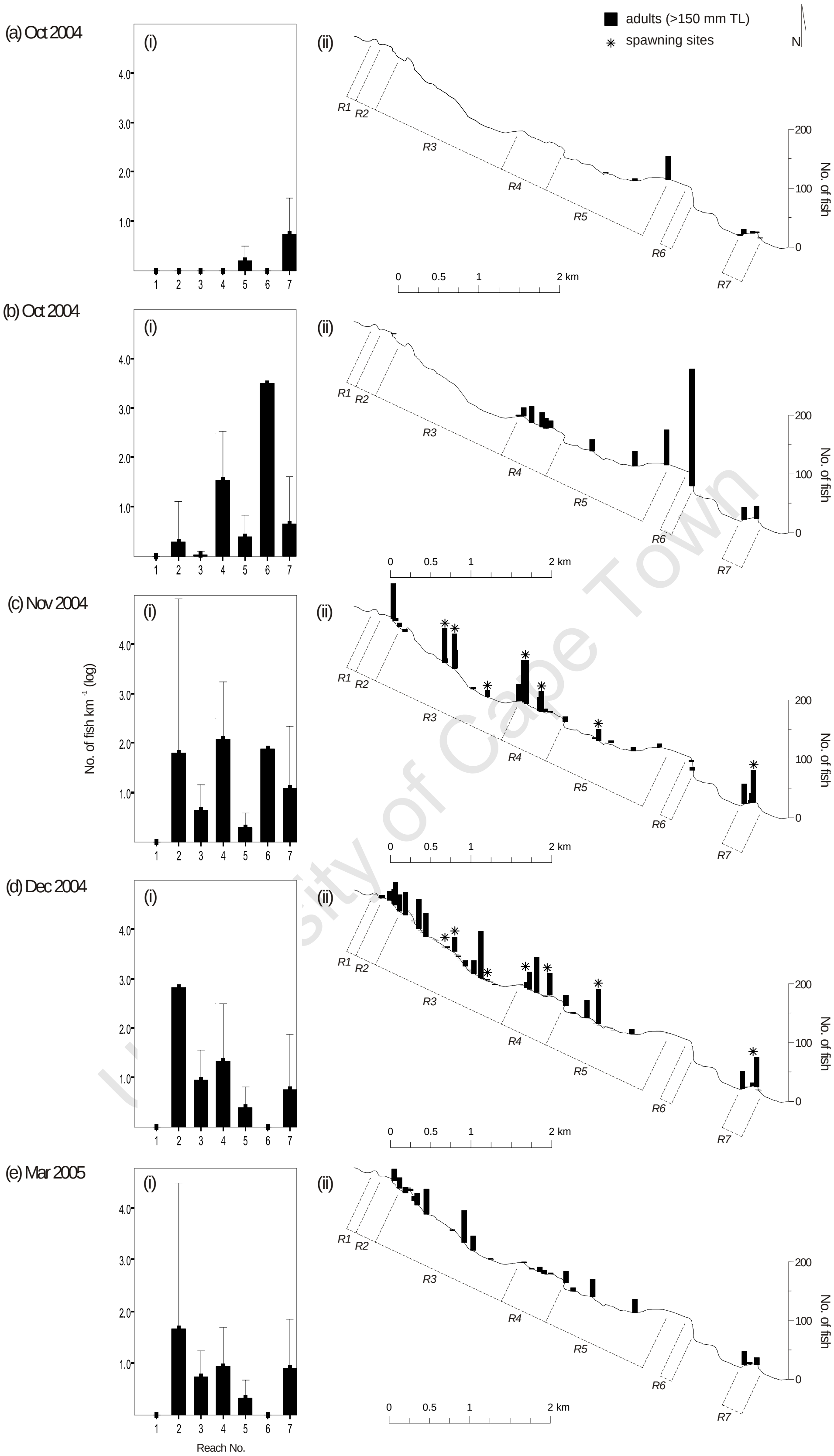

Figure 4.2 Seasonal distribution of adult sawfin in the Driehoeks River between (a) October 2004 and (e) March 2005 represented by: (i) bar charts of the mean number of fish per km of each reach (Reach no. 1-7) (log transformed) and (ii) a north oriented map of the Driehoeks River with total counts of fish superimposed (black-shaded bars, scale bar to the right). Asterisks above the bars represent spawning sites selected in November and December. Error bars represent 95% confidence intervals of the mean.

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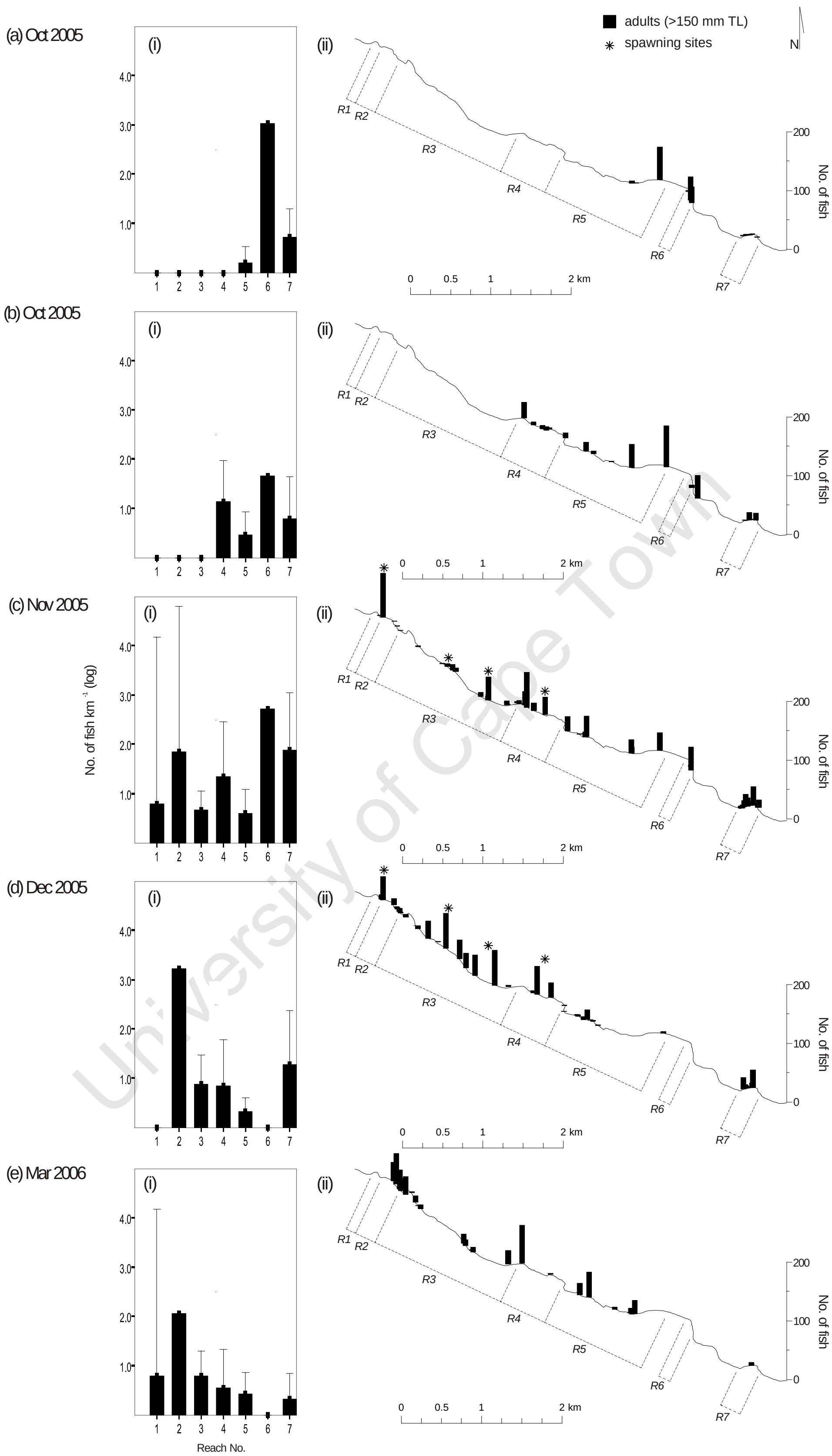

Figure 4.3 Seasonal distribution of adult sawfin in the Driehoeks River between (a) October 2005 and (e) March 2006 represented by: (i) bar charts of the mean number of fish per km of each reach (Reach no. 1-7) (log transformed) and (ii) a north-oriented map of the Driehoeks River with total counts of fish superimposed (black-shaded bars, scale bar to the right). Asterisks above the bars represent spawning sites selected in November and December. Error bars represent 95% confidence intervals of the mean.

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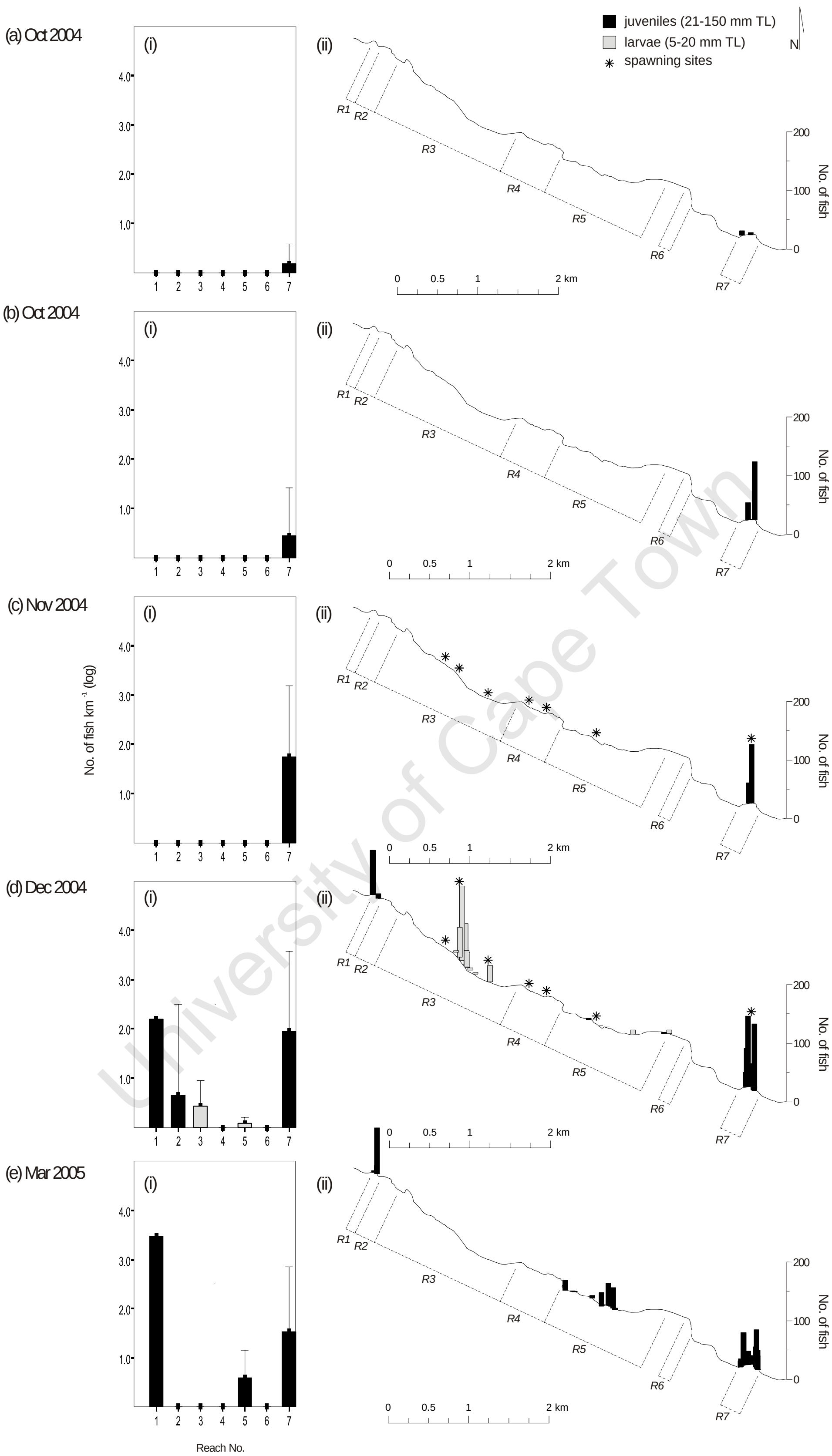

Figure 4.4 Seasonal distributions of juvenile and larval sawfin in the Driehoeks River between (a) October 2004 and (e) March 2005 represented by: (i) bar charts of the mean number of fish per km of each reach (Reach no. 1-7) (data log transformed) - juveniles represented by black-shaded bars and larvae by grey-shaded bars, and (ii) a north-oriented map of the Driehoeks River with total counts of fish superimposed as black- (juvenile) and grey- (larval) shaded bars (scale bar to the right). Asterisks above the bars represent spawning sites selected in November and December.

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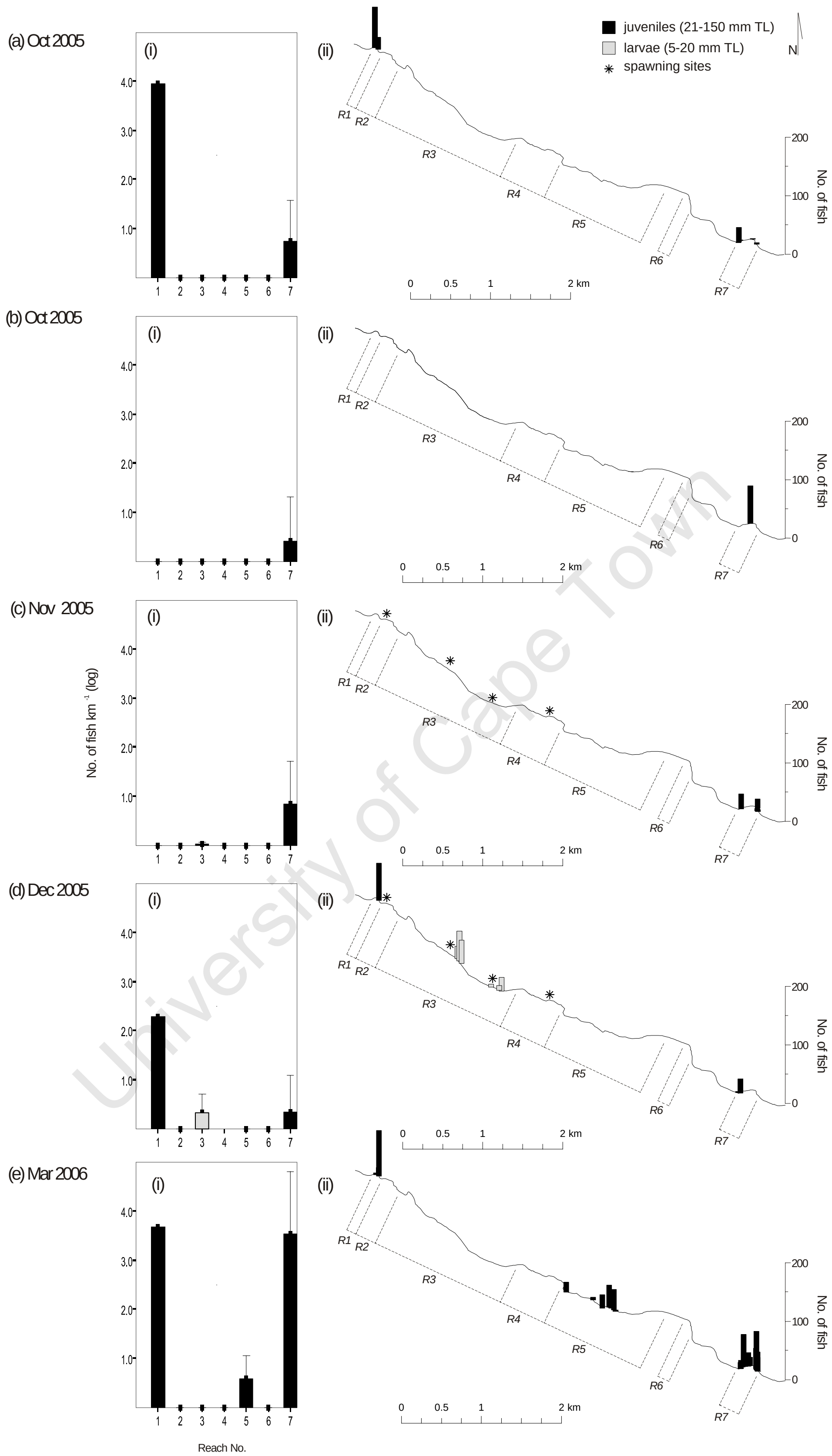

Figure 4.5 Seasonal distributions of juvenile and larval sawfin in the Driehoeks River between (a) October 2005 and (e) March 2006 represented by: (i) bar charts of the mean number of fish per km of each reach (Reach no. 1-7) (data log transformed) - juveniles represented by black-shaded bars and larvae by grey-shaded bars, and (ii) a north oriented map of the Driehoeks River with total counts of fish superimposed as a black- (juvenile) and grey- (larval) shaded bars (scale bar to the right). Asterisks above the bars represent spawning sites selected in November and December.

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By mid-December of both years, higher overall abundances of juvenile sawfin were apparent in *Reaches 1* and *7* and larval sawfin were evident immediately downstream of the main spawning sites in *Reach 3*. Estimated abundances of larval sawfin were higher in 2004 than in 2005. In both years, the highest concentration of larvae was found downstream of the upper three spawning sites in *Reach 3* (Figures 4.4d and 4.5d). By March of both years, this same 0^+ cohort was found in *Reach 5* (Figures 4.4e and 4.5e).

4.3.3 Fish tagging

A total of 249 fish were tagged between October 2004 and March 2006 (Table 4.4; APPENDIX B.5). Of these, 90 were tagged in 2004 and 159 in 2005. No recaptures were made of fish tagged in 2004. However, of the 159 tagged during the course of October and November 2005, 10 were recaptured (Table 4.4). Of these, four that were tagged in Reach 4 were recaptured at the same locality one day after they were tagged. Two individuals (D29 and D41) were recaptured in Reach 3 one and two days respectively after tagging and 0.78 km upstream of their initial point of capture (Reach 4). Between 8 and 11 November, three sawfin that had been tagged in Reach 4 (D61, D68 and D40) travelled 2.7 km upstream where they were found spawning in Reach 2 and a single individual (S94) tagged in *Reach 4* twenty-two days earlier (21 October 2005), was also recaptured.

TABLE 4.4. List of recaptures showing species, tag number, date on which the fish was tagged, location, date of recapture, direction, time between tagging and recapture and distance travelled.

			Tagged		*Recaptured*				
Species	TL (mm)	Tag No.	Date	Reach	Date	Reach	Direction	Time (day)	Distance (km)
B. serra	258	D81	08-Nov-05	4	09-Nov-05	4	-	1	0
B. serra	310	D85	08-Nov-05	4	09-Nov-05	4	-	1	0
B. serra	275	D63	08-Nov-05	4	09-Nov-05	4	-	1	0
B. serra	287	D89	08-Nov-05	4	09-Nov-05	4	-	1	0
B. serra	300	D29	09-Nov-05	4	10-Nov-05	3	upstream	1	0.78
B. serra	246	D41	08-Nov-05	4	10-Nov-05	3	upstream	2	0.78
B. serra	319	D61	08-Nov-05	4	10-Nov-05	2	upstream	2	2.7
B. serra	299	D68	08-Nov-05	4	11-Nov-05	2	upstream	3	2.7
B. serra	230	D40	08-Nov-05	4	11-Nov-05	2	upstream	3	2.7
B. serra	311	S94	21-Oct-05	4	11-Nov-05	2	upstream	22	2.7

Plate 4.1 Adult sawfin gathered in groups of over 75 individuals and spawned in shallow, fast-flowing water with a loosely embedded cobble-gravel substratum. Here sawfin spawn in one of the study reaches in the Driehoeks River during November 2006 (photo Dr. J. Cambray).

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4.3.4 Seasonal habitat selection of adult sawfin

Sawfin in the Driehoeks River were encountered most commonly in depths of between 1.2-1.8 m in slow flowing areas with a sand-gravel substratum throughout the study period (Figure 4.6).

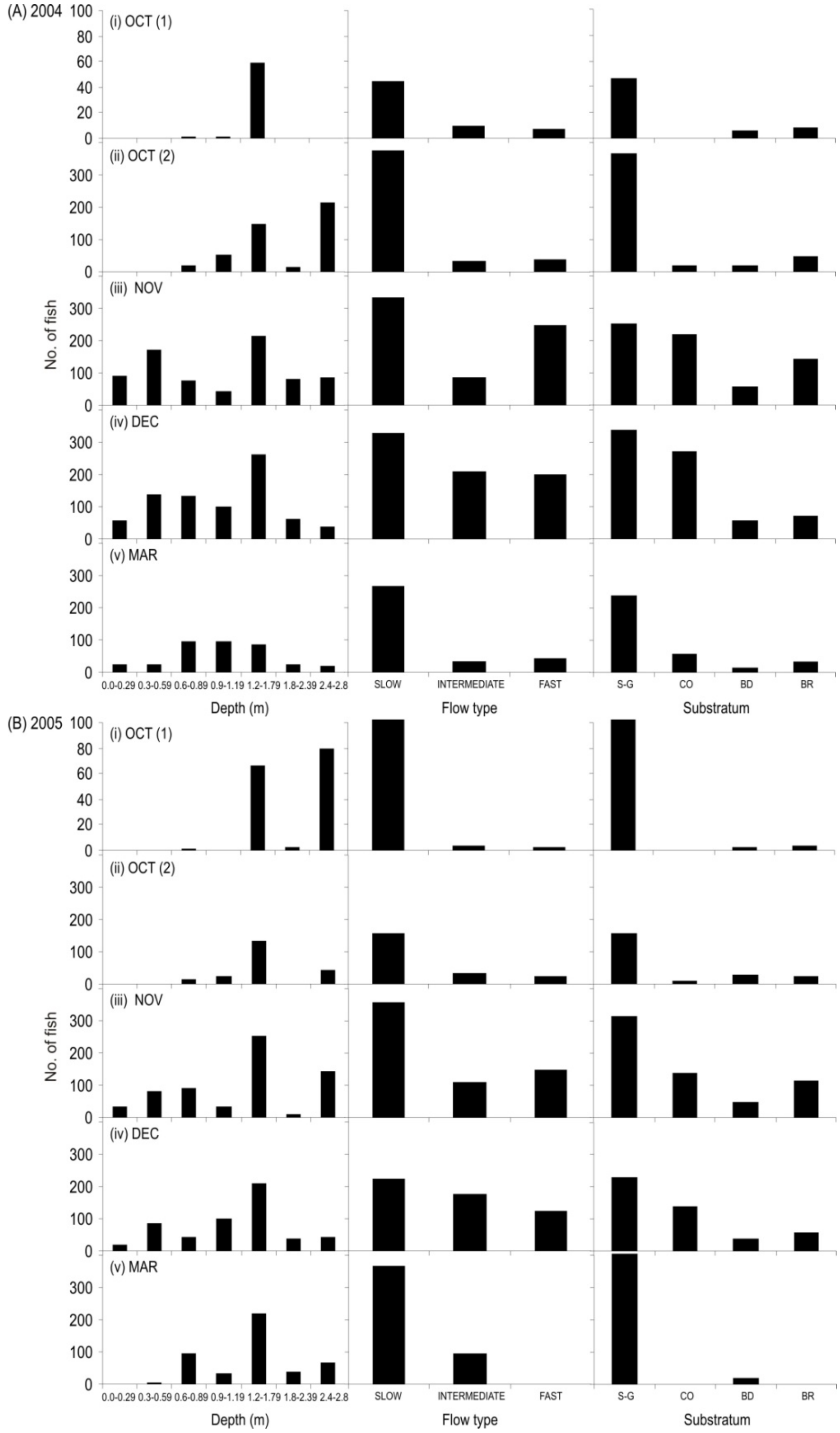

Figure 4.6 Occurrence of adult sawfin in depth, flow and substratum categories between October and March of (a) 2004 and (b) 2005. Fish counts and physical habitat data were obtained during the course of dive surveys and these were pooled for all morphological units (APPENDIX B.1). S-G=Sand-Gravel, CO=Cobble, BD=Boulder, BR=Bedrock.

During October of both years, very few sawfin were located in areas that were shallower than this. However, during November and December of both years, a second modal range, centered around depths of 0.3-0.59 m is evident, and sawfin were encountered more frequently in areas with intermediate to fast flow and a cobble substratum (Figure 4.6a-iii and –iv and 4.6b-iii and –iv). During March, many sawfin were associated with intermediate depth and flow conditions. (Figure 4.6a-v and 4.6b-v).

The association between the relative abundances of adult sawfin, time of the year and three environmental variables: depth, flow and substratum, was tested for significance by means of the Chi-Squared tests of independence (APPENDIX B.6). There was a significant dependence between months of the year and depth (Chi-Squared 1297, df=42, p=0.001), flow (Chi-Squared 634.04, df=14 , p=0.001) and substratum (Chi-Squared 775.55, df=21, p=0.001).

There was a strong association between deeper areas and the relative abundance of sawfin in October 2004 (contribution to the total Chi-Squared statistic 16%) and shallower areas (0.1-03 and 0.31-0.6 m depth class) in November 2004. The association of fish at intermediate depths (1.2 m) in March 2006 contributed 6% to the total Chi-Squared Statistic. Thus, in general, although sawfin appeared to use slow-flowing deep areas throughout the year, they began using shallower areas with intermediate to fast flowing waters (associated with larger substratum particle sizes) during November and December. During late summer (March), the number of observations in the shallower habitats declined once more, suggesting a movement back to deeper areas.

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4.4 DISCUSSION

Lucas and Batley (1996) contended that the significance of movement in the life cycles of non-salmonid fish, particularly those from temperate latitudes, has been under-estimated. Pre-spawning migrations have been reported for a number of species in this group including *inter alia* barbel (*Barbus barbus*) in Europe (Lucas and Batley 1996; Lucas 2000); Colorado pikeminnow (*Ptychocheilus lucius*) in the south western United States (Tyus and McAda 1984) and Murray cod (*Maccullochella peelii peeli*) in Australia (Koehn 1996). Large-bodied cyprinids are a major component of many African river fish faunas (Skelton 1994), both in terms of biomass and abundance, and yet little is known about their movement or habitat requirements. In the Western Cape's Olifants and Doring Rivers, coordinated movements by cyprinids in the mainstem have been reported (Harrison 1977), but their extent and importance for recruitment has been little appreciated.

Underwater visual survey techniques have been successfully applied as a means of estimating the abundances, distribution and behaviour of river fish at local scales (Hicks and Watson 1985; Hankin and Reeves 1988; Ensign *et al*. 1995; Dolloff *et al*. 1996), but they have rarely been used continuously over more extensive distances (but see Torgersen *et al*. 1999) or to infer movement. Variations in catch-per-unit-effort (*cpue*), however, by means of electrofishing have been used to reveal seasonal and diel shifts in the distribution of both adult and juvenile river fish (e.g. Rodriquez-Ruiz and Granado-Lorencio 1992; Baras and Nindaba 1999).

Given the cost of telemetry equipment, the clarity of the water and the relatively small size of the river channel (<10 m), underwater visual survey techniques, together with fish tagging (mark-recapture) studies, were considered the most appropriate means of assessing the seasonal distribution of fish in the Driehoeks River – and inferring from this their movement patterns. Both these techniques had drawbacks. The principal disadvantage of the underwater visual surveys were the inability to determine distances and directions moved by individual fish, whereas the principal disadvantage of the tagging studies were the low recapture rates. Successful mark-recapture studies require large numbers of fish to be tagged and considerable investment of effort and manpower for meaningful results to be obtained. The limited recaptures obtained in the present study were considered acceptable given its small scale. Mark-recapture is not considered practical in larger river systems unless the populations are intensively fished and monitored. In these systems, telemetry methods would give better returns on investment in capital and equipment and effort.

The expansion of the upstream limit of adult sawfin distribution in the Driehoeks River during October and November, together with the recaptures of tagged fish, suggest that they begin migrating from the lower reaches of the study segment (*Reaches 6* or *7*) at the end of the high flow season, as flows are subsiding and temperatures rising. This movement appears to be associated with the increased availability of suitable spawning riffles in *Reaches 3* and *4*. Over the spawning season, adult sawfin were fairly evenly distributed throughout the study segment, signifying that distances moved by individual fish or shoals vary widely. This suggests that migration may serve to distribute individual fish or shoals evenly throughout the system until all spawning and feeding sites are occupied in a manner suggested by Fretwell and Lucas' (1970) ideal free distribution model whereby dispersion between key habitats maximises individual fitness.

The redistribution of fish through the system occurred from the downstream reaches yet, as pointed out in Section 4.2.1, the waterfall in *Reach 7* (over 3 m high) was considered impassable to fish moving upstream. The reason for the lower abundances of sawfin counted towards the beginning (October) and end (March), of the low-flow season is therefore attributed to fish making greater use of deeper pools or hydraulic cover such as bedrock shelves and boulders where they were less easily observed rather than to emigration or immigration to or from downstream reaches. This is supported by the absence of fish in shallower water early in spring and the presence of an unusually large school of sawfin observed in *Reach 7* in October 2004 (estimated >400 fish). Towards the end of the summer low-flow period (March) the greater abundances of sawfin that were observed in the upper reaches of the study segment where there were also deep pools (*Reaches 2* and *3*), suggests that at some point prior to or during the high-flow season, a downstream displacement of adult fish back to the pools in *Reach 6*, or the more structurally complex habitat in *Reach 7*, takes place. This pattern is consistent with the annual cyclic migrations of other cyprinids that move downstream in autumn and upstream in spring and early summer (Lucas and Batley 1996).

Longitudinal migrations are often accompanied by a shift from shallow, temporally variable habitats in summer to deeper, more stable or structurally complex habitats in winter and late summer (Schlosser 1991; Labbe and Fausch 2000; Muhlfeld *et. al* 2001; Magoulick and Kobza 2003). Sawfin moved from deeper pools (>1.8 m) in spring (October) into shallower runs and riffles (<1.2 m) in summer (November and December) where they spawned and fed in large schools. However, they continued to use intermediate depths (1.2-1.8 m) throughout the spawning season. The reduced overall abundances of both juvenile and adult fish during spring is attributed to their occupation of deeper habitat as well as their lower mobility and therefore visibility over this period. It is considered improbable that populations would have been supplemented by

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immigrants from downstream due to the presence of a 3 m-high waterfall at the downstream end of the study segment.

The only time juvenile fish were encountered in the middle reaches of the study segment (*Reaches 2-6*) was towards the end of the low-flow period (March) where they were aggregated in *Reach 5* (Figure 4.4e and 4.5e). It is likely that these fish were the previous year's cohort that had been spawned in *Reaches 3* and *4* and subsequently drifted downstream during the course of the summer. The age structure of these schools, ascertained by otolith analysis, makes this explanation plausible (Chapter 7). They occurred at the same location in both years, indicating that as larvae and juveniles they had actively moved, or were transported, a distance of roughly 2.5 km downstream of their natal habitat over a 3-4 month period beginning on the date of their spawning. This movement would have coincided with the ontogenetic shift of the young fish to deeper waters (Chapter 6). Seasonal drift by larval fish is an important component in the life history of a number of fish species, with important implications for population and species assemblage dynamics (Robinson *et al*. 1998; Reichard *et al*. 2002; Gilligan and Schiller 2003; Zitek 2004). Since there were no high flows during the summer and several deep slow-flowing pools between the spawning areas and *Reach 5*, it is assumed that the downstream movement by the juveniles was active. Active downstream migration of young-of-the-year fish has been widely reported for salmonids (e.g. Spicer *et al*. 1995; Giorgi *et al*. 1997), but not for riverine cyprinids. The function of the movement in the Driehoeks River appears to be related to the availability of suitable habitat.

Reaches 1 and *7* were the only bedrock- and boulder-dominated reaches throughout the study segment, and during early spring (October) of both sampling years shoals of juvenile sawfin sheltered beneath boulders or in bedrock fissures. Young fish are particularly vulnerable to high flows and predation because of their limited swimming capacity and small size. They are therefore frequently associated with shallow, slow-flowing backwater or floodplain habitats (Rincón *et al*. 1992; Sempeski and Gaudin 1995) or snags and woody debris (Angermeier and Karr 1984; Todd and Rabeni 1989). In the Western Cape, mountain and foothill rivers channels are geomorphologically constrained and therefore lack extensive backwaters or floodplains. In addition, there is little in the way of large woody debris that could be used as cover for young fish due to the nature of the vegetation. While pools may provide hydraulic cover during spates, they would not provide cover from aquatic predators, whereas bedrock-controlled reaches with numerous shelves and large boulders are likely to provide both hydraulic and predation cover. Sawfin populations elsewhere in the system appear to be strongly associated with these more structurally complex reaches (Paxton *et al*. 2002). Where these conditions prevail, i.e. the lower reaches of the Doring River and headwater tributaries of both the Olifants and Doring Rivers, sawfin are often the most numerous of the three large-bodied endemic cyprinids (Paxton *et al*. 2002).

Highest abundances of larval sawfin were located immediately downstream of spawning sites in December 2004 and 2005. Rearing studies indicated that the free embryos are photophobic upon hatching and remain so for ten days (Chapter 7 this document). Thus it is assumed that they remain in the cobble substratum of spawning riffles until swim-up when they are washed into the shallow littoral slackwaters immediately downstream. The abundances and distribution of larvae (Figures 4.4d and 4.5d) suggests that the spawning sites were not equally productive. Although there was evidence for spawning site fidelity in that three of the four sites selected in 2004 were also selected in 2005, only one of these was occupied by spawning

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aggregations almost continuously over the spawning period in both years. Over 90% of the larvae were located immediately downstream of this site in *Reach 3* (Figures 4.4d and 4.5d). The productivity of spawning habitats may be related to the hydraulic and geomorphological conditions of the site itself (Chapter 5), or it may be related to the habitat conditions immediately downstream. Immediately after swim-up, sawfin larvae gather in shallow (0.05-0.14) slow-flowing (0.01 m s^{-1}) marginal slackwaters that are free of aquatic predators and where growth is promoted by higher temperatures and increased primary productivity (Chapter 5 this document). These conditions were met at two sites in *Reach 3*, but not at many of the other sites that either had deep pools or fast runs immediately downstream. It is not considered likely that choice of spawning site is influenced by the presence of larval habitat downstream, but it did appear to be important for recruitment success in a given reach.

Sizeable populations of sawfin, although growth-limited in the Driehoeks River, are able to persist in a relatively short segment of river (6 km) since all the conditions necessary for them to complete the various phases of their life history are present. Kocik and Ferreri (1998: 194) have proposed the existence of discrete Functional Habitat Units (FHUs) defined as being 'natural partitions within the river system that contain all the necessary habitat elements to support all life history stages of interest'. It would appear therefore, that the river segment in this study corresponds to one such FHU since it contains all the morphological units necessary to support sawfin from egg to adult. Destroying habitat, or obstructing movements between *Reaches 3* or *7*, would compromise it as a FHU and cause significant declines in population abundances, if not local extinction. The extent of movement by adult fish elsewhere in the Olifants and Doring Rivers system and their tributaries, and the dispersal of young fish from the natal habitat, can therefore be expected to be determined by the availability of and distance between critical habitat patches within the riverscape. The extent to which the movement of larger populations of larger-bodied sawfin increases in the mainstem reaches, where habitat units and therefore distances that would need to be travelled are correspondingly greater, is presently unknown. Future studies to determine the timing and extent of these mainstem movements will need to be ascertained by means of telemetry.

4.4.1 Conclusions

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Research has shown that riverscape scale factors such as disturbance, dispersal and habitat patch mosaics may be more important for controlling fish population dynamics at a local scale than biotic or microhabitat conditions (Schlosser 1998; Labbe and Fausch 2000). Understanding ecological processes at the riverscape scale emphasises not only the importance of different habitat patches but also their spatial context, i.e. their adjacency and connectivity. Successful completion of various life stages depends on access to and therefore connectivity between these habitat types. Traditionally, ecological studies of river systems have been conducted at the scale of the stream reach (Johnson and Gage 1997). In this study, continuous, georeferenced dive surveys across scales approximating that of the river segment (> 10^3 m) allowed processes that occur at the riverscape scale to be detected. It is unlikely that more conventional random or stratified random sampling approaches would have revealed the highly aggregated nature of fish distribution within the study segment or the correspondingly patchy nature of stream habitat. The strong cyclical patterns in the distribution and abundance of adult sawfin in the Driehoeks River implies an upstream migration in spring associated with spawning activity and a downstream return sometime during the winter months. The differentiation between natal and rearing habitats suggests that the spatial distribution of key resource areas, together with dispersal to and from these areas, plays a major role in the population dynamics of sawfin within the system. Perhaps the most salient finding to emerge from the current study is that the existing or potential spawning habitat for sawfin in the Driehoeks River comprised less than 1% of the total length of the study segment (from measures of habitat unit length and type) and an even smaller proportion of that habitat was responsible for over 90% of fish production. Similar low spawning habitat area to fish production ratios have also been reported for brook trout (*Salvelinus fontinalis*) in Appalachian streams (Petty *et al*. 2005) and chinook salmon *Oncorhynchus tshawytscha* in the Sixes River, Oregon (Reimers 1973). The availability and condition of spawning areas is therefore likely to have a profound influence on the persistence of sawfin in any given reach. The value of preserving these shallow, temporally variable habitats and ensuring their hydraulic and geomorphological integrity is therefore demonstrated. Other key habitats identified in this study include: nursery habitat for larval fish (shallow marginal slackwaters immediately downstream of spawning habitat), rearing habitat for juvenile sawfin (bedrock- and boulder-dominated reaches) and deeper, winter refugia for adult fish.

The understanding acquired in this study will help to identify appropriate scales of management; explain range restrictions and local declines in abundances; and guide plans for river rehabilitation and recovery of sawfin populations. More specific conservation and management actions relating to aquatic habitat in the Olifants and Doring Rivers, together with additional research needs, will be discussed in greater detail in Chapter 8.

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CHAPTER 5 Behaviour, diel and life stage-specific habitat shifts by Clanwilliam yellowfish and sawfin and in the Driehoeks River

5.1 INTRODUCTION

The magnitudes and distributions of the depths, current speeds and substratum types in a river affects the growth and mortality of fish through the delivery of nutrients and oxygen to eggs and developing embryos (Coble 1961), the displacement and dispersal of young fish (Robinson *et al*. 1998), by inducing trade-offs between metabolic swimming costs and foraging efficiency (Fausch 1984, Laurence and Keckeis 1998), and by providing refugia from predation or disturbances (Harvey 1991; Magoulick and Kobza 2003). Human modifications of river systems through regulation and water abstraction alter the magnitudes and distributions of depths and velocities and thereby the availability and quality of instream habitat (Ligon *et al*. 1995; Poff *et al*. 1997; Marmulla 2001). Understanding how the biota respond to altered flows presents one of the most challenging aspects of the science behind EWR assessment (Gore and Nestler 1988; Castleberry *et al*. 1996).

The most common method for establishing the linkages between river flow and the biota is Habitat Suitability Criteria (HSC) (Bovee 1986) developed for use within the habitat component (PHABSIM: Milhous *et al*. 1989) of the Instream Flow Incremental Methodology (IFIM: Bovee 1982). HSC were developed in order to translate the hydraulic and geomorphological conditions in rivers into indices of habitat quality by observing and recording the habitat selection of individual organisms across a range of the three primary physical habitat variables, i.e. current speed, depth and substratum particle size. They have been criticised on a number of levels, however, for a range of inherent assumptions and potential biases that could be introduced at any stage of their construction – from the collection of input data to their analysis and interpretation (Mathur *et al*. 1985; Orth 1987; Castleberry *et al*. 1996; Hudson *et al*. 2003, but see Section 2.3 for a full discussion).

The most frequently cited criticisms include: poor transferability between river systems that have different proportions of available habitat (Pollard 2000; Holm *et al*. 2001); the assumption that fish habitat selection is independent of discharge (Holm *et al*. 2001; Ibbotson and Dunbar 2002); the fact that HSC models are correlative and do not address underlying mechanisms (Grossman *et al*. 2002) and that the correlations between simulated habitat and fish standing stock are poor (Mathur *et al*. 1985). This last limitation can be attributed to the failure of most habitat models to account for factors other than habitat that play important roles in regulating fish populations such as water quality, temperature and biotic interactions (Orth 1987).

Critique of HSC-based methods by South African scientists has focussed on their intensive data requirements, species-specificity and inability to address all parts of the river ecosystem, stressing the fact that they may be inappropriate for developing countries where data, manpower and resources are constrained and where maintenance of healthy ecosystems is vital because of the large numbers of subsistence users (King and Tharme 1994; King *et al*. 2004). South African researchers have therefore directed their attention to developing holistic, whole-ecosystem approaches that can be used in both data-rich and data-poor situations such as the Building Block Methodology (BBM, Tharme and King 1998) and the Downstream Response to Imposed Flow Transformation methodology (DRIFT, King *et al*. 2003; King *et al*. 2004). DRIFT is a multi-

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criteria knowledge-based system that is able to incorporate expert knowledge at a range of confidence levels. Confidence in the output of any methodology, however, is only as good as the net reliability of deliberations by the specialists. In situations where data are poor to non-existent, specialists must base their predictions of individual species or community level responses to changes in flow on research of related species elsewhere in the world or on general knowledge of how river ecosystems function. Without a basic ecological understanding of how individual species or communities respond to changes in flow, levels of confidence in the predictions of EWR assessments will remain low. This is of special concern in high-profile cases of river systems that have species of outstanding social, economic or conservation importance, or where predictions of change may be legally contested. In these cases, quantitative methods are needed to defend EWR assessments. This chapter, while acknowledging the limitations of HSC-based methods, adopts the position of Castleberry *et al.* (1996) and Tharme (2003) that they remain the most effective means of providing quantitative estimates of habitat use by river organisms provided they are correctly applied and that the complexity of habitat use is recognised. The application of HSC-based methods in this context is further defended on the grounds that the target species are endangered and therefore their protection is a requirement under the National Environmental Management Biodiversity Act of South Africa (10 of 2004). Preservation of macro-, meso- and microhabitat conditions is key to the strategy for the recovery of threatened organisms (Knight and Arthington 2008).

Studies aimed at developing quantitative models for predicting the biological outcome of changes in physical habitat as a function of discharge are still in their infancy in South Africa. Habitat studies focussing on river fish in particular have been few (Gore *et al*. 1991; King and Tharme 1994; Weeks *et al*. 1996; Niehaus *et al*. 1997; Pollard 2000; Arthington *et al*. 2003b) and for the most part limited to the examination of only one or two life stages (adult and juvenile) (but see King *et al*. 1998). In addition, they have not taken the behaviour of individual fish at the time of sampling into account. Hardy *et al.* (2006) argued that current fish habitat models relying on biological response functions to a range of habitat variables are too simplistic to represent the complex interplay of factors that cause a fish to select a particular habitat type. They have therefore emphasised the need for incorporating features such as proximity to certain other habitat variables (e.g. velocity or cover). In their study, Hardy *et al.* (2006) derived behaviour-based decision rules for the proximity of chinook fry to escape cover.

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In this chapter, HSC have been used to describe the hydraulic (velocity and depth) as well as substratum habitat utilisation by sawfin and Clanwilliam yellowfish. The study included habitats deemed most limiting to fish production, i.e. those used for foraging, early life stages and reproduction. Although a distinction was made between juvenile and adult Clanwilliam yellowfish, no reproductive activity was observed and spawning and larval habitat could therefore not be described. However, more focussed attention was given to drift-feeding Clanwilliam yellowfish. Drift-feeding fish will minimise energy expenditure while maximising energy intake by selecting hydraulic cover in the form of velocity shears or substratum particles in close proximity to areas of higher velocity that deliver suspended drift (Bachman 1984; Grossman *et al*. 2002). Ideal foraging sites therefore tend to be areas of slower current speed in proximity to high velocity shears produced by channel morphology. Although few studies have accounted for adjacent velocities (but see Fausch and White 1981; Hayes and Jowett 1994), the importance of incorporating these into habitat models is becoming increasingly apparent (Hardy 2006). In this study therefore, a distinction was made between non-feeding (refuge) and drift-feeding (foraging) Clanwilliam yellowfish habitat (Bachman 1984) and HSC were derived for cover positions as well as for areas of higher flow where fish were observed making short forays to feed on drift. These criteria will be included in behaviour-based rules and incorporated into a two-dimensional hydrodynamic model in Chapter 6.

5.2 METHODS

5.2.1 Study area

Data collection was conducted in the Driehoeks-Matjies River between 19-27 November and 4-25 December 2005. The area from which data were collected for this component of the study comprised a continuous 1.2 km segment of river contained within the broader 5.9 km study segment (Figure 3.4). Discharge over the sampling period varied between 0.19 and 0.36 m^3s^{-1}. The 1.2 km study segment from which habitat data were collected consisted of a series of shallow sandy runs alternating with riffles dominated by small cobble and gravel substrata. The mean gradient of the segment was 0.04 and the maximum gradient 0.14. The deepest pool in the study area was Pool 7 (D_{max}= 2.7 m) (Figure 3.4) which was located near the downstream end of the area. River widths ranged between 0.25 and 8.7 m ($\bar{x}$=2.1 m). Riparian vegetation consisted primarily of restios (*Elegia* spp.) with shrubs and grasses and some oak (*Quercus* spp) present on the right banks.

5.2.2 Fish Sampling

The number of habitat-use observations that were obtained was relatively low due to the low densities of fish in the study segment (Clanwilliam yellowfish $\bar{x}$ = 22.3 fish river-km^{-1}; sawfin >150 mm TL $\bar{x}$ = 67.9 fish river-km^{-1}). This, combined with their isolation and patchy distribution within the Olifants-Doring Rivers catchment as a whole due to local extinctions, placed a constraint on the total amount of habitat-use data that could be collected. Thus, significantly less than the 100-200 data points recommended by Bovee (1986) were collected per size class. Physical habitats selected by sawfin and Clanwilliam yellowfish were identified by snorkelling the 1.2 km study segment. Data were collected by a single diver swimming in an upstream direction to minimise disturbance to the fish. Due to the good underwater visibility and relatively small size of the river, both banks were visible to the diver. Each fish was observed for a minimum of 2-5 minutes to establish whether it had selected a position or been disturbed. Fleeing fish, or fish attracted to the observer, were ignored. The behaviour of the fish (whether it was feeding, stationary or spawning) was noted. Observations of larval habitat selection in water that was too shallow to snorkel were made from the bank. Numbered and weighted marker buoys were dropped where fish were observed and the species, size class (estimated by means of a calibrated writing slate) and activity were recorded for each marker buoy. Size class estimates were later validated by means of seine and fyke netting and measuring fish lengths. Where drift-feeding fish were observed performing short excursions upstream to collect food items before returning to a holding area, both the holding area as well as the adjacent flow from which drift was being collected (feeding area) were marked. The distance between holding areas and feeding areas was measured and found to range between 0.5 and 1.0 m. After 30 minutes of snorkelling, the physical habitat variables of interest, i.e. depth (m), velocity (m^3s^{-1}) and substratum were measured at each marker buoy. Mean water-column velocity was measured at 0.6 of the depth from the surface over a 30 s period using a Flo-Mate Marsh McBirney® electromagnetic current meter. HSC for spawning sawfin were derived by taking a single measurement of depth and velocity near the head of the school. Since spawning took place over a general area, however, an additional four points were selected within 0.3 m of the first measurement in the region of the spawning

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school. The total available habitat throughout the 1.2 km study segment was estimated over the same time period that habitat-use data were collected. Measuring these variables was done by placing cross-sections on visually distinguished longitudinal transitions in the flow (depth or velocity) and at each transition along the cross-section. Depth, velocity and substratum measurements were taken at 110 cross-sections spaced an average of 16 m apart and along each cross-section at intervals between 0.5 and 1.5 m. The area of each cell (width along the cross-section × length between cross-sections) was calculated and these areas were summed over the whole study segment to give an estimate of the total area occupied by each depth, velocity and substratum class interval. At each measured point, a single substratum particle that was visually assessed as being representative of the size of the bed particles in the immediate vicinity, and that was larger than sand (<2 mm), was measured (β axis) and classified according to a modified Wentworth scale; (Gravel 2-16 mm; Course Gravel 16-64 mm; Small Cobble 64-120 mm; Large Cobble 120-250 mm; Boulder >250 mm and Bedrock).

Spawning habitat was described using sites both within and outside the defined boundaries of the study segment (upstream and downstream) due to the limited numbers of sites available within the defined study segment. A spawning site was identified on the basis of visual observation of large aggregations of actively spawning fish, followed by the collection of eggs from between the particles of bed material. Measurements were taken from the area where most of the spawning activity by males and females was taking place and where the highest density of eggs was observed. Mean water-column velocities were measured at this point.

To investigate whether diel migrations by 0^+ juvenile sawfin between shallow marginal slackwaters and deeper areas (>1 m) were related to temperature, hourly counts of the numbers of 0^+ juvenile sawfin were made in two shallow habitats between 07h00 and 20h00 over an 86-hour period in November 2005. Temperatures were monitored in a shallow marginal embayment and in the deeper main channel of the Driehoeks River in Reach 1 over the same 86-hour period by means of two thermistor temperature sensors coupled to data loggers (HOBO® Water Temp Pro) accurate to ± 0.2°C at 25°C. Water surface elevations on the Driehoeks River were monitored continuously by means of a piezoresistive pressure sensor coupled to a data logger (STS® data logger DL/N 641) installed 1.2 km upstream of the study reach. The STS® data logger measures depth in metres (m). The sampling rate was set at 30 min intervals.

5.2.3 Analyses

HSC for Clanwilliam yellowfish and sawfin were derived using mean water column velocity since this is more meaningful than focal-point velocity for hydraulic modelling and flow management purposes (Hayes and Jowett 1994, Gibbins and Acornley 2000). HSC were derived for four size classes of sawfin: 5-20 (larvae); 21-75 (0^+ juvenile); 76-150 (1^+ juveniles and young adults) and > 150 (adults) mm TL; and two size classes of yellowfish: 75-150 (1^+ juvenile) and > 150 (adult) (no larvae or 0+ juvenile yellowfish were observed in the study area). Each observation was counted as a single datum point, thus observations of schools of fish were treated as equivalent to single fish and no weighting was given to larger schools.

Habitat utilisation curves (see Chapter 2, Section 2.3.2) were derived for each habitat variable, i.e. depth, velocity and substratum, species, size classes and behaviours using the *X*, *Y* coordinates produced from kernel smoothed density estimations (Silverman 1986) using the statistical package '*R 2.3.0*'. Kernel density estimation smooths out the contribution of each observed data point over a local neighbourhood of the data

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point by placing a kernel (e.g. a Gaussian distribution) over the data point. The contribution of each data point to the density is then summed to an overall estimate. The resulting curves were then normalised by dividing by the maximum *Y* ordinate to obtain a utilisation index of between 0 and 1. The optimal habitat range was defined as having a utilisation value > 0.85 (Waddle 2001). Significant differences in habitat use by species, size-classes and behaviour were tested using Kolmogorov-Smirnov two-sample tests on the raw data (Sokal and Rohlf 1981).

5.3 RESULTS

5.3.1 Sawfin

A total of 154 separate observations were used to derive HSC for sawfin, although numbers of individual fish estimated for each observation ranged between 70-200 fish in the case of schooling juveniles and spawning adults (APPENDIX C.1). This gave rise to small datasets, but the presence of large numbers of fish in these locations suggested that selection was not random. A total of 948 depth and velocity, and 735 substratum measurements were taken to characterise available habitat over the 1.2 km reach. Kernel density distributions of depth (m) and velocity (m s^{-1}) use and frequency distributions of substratum use for each size class of sawfin, together with the corresponding distributions of available habitat are illustrated in Figure 5.1. All size classes selected depth and velocity conditions that were significantly different from the most commonly available habitat conditions (Table 5.1, P <0.01).

Larvae and early juveniles (5–20 mm TL)—Larval and early juvenile sawfin (5–20 mm TL, < 30 days old, Chapter 7 this report) were found in very shallow marginal slackwaters at the base of riffles. Optimum depth use ranged between 0.05 – 0.14 m (Figure 5.1 a). Over 75% of the observations were made in water depths of less 0.2 m. Velocity use never exceeded 0.06 m s^{-1} with optimal values being around 0.01 m s^{-1}. Both depth and velocity use differed significantly from available conditions (Table 5.1). Substratum use consisted predominantly of sand, which was also the predominant substratum type in the slackwaters. Fish in this size class were occasionally, but not exclusively, associated with overhead or instream cover (aquatic macrophytes or riparian trees).

0^+ juvenile (21–75 mm TL)—0^+ juvenile sawfin (30 – 90 days old, Chapter 7 this report) exhibited schooling behaviour and selected slightly deeper marginal slackwaters than larvae and early juveniles (Figure 5.1 b; Kolmogorov-Smirnov tests; D = -0.7 P < 0.001; Table 5.2). Optimum depth use ranged between 0.3 – 0.4 m. However, sawfin in this size class continued to select slow velocities of < 0.01 m s^{-1} (Figure 5.1b). They were found predominantly in bedrock-dominated reaches in the vicinity of riffles and bedrock cascades. They were never in water deeper than 0.5 m during the day and were observed to move to deeper waters at night, thus the utilisation curves reflect daytime habitat selection only. No overhead cover was present at any of the observed locations.

1^+ juveniles and young adults (76–150 mm TL)—sawfin in this size class were frequently observed at the base of riffles and cascades feeding on invertebrate drift. Optimum depth and velocity use was significantly greater than 0^+ juvenile ranging between 0.7 – 1.0 m and 0.01 – 0.1 m s^{-1} respectively (Figure 5.1 c; Kolmogorov-Smirnov tests for depth; D = -0.85 P < 0.001 and velocity differences; D = -0.74 P < 0.001;

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Table 5.2). Hydraulic cover, in the form of large bed particles (>250 mm) was used by fish in this size class during feeding.

Adults (>150 mm TL)—Adult sawfin that were not spawning were observed schooling in deeper runs and pools (0.6 – 1.0 m) and were infrequently seen drift-feeding over the spawning season (Figure 5.1 d). There were no significant differences between depth and velocity use between adults and 1+ juveniles (Table 5.1).

Spawning adults—sawfin spawned in relatively shallow water, with optimum depths between 0.13-0.36 m (Figure 5.1 e) and loosely embedded gravel, cobble and boulders (16-250 mm). Optimum velocities were the highest recorded for this species and ranged between 0.3-0.8 m s^{-1}. The broad range of velocities recorded at spawning sites was a consequence of turbulence at these sites. Spawning sawfin selected significantly shallower water and faster current speeds than did non-spawning adults (Kolmogorov-Smirnov tests for depth; D = 0.43 P < 0.001 and velocity differences; D = -0.57 P < 0.001; Table 5.2).

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5.3.2 Clanwilliam yellowfish

A total of 173 observations were used to derive HSC for yellowfish juveniles and adults. Three principal habitat groups were identified amongst yellowfish: juvenile (75-150 mm TL), young adult and adult (> 150 mm TL) and adult foraging (Figure 5.2 a). Yellowfish did not spawn during the course of sampling and therefore no information regarding spawning habitat could be obtained. Unlike sawfin, however, yellowfish were frequently encountered drift-feeding downstream of riffles. Only juvenile yellowfish depth use differed significantly from available depths (Kolmogorov-Smirnov tests; D = -0.5 P < 0.001, Table 5.3), but velocity use was significantly different from the most commonly available velocities for all size classes (Table 5.3) in that rare areas of higher velocity were selected.

1^+ Juvenile (75-150 mm TL)—Juvenile yellowfish were frequently encountered in shallow (0.2-0.4 m), fast flowing riffles with optimum velocities ranging between 0.1-0.4 m s^{-1} and a loosely embedded cobble substratum that they used for cover (Figure 5.2 a).

Adult (>150 mm TL)—Adult yellowfish selected significantly deeper runs with slower velocities than juveniles (Kolmogorov-Smirnov tests for depth; D = 0.67 P < 0.001 and velocities; D = -0.65 P < 0.001, Table 5.4). Optimum depths for this group ranged between 0.5-0.8 m and velocities between 0.01-0.2 m s^{-1} (Figure 5.2 b).

Adult drift-feeding (>150 mm TL)—A high proportion of yellowfish was observed feeding from the drift during the course of dive surveys. Fish sought cover in the lee of a cobble or boulder, or in the vicinity of a velocity shear (a high velocity gradient) from where they made short excursions into the faster current to collect drift. Optimum cover velocities for foraging were similar to those used by 1^+ juvenile yellowfish and ranged between 0.1-0.3 m s^{-1}. Adjacent velocities, i.e. those areas into which fish would move to collect drift particles, ranged between 0.3-0.5 m s^{-1}. (Figure 5.2 c). Adjacent depths were similar to cover depths (0.4-0.7 m).

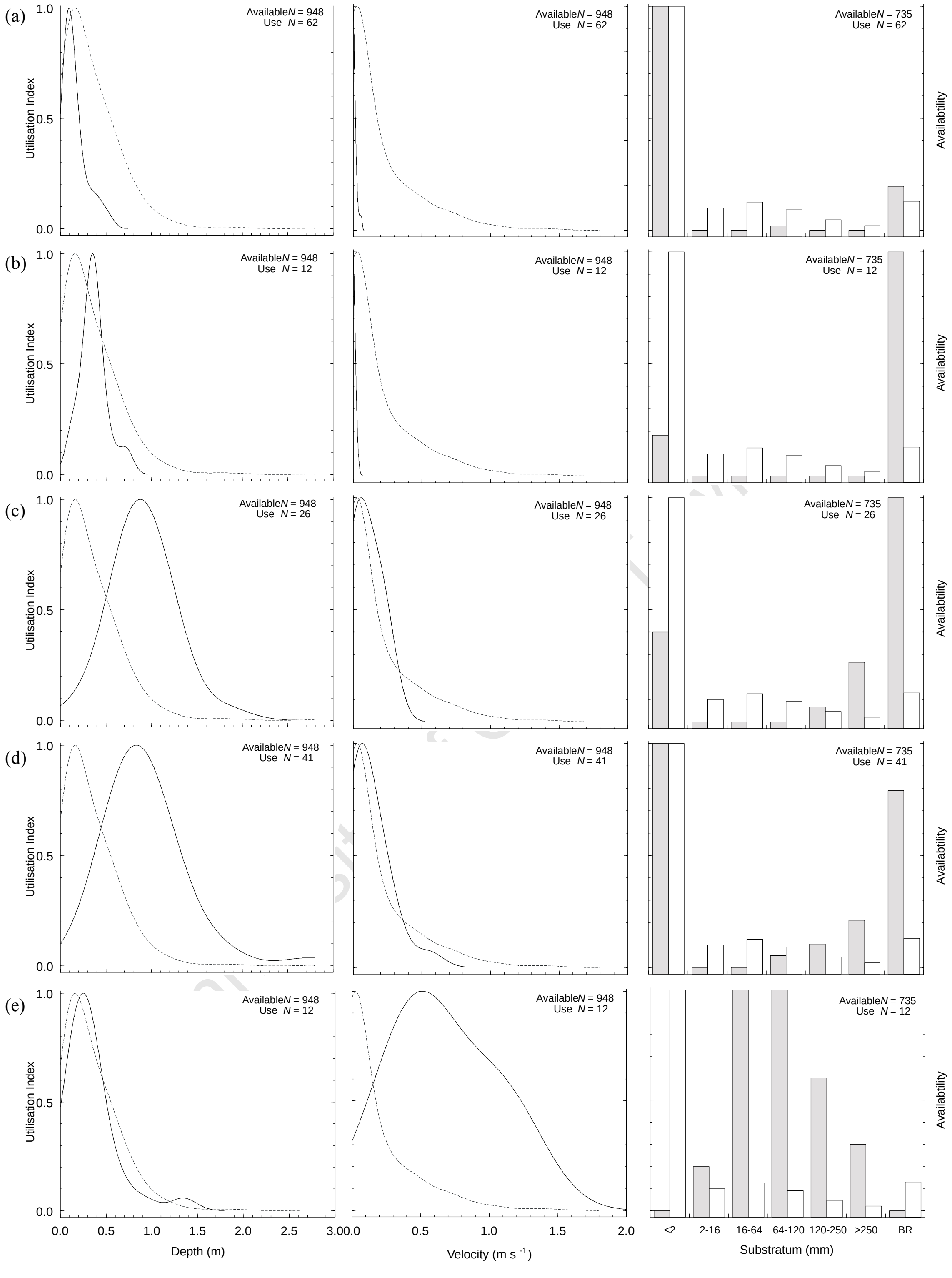

Figure 5.1 HSC derived for sawfin. Kernel-smoothed density distributions of depth (m) and velocity (m s^{-1}) (broken lines = availability, solid lines = use) and frequency distributions of substratum utilisation (open bars = availability, shaded bars = use) for (a) 5-20 mm TL; (b) 21-75 mm TL; (c) 76-150 mm TL; (d) >150 mm TL and (e) spawning sawfin.

TABLE 5.1 Comparison between available depth and velocities and habitat use by sawfin according to size class and behaviour (spawning and non-spawning). The Kolmogorov-Smirnov D-statistic is reported in the final two columns. Alpha was set at 0.01. Asterisks denote significant differences (P < 0.01* or P <0.001**).

		Depth (m)	Velocity ($m\ s^{-1}$)			Depth (m)	Velocity ($m\ s^{-1}$)	Depth comparison	Velocity Comparison
	N	Mean±SD	Mean±SD		*N*	Mean±SD	Mean±SD	*D*-statistic	*D*-statistic
Available	948	0.30±0.32	0.17±0.26	5-20 mm TL	62	0.15±0.12	0.00±0.02	-0.30**	-0.52**
Available	948	0.30±0.32	0.17±0.26	21-75 mm TL	14	0.36±0.15	-0.01±0.02	0.45*	-0.59**
Available	948	0.30±0.32	0.17±0.26	76-150 mm TL	26	0.91±0.31	0.10±0.10	0.77**	-0.25
Available	948	0.30±0.32	0.17±0.26	>150 mm TL	41	0.93±0.44	0.12±0.14	0.72**	0.26*
Available	948	0.30±0.32	0.17±0.26	spawning	44	0.67±0.32	0.36±0.29	0.55**	0.53**

TABLE 5.2 Comparison of habitat use by sawfin between different size classes and behaviours (spawning and non-spawning). The Kolmogorov-Smirnov D-statistic is reported in the final two columns. Alpha was set at 0.01. Asterisks denote significant differences (P < 0.01* or P <0.001**).

		Depth (m)	Velocity\ ($m\ s^{-1}$)			Depth (m)	Velocity ($m\ s^{-1}$)	Depth comparison	Velocity comparison
	N	Mean±SD	Mean±SD		*N*	Mean±SD	Mean±SD	*D*-statistic	*D*-statistic
5-20 mm TL	62	0.15±0.12	0.00±0.02	21-75 mm TL)	14	0.36±0.15	-0.01±0.02	-0.70**	0.25
21-75 mm TL	14	0.36±0.15	-0.01±0.02	76-150 mm TL)	26	0.91±0.31	0.10±0.10	-0.85**	-0.74**
76-150 mm TL	26	0.91±0.31	0.10±0.10	>150 mm TL)	41	0.93±0.44	0.12±0.14	0.11	-0.15
>150 mm TL	41	0.93±0.44	0.12±0.14	spawning	44	0.67±0.32	0.36±0.29	0.43**	-0.57**

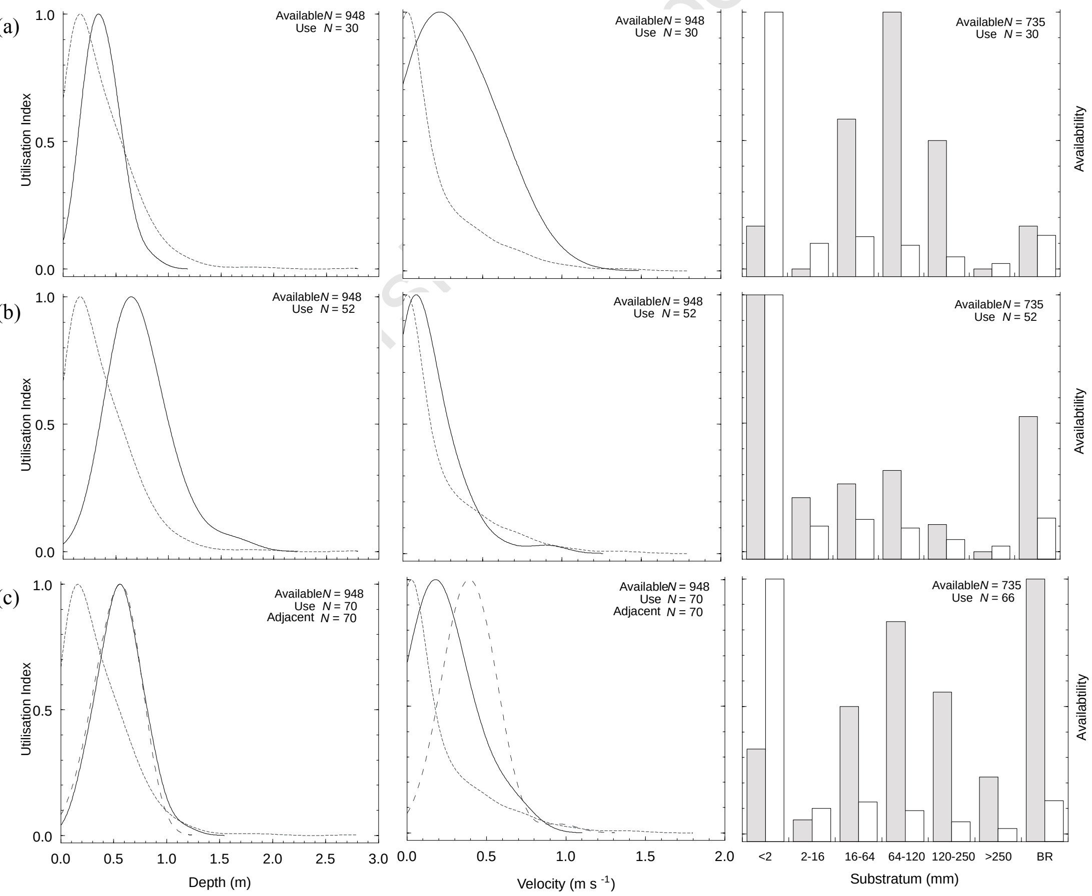

Figure 5.2 HSC derived for yellowfish. Kernel-smoothed density distributions of depth (m) and velocity ($m\ s^{-1}$) (broken lines = availability, solid lines = use, dashed lines = adjacent) and frequency distributions of substratum utilisation (open bars = availability, shaded bars = use) for (a) 75-150 mm TL; (b) >150 mm TL; and (c) drift-feeding yellowfish (dashed lines indicate drift-feeding areas adjacent to holding positions).

TABLE 5.3 Comparison between available depth and velocities and habitat use by yellowfish according size class and behaviour (drift-feeding). The Kolmogorov-Smirnov D-statistic is reported in the final two columns. Alpha was set at 0.01. Asterisks denote significant differences ($P < 0.01$* or $P < 0.001$**).

		Depth (m)	Velocity ($m\ s^{-1}$)			Depth (m)	Velocity ($m\ s^{-1}$)	Depth comparison	Velocity comparison
	N	Mean±SD	Mean±SD		*N*	Mean±SD	Mean±SD	*D*-statistic	*D*-statistic
Available	948	0.30±0.32	0.17±0.26	75-150 mm TL	30	0.37±0.14	0.30±0.23	0.50**	0.42**
Available	948	0.30±0.32	0.17±0.26	(>80 mm TL	51	0.72±0.28	0.17±0.20	-0.23	0.80**
Available	948	0.30±0.32	0.17±0.26	drift-feeding	66	0.22±0.19	0.56±0.20	-0.16	0.71**

TABLE 5.4 Comparison of habitat use by yellowfish between size classes and behaviours (drift-feeding and non-drift feeding). The Kolmogorov-Smirnov D-statistic is reported in the final two columns. Alpha was set at 0.01. Asterisks denote significant differences ($P < 0.01$* or $P < 0.001$**).

		Depth (m)	Velocity ($m\ s^{-1}$)			Depth (m)	Velocity ($m\ s^{-1}$)	Depth comparison	Velocity comparison
	N	Mean±SD	Mean±SD		*N*	Mean±SD	Mean±SD	*D*-statistic	*D*-statistic
75-150 mm TL	30	0.37±0.14	0.30±0.23	>150 mm TL	51	0.72±0.28	0.17±0.20	0.67**	-0.65**
>80 mm TL	51	0.72±0.28	0.17±0.20	drift-feeding	66	0.22±0.19	0.56±0.20	-0.29	-0.31*

5.3.3 *Comparison between species*

Both yellowfish and sawfin juveniles selected similar depth ranges (0.2-0.4 and 0.3-0.4 m respectively), but whereas sawfin juveniles were found in slackwaters with low velocities (<0.01 $m\ s^{-1}$), juvenile yellowfish were associated with riffles with significantly higher velocities (0.1-0.4 $m\ s^{-1}$; Kolmogorov-Smirnov tests; $D = -0.93$ $P < 0.001$; Table 5.5) and a gravel-cobble substratum. There were no significant differences between adult sawfin and yellowfish depth and velocity use (Table 5.5).

TABLE 5.5 Comparison of depth and velocity habitat use between species (sawfin (*Bs*) and yellowfish (*Lc*)) in comparable size classes. The Kolmogorov-Smirnov D-statistic is reported in the final two columns. Alpha was set at 0.01. Asterisks denote significant differences ($P < 0.01$* or $P < 0.001$**).

		Depth (m)	Velocity ($m\ s^{-1}$)			Depth (m)	Velocity ($m\ s^{-1}$)	Depth comparison	Velocity comparison
	N	Mean±SD	Mean±SD		*N*	Mean±SD	Mean±SD	*D*-statistic	*D*-statistic
Bs (21-75 mm TL)	14	0.36±0.15	-0.01±0.02	*Lc* (20-80 mm TL)	30	0.37±0.14	0.30±0.23	0.19	-0.93**
Bs(>150 mm TL)	41	0.93±0.44	0.12±0.14	*Lc* (>80 mm TL)	51	0.72±0.28	0.17±0.20	-0.26	-0.14

5.3.4 *Diel shifts in habitat use by 0^+ juvenile*

Temperature changes were more extreme in the shallow slackwaters, varying by up to 10 °C (17-27 °C), than in the deeper areas (> 1 m) of the main channel where daily temperature variations did not exceed 4 °C (19-23°C) (Figure 5.3). Temperatures in the shallow slackwaters were up to 4 °C warmer during the day, but 1-1.5 °C colder than in the main channel at night. Sawfin moved out of the shallow habitats to deeper areas in the main channel (>1 m) between 19h00 and 20h00 in the evening as soon as temperatures in these areas had equalled or dropped below the temperature in the main channel (~19 °C). They migrated back to the shallow areas between 09h00 and 12h00 when temperatures there exceeded those in the main channel. The largest numbers of fish in the shallow marginal habitats corresponded to the highest temperatures in these areas (Figure 5.3).

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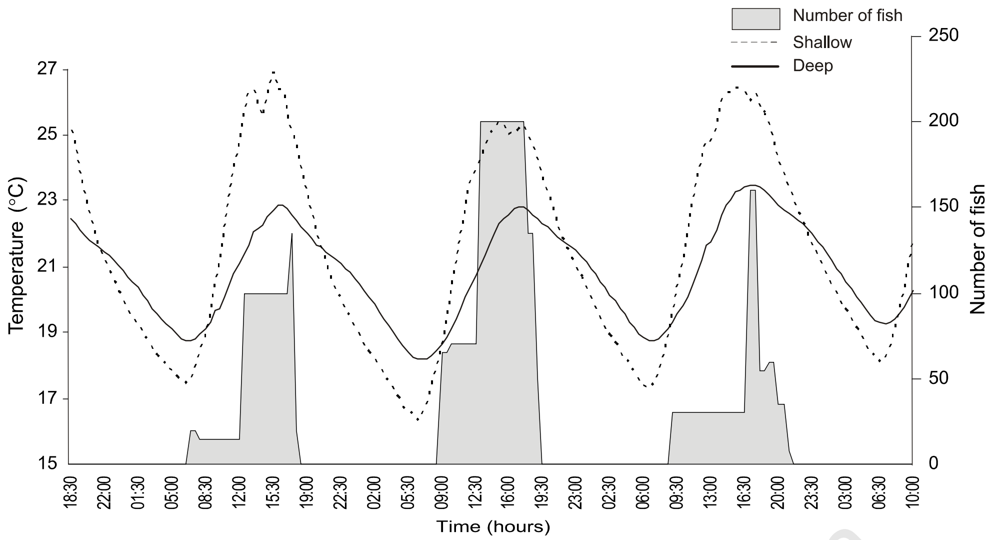

Figure 5.3 Diel temperature differences (primary *y*-axis) recorded in deep water (> 1 m) (solid line) and shallow slackwaters (dashed line) together with estimates of the abundance of 0^+ juvenile sawfin (solid line) counted in the shallow slackwaters (<0.3 m; <0.01 m s^{-1}) (secondary *y*-axis) over an 86 hour period during November 2005.

5.4 DISCUSSION

Although widely criticised, HSC-based approaches remain an effective means of establishing links between a river's biota and its physical habitat (Castleberry *et al.* 1996). Category III criteria, or 'suitability curves', that express HSC as a proportion of available habitat, are generally preferred over the simple utilisation curves presented in this chapter (Category II criteria; Bovee 1986). A number of workers have disputed the incorporation of available habitat into utilisation curves, however, since this introduces distortions of its own (Lambert and Hanson 1989; Pollard 2000). This study adopted the latter view and used available habitat only as a means of testing whether fish are equally distributed through the range of depth and velocity conditions available to them. In all cases, there were significant differences between depth and velocity use by sawfin and available depth and velocity distributions within the study reach, suggesting that the distribution of fish within the river was non-random.

Another criticism of the use of HSC is that they are single, univariate response functions whereas fish habitat selection is dynamic, varying between seasons (Nickelson *et al*. 1992), discharges (Holm *et al*. 2001), life stages (Rosenberger and Angermeier 2003) and behaviours (Aadland 1993). Differences in fish size and resource use may be so large that larvae, juveniles and adults may be considered separate ontogenetic units. This study has attempted to address this complexity by focussing on those life stages and behaviours considered most limiting to fish production, i.e. early life stage, foraging and spawning. Thus, in addition to differences between species, this study has provided clear evidence for differential habitat selection related to ontogeny and growth in both sawfin and Clanwilliam yellowfish.

Larval sawfin measuring between 5-20 mm TL selected very shallow slackwaters (<0.15 m) along river shorelines and the edges of sandbars for the first 30 days post-spawning. Selection of littoral slackwaters, backwaters and floodplains by young fish has been postulated as being due to their reduced swimming capacity (Nykänen and Huusko 2004), a mechanism to minimise predation risk from aquatic predators

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(Harvey 1991; Eklov 1994) and due to the increased availability of food in the form of benthic microbes and zooplankton as a result of higher temperatures and increased water retention in these areas (Humphries *et al*. 2002; Thorp and Mantovani 2005). The availability of these habitat types has been found to have a marked influence on the abundance of rheophilic cyprinids in rivers (Copp 1990). Larvae are unlikely to occur in regions where current speeds exceed their maximum sustained swimming speed (Schiedegger and Bain 1995). Webb (1975) estimated that sustained swimming speeds for most fish were in the region of 3-5 body lengths per second, which in this case would translate to a range of between 0.02 to 0.1 m s^{-1} – a similar range to the velocities occupied by sawfin larvae in this study.

At some point between January and March, older juvenile sawfin (> 30 days old) began exhibiting schooling behaviour and migrated several kilometres downstream (Chapter 4, this report). These sawfin that fell within the 21-75 mm TL size class made use of slightly deeper inshore bays (< 0.5 m) during the day. Shifts in habitat use from shallow to deeper waters such as these have been found to accompany the morphological transition from larvae to juveniles in other cyprinid species (Simonović *et al*. 1999).

The shift from shallow slackwaters to deeper inshore bays by 0^+ juvenile sawfin was also accompanied by diel migrations to and from the main channel. In the evening (~19h00), juvenile sawfin moved from the inshore slackwaters into deeper waters (>1 m) in the main channel, returning to the bays between 10h00 in the morning and mid-day. Temperatures drop more rapidly in the shallows at night due to the decreased specific heat capacity of smaller volumes of water, and the inshore-offshore migrations appeared to correspond to the period during which temperatures equilibrated between the shallow and deep areas. Schools of juvenile sawfin were observed taking cover under bedrock shelves in the deeper main channel areas.

Few studies have addressed diel patterns of habitat use by juvenile cyprinids in rivers. However, similar temperature variations between shallow and deep areas with corresponding diel shifts in habitat use by minnows (*Phoxinos phoxinos*) were reported by Garner *et al*. (1998) who reported that the minnows moved from warm shallow waters during the day to the main channel during the evening and morning to feed. They hypothesised that a trade-off existed that maximised somatic growth by balancing a higher prey density and lower temperatures in the main channel at night and morning, with lower prey density and higher water temperature in the shallows during the day. Baras and Nindaba (1999) showed that 0^+ chub (*Leuciscus cephalus*) and dace (*Leuciscus leuciscus*) shifted from the exclusive use of shallow inshore bays, to a diel pattern of inshore-offshore movement. They also hypothesised that trade-offs between food availability and predator avoidance drive this kind of behaviour. Hohausová *et al*. (2003) found that water levels, temperature and illumination were the most important factors influencing fish movement in and out of backwaters on the River Morava in the Czech Republic.

The variability in habitat use amongst sawfin even during these earlier life stages demonstrates some of the difficulties of characterising instream habitat conditions for any particular species by means of single univariate response curves and explains in part why HSC-based methods have given rise to such heated debates in the literature. However, given sufficient knowledge of the species, it would be possible to isolate the more critical habitat units that are most susceptible to river flow modification such as daytime feeding or spawning areas, as has been done in this study. Ideally, these habitat bottlenecks that may have a disproportionate influence on fish growth and survival should be determined empirically (Bovee *et al*. 1994).

However, in most cases, including in the current study, these types of data are not available and bottlenecks would need to be identified *a priori* using best available knowledge on the species or habitat guild.

In addition to differences between life stage-specific and diel habitat use, there were also significant differences between species. Where sawfin 0^+ juveniles selected bedrock-dominated reaches, 1^+ juvenile Clanwilliam yellowfish selected riffles with higher current speeds over gravel and cobble where they were found feeding on drift. Although few in numbers due to low recruitment levels in the Driehoeks River, these juvenile yellowfish were associated almost exclusively with these habitat types. Due to their high turbulence and elevated topography, riffles are some of the most productive habitats in rivers (Brussock and Brown 1991). These areas would therefore provide profitable foraging areas for young yellowfish able to withstand the stronger currents.

Hardy *et al*. (2006) argued that the use of traditional habitat utilisation models in instream flow assessments sometimes results in 'irrational' relationships between river discharge and instream habitat. These frequently contradict the scientist's intuitive understanding of river function and give rise to predictions that are detrimental to the ecosystems they were designed to protect. Hardy *et al*. (2006) suggested that part of the reason for this is that these models are overly simplistic and in particular, fail to take into account adjacent stream attributes. In their study, Hardy *et al.* (2006) derived habitat measurements based on the proximity of chinook salmon fry (*Oncorhynchus tschawytscha*) to escape cover. In this study, it was felt that a single focal-point velocity would be inadequate for characterising foraging habitat by adult yellowfish since their selection of foraging habitat appeared to depend on both vertical and lateral velocity shears, i.e. bands of slow flowing water in close proximity to areas with higher current speeds. These velocity shears arose due to channel morphology or the presence of large bed particles. Two utilisation curves for each hydraulic variable of depth and velocity were therefore derived for drift-feeding yellowfish: one focal-point velocity and a second for the area into which the fish was observed making repeated forays to collect drift. The ability of the more traditional HSC habitat models and the adjacent velocity models to predict yellowfish feeding habitat in a two-dimensional hydrodynamic model will be tested in Chapter 6.

Prior to the current study, the spawning habitat and behaviour of sawfin were known only from anecdotal accounts. This study has confirmed that, like the Clanwilliam yellowfish, sawfin are non-guarding, open substratum, lithophilic spawners (A.1.3) (Balon 1975; Cambray *et al*. 1997), selecting riffles and runs with loosely embedded gravel, cobble and boulder substrata, significantly shallower water and faster current speeds than non-spawning adults. Sawfin gathered in these habitat types in schools that sometimes exceeded 70 individuals. Females near the upstream end of the school released eggs into the interstices between the substrata were seen to be fertilised by attendant males. Although measured current speeds at the spawning sites were highly variable due to turbulence (0.3-0.8 m s^{-1}) all sites were situated in close proximity (< 8 m) to some of the highest current speeds measured in the study reach (> 0.8 m s^{-1}). Shallow riffles with swifter currents and gravel and cobble substrata are used for spawning by a number of rheophilic cyprinid species, including the common barbel (*Barbus barbus*) (Hancock *et al*. 1976) and nase (*Chondrostoma nasus*) (Keckeis 2001) in Europe, and many of the larger-bodied rheophilic cyprinids in South Africa including *inter alia* the largemouth yellowfish *Labeobarbus kimberlyensis*, the smallmouth yellowfish *L. aeneus* (Tómasson *et al*. 1984) and the Kwazulu Natal yellowfish *L. natalensis* (Crass 1964). The higher concentration and rate of oxygen delivery in these areas relative to other habitat types, resulting from the increased turbulence and

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the entrainment of air bubbles near the surface, make them ideal environments for incubating fish eggs (Soulsby *et al*. 2001). Clanwilliam yellowfish did not spawn during the study period and the possible reasons for this will be dealt with in Chapter 8.

5.4.1 Conclusions

In this chapter utilisation curves for three principal physical habitat variables (depth, velocity and substratum) were derived for sawfin and Clanwilliam yellowfish. Significant differences were found between larval, juvenile and adult life stages, as well as between species. Since habitat bottlenecks may occur at any stage in a fish's life history, the importance of considering multiple life stages when providing input to EWR assessments is underscored. At the scale of the river reach, these critical sawfin habitats included: riffles with fast flowing water and loosely embedded cobble substratum for spawning, shallow slackwaters along shoreline or sandbar edges for larval sawfin, and inshore bays for older juveniles. Critical habitats for yellowfish included shear zones near the base of riffles for foraging adults and riffles for juvenile yellowfish.

The results presented here suggest that for spring irrigation releases, a careful balance needs to be struck between providing adequate hydraulic conditions that will promote spawning and successful incubation of eggs, without drowning out larval and juvenile habitat and displacing these early life stages into unfavourable habitat where they would be vulnerable to predation and starvation. More detailed management recommendations relating to the species of concern will be presented in Chapter 9.

The findings of this chapter should be treated with some caution for a number of reasons. Firstly, the limitations of HSC discussed in the introduction to this chapter and in more detail in Chapter 2 should be borne in mind. In particular it should be noted that the site, the river and the time of collection and the discharge has a significant effect on the shape of utilisation curves (Mathur *et al*. 1985; Holm *et al*. 2001). HSC are best compiled by comparing or combining data from several rivers at different discharges. Since the HSC derived here will only be used in the source river, this is not an important consideration. However, the Driehoeks River is a first order tributary system where adult sawfin and yellowfish are growth-limited due to low habitat volume and temperatures. Thus care should be exercised when extrapolating the results to larger-bodied mainstem populations where physical-habitat conditions are likely to be different. Regional HSC (habitat models that encompassed the entire geographic range of the species) would require that data be included from mainstem reaches.

A further consideration highlighted in this study relates to the difficulty of representing the dynamic nature of habitat use by fish by means of a univariate response function. Observations of 0^+ juvenile sawfin behaviour revealed that they undertook diel migrations between shallow inshore bays and the main channel in the evening and the mornings. This emphasises the importance of identifying critical habitats for a species, i.e. habitats most likely to affect abundances and that are sensitive to flow modification, before an EWR assessment is undertaken.

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CHAPTER 6 Using a two-dimensional hydraulic model (River2D) to simulate Clanwilliam yellowfish and sawfin habitat in the Driehoeks River: model validation based on fish spatial distribution

6.1 INTRODUCTION

Hydraulic-habitat simulation models were developed for predicting the ecological implications of flow alteration in rivers subjected to water abstraction and flow regulation. They typically combine predictions from hydraulic models with empirically derived species and life stage-specific hydraulic habitat relationships (Hydraulic Suitability Criteria HSC, Chapter 5 this report) to predict how changes in discharge affect the availability of aquatic habitat. Predictions of habitat availability are then used within environmental flow methodologies as one of the inputs for creating alternative flow scenarios. The Instream Flow Incremental Methodology IFIM (Bovee 1982) was the first water resource planning methodology to use a habitat simulation approach – the Physical HABitat SIMulation model PHABSIM (Milhous 1989) which is contained within the IFIM. Developed by the Co-operative Instream Flow Service Group of the US Fish and Wildlife Service in the 1970s, the IFIM is still the most widely used methodology in the world (Tharme 2003). However, a range of similar hydraulic simulation techniques has been developed in a number of countries to meet local needs and capacities. These have included *inter alia* the river hydraulics methodology in New Zealand RHYHABSIM (Jowett 1996), the habitat evaluation method in France EVHA (Souchon *et al*. 1989) and the Canadian habitat modelling system HABIOSIM (Dunbar *et al*. 1998).

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Amongst the litany of criticisms that has been levelled at these methodologies (discussed in more detail in Chapter 2), one concern relates to the inadequacies of the hydraulic models themselves (Scruton *et al*. 1998). Earlier hydraulic modelling approaches, including PHABSIM, made use of one-dimensional (1-D) hydraulic models that predicted an average Water Surface Elevation (WSE) and an average velocity at river cross-sections for any discharge of interest. The transect profile was intersected by a number of survey points that form the centre or edge of an area of the channel referred to as a cell. Based on the average velocity at each cross-section, velocities were allocated to each cell of the cross-section either using measured velocities for calibration or estimating velocity based on local channel conditions. Weighted Usable Area (WUA) – an index of the habitat available to an organism calculated from the wetted area of the modelled reach weighted by its suitability for use by that organism – can then be calculated. 1-D models have a number of limitations, however. One of the most important of these is that they assume uniform conditions across the width and length of each cell and therefore are unable to adequately represent the mosaic of heterogeneous hydraulic conditions in the river at resolutions relevant to fish (<1 m^2) (Leclerc *et al*. 1995; Scruton *et al*. 1998). Also, they are not accurate for describing low-flow hydraulics in rivers with complex morphologies, particularly for parts of the channel that may be subject to wetting and drying (Leclerc *et al*. 1995) or where Water Surface Elevations (WSEs) in multiple channels are at different heights (Dr. J.M. King, *pers. comm*.). They require a large amount of data for calibration and validation and are time consuming and expensive (Armour and Taylor 1991; King and Tharme 1994).

The last decade has seen the increasing use of two-dimensional (2-D) depth-averaged hydraulic models for flow simulation. Whereas 1-D models depict the river in terms of a number of cross-sections, 2-D models depict it as a continuous grid of computational nodes or cells for each of which a depth and a depth-averaged velocity is predicted using shallow-water equations (Blackburn and Steffler 2002). Unlike 1-D models, 2-D models are able to include the downstream and transverse velocity components between cells (or nodes). Apart from their ability to represent the heterogeneity of conditions in river channels more accurately and at much higher resolutions than 1-D models, one of their most important advantages is that they are spatially explicit, having the ability to predict not only the frequency distribution, but also the location of point depth and velocity values, across the modelled reach. This has numerous advantages, including the ability to calculate measures of habitat heterogeneity (Bovee 1996), to query the juxtaposition of different habitat types and to incorporate behaviour-based decision rules (Hardy *et al*. 2006). Another major advantage of spatially-referenced hydraulic models is that they facilitate simple validation by correlating predicted habitat suitability with observed fish microposition choice. Using this approach, both Boudreau *et al*. (1996) and Guay *et al.* (2003) found significant and positive relationships between Atlantic salmon (*Salmo salar*) parr densities estimated from surveyed fish positions and habitat quality indices predicted by a 2-D hydraulic model.

In South Africa, the South African National Water Act of 1998 (NWA No. 36 of 1998) stipulates that a proportion of water in a river (the Reserve) be set aside to protect and maintain the aquatic ecosystem. Together with water to meet basic human needs, the National Water Act ensures the Reserve is accorded the highest priority for water allocation and is therefore determined before water-licence applications are processed (Brown *et al*. 2006). A variety of different approaches with varying levels of sophistication and data requirements has been explored for setting the Reserve for local river systems (King and Tharme 1994, King and Louw 1998; Rowntree and Wadeson 1998; Hughes and Hannart 2003; King *et al*. 2003). Despite advances in hydraulic modelling techniques, the adoption of habitat simulation approaches in South Africa, whether they be 1-D or 2-D, has met with considerable resistance from local scientists who have focussed their criticisms on the data-intensive requirements of such methods and their species specificity (King and Tharme 1994; Pollard 2000, Tharme 2003). In addition, lack of capacity and financial constraints has limited the widespread application of these methods. Instead, scientists here have focused on the development of whole-ecosystem approaches that rely on some data collection and available knowledge gleaned from experts and that have the ability to integrate the social outcomes of altered flows into assessment procedures – a vital consideration in developing countries (King and Louw 1998; King *et al*. 2003). A diverse combination of alternative sources of hydrological and hydraulic data has therefore been used to evaluate the consequences of flow change in this country. This has included: measured depth and velocity data, cross-sectional profiles, flow duration curves and flood-class frequencies (Brown *et al*. 2006). The standard hydraulic data used in Ecological Water Requirement (EWR) assessments are a stage-discharge relationship and an average velocity per cross-section calculated as a function of discharge or stage (including width, maximum or average depth, wetted perimeter and average velocity). Levels of complexity in Reserve determinations (Rapid, Intermediate and Comprehensive) differ only in terms of the quantity of rating data that are measured and the number of cross-sections per site (MacKay 1999; Jordanova *et al*. 2004). This information can be supplemented with fixed-point photography and hydraulic-biotope mapping (Wadeson and Rowntree 2001).

Inferring fish and invertebrate responses from the aforementioned data types presents ecologists with considerable challenges because of the spatial resolution of the hydraulic outputs, the difficulty of estimating

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changes in the spatial extent of usable habitat and the limited predictive capabilities associated with photography and mapping. There exists therefore considerable scope for improving confidence in South African EWR assessments through more widespread application of 2-D hydraulic modelling techniques. This may be particularly important in water-stressed catchments where fish or invertebrates are accorded high conservation status, or may be in imminent danger of extinction (as is the case in the Olifants/Doring Rivers system) and so a greater degree of scientific certainty is desired. In recent years, the increased availability and user-friendliness of habitat-simulation software has provided the incentive to test the applicability of these tools in local river systems.

The primary of objective of this chapter was therefore to evaluate the suitability of a 2-D hydraulic modelling programme – River2D (Blackburn and Steffler 2002; University of Alberta 2002) – for simulating Clanwilliam yellowfish and sawfin habitat. This component of the study formed part of a collaboration with a related WRC Project "Ecohydraulic modelling in river systems" (WRC Report No. 1508/1/07; Hirschowitz *et al*. 2007) that aimed to investigate a range of alternative methods – including 2-D hydraulic modelling – for predicting the impacts of flow modification on habitat-defining hydraulic conditions in rivers. In this chapter, the HSC derived for Clanwilliam yellowfish and sawfin in Chapter 5 were combined with the simulated depths and velocities generated by River2D and measured substratum particle sizes into Combined Suitability Indices (CSIs). To evaluate the consequences of alternative flows on habitat availability, WUA was then calculated for each species and life stage and for each site over a range of discharges. To test the ability of River2D to accurately predict microposition choice by yellowfish and sawfin, the correspondence between observed fish positions and the spatial distribution of the simulated habitat suitabilities was investigated; the assumption being that high model accuracy would be reflected by a strong relationship between these two parameters.

6.2 METHODS

6.2.1 Study sites and species

Three sites, distributed over a 700 m segment of the Driehoeks River, were selected for hydraulic modelling purposes (Figure 3.4). The river along this segment consisted of a series of shallow riffles with cobble substrata alternating with deeper runs and shallow pools with a combination of bedrock and sand substrata. Maximum depths along the segment did not exceed 1.6 m and river widths ranged between 2 and 14 m. River gradients ranged between 0.004 and 0.14 and the mean gradient over the entire segment was 0.04. Where the gradient was higher, the river channel braided between vegetated islands (predominantly *Elegia* spp.), whereas it formed a single channel in the intervening lower gradient reaches. The three modelling sites were selected because they contained a wide range of available habitat conditions as well as the presence of several life stages of the species of interest, i.e. the Clanwilliam yellowfish and sawfin. The sites from upstream to downstream were: Upper Tafelberg (~35 m in length); Lower Tafelberg (~40 m in length) and Sneeuberg (~55 m in length) (Figure 3.4). Lower Tafelberg was 110 m downstream of Upper Tafelberg and Sneeuberg was another 420 m downstream of Lower Tafelberg.

The Upper Tafelberg site consisted of two riffles and two runs with two side channels on the left bank, separated from the main channel by vegetated islands, that only flowed at intermediate discharges. The instream substratum at this site consisted predominantly of cobble (37%) in the higher-velocity riffles (see Section 5.2.2 for substratum class descriptions) with sand (16%) and bedrock (15%) dominant in the remainder of the reach. Lower Tafelberg site (Plate 6.1) consisted of a single riffle with part of a run immediately downstream. Cobble formed the largest component of the substratum (31%), with sand (25%) on bedrock (19%) comprising the remainder. Sneeuberg site consisted of a run-riffle-run sequence with a considerable amount of slackwater on the right bank that flowed only at higher discharges. The substratum consisted predominantly of sand (30%), cobble (21%) and gravel (11%).

Plate 6.1 Lower Tafelberg site showing the spawning riffle and run immediately downstream

6.2.2 Data collection

Hydraulic model— Topographic data, together with the hydraulic data required to calibrate the hydraulic models, were collected over the winter high flow period (July 2005), as well as the early (December 2005) and late summer (March 2006) low flow period.

Bed elevation was surveyed with a total station from benchmarks situated along the length of the study segment. Topographic survey points were situated either on selected cross-sections or at large features expected to influence hydraulics, such as the boundaries of vegetation islands. Cross-sections were situated at intervals along the length of each site where irregularities in channel geometry, current speed, bed slope and/or substratum type could be visually distinguished and were deemed to have an influence on local hydraulics. Within each cross-section, points of obvious change in slope were surveyed in order to allow a good approximation of the cross-section profile. All edge water points were also surveyed. Additional features expected to influence hydraulics, such as the presence of large boulders or the boundaries of vegetated islands, were surveyed, generally using tape and offset survey.

Hydraulic data were measured along cross-sections within each site, several of which coincided with the topographic survey cross-sections. Measurement points along each of the cross-sections were spaced at equal intervals (0.5-1.0 m) if habitat conditions were uniform or at local changes in channel geometry if they were not. At each measurement point, depth was recorded for hydraulic model calibration and substratum size (median axis) was measured. Mean water-column velocity was measured at 0.6 of the depth from the surface over a 30-s period using a Flo-Mate Marsh McBirney® electromagnetic current meter. All three sites were linked to a common datum by means of permanent benchmarks set up along the banks. Water Surface Elevation was monitored continuously by means of a piezoresistive pressure sensor coupled to a data logger (STS® data logger DL/N 641) installed at a site 1.2 km upstream of the modelled sites. No tributaries entered the river between these two areas. The sampling rate was set at 30 min intervals and a gauging plate was erected to calibrate the logger. A rating curve was developed using stage at the stage logger and discharge measured by the velocity-area method at a cross-section at Site 2: Lower Tafelberg (APPENDIX F.3).

Biological habitat models (HSC)—HSC were derived using the visual observation techniques described in Chapter 5 (Bovee 1997). Ideally, models should not be validated using data that were initially used to develop the model (Boudreau *et al*. 1996). Due to the low number of rivers in the Olifants/Doring catchment that support all life stages of the target species and the difficulty of accessing many these rivers, it was not possible to obtain sufficient HSC data from areas that did not include the modelled reaches. Even within the Driehoeks River, there were few opportunities for collecting data from elsewhere in the river since most of the fish were concentrated in these reaches. Thus due to the limited study area available, habitat simulations were performed using the HSC derived from the 1.2 km river segment described in Chapter 5 that included the three modelled sites. The modelled sites were included during derivation of the HSC, since exclusion of data from these sites would have given rise to biases in the HSC models. That said, the greater proportion of the HSC data came from observations made in the intervening reaches between the modelled sites, as well as the reaches immediately upstream and downstream of those sites.

HSC were derived for four estimated size classes of sawfin: larval sawfin (5-20 mm Total Length (TL)), 0+ sawfin (21-75 mm TL), juvenile sawfin (76-150 mm TL) and adult sawfin (>150 mm TL), as well as for spawning sawfin (see Chapter 5, Section 5.2.2 for a detailed report on the methodology used to derive HSC). For the modelling procedure, however, the last two size classes were combined into a single size class (>75 mm TL) since no significant differences in habitat use between these two size classes were detected. Since no yellowfish < 75 mm TL were observed, Clanwilliam yellowfish were separated into two size classes: juvenile (75-150 mm TL) and adult (>150 mm TL).

6.2.3 Habitat simulation

A hydraulic habitat simulation was performed using the software River2D according to the procedure outlined by Steffler and Blackburne (2002). A description of the procedure for hydraulic simulation in this study are beyond the scope of this chapter, but have been reported by Hirschowitz *et al*. (2007). The survey data used in the modelling procedure in this study are also available in APPENDIX A of Hirschowitz *et al*.'s (2007) report. The calibration of hydraulic models is also discussed in that report. The surveyed topographic data collected between July 2005 and March 2006 (Section 6.2.2 above), were used to develop a Triangular Irregular Network (TIN) (an irregular digital mesh of nodes and lines forming triangles) representing the bed topography. For all three sites, boundary conditions at the inflow section were set at the discharge of interest and fixed water surface elevations were set at the outflow section by interpolation of the surveyed elevations.

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The equivalent sand grain roughness (*ks*) within each area of the model was estimated based on the predominant substratum and vegetation characteristics. In River2D a Composite Suitability Index (CSI) is calculated at each computational node in the TIN of the hydrodynamic model as the product of the depth and velocity indices and the Channel Index (CI) (substratum and/or cover) as determined for each species and life stage of interest (Chapter 5):

$$\text{Composite SI} = \text{depth SI} \times \text{velocity SI} \times \text{Channel Index}$$

WUA in River2D is based on the PHABSIM concept and is calculated as an aggregate of the product of the CSI at each node at the vertices of the triangle and the area associated with that node (CSI × surface area). Since CSI is a dimensionless number, the units for WUA remain m^2.

WUA estimates for each species and size class of interest in this study were calculated at discharge intervals of 0.1 $m^3\ s^{-1}$ between the discharges of 0.1 $m^3\ s^{-1}$ and 1.2 $m^3\ s^{-1}$. River2D became unstable at simulated discharges above or below these values, either because flow extended outside of the model boundaries or flow through the model boundaries was supercritical. The effect of these discharges on WUA could not be investigated.

6.2.4 Model performance

The performance of the model was tested by comparing simulated CSI values and their locations with actual fish positions determined in the same way that HSC were derived in Chapter 5 except that no physical habitat data were collected. Between 16 and 22 November 2005, the positions of both Clanwilliam yellowfish and sawfin in all life stages were ascertained by snorkelling all three sites. Marker buoys were dropped where fish were observed and the positions of these marker buoys were later georeferenced with a total station, yielding maps of fish distribution across the three sites. Hydraulic conditions at the three sites were simulated at the average discharge that prevailed between the 16 and 22 of November 2005, i.e. 0.29 $m^3\ s^{-1}$. This discharge also approximated the median flows (0.27 $m^3\ s^{-1}$, SD = 0.12; min = 0.2 $m^3\ s^{-1}$; max = 0.9 $m^3\ s^{-1}$) that prevailed during the month of November 2005. Using River2D, CSIs were calculated for each node in the model in the manner described in Section 6.2.3 above. The CSI values, together with their spatial coordinates, were exported from River2D as a regular grid (0.1 and 0.2 m intervals) into a GIS database ArcGIS 9.1 © (ESRI, 2005). The georeferenced fish positions were then overlayed on the grid and the association between simulated CSI values associated with each cell in the grid and observed fish positions was explored using the 'proximity' tool in ArcGIS. The correspondence between these two parameters was then investigated using a method modified from Guay *et al.* (2000): CSI values were grouped into ten classes and the total surface area occupied by each of these classes in the modelled site was determined in ArcGIS. The density of fish in each of the ten CSI classes was calculated by dividing the total number of fish in each CSI class by the aerial extent of that class. The strength of the relationship between simulated CSI values and fish density in each CSI class was then tested by means of regression. A positive correlation between simulated CSI values and fish density in each CSI class was expected.

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6.3 RESULTS

6.3.1 Surveyed fish positions

A total of 94 individual fish positions and four spawning sites were surveyed across the three sites (Table 6.1 and APPENDIX D.1). Estimated densities of fish were low ranging between 0.02 and 0.07 fish m^{-2} (Table 6.1). At each of the three sites all adult sawfin were actively engaged in spawning. Each school of spawning sawfin was estimated to comprise between 40 and 70 individuals. Fish species and life stages were unequally distributed through the three sites and no 0+ juvenile sawfin were present anywhere in the reach that included the three modelling sites.

Spawning sawfin—Schools of spawning sawfin were observed at all three modelled sites. In all cases the solid black circles in Figures 6.1 (a), 6.2 (a) and 6.3 (a) indicate the upstream end of the school where most of the spawning activity was focused. A large shoal of sawfin (~70 adult fish) was observed spawning at the Upper Tafelberg site (Figure 6.1 a). Sawfin selected this same location for spawning in all three years of the study (2004 – 2006). At the Lower Tafelberg site, a shoal of ~40 adult sawfin was observed spawning in the riffle at the location indicated in Figure 6.2 (a). At the Sneeuberg site, sawfin were observed spawning in the upstream riffle as well as the downstream run (Figure 6.3 a).

TABLE 6.1 Numbers and densities of fish surveyed at each of the three modelling sites.

Species and size class	Upper Tafelberg site ($228\ m^2$)		Lower Tafelberg site ($250\ m^2$)		Sneeuberg site ($328\ m^2$)	
	No.	Density (fish m^{-2})	No.	Density (fish m^{-2})	No.	Density (fish m^{-2})
Adult spawning sawfin	~70	-	~40	-	~60	-
Larval sawfin (5-20 mm TL)	0	0	10	0.04	0	0
Juvenile sawfin (21-75 mm TL)	0	0	0	0	0	0
Clanwilliam yellowfish juvenile (75-150 mm TL)	16	0.07	10	0.04	7	0.02
Clanwilliam yellowfish adult (>150 mm TL)	11	0.05	0	0	23	0.07

Larval sawfin—No larval sawfin were found within the Upper Tafelberg or the Sneeuberg modelling sites, although they did occur approximately 150 m downstream of the latter site. At the Lower Tafelberg, site the positions of ten larval sawfin were surveyed at the locations indicated in Figure 6.2 (b). In all cases, larvae aggregated in the shallow marginal slackwaters downstream of the spawning sites.

Clanwilliam yellowfish juveniles—Juvenile yellowfish were present at all three of the sites. In all cases, they occupied positions in areas that had a relatively high current speed where they used cobble for cover and from where they could make short excursions into the current to feed off the drift. Densities of juvenile yellowfish were highest at the Upper Tafelberg site (0.07 fish m^{-2}) where 16 positions were surveyed (Table 6.1 and Figure 6.1 b). The surveyed positions of the 16 juvenile yellowfish at the Lower Tafelberg site are shown in Figure 6.2 (c). The Sneeuberg site had the lowest densities of juvenile yellowfish (0.02 fish·m^{-2}) and seven fish positions were surveyed at this site (Table 6.1 and Figure 6.3 b).

Clanwilliam yellowfish adults—eleven adult yellowfish positions were surveyed at the Upper Tafelberg site (0.05 fish m^{-2}) (Table 6.1 and Figure 6.1 c). Although adult yellowfish had been seen at the Lower Tafelberg site on previous occasions, there were none present at this site at the time of the survey. Highest numbers (23) and densities (0.07 fish·m^{-2}) of adult yellowfish were found at the Sneeuberg site (Table 6.1 and Figure 6.3 c).

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No yellowfish showed any sign of spawning activity throughout the study period and most were engaged in drift-feeding downstream of riffles at the time of the survey.

6.3.2 Habitat simulation

Upper Tafelberg site—CSI values predicted for spawning sawfin habitat ranged between 0-0.99, of which only 7 % were predicted as being above 0.6 (Figure 6.1 a). The CSI value predicted by River2D at the surveyed spawning bed indicated by the solid black circle in Figure 6.1 (a) was 0.4 and the location of this spawning site did not coincide with highest CSI values.

The highest CSI values as well as the greatest aerial extent of suitable spawning habitat was predicted by River2D to be further downstream (Figure 6.1 a). The maximum CSI values predicted for juvenile yellowfish at the Upper Tafelberg site did not exceed 0.59 and <8% of the predicted CSI values exceeded a value of 0.3 (Figure 6.1 b). The positions of the juvenile yellowfish in most instances, however, corresponded to the highest CSI values and greatest aerial extent of those values predicted by River2D. Similarly, for adult yellowfish, maximum CSI values did not exceed 0.58 and only 8% exceeded a value of 0.3 (Figure 6.1 c). Adult yellowfish were grouped in positions at or near areas predicted by River2D to have the highest CSI values.

Lower Tafelberg site—At the Lower Tafelberg site the maximum CSI value simulated for sawfin spawning habitat ranged between 0-0.99 (Figure 6.1 a) of which 15 % were predicted to be over 0.6. The CSI value simulated at the spawning bed indicated by the solid black circle in Figure 6.2 (a) was 0.8 and it was located within 1 m downstream of the greatest aerial extent of suitable spawning habitat predicted by River2D. CSI values predicted for larval sawfin (Figure 6.2 b) ranged between 0-0.8 and most of the most suitable locations were predicted to be along the marginal slackwaters immediately downstream of the riffle. There was a good spatial correspondence (visual association) between the highest CSI values and surveyed larval fish positions. CSI values predicted for juvenile yellowfish at the Lower Tafelberg site ranged between 0-0.59 with only 10 % of the values being >0.3 (Figure 6.2 c) and in most instances, there was a good spatial agreement between the highest simulated CSI values and surveyed fish positions.

Sneeuberg site—River2D predicted CSI values for spawning sawfin ranging between 0-0.99 (Figure 6.3 a). Roughly 30% of the Sneeuberg site had a CSI value >0.6 for spawning sites – the highest proportion of available spawning area of the three sites. River2D predicted the location of the spawning site upstream site well – the CSI value here being 0.94 – while the CSI value at the downstream site was much lower (0.23). The downstream site, however, was within 1 m of an area where CSI values ranged between 0.4 and 0.7. River2D predicted a maximum CSI value of 0.6 for juvenile as well as adult yellowfish. There was a strong spatial correspondence between adult and juvenile yellowfish positions and the highest CSI values predicted by River2D.

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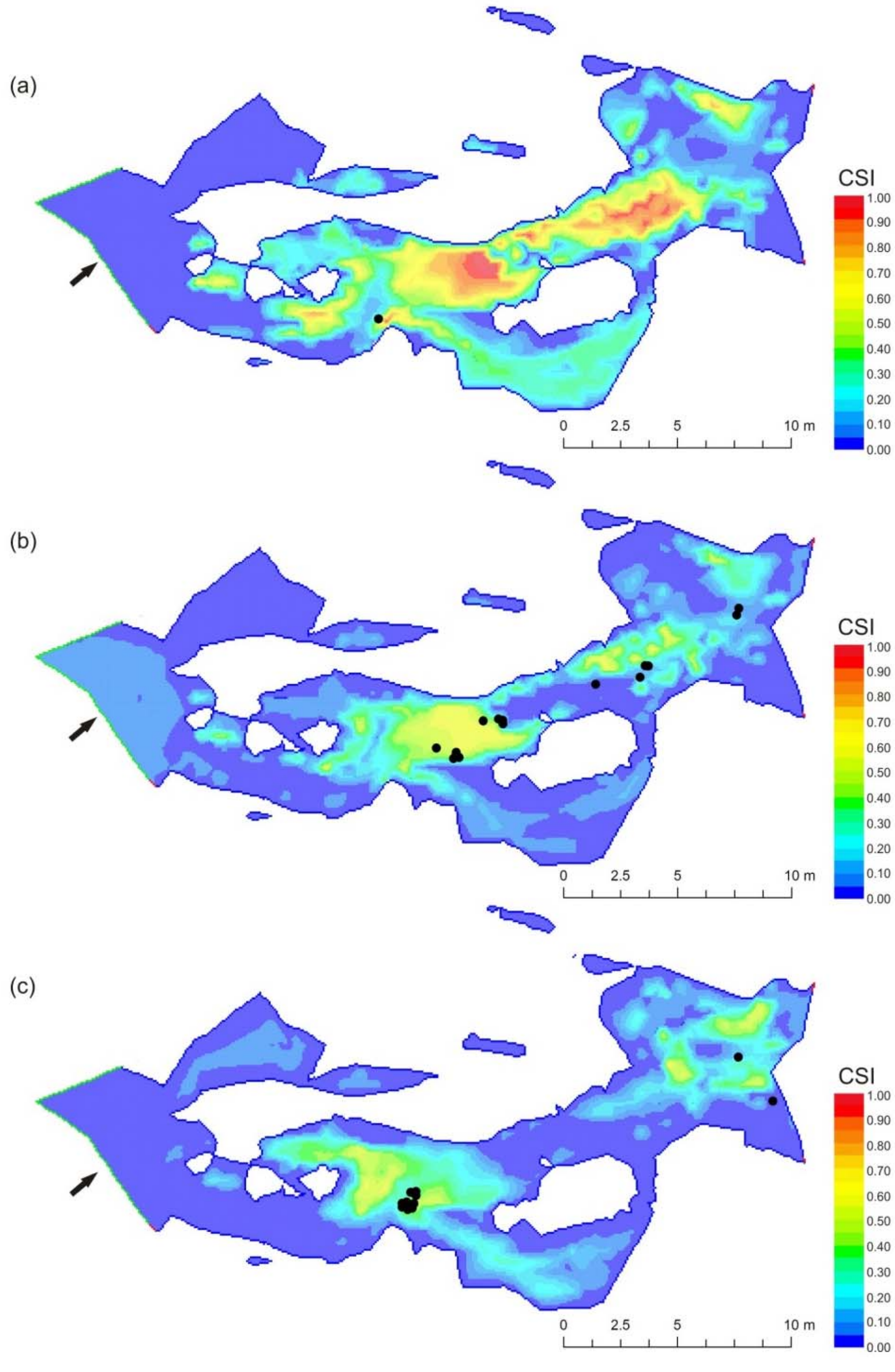

Figure 6.1 Simulated habitat conditions at Upper Tafelberg at a discharge of 0.29 $m^3 s^{-1}$ showing CSI values for (a) sawfin spawning habitat, (b) juvenile yellowfish and (c) adult yellowfish habitat. Solid black circles indicate surveyed fish positions. Arrows indicate the direction of flow

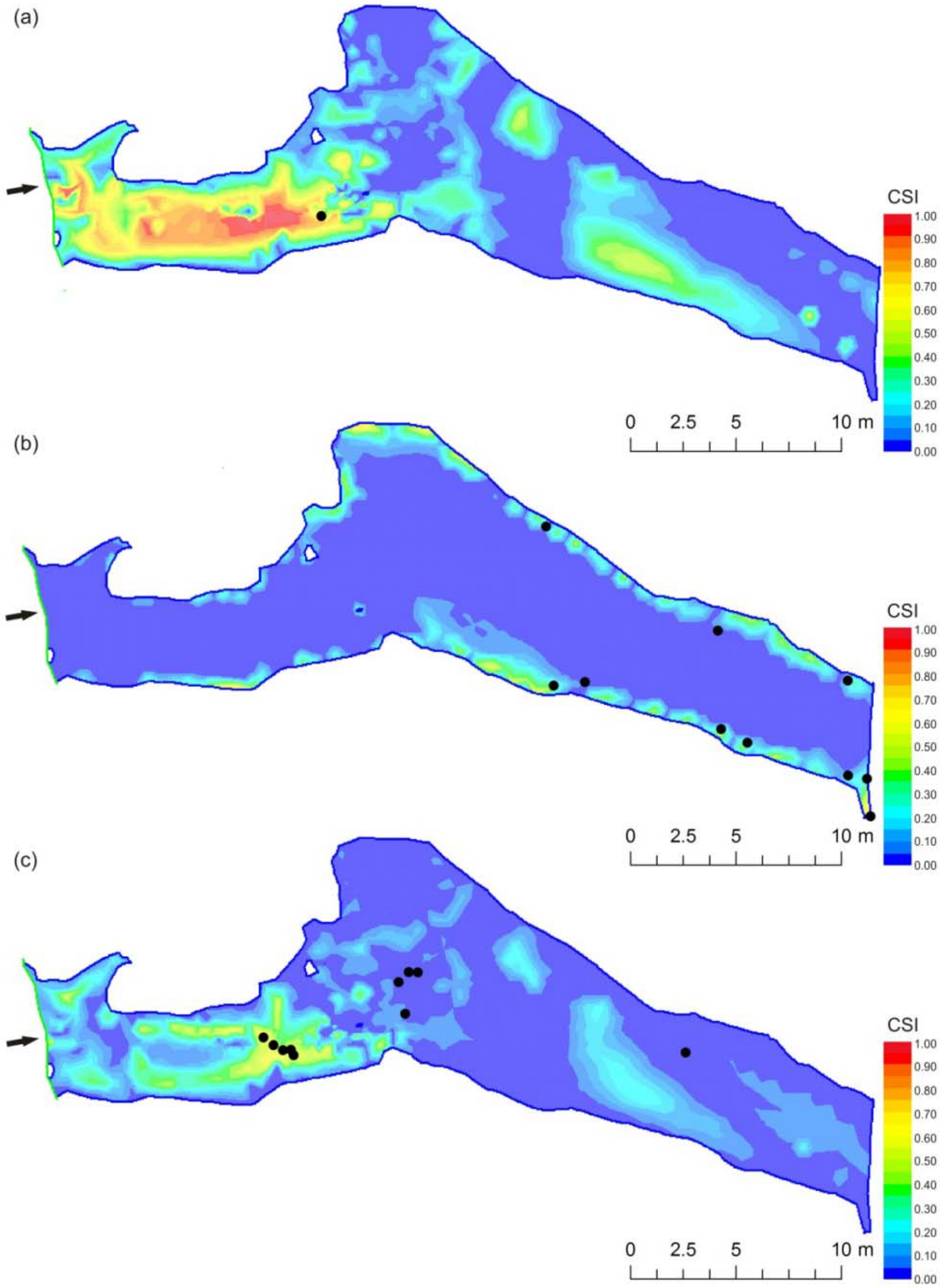

Figure 6.2 Simulated habitat conditions at Lower Tafelberg at a discharge of 0.24 $m^3 s^{-1}$ showing CSI values for (a) sawfin spawning habitat, (b) larval sawfin and (c) juvenile yellowfish habitat. Solid black circles indicate surveyed fish positions. Arrows indicate the direction of flow.

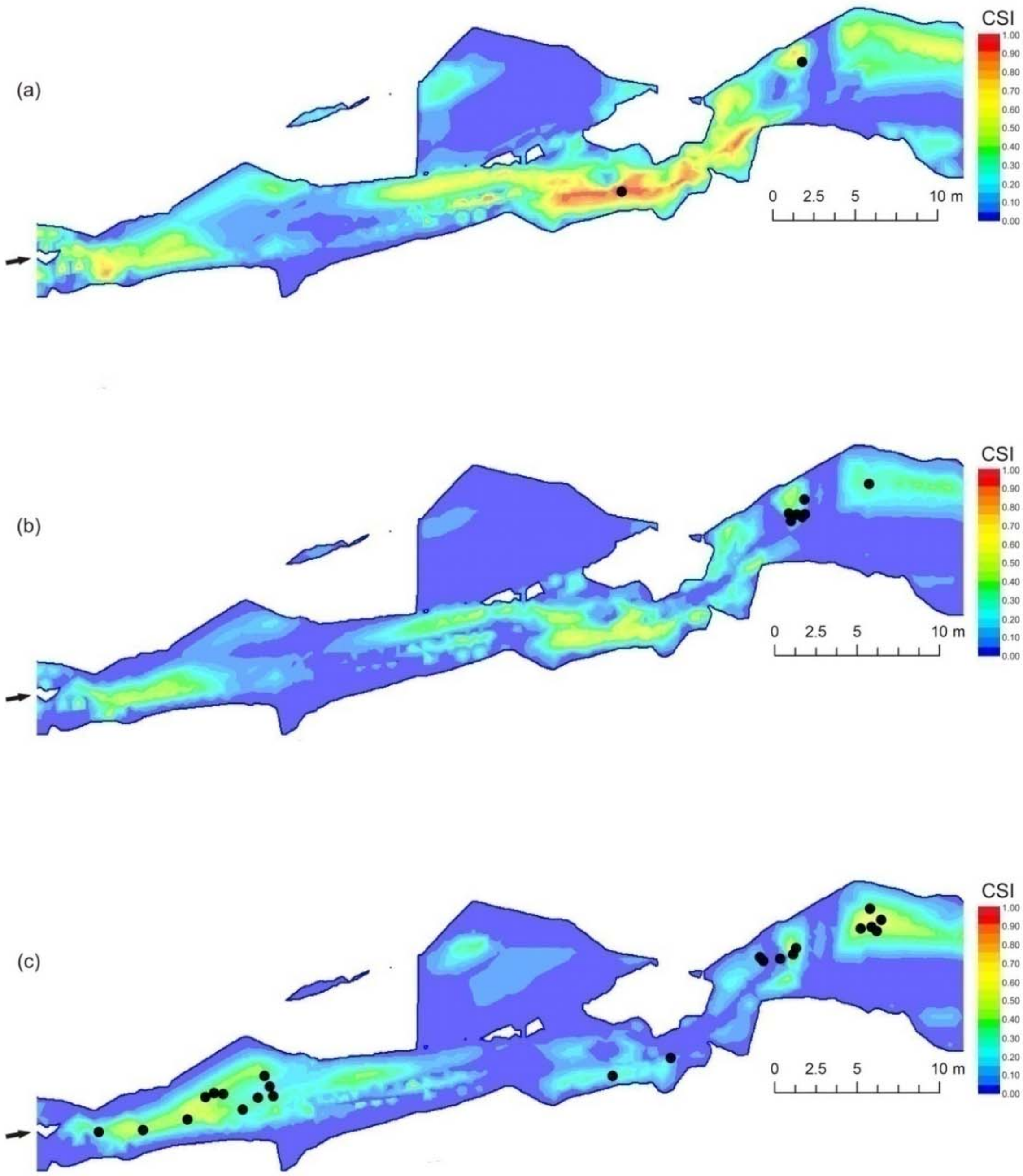

Figure 6.3 Simulated habitat conditions at Sneeuberg at a discharge of 0.29 m^3 s^{-1} showing CSI values for (a) sawfin spawning habitat, (b) juvenile yellowfish and (c) adult yellowfish habitat. Solid black circles indicate surveyed fish positions. Arrows indicate the direction of flow.

6.3.3 Correlation between predicted CSIs and surveyed fish positions

The CSI outputs simulated by River2D at each of the three sites and fish densities were pooled for the three sites. Due to the small sample size and therefore reduced statistical power, the focus of this analysis is on the shape of the plot and the correlation coefficient rather than statistical significance. Fish densities in each CSI class (0.1-1.0) varied between 0 and 1.1 fish m^{-2}. The correlation between simulated CSI values and yellowfish densities per surface area of each CSI class at a discharge of 0.29 $m^3.s^{-1}$ was positive for both juvenile yellowfish (r^2 = 0.67) and adults (r^2 = 0.98) (Figure 6.4 a and b).

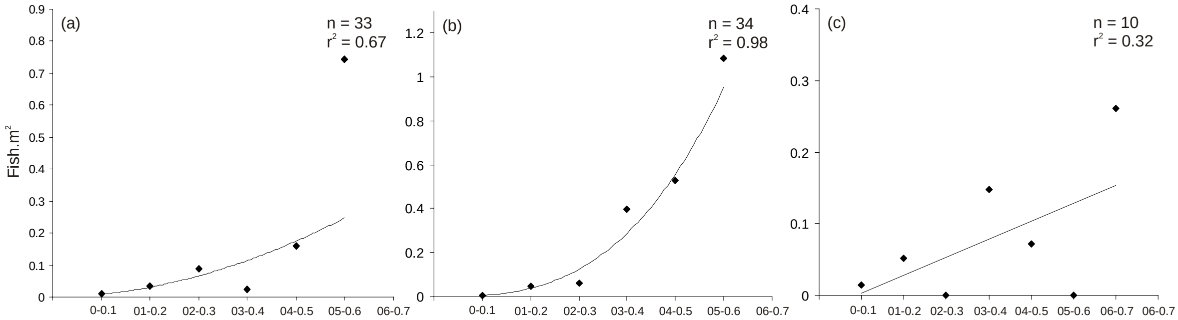

Figure 6.4 Regression between CSI classes at (at 0.1 intervals) and observed fish densities per aerial surface area of each CSI class at 0.29 m^3.s^{-1} for (a) juvenile yellowfish and (b) adult yellowfish and (c) sawfin larvae.

In both instances, the relationship appeared to be non-linear and a power curve was therefore fitted, suggesting that areas with higher CSIs are used to a far greater extent than those with lower. The correlation between larval sawfin densities and predicted CSI values was also positive but linear (Figure 6.4 c). The low sample size (n = 10) may have contributed to the lower r^2 here (r^2 = 0.32).

6.3.4 Weighted Usable Area (WUA)

Upper Tafleberg site—At the Upper Tafelberg site (Figure 6.5a; APPENDIX D.2), simulated WUA values increased steadily with increasing discharge for juvenile (15 to 42 m^2) and adult yellowfish (16 to 33 m^2), as well as spawning (32 to 73 m^2) and sawfin >75 mm TL (18 to 67 m^2). WUA for larval sawfin (5-20 mm TL) was low (12-15 m^2) at discharges <0.4 m^3 s^{-1} but increased sharply at higher discharges due to the opening up of secondary channels with attendant slackwaters. Maximum WUA for larval sawfin (39 and 25 m^2) occurred at discharges of between 0.7 and 0.9 m^3 s^{-1} and tailed off gradually at higher discharges as increased velocities in secondary channels drowned out the additional slackwaters. Due to the absence of suitable substratum (bedrock and boulders) WUA for juvenile sawfin remained consistently low (3.5-5.5 m^2) across the full discharge range.

Lower Tafelberg site—At the Lower Tafelberg site, WUA estimates for each species and size class of interested were calculated at the same discharge intervals and over the same range as those for Upper Tafelberg (Figure 6.6; APPENDIX D.2). Although, in general, WUA was lower for juvenile yellowfish than adult yellowfish (Figure 6.6 a), WUA for both size classes showed an increase between discharges of 0.1 and 0.4 m^3 s^{-1} before declining towards the higher simulated discharge values. WUA for sawfin spawning habitat increased from 39.2 m^2 at a discharge of 0.1 m^3 s^{-1} before reaching a maximum WUA of 64.7 m^2 at a discharge of 0.7 m^3 s^{-1} (Figure 6.6 b). WUA for sawfin >75 mm TL showed two peaks at 0.2 m^3 s^{-1} and 0.5 m^3 s^{-1}, but otherwise exhibited a declining trend towards the higher simulated discharges. WUA for sawfin larvae showed little change across the full range of discharges. As for the Upper Tafelberg site, WUA for juvenile sawfin (21-75 mm TL) remained low (5.5-6.6 m^2) across the entire simulated discharge range due to the absence of a suitable substratum.

Sneeuberg site—At the Sneeuberg site, simulated changes in WUA for both juvenile and adult Clanwilliam yellowfish (Figure 6.7 a; APPENDIX D.2) were similar across the range of discharges, increasing from ~30 m^2 at 0.1 m^3.s^{-1} to ~50 m^2 at 1.2 m^3.s^{-1}. River2D predicted a maximum WUA for spawning sawfin at a discharge of 0.7 m^3.s^{-1} (110 m^2). Maximum WUA for adult sawfin peaked at 1.2 m^3.s^{-1} (108.8 m^2). As for

Lower Tafelberg, larval sawfin habitat remained relatively unchanged across the full discharge range (~20 m^2) and juvenile sawfin habitat was consistently low throughout all discharges (~3 m^2).

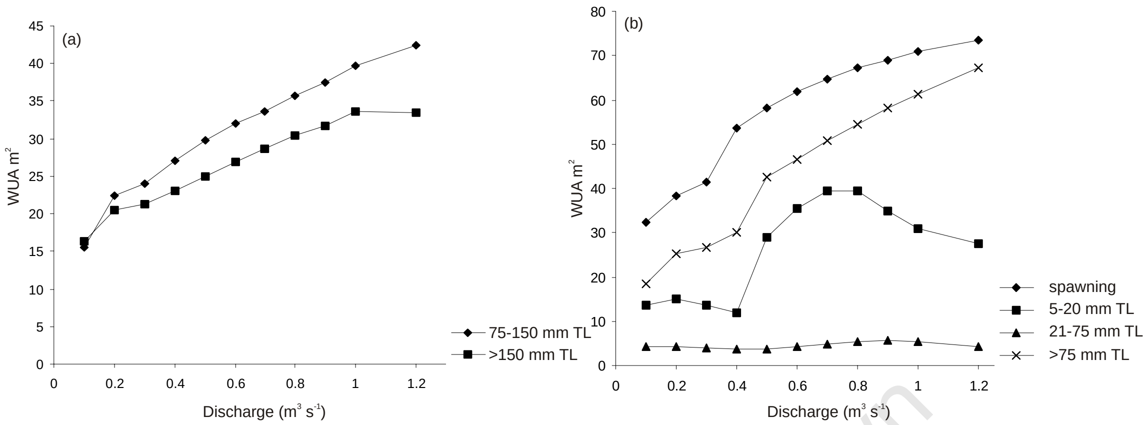

Figure 6.5 Relationship between WUA and discharge at Upper Tafelberg for (a) Clanwilliam yellowfish and (b) sawfin.

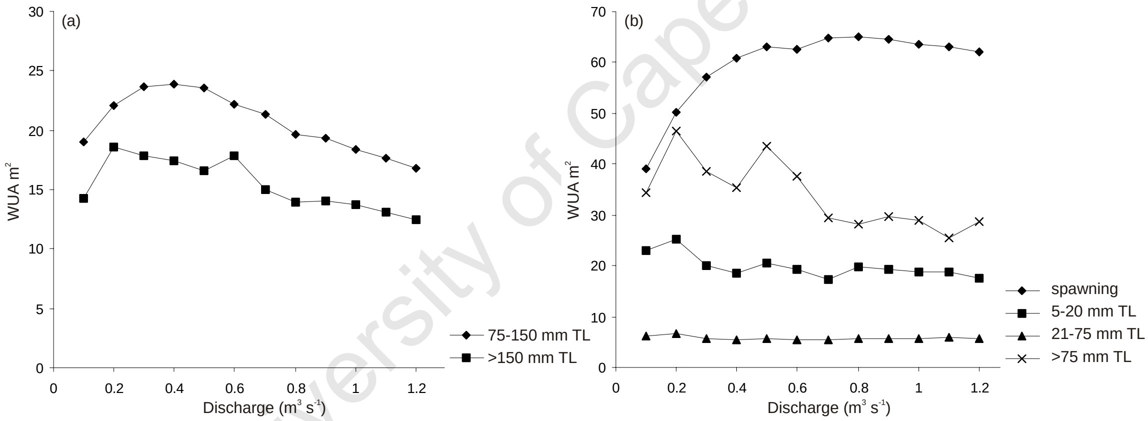

Figure 6.6 Relationship between WUA and discharge at Lower Tafelberg for (a) Clanwilliam yellowfish and (b) sawfin.

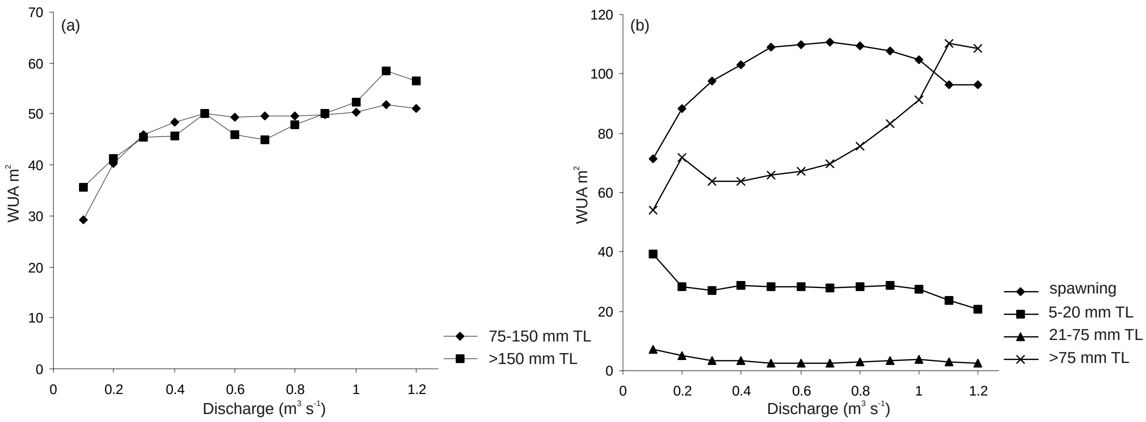

Figure 6.7 Relationship between WUA and discharge at Sneeuberg for (a) Clanwilliam yellowfish and (b) sawfin.

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6.4 DISCUSSION

Two important constraints in this study were the scarcity of rivers containing indigenous fish in the Olifants/Doring catchment and the inaccessibility of those rivers that do support populations. It was not therefore possible to validate the models using HSC developed in reaches other than those that included the modelled sites. Despite this, a good correspondence between CSIs and surveyed fish densities (Section 6.3.3) suggests that, in general, the River2D models provided a reasonably accurate indication of habitat quality in the Driehoeks River and, thereby, fish distribution.

WUA-discharge relationship—River2D predicted a similar WUA trend for increasing discharge for sawfin spawning habitat at all three of the sites with peaks between 0.7-1.2 $m^3.s^{-1}$. Because of differences in topography at the three sites, however, there were considerable between-site differences in the relationship between WUA and discharge for other species and life stages. For example, for both juvenile and adult yellowfish at the Upper Tafelberg site, River2D predicted a continuously increasing trend in WUA with increasing discharge. At this site, the maximum WUA for these two life stages was predicted as occurring between 1-1.2 m^3 s^{-1}. At the Lower Tafelberg site, however, River2D predicted an overall declining trend in WUA with increasing discharge for these same two life stages. Maximum discharge at this site was predicted at 0.3-0.4 m^3 s^{-1}. WUA for larval sawfin remained relatively unchanged across the full range of modelled discharges at Lower Tafelberg and Sneeuberg sites, whereas it peaked at a discharge of 0.7 m^3 s^{-1} at Upper Tafelberg. This was primarily due to the opening of additional side channels at this site which increased the availability of shallow slackwaters.

These discrepancies between sites highlight one of the dilemmas faced by ecologists when interpreting results from sites with different topographies. The use of inflection points in the WUA-discharge relationship for identifying critical discharges for organisms has been criticised on a number of occasions for inherent weaknesses (Hudson *et al*. 2003; Pusey 1998, Waddle 2001). In this study the identification of inflection points was complicated by the fact that WUA was either unchanging, gradually changing, or showed no signs of becoming asymptotic. These problems have also been taken up by Pusey (1998). The River2D model became unstable at discharges under 0.1 m^3 s^{-1} or over 1.2 m^3 s^{-1} –because of the difficulty of modelling very low flows, or the fact that the flow became supercritical, or because flows exceeded the boundaries of the model at very high discharges. Inflection points beyond these values may have been more evident were they modelled. The most consistent pattern in the WUA-discharge relationships showed a decline in WUA at discharges below 0.1 m^3 s^{-1} – particularly for sawfin spawning habitat – suggesting that this was indeed an important threshold for both species and their respective life stages. The importance of including more extensive bank and macro-channel features in hydraulic models is illustrated by the fact that River2D became unstable even at a moderate upper limit (1.2 m^3 s^{-1}) and any future use of the model should take this into consideration. The absence of inflection points could also point to generally broad tolerances for flow conditions of the organisms themselves and/or the diversity of channel conditions at a range of discharges.

Where multiple species and life stages are being considered, the problem arises of inconsistent or competing critical discharges. This highlights the main criticisms of habitat simulation methods, i.e. that they are species, life-stage, site and season specific (Orth 1987). Where the flow requirements of many species or life stages are being considered and where the focus is often not on a commercially or recreationally important target species, but rather on the whole ecosystem (as is the case with many South African EWRs), a

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compromise will always need to be reached according to the management objectives in the system. Arthington *et al*. (1992; cited in Pusey 1998) proposed adopting a 'band' of flows rather than a single flow to overcome this. Alternatively, priorities can be assigned to particular species, life stages or behaviours and these can be used as indicators for different periods of the year. Using the case of the Driehoeks River in this study, for example, priority could be assigned to sawfin spawning habitat during November and December, whereas between January and March, priority could be given to flows that maximised the availability of larval and juvenile sawfin habitat. As a means of simplifying the interpretation of numerous WUA-discharge curves, Waddle (2001) suggested normalising each species and life stage WUA curve and then using a weighted arithmetic mean to produce a single curve. Figure 6.8 shows a WUA-discharge curve representing all life stages for both species in the Driehoeks River for November and December. Sawfin spawning habitat has been given the heaviest weighting (0.6) since this is one of the most critical habitat types and most vulnerable to flow change, followed by larval habitat (0.3), while the remainder of the habitat types have been weighted at 0.1. According to this figure, optimal WUA in the Driehoeks River for November and December occurs at around 0.8 and 0.9 $m^3 s^{-1}$.

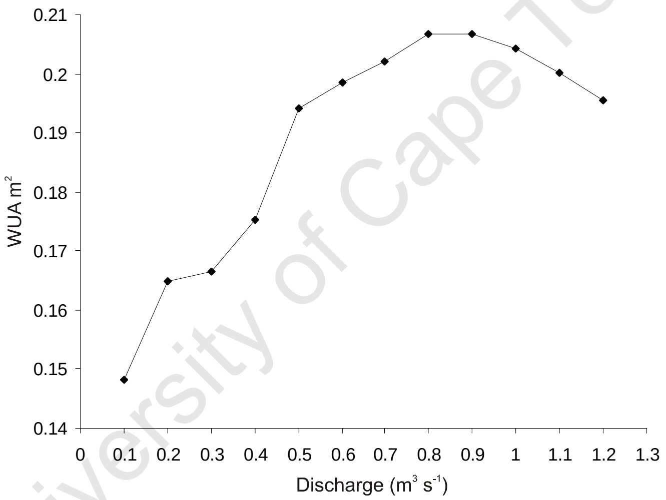

Figure 6.8 Weighted arithmetic mean relationship between WUA and discharge for all sites (Upper Tafelberg, Lower Tafelberg and Sneeuberg), species (Clanwilliam yellowfish and sawfin) and size classes for November and December. Weighting factors: sawfin spawning (0.6); larval sawfin (0.3); 21-75 mm TL sawfin (0.1); >75 mm TL sawfin (0.1); 75-150 mm TL yellowfish (0.1); >150 mm TL yellowfish (0.1).

Although no long-term hydrological data exist for the Driehoeks River, the flows suggested in Figure 6.8 appear to be unrealistically high flows for this time of year. From the flow record in this study discharges in the region of 0.8 $m^3 s^{-1}$ had an exceedance value of <1% in November 2005. This may simply mean that flows in the Driehoeks River over the spawning period are 'naturally' sub-optimal for all species. In cases where habitat simulation programmes predict optimal flows that exceed median monthly flows, Waddle (2001) suggested that investigators work from median monthly flows and evaluate whether reductions below these values would constitute a significant reduction in WUA.

WUA and fish densities—The sites with the highest simulated WUA for a species and life stage did not necessarily correspond to the greatest abundances of fish. For instance, although there appeared to be similar quantities of larval habitat at all three sites, larval sawfin were found only at Lower Tafelberg. Scott and Shirvell (1987) found that in 74% of the studies they reviewed there was a poor correspondence between

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WUA and fish biomass. They speculated that this was particularly the case where some other limiting factor such as flow perturbation, competition or predation affected fish abundances. Although there were no major flood events during the course of the study that would have depressed fish abundances in the Driehoeks River, Clanwilliam yellowfish and sawfin populations may be under carrying capacity due to biological interactions such as inter and intraspecific competition and/or predation by largemouth bass that are present in the river, albeit in small numbers. Poor correlations with WUA in this river are considered here to be most likely related to contingencies such as the quantity and quality of upstream spawning habitat and the broader-scale processes such as migration and dispersal discussed in Chapter 4. With respect to the distribution of larval sawfin, the greatest concentrations were found at Lower Tafelberg, but none at either Upper Tafelberg or Sneeuberg. The most productive spawning beds (from larval abundance estimates, Chapter 3) were Upper and Lower Tafelberg. The only other larval source was a spawning site located a considerable distance upstream. From WUA estimates (Figure 6.5b) it will be noted that at discharges 0.29 $m^3 s^{-1}$ (roughly the flow conditions prevailing in the river at the time of sampling) there is very little larval habitat at Upper Tafelberg and a large proportion of this was located upstream of the spawning site (*pers. obs*.). Thus upon emerging from the cobble bed, the larvae would immediately become entrained in the current and wash through the site. Since Upper and Lower Tafelberg were located within 100 m of one another, the shallow slackwaters along the margins of the run immediately downstream of Lower Tafelberg provided a catchment for larvae from both sites. Although River2D predicted sufficient larval habitat at Sneeuberg, this was located upstream of both spawning beds. Hatched larvae from this site were found in slackwaters further 150 m downstream of these spawning beds.

The primary reason for consistently low WUA values for juvenile sawfin was due to their association with large bedrock areas and boulders and the absence of these habitat features from the modelled sites. In Chapter 4 it was noted that larval and then juvenile sawfin undertake a gradual downstream displacement in the first three to four months post-spawning. Thus all juvenile sawfin were found concentrated in a bedrock/boulder dominated reach several kilometres downstream of the modelling sites. Their selection of these reaches may be related to the availability of cover from predation and winter flows afforded by bedrock shelves and large boulders (see Chapter 3 for further discussion). Juvenile yellowfish, however, selected riffles with a cobble substratum in which they would hide or from which they would make short excursions to feed. Their greater abundances in the modelled sites reflected the predominance of these types of habitat conditions. There was therefore clear niche separation between sawfin and yellowfish juveniles.

***Spawning habitat*—**One of the principal objectives of this study was to characterise hydraulic features of sawfin spawning habitat, the assumption being that the quality and quantity of spawning habitat available in the river would have a significant effect on sawfin abundances because of their importance as sites of fish production and their sensitivity to flow changes. During the course of continuous dive surveys over two years, 12 separate spawning beds (e.g. Plate 6.1) were identified in the 6 km segment (Chapter 3) – not all of which were occupied simultaneously, or in the same year. At each of these beds, sawfin gathered in a single nuptial school consisting of between 30-70 adult fish. Although the whole school would extend for a meter or more downstream, only the upstream end of the school was surveyed since this was where most of the spawning activity took place.

River2D overestimated the quantity of spawning habitat and in all cases, except the upstream bed at Sneeuberg, sawfin selected areas that were predicted by the model to be sub-optimal (CSI values <0.6). The

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overestimation of the quantity of spawning habitat by River2D and its inability to accurately predict spawning bed location could either mean that the HSC were inaccurate due to a low sample size, or that sawfin select hydraulic characteristics not captured by standard HSC models (see Chapter 5 for detail on how these were derived), or that habitat selection by spawning sawfin is fairly flexible within given limits. This last alternative is considered most likely since in some instances during 2005 sawfin were observed selecting locations in similar hydraulic conditions but adjacent to the 2005 sites. Another possible criterion for selection of spawning bed location that would not have been captured by HSC could be their proximity to areas of turbulence associated with regions of flow exceeding 1 m s^{-1}. All the spawning beds were located immediately downstream of shallow, high velocity hydraulic features such as a chute or waterfall where a steep gradient caused turbulence and induced the entrainment of air bubbles. Presumably this turbulence, apart from ensuring high oxygen saturation levels, would also increase interstitial flow pathways through cobble thereby aiding the incubation of eggs and elimination of metabolites (Chapman 1988). These types of conditions would be difficult to simulate in a hydraulic model although there is considerable potential for incorporating additional characteristics such as gradient and river bed topography into WUA in River2D that could be used as proxies for turbulence. It was not considered feasible to use the existing data for developing more sophisticated models of sawfin spawning habitat that would have included additional geomorphic or hydraulic features. A more focussed study that included a greater number of spawning sites in other rivers would be required for this. A study of this nature should take into consideration the change in spawning behaviour and/or location with a change in flow using the gradient approach proposed by Arthington *et al*. (2006), whereby an ecological response (in this case spawning) is measured across a gradient of natural to impaired flow conditions. The objective would be to identify a critical threshold that would reduce the potential of a site to support spawning.

Interpretation of WUA—WUA in River2D is calculated by the multiplication of an area by the corresponding habitat suitability index (a dimensionless number) and it has been reported in this document as a unit of area. King and Tharme (1994) and Payne and Riley (2007), however, noted that the representation of WUA in units of area was a wrong interpretation of the data and that it should rather be represented as units of habitat 'worth'. Similar problems of interpretation were highlighted by Guay *et al*. (2000) who noted that because of the way in which WUA was calculated using the weighting procedure, different areas of habitat and different suitability values could end up giving the same WUA value, whereas there was no reason to believe that these areas had identical value to fish. WUA is therefore best considered as a unit of habitat quality rather than area that can only be interpreted in terms relative to itself, or to some other parameter that is directly linked to fish biomass or abundance.

Apart from uncertainties over how WUA should be represented or interpreted, the ecological significance of WUA has come under scrutiny in a number of studies and reviews (Mathur *et al*. 1985; Scott and Shirvell 1987; Gore and Nestler 1988). An enduring criticism of the concept of WUA has been whether it is a valid predictor of fish abundance or biomass (Gore and Nestler 1988). In this respect, Bovee (1996) questioned whether 2-D hydraulic models represent a significant advance over 1-D models. Despite the fact that 2-D models provided better estimates of WUA and that they were spatially explicit, the ecological implications of changes in WUA remain unclear. Rosenfeld (2003) made a distinction between habitat 'selection' and habitat 'requirement'. Rosenfeld (2003) defined habitat selection as occurring when an organism uses a particular habitat more frequently than others as suggested by higher densities or frequencies of occurrence by the

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organism in that habitat (the basis of HSC). Habitat requirements on the other hand, are features of the environment necessary for actual fitness or survival – measurable outcomes in terms of the health or abundance of organisms. Habitat models such as the one presented in this chapter only address habitat selection or microposition choice (Scruton *et al.* 1998) and don't address the fitness or survival consequences of a habitat loss. Also, as Orth (1987) pointed out, habitat models address only instantaneous habitat, whereas fish abundances may be controlled by preceding habitat conditions. Thus, whatever their level of sophistication, very little can be surmised from habitat models, 2-D or otherwise, regarding the actual outcomes of altered flows on the standing crop of fish in rivers unless they are linked to population models and include habitat time series (Stalnaker *et al*. 1995). Practitioners and managers should understand these limitations and acknowledge, as Gore and Nestler (1988) suggested, that they are tools for aiding decisions regarding water resource allocation rather than realistic biological models.

In summary, this study has highlighted several points that need to be considered when applying habitat simulation approaches. Firstly, simulating very high or very low flows using River2D is problematic. The former problem can be attributed to insufficient data points surveyed for high flows, while the latter can be attributed to uncertainties in model performance at very low flows (Nicholas 2003). More detailed investigations, not possible within the scope of the current project, would be necessary to determine what the causes were in this instance. Secondly, habitat availability as measured by WUA may be relatively constant over the range of simulated flows, even for relatively specialised habitats such as spawning habitat, making it difficult to identify inflection points for optimal flows. Thirdly, because of lateral and longitudinal variability in bed topography and differences between species and life stages there may be significant between-site differences in habitat availability that produce contradictory predictions for optimal flows.

6.4.1 Conclusions and recommendations

This study has evaluated the use of River2D to simulate hydraulic habitat for two indigenous fish species in the Driehoeks River. While low fish numbers and their patchy distribution limited the evaluation of model performance – particularly because data used to test model performance necessarily came from observations that included the modelled sites – River2D appeared to predict most habitat quality fairly accurately, although the quantity of sawfin spawning habitat was overestimated in some cases.

The advantage of a 2-D hydraulic model over a 1-D model or frequency distribution model lies not only in its greater accuracy and resolution at scales relevant to fish, but also in the spatially explicit nature of the predictions. This advantage becomes particularly apparent when these models are linked to the behaviour-based habitat models such as those suggested by Hardy *et al*. (2006) or for assessing changes in habitat diversity (Bovee 1996). Behaviour-based rules – such as proximity of holding positions to drift-feeding areas – were tested in a related study (Hirschowitz *et al*. 2007) and although it was found that these improved predictions of habitat quality, these were not developed further in this study because they added significantly to the complexity of the procedure. Only standard HSC approaches were therefore used here. The measurement of adjacent habitat conditions such as drifting-feeding areas (Chapter 5), however, proved a valuable exercise and captures some of the complexity of the dynamic nature of fish habitat use.

The free availability and user-friendliness of River2D make it an attractive tool for application in local EWR assessments. In South Africa, however, the current technology available to simulate hydraulic conditions in

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rivers far exceeds our ability to interpret their biological meaning. Thus, while a 2-D model represents an advance over a 1-D model and habitat mapping approaches in terms of its ability to accurately simulate habitat conditions at scales relevant of fish, until we arrive at some understanding of the proximate causes of population fluctuations in local rivers, the value to the ecologist of using more sophisticated modelling techniques is debatable. If our current understanding of fish responses to changing aquatic habitat is to be advanced, then a more convincing link with hydraulic-habitat model outputs will need to be established. Focussing research at integrating habitat models with fish population models that incorporate mortality rates, migration and estimates of habitat carrying capacity (e.g. SALMOD: Bartholow *et al.* 1993), would therefore be of greater value than applying more sophisticated modelling procedures. In addition, while this study has evaluated the ability of a 2-D model to predict fish microposition choice from simulated habitat quality indices, this does not represent a complete validation exercise. Bovee (1982) has suggested 'backcasting' as a method of validating model predictions. This method combines a habitat time-series analysis with an historical analysis of indicators of fish response such as year-class strength, growth rates and survival. This option would be unrealistic in South Africa unless long-term monitoring of freshwater fish populations was implemented.

In Australia, Pusey (1998) questioned whether methods that focus on preserving certain quantities of habitat are appropriate unless habitat selection has been shown to be indisputably important in any particular case. The reasons include that fact that flows in Australian rivers are highly variable (as they are in South African rivers), that the species in these rivers are consequently habitat generalists and that habitat is therefore not a limiting resource. The consequences of such a formulation for South African conditions will be addressed in Chapter 9 (Section 9.2).

6.4.2 Calculating WUA in River2D and PHABSIM

In PHABSIM, the river segment to be modelled is divided into a number of cross-sections comprising a matrix of cells, each with associated depth, velocity and Channel Index (CI) values (Figure 6.9).

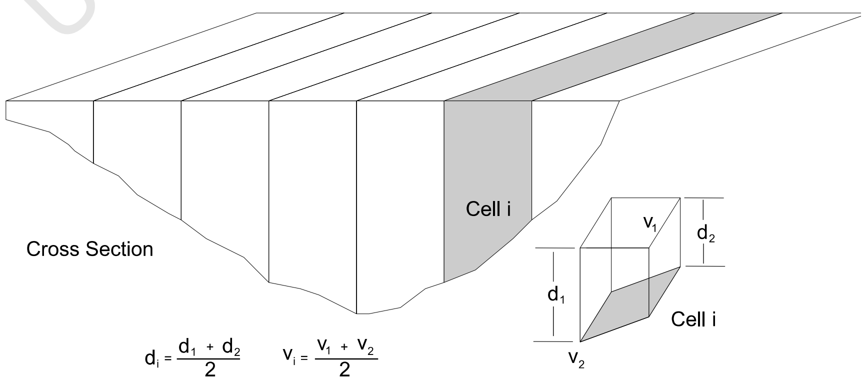

Figure 6.9 Cross-sectional profile of a river segment as it represented in PHABSIM. A series of transects defines a matrix of habitat cells in a river segment, each with their associated depth, velocity and Channel Index (CI: cover or substratum) attributes. These form the basis of the computational cells in the hydraulic model. The vertical components of the cells are measured in the field and the hydraulic model simulates the depths and velocites one half the distance from the first vertical to the next (d_1-d_2, v_1-v_2). The depth, velocity and CI values in each cell are converted to indices of habitat suitability by means of HSC.

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The calculation of a composite SI is calculated in the same manner as it is in River2D, by multiplying the depth velocity and CI together for each cell. WUA is then calculated by multiplying the surface area of each cell by its CI, summing these across cells and representing the final value per 1000 ft of river:

$$\text{WUA} = \frac{\sum_{i=1}^{n} A_i C_i}{\text{Reach Length (1000ft)}}$$

where A_i is the surface area of cell i and C_i is the composite SI of the cell.

In River2D, the depth, velocity and CI are represented as nodes in a triangular mesh. River2D is based on the PHABSIM concept of WUA and, as pointed out in Section 6.2.1 is calculated as an aggregate of the product of the CSI at each node at the vertices of the triangle and the area associated with that node (CSI × surface area) (Figure 6.10). Since CSI is a dimensionless number, the units for WUA remain m^2. Unlike PHABSIM, it is not standardised as a proportion of a length of river, but can be compared with the total are of the modelled site.

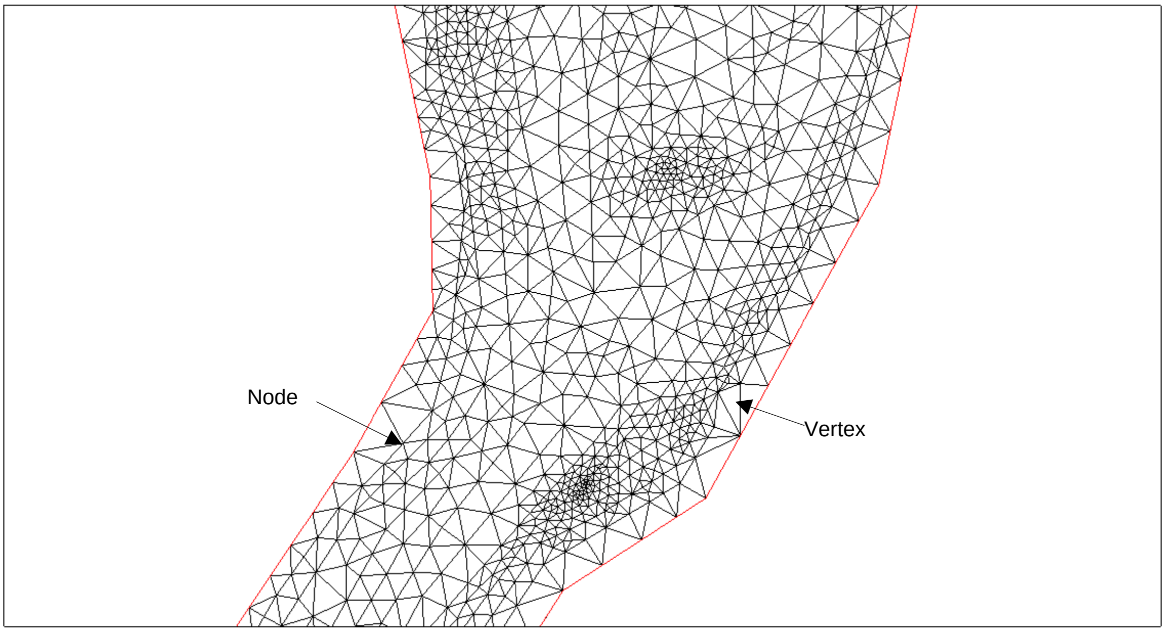

Figure 6.10 A river reach in River2D is modelled as a TIN with each node associated with a set of depth, velocity and CI (cover or substratum) attributes. HSC are used to transform these values into a set of Habitat Sutiability Indices (SI) and the CSI is calculated as the product of these. WUA is then calculated as the product of the CSIs at each node of the vertices of the triangle and the area associated with that node (CSI × surface area).

CHAPTER 7 Early development, age estimation and validation of otolith increment deposition rate in larval and juvenile sawfin in the Driehoeks River

7.1 INTRODUCTION

Knowledge concerning the age structure of fish populations obtained from counts of otolith growth increments can yield valuable information on growth and mortality rates, recruitment patterns and response to environmental variability such as changes in water temperature and food availability (Savoy and Crecco 1988; Bestgen and Bundy 1998; Campana and Thorrold 2001). Age estimation has therefore become an important tool for devising, implementing and evaluating management strategies for both freshwater and marine fish species. Age estimation of fish involves an assessment of the age of individual animals by means of enumerating the daily, seasonal, or annual variations in growth in their calcified structures. Structures that have been used for age estimation include: fin rays (e.g. Rien and Beamesderfer 1994) and spines (e.g. Buckmeier and Irwin 2002); vertebrae (e.g. Prince *et al*. 1985); opercular bones (e.g. Blake and Blake 1978); scales (e.g. Booth *et al*. 1995) and otoliths (e.g. Moksness and Wespestad 1989). Otoliths, however, are the preferred method for aging since these are usually the first calcified structures to be laid down during the early life stages and are also believed to reflect growth more accurately than other structures (Campana and Neilson 1985). There are three pairs of otoliths within the vestibular apparatus, which is located on either side of the head just posterior to the cranium (Figure 7.1).

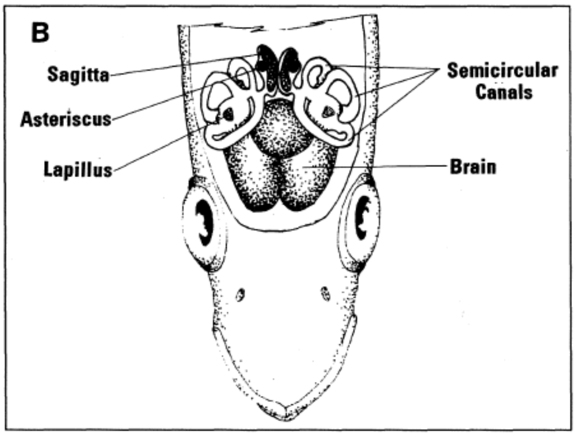

Figure 7.1 Location of the three pairs of otoliths; the sagitta, asteriscus and lapillus in the vestibular apparatus of a fish (from Secor *et al*. 1992).

The sagittae, the largest of the three pairs, are located in proximity to the asterisci and both of these are posterior, medial and ventral to the lapillae. Most commonly, annual rings (annuli), that are deposited in otoliths as a result of alternating periods of fast (summer) and slow (winter) growth, are used to age adult fish (Campana 2001). The discovery by Panella (1971), however, that fish lay down daily growth increments has opened new opportunities for estimating the age of much younger (0^+) fish. The techniques subsequently developed for enumerating daily growth increments have offered a means of investigating recruitment patterns in detail, determining hatch dates and relating these parameters to environmental variability. Daily growth increments result from the differential deposition of calcium carbonate (in the aragonite[2] configuration) and a protein (otolin) over a twenty-four hour period, resulting in a sequence of contrasting opaque and hyaline bands through the otolith. Both sagittae and lappilli have been found to be useful for aging, whereas Barkman (1978) found the asterisci to be less reliable. Campana and Neilson (1985) propose a hypothesis of daily increment formation that is in agreement with most published work. They suggest that formation is attributable to an endocrine-driven endogenous circadian rhythm that is entrained by photoperiod. The periodicity of daily increment deposition by teleost fish is therefore regarded as being a more reliable indicator of fish age than annuli that are affected by seasonality (Campana and Neilson 1985). The rate of increment deposition is species-specific (Jones 1986) and additional asynchronous variables, such as fluctuating temperatures (e.g. Brothers 1978) or feeding patterns (e.g. Neilson and Geen 1985), may mask the circadian rhythm or amplify it, resulting in the loss of daily synchronisation and leading to under- or overestimation of actual age (Campana 1992). A major source of error in age estimation therefore arises from incorrectly assigning a frequency to the rate at which increments are laid down. Thus validation of daily increments, i.e. empirically ascertaining the periodicity of formation of growth increments, is now considered a prerequisite for aging studies (Geffen 1992).

Two of the more commonly employed techniques for validating the rate of increment deposition include: marking with chemical compounds such as oxytretracyline hydrochloride (OTC) (e.g. Lang and Buxton 1993) or rearing known-age larvae (e.g. Miller and Storck 1982). Chemical marking of wild-caught fish and their subsequent recapture is generally regarded as the most effective validation method because fish released back into the wild will be exposed to normal environmental fluctuations (Campana 2001). However, this method is not suitable where the supply of fish is limited or where the species is rare or endangered because of the large numbers required for capture, marking and recapture. Where feasible therefore, rearing young fish in the laboratory under conditions approximating as closely as possible those of the wild provides a viable alternative for daily increment formation, but not necessarily for annulus formation (Geffen 1992; Campana 2001). An added advantage of laboratory-based methods is that they provide information on age-at-first increment formation – especially important for studies where spawning and hatch dates need to be accurately determined. The success of rearing known-age larvae in the laboratory that accurately reflect growth rates depends on the degree to which the environmental conditions including photoperiod, diurnal temperature fluctuations and food availability can be simulated (Geffen 1992). Campana (1984), in a study of laboratory-reared starry flounder *Platichthys stellatus*, attributed the poor clarity and irregularity of increments in the otoliths to the absence of diurnal temperature fluctuations.

An additional factor to consider when aging fish is the onset of increment deposition that may vary between species by as much as one day before hatching in carp (Smith and Walker 2003) to as many as nine days after hatching in European smelt *Osmerus eperlanus* (Sepulveda 1994). Determining an estimate of the number of days to the onset of increment deposition was thus an important objective of this study. Without this step, age estimations would have been consistently incorrect by a constant amount (Campana 2001).

While most studies aimed at aging fish by means of daily increments have been conducted on marine species, the technique is increasingly being used as a tool for investigating the age and growth of fish in temperate freshwater ecosystems and a number of these studies have focussed on cyprinids (Victor and Brothers 1982;

[2] One of two alternative crystal lattice configurations of calcium carbonate.

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Bestgen and Bundy 1998; Vilizzi 1998; Smith and Walker 2003; Durham and Wilde 2005).

In South Africa, daily growth increments have been used to study the early growth (Waldron 1994) and hatchdate distributions (Wilhelm *et al.* 2005) of anchovy (*Engraulis capensis*) and for validating the ages of horse mackerel (*Trachurus trachurus*) (Waldron and Kerstan 2001). A few freshwater fish studies have focussed on elucidating early life history characteristics of certain species, including the chubby-head barb (*Barbus anoplus*) (Cambray 1983); the Maluti minnow (*Pseudobarbus quathlambae*) (Cambray and Meyer 1988); the Cape kurper (*Sandelia capensis*) (Cambray 1990b) and the Clanwilliam yellowfish (*Labeobarbus capensis*) (Cambray *et al*. 1997). To date there have been no early growth studies despite their value for understanding recruitment processes and population dynamics.

The early life history of the sawfin is poorly known. The primary aim of this component of the study was therefore to establish an age-length relationship for larval and early juvenile sawfin. Secondary aims included establishing the age of first increment deposition and identifying key stages in the early development of the larvae. This was not done for Clanwilliam yellowfish since they did not spawn during the course of the study. Following this Introduction, the chapter has been divided into three parts. Section 7.2 deals primarily with the larval rearing experiments that were carried out in November 2006. The objectives in this component of the study were (1) to validate the increment deposition rate of known-age larvae reared under laboratory conditions and (2) record the early development stages of sawfin eggs and larvae. Section 7.3 deals with establishing age-length relationships for both the laboratory-reared fish and the wild-caught fish that were collected from the Driehoeks River between December 2004 and March 2006. The results of the two separate components of the study are then brought together and discussed in Section 7.4. In Chapter 8, the information presented in this chapter will be used to determine hatch dates in order to investigate environmental conditions that prevailed over peak spawning periods.

7.2 LARVAL DEVELOPMENT AND VALIDATION OF INCREMENT DEPOSITION RATE IN LABORATORY-REARED FISH

7.2.1 Objectives

The accuracy of age estimation using otoliths depends on correctly assigning a frequency to the rate at which increments are laid down (Campana and Neilson 1985). Age validation studies have made use of chemical markers such as OTC (e.g. Lang and Buxton 1993, Fowler 1989), as well as laboratory-reared known-age larvae (e.g. Moksness and Wespestad 1989; Bestgen and Bundy 1998). Validation using known-age larvae is considered a more reliable means of validation (Geffen 1992) and has the additional advantage of being able to establish age-at-first increment deposition. The initial intention of this component of the study was to use known-age larvae and corroborate their ages with OTC treatments. It became clear that considerably more time than was allocated to the study would have been needed to establish the correct OTC concentrations and emersion times. Thus validation of age in this study is based solely on comparing increment counts with known ages. Subsidiary objectives included: to record important developmental stages of sawfin embryos and larvae; determine the onset of increment deposition and determine the accuracy and precision of increment counts. The effect of variation in water temperatures on increment formation is also investigated.

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7.2.2 Methods

Collection and rearing of fertilised eggs and larvae—Milt was collected from three adult ripe-and-running male sawfin caught in a fyke net set in the Driehoeks River in Pool 6 (Figure 3.4) on the 13 November 2006. The milt was set aside in a cooler box and used to fertilise eggs stripped from three female sawfin (288, 299 and 295 mm TL) caught on the same day. The fertilised eggs from each female (BS01; BS02 and BS03) were transferred to a temporary field hatchery on site where they were hatched and the larvae reared in aerated plastic containers. From the moment of fertilisation, samples of the developing eggs and larvae were collected at regular intervals and their total lengths (to the nearest 0.5 mm TL) were recorded. Half of each sample was set aside for cataloguing in the Albany Museum and was therefore preserved in formalin; the other half was preserved in 96% ethyl alcohol for later otolith analysis. Development stages were photographed using a Nikon D100 camera mounted on a dissecting microscope. The larvae hatched in the field remained in the hatcheries on site for ten days during which time they fed off their yolk sacs. Over the course of this period, a small sample of embryos and larvae was collected from spawning beds in the Driehoeks River for later comparison of their otoliths with laboratory-reared fish. On the 20 November 2006, a fourth batch of eggs was collected and fertilised from a female (BS04). These eggs, together with the hatched larvae from the first three batches, were transported back to temperature control rooms at the University of Cape Town on the same day. During transport, the eggs and larvae were held in aerated polyethylene bags held in cooler boxes to prevent overheating. On arrival, the eggs and larvae were then transferred to aquaria in the temperature-control rooms.

Conditions in the temperature control rooms were set to simulate, as closely as possible, the diel light cycles and temperatures that the fish would be exposed to over the growing season (Thresher 1988; Fowler 1989; Geffen 1992). These temperature cycles were based on conditions that had been recorded in the river by temperature loggers over the previous two sampling seasons (2004 and 2005). Ambient temperature in the control room was set to 18 ºC. An immersion heater-thermostat in the aquaria linked to a timer switch was set to increase temperatures from the ambient temperature at 09h00 to 24 ºC at 18h00 daily. The heater-thermostat was set to turn off after 18h00 and the temperature left to return to ambient room temperature overnight. Photoperiod was set at 12 hours 07h00 in the morning to 07h00 in the evening. Temperature was monitored in the tanks throughout the experimental period by means of a thermistor temperature sensor coupled to a data logger (HOBO® Water Temp Pro) accurate to ± 0.2°C at 25°C. Early larvae and juveniles were fed on newly hatched *Artemia* nauplii for the first 20 days and on commercially available dry food thereafter. Throughout the period that they were kept in the laboratory, sampling and recording of lengths continued at hourly and daily intervals for eggs and at multi-day intervals (2,5,10 days) for larvae. Photography of the development stages also continued (SMZ1500 Nikon stereoscopic microscope). Sampling ceased on 8 January 2007 after which the increments became increasingly difficult to discern due to very slow growth and consequent compression of increment widths. Attempts were made to confirm the periodicity of increment deposition by means of Oxytetracycline hydrochloride (OTC) marking. Fish were immersed in 250 mg l^{-1} in OTC for eight hours. However, preliminary attempts failed due to the high mortality of the specimens and this component was therefore abandoned due to time constraints. The otoliths from the sampled fish were set aside for extraction, processing and analysis.

Age estimation—The ages of the larval and 0^+ juvenile sawfin were estimated by enumerating daily growth increments on the otoliths. The sagittae and lapilli were retrieved from the vestibular apparatus after lysing

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the non-calcareous tissue with sodium hydroxide and mounting these on a glass slide using thermoplastic cement (Crystalbond 509®). For older juveniles, rings were clearer on the lapillae and these otoliths were used for all subsequent increment counts. For fish >15 mm TL the otoliths were polished through to the core. A 1500 grade sandpaper was used to polish the cement to the depth of the otolith in the cement. Thereafter a 0.3 µm aluminium suspension polishing compound (Buehler Micropolish II) was used to abrade and polish the otolith down to the core. Once the core was reached, the cement was then re-melted to seal the polished surface of the otolith. Both sagittae and lapilli were polished through the lateral surface to produce a sagital section. Counting was carried out by means of a light microscope at 400× magnification. Counting commenced from the nucleus (primordium) and proceeded outwards across the longest radius of the otolith to the margin, along a path that presented the clearest and most unequivocal increment formation. Increments were counted 'blind', i.e. without knowledge of the age of the fish, by one counter on two separate occasions. The precision and accuracy of increment counts were tested on a sub-sample of sawfin lapilli by comparing the mean of three blind counts by the author and one other researcher.

Analysis—Least squares regression of the known age (post-fertilisation) as a function of estimated age (increment count) was used to test the hypotheses that (1) increments were formed at fertilisation and (2) that increments were formed on a daily basis. The age-at-first increment deposition was assumed to be the *y*-intercept. If *y*-intercepts were not significantly different from 0, this would support hypothesis (1) and if the slope of the regression was not significantly different from one then the hypothesis (2) would be supported. The age post-fertilisation was chosen as 0 age rather than the hatch date since the former was known precisely, whereas the latter was found to differ by up to 20 hours (Section 7.2.2).

7.2.3 Results

Development stages—sawfin eggs immediately after fertilisation were adhesive and negatively buoyant (Plate 7.1). Egg diameters were ~1.8 mm. The first cell division commenced after 2-3 hours and blastopore closure occurred after 18 hrs. After 22 hours serial muscle bundles (myomeres) were evident (Plate 7.2; Table 7.1). Hatching commenced between 50 (10-20 %) and 70 (100 %) hours (2-3 days) where mean temperatures over the incubation period were 19.8 (SD±0.88) and 20.3 °C (SD±3.08) in the field and laboratory hatcheries respectively (Table 7.1). Upon hatching, the larvae were photophobic, attaching themselves to the substratum of the hatcheries by means of an adhesive pad on the head.

Plate 7.1 Sawfin eggs collected from the Driehoeks River adhering to the underside of a cobble

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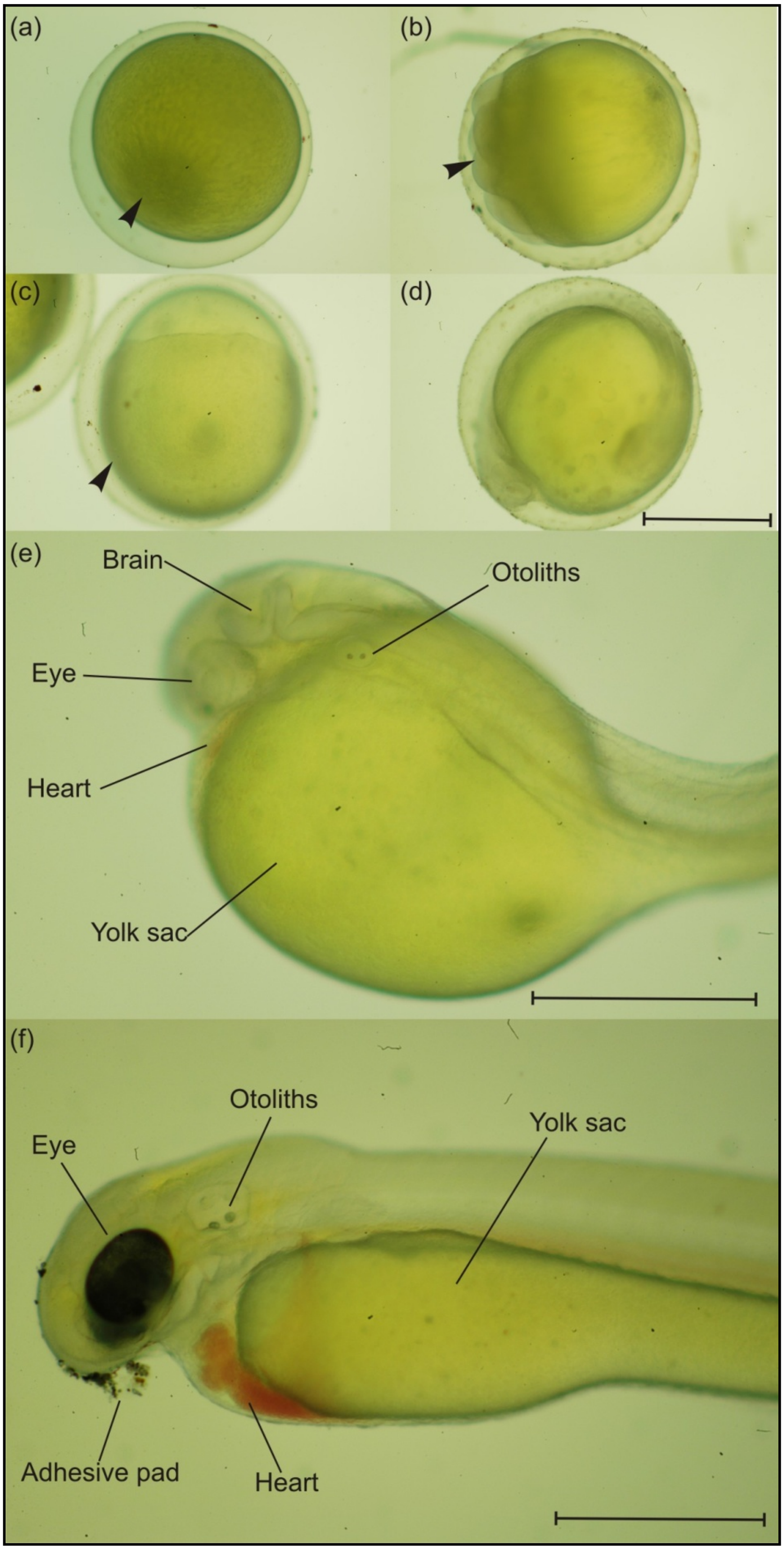

Plate 7.2 Development of sawfin eggs and larvae (BS03): (a) protoplasmic streaming, 1 hr; (b) eight cell division, 3 hours; (c) cell division 2/3 over yolk, 14 hours (d) head and tail visible, 26 hours; (e) hatched free-embryo, (66 hours); (f) larvae (4 days) adhesive pad is visible above the mouth. Scale bar = 1 mm.

TABLE 7.1 Development stages of the four batches (BS01-BS04) of sawfin larvae reared in the field and laboratory.

Date	Development stage	Time	Size (mm TL)
BS01 (Field hatched)			
13/11/2006	Fertilisation	0 hours	1.8
13/11/2006	Cell division	3.5 hrs	
15/11/2006	10% hatching	50 hrs	
16/11/2006	90% hatching	70 hrs	6.0
23/11/2006	20% swim-up	10 days	8.5
24/11/2006	Swim bladder visible	11 days	
24/11/2006	100% swim-up	11 days	
BS02 (Field hatched)			
13/11/2006	Fertilisation	0 hrs	1.8
13/11/2006	4 cell division	3 hrs	
13/11/2006	Cell division 2/3 over yolk	15 hrs	
15/11/2006	Tail free		
15/11/2006	5% hatching	49 hrs	
16/11/2006	90% hatching	70.5 hrs	6.0
22/11/2006	BS02 all died		
BS03 (Field hatched)			
13/11/2006	Fertilisation	0 hrs	1.8
13/11/2006	Protoplasmic streaming visible	1 hrs	
13/11/2006	2-4 cell division	2 hrs	
13/11/2006	8 cell division	3 hrs	
14/11/2006	Cell division 2/3 over yolk	14 hrs	
14/11/2006	Yolk closure	17 hrs	
14/11/2006	Blastopore closure	18 hrs	
14/11/2006	5 myomeres visible	22 hrs	
16/11/2006	60-70% hatching	66 hrs	6.0
25/11/2006	50% swim-up	12 days	9.0
26/11/2006	100% swim-up	13 days	
BS04 (Laboratory hatched)			
20/11/2006	Fertilisation	0 hrs	1.8
22/11/2006	20% hatching	51.5 hrs	
23/11/2006	90% hatching	69.5 hrs	6.0
1/12/2006	10% swim-up	11 days	8.5
2/12/2006	90% swim-up	12 days	

Swim-up – the stage at which larvae make the transition from yolk-sac feeding to external feeding and swim into the water column (Bagatto *et al*. 2001) – occurred between 11 (BS01) and 13 days (BS03) post-fertilisation shortly after development of the swim bladder and the exhaustion of the yolk sac. Exogenous feeding commenced a day after swim-up. Embryo and larval mortality was high prior to swim-up, but considerably lower thereafter.

Otolith location and structure— Sagittae and lapilli were visible in the otic capsule of sawfin 50 hours after fertilisation through a light microscope at 400× magnification (Plate 7.3). The lapilli were anterior and distal to the sagittae. Asterisci were not visible until the fish was at least 30 days old and were therefore unsuitable for aging purposes. With increasing age, the disc shaped sagittae become more circular and convex-concave in cross-section, whereas the lapilli become increasingly ovoid (Plate 7.4). The centre of each otolith consisted of an opaque zone considered to be the primordium. Visible increments deposited from the primordium through to the margins were present in sagittae and lapilli, suggesting that either would be suitable for increment analysis. The sagittae were the largest otoliths and therefore easier to remove and mount. With increasing age, however, the sagittae exhibited numerous concentric fissures that obscured the daily increments and were consequently difficult to read (Plate 7.4).

In addition, the convex-concave shape of the sagittae complicated the grinding procedure. Lapilli were therefore the preferred otoliths for age estimation in older specimens. What were assumed to be daily increments on the lapilli were visible as paired, widely spaced hyaline (translucent) and opaque (dark) bands on the surface of the sectioned otolith when viewed through a light microscope (Inset Plate 7.4). Sub-daily increments were also visible as regularly spaced bands, but were much narrower and far less visually prominent than daily increments. Where there was some ambiguity between daily and sub-daily increments, it was possible to eliminate sub-daily increments from the field of view by adjusting the focus.

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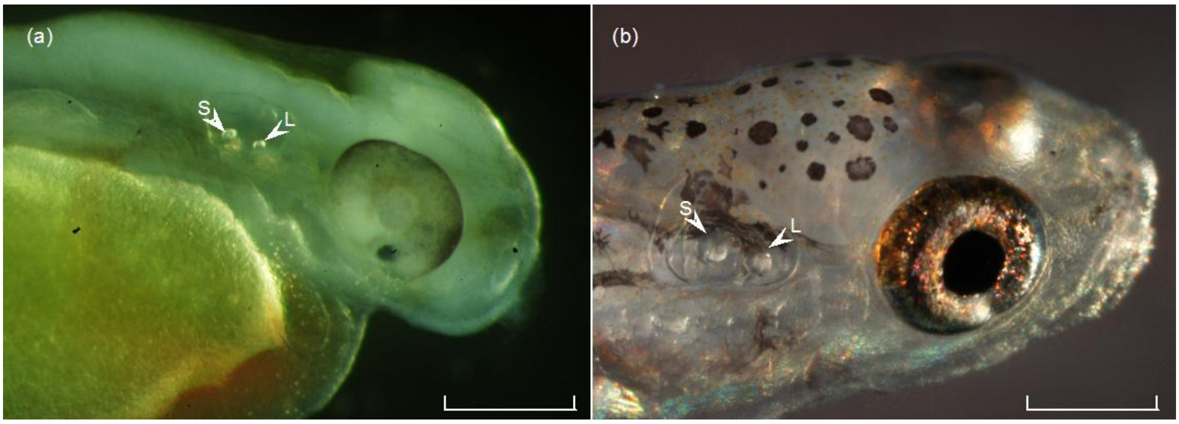

Plate 7.3 Sawfin larvae showing the position of the sagitta (S, posterior) and lapillus (L, anterior) in the otic capsule (a) 2 day post-hatching and (b) 16 day old post-hatching (scale bars = 500 µm).

Plate 7.4 Micrograph of a polished lapillus (L) and unpolished sagittus (S) of a 92 day old juvenile sawfin. The inset shows an enlargement of a region of the lapillus and the appearance of alternating opaque and hyaline bands laid down as daily increments. (Scale bar = 100 μm). Concentric fissures in the surface of the larger sagittae that made them difficult to read are visible.

Validation of otolith increment deposition rate—The relationship between the increment count and the known-age (post-fertilisation) was investigated using 41 laboratory-reared larvae (APPENDIX E.1). Increments in fish older than 20 days were more difficult to discern near the primordium and towards the margins than in fish less than 20 days old. In order to estimate the onset of increment formation more accurately therefore, the relationship between estimated age and mean actual age was determined for two separate age groups: one for larvae <20 days, one for juveniles >20 days post-fertilisation. The former relationship was used to estimate the age at increment formation. The regression line for both age groups is described by a linear equation (Figure 7.2). Neither slopes of the regression lines in Figures 7.2 (a) and (b) were statistically different from 1 (t-test; Table 7.2). Thus the increment deposition rate closely approximated one per day in both size classes (0.987 and 1.046 increments per day for <20 and >20 day old fish respectively). The y-intercept of the equation describing the smaller group (<20 day old larvae), suggests that where the increment count is 0, actual age is 2.98 days post-fertilisation. Additional evidence for the timing of the first increment deposition, however, comes from counts of increments on the clearest and least ambiguous otoliths which suggested that the first visible increment is deposited two days post-fertilisation (Plate 7.5). From these two lines of evidence therefore, the time to first increment deposition is assumed to be between two and three days post-fertilisation. The *y*-intercept for >20 day old larvae was much higher (5.3 days). This was assumed to be the result of undercounting increments belonging to older fish (see below).

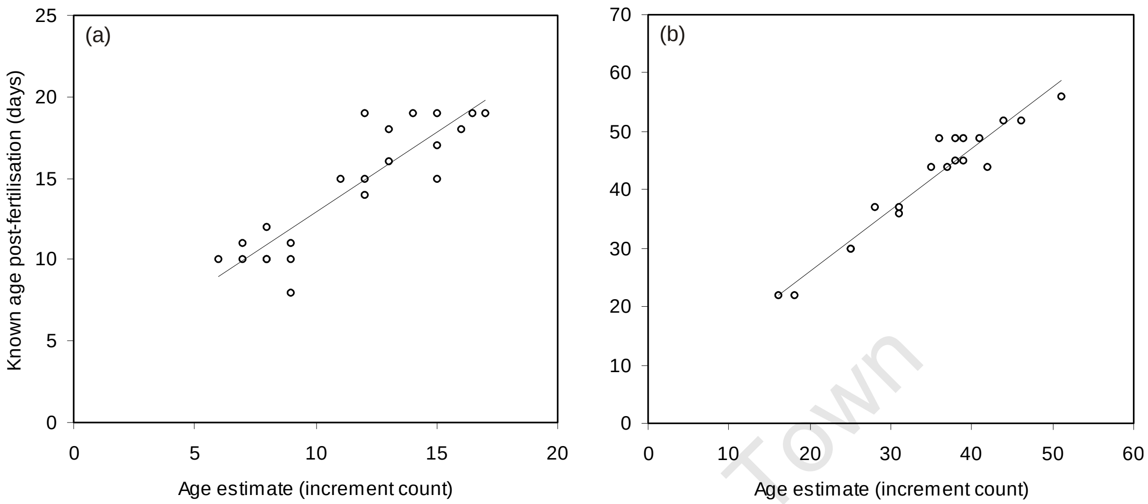

Figure 7.2 Regression of known post-fertilisation ages and increment counts for laboratory-reared larvae: (a) <20 days post-fertilisation and (b) >20-56 days post-fertilisation. The regression line for (a) is described by the equation: known age post-fertilisation (days) = 0.987 [increment count] + 2.982 (r^2 = 0.79, n = 19). The regression line for (b) is described by the equation: known age post-fertilisation (days) = 1.046 [increment count] + 5.338 (r^2 = 0.93, n = 22).

TABLE 7.2 Results of the regressions of age estimates against known age for <20 day old sawfin larvae and >20 day old larvae: $H_0\ \beta = 1$; $H_A\ \beta \neq 1$ and $H_0\ a = 0$; $H_A\ a > 0$.

Group	*Statistic*	*Coefficients*	*Std. Error*	*t-stat*	*P-value*	*Lower 95%*	*Upper 95%*
Larvae <20 days old	Intercept (*a*)	2.98	1.36	2.19	0.05	0.15	5.81
	Regression coefficient (*β*)	0.99	0.11	-0.11	0.05	0.74	1.24
Larvae >20 days old	Intercept (*a*)	5.34	2.46	2.19	0.05	0.15	5.82
	Regression coefficient (*β*)	1.05	0.07	0.68	0.05	0.90	1.20

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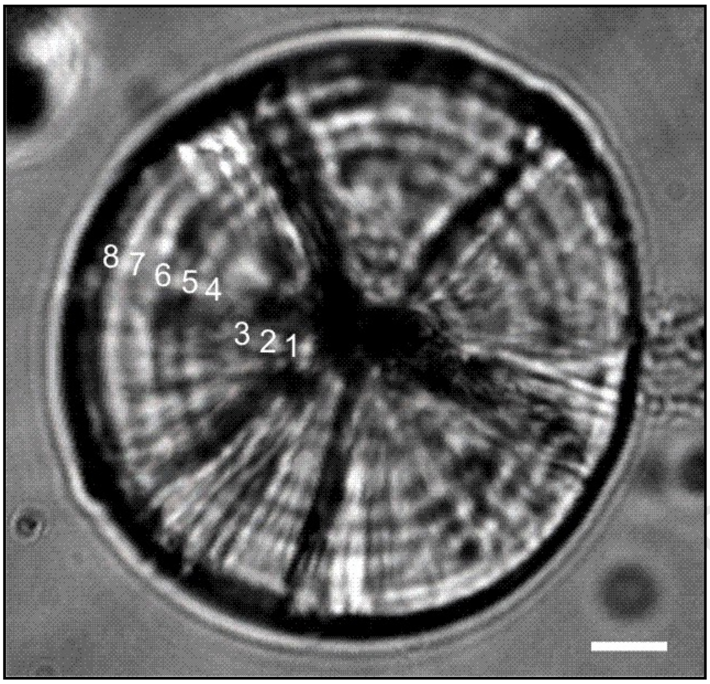

Plate 7.5 Micrograph of a sagittal otolith extracted from a 10 day old larvae showing eight increments from the primordium. The primordium is visible as the dark area at the centre of the otolith (Scale bar = 10 μm).

***Counting precision and accuracy*—**Three blind counts by the author and one other researcher of daily growth increments on 19 sawfin lapilli showed a good agreement between counters, with the mean difference being two increments (Table 7.3). These differences were not significant (*t*-test: $p<0.05$; df = 34; t=-0.13). There was a trend of increasing difference between actual and estimated age with increasing age of the fish (Figure 7.3). This was assumed to be due to reader error as a result of a greater number of increments and narrow increment widths in older fish and/or the difficulty of resolving the very first increments close to the primordia and margins of the otolith.

TABLE 7.3 The mean of three counts of the same otolith (lapillis) in 19 sawfin by two counters (Counter 1 and Counter 2) are shown in column $\bar{x}$ R1 and $\bar{x}$ R2. The absolute difference between the mean of the two counts is shown in column D. The mean difference and the 95% confidence interval of the mean difference are shown in the final two rows.

	Counter 1				Counter 2				
TL (mm)	1	2	3	$\bar{x}$ R1	1	2	3	$\bar{x}$ R2	D
8.0	9	9	9	9	8	8	8	8	1
13.0	12	13	12	12	13	13	13	13	1
14.0	15	15	15	15	14	14	14	14	1
14.0	16	16	17	16	14	14	14	14	2
17.0	16	18	18	17	17	17	17	17	0
18.1	16	18	18	17	19	18	18	18	1
21.9	20	21	20	20	21	22	22	22	1
25.0	26	25	26	26	25	25	25	25	1
48.7	50	48	49	49	50	49	48	49	0
53.0	54	54	51	53	53	53	53	53	0
57.0	54	53	55	54	57	56	58	57	3
64.1	55	60	65	60	61	66	63	63	3
67.0	62	63	63	63	67	67	67	67	4
69.0	68	69	68	68	69	69	69	69	1
72.6	68	70	68	69	73	77	68	73	4
94.3	89	90	91	90	93	95	94	94	4
96.2	96	90	90	92	98	95	97	97	5
96.3	91	95	98	95	95	95	98	96	1
								$\bar{x}$ Difference	2
								95% CI	0.69

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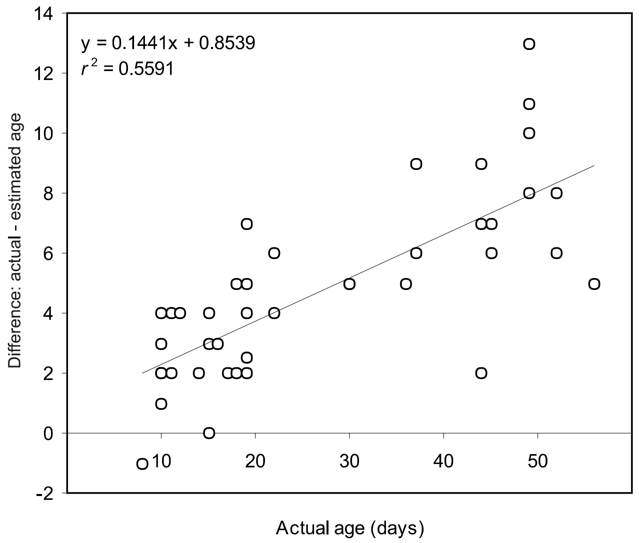

Figure 7.3 Actual age of larvae (days) plotted against the difference between the actual age and the estimated age (increment counts).

Effect of temperature on increment formation—Three batches of eggs (BS01, BS02 and BS03) from each of three females caught on the 13 November 2006 were kept in field hatcheries until the 20 November 2006 when they were transferred to temperature-control rooms in Cape Town. It was not possible to control temperatures in the field hatcheries and therefore the first three batches (BS01, BS02 and BS03) were subject to ambient temperatures during the first seven days of their development (Figure 7.4). The water temperatures in the field hatcheries ranged between 18.2 and 21.6 °C ($\bar{x}$ 19.7 ±0.83°C). The fourth batch of eggs, fertilised on the 20 November 2006 (BS04), were packed into sealed polystyrene cooler boxes with ice and transported directly to the temperature-control rooms in Cape Town. During transport, temperatures rose to a maximum of 24 °C. On arrival, the eggs and larvae were kept in aerated plastic trays in the temperature-control rooms for the first ten days. These trays facilitated the daily removal of dead eggs and larvae. Daily fluctuations in water temperature in the trays were high (between 15.9 and 26.6 °C; $\bar{x}$ 21.6 ±2.6 °C) due to the smaller volumes of water. After swim-up, the larvae were transferred to larger aquaria to facilitate growth. Water temperature variations were less in these tanks, ranging between 17.9 and 24.3 °C ($\bar{x}$ 21.9) and remained between these levels until the termination of the experiment on 21 January 2007 (Figure 7.4). These temperatures were lower than the temperatures recorded in the Driehoeks River over the same time period in 2005, i.e. 16.6 and 30.7 °C ($\bar{x}$ 22.1 °C).

Plate 7.6 shows that there were visual differences between otolith increments formed between fish that were hatched in the field (BS01), larvae that were hatched in the laboratory (BS04) and larvae that were collected from spawning beds in the Driehoeks River during the course of fieldwork (20/11/2006). Increments formed in the otoliths of BS04, that were exposed to the fluctuating temperatures in the laboratory, are considerably more pronounced and unambiguous near the primordium than those formed by the field-hatched larvae (BS01) that were exposed to less variable temperature conditions. Increments formed close to the primordium in BS01 (those formed for the first few days after hatching) are almost indistinguishable. The clarity of increments formed by the wild-caught larvae were intermediate between the two.

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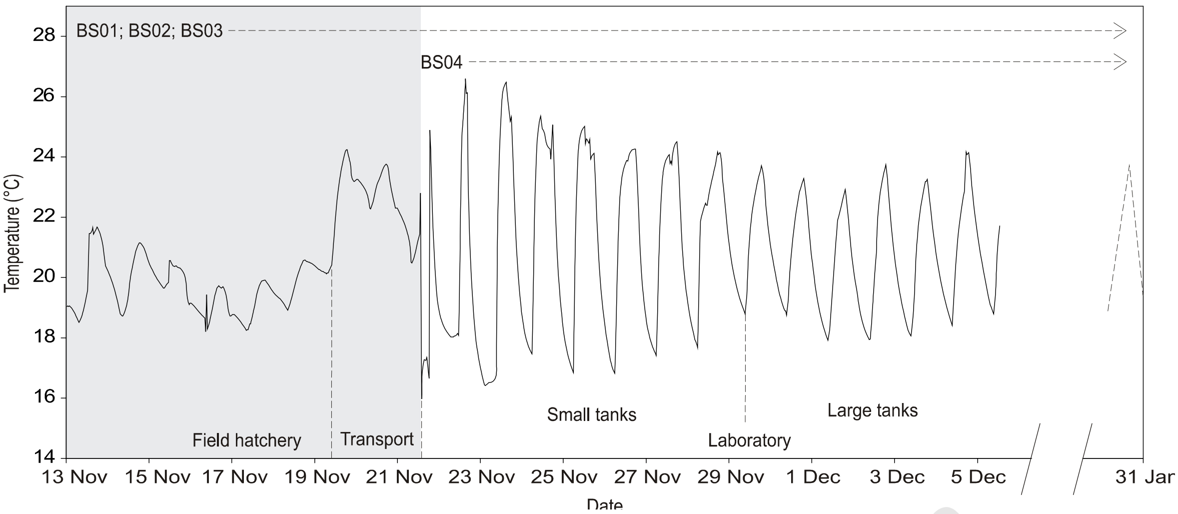

Figure 7.4 The water temperature regime over the experimental period. The first stage (grey block: 13 November 2006 to 20 November 2006) shows the temperature regime in the field hatcheries where the first three batches were hatched out (BS01, BS02, BS03) and transported to Cape Town. The second stage (20 November 2006 to 31 January 2007) shows the temperature regime in the control rooms for all four batches.

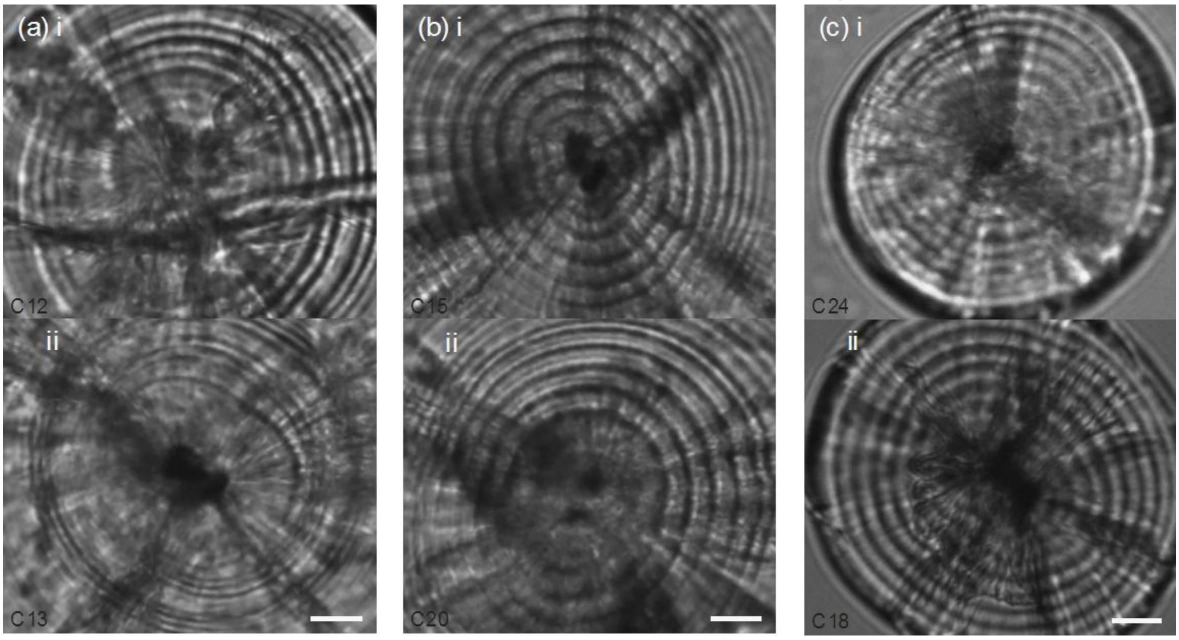

Plate 7.6 Micrograph of larval sawfin sagittal otoliths: (a) (i and ii) hatched in the field, laboratory-reared (BS01); (b) (i and ii) laboratory-reared, hatched in the temperature-control rooms (BS04) and (c) (i and ii) wild-caught from Driehoeks River 20/11/2006 (Scale bar = 10 μm).

7.3 AGE-LENGTH RELATIONSHIPS OF LABORATORY-REARED AND WILD-CAUGHT LARVAE

7.3.1 Objectives

The primary objective of this component of the study was to examine the otoliths of wild-spawned 0+ larvae and juvenile sawfin collected from the Driehoeks River in 2004/5 and 2005/6, to develop age-length relationships for the first few months of life and to compare growth rates between years and between wild-caught and laboratory-reared larvae.

7.3.2 Methods

Collection of fish—Replicate sampling of larval and juvenile sawfin was not considered feasible because of the highly clumped nature of their distribution and since this approach would have entailed a higher mortality than was considered acceptable. Only two sampling trips were therefore planned per year – one in December and another in March to ensure the sampled cohort included individuals from near the first and last spawning events. Larval sawfin were collected from the Driehoeks River between 3-6 December 2004 (n = 159) and 10-13 December 2005 (n = 51) by means of hand nets, drift nets and quatrefoil light traps immediately downstream of a known spawning bed (Lower Tafelberg, Chapter 6). Juvenile fish from the 2004 cohort were collected on the 23-26 February 2005 (n = 116) and from the 2005 cohort 24 March 2006 (n = 174). These fish were caught between one and two kilometers downstream of the spawning sites using a 5 m seine net (6 mm mesh). Since no other juvenile fish were found in the intervening reaches, it was assumed these fish came from these upstream spawning sites (See Chapter 4 for a detailed discussion of juvenile distribution patterns). The total length of live fish was measured to the nearest 0.5 mm and those retained for otolith analysis were preserved whole in 96% neutral buffered ethyl alcohol. A total of 167 otoliths from laboratory-reared and wild-caught fish ranging in size between 7 and 65 mm TL were prepared in the manner described in Section 7.2.1. Of these, 111 (66 %) were suitable for reading and included in the analysis: 36 from wild-caught fish that hatched during the 2004/5 spawning season, 34 from 2005/6, and 41 from laboratory-reared fish (described in Section 7.2). Linear regression is the preferred growth model for short growth intervals where no upper asymptote is expected, as is the case with larval and juvenile growth (Townsend and Graham 1981; Jones 1992), and a linear equation was therefore used for this analysis. Significant differences between years and between wild-caught and laboratory-reared sawfin were tested by means of a paired-sample *t*-test.

7.3.3 Results

Age-length—Age-length relationships for wild-caught larval and juvenile sawfin were ascertained for fish sampled from the Driehoeks River during the summers of 2004 and 2005. Wild-caught fish ranged in age from roughly one week to five months and during this time increased their length from 9 to 60 mm TL (Figure 7.5) (APPENDIX E.2). The age-length relationships for the wild caught fish were described by the equations:

Equation 1 (2004/5): *Length (TL)* = 0.3651 [*age*] + 7.0 (r^2 = 0.950; n = 36)

Equation 2 (2005/6): *Length (TL)* = 0.4413 [*age*] + 5.1055 (r^2 = 0.99; n = 34)

These equations are used later in Chapter 8 for back-calculating larval spawning dates. In addition to wild-caught sawfin, the age-length relationship of laboratory-reared sawfin was also ascertained:

Equation 3 (2006/7): Length (TL) = 0.10 [age] + 8.13 (r^2 = 0.87, n = 35)

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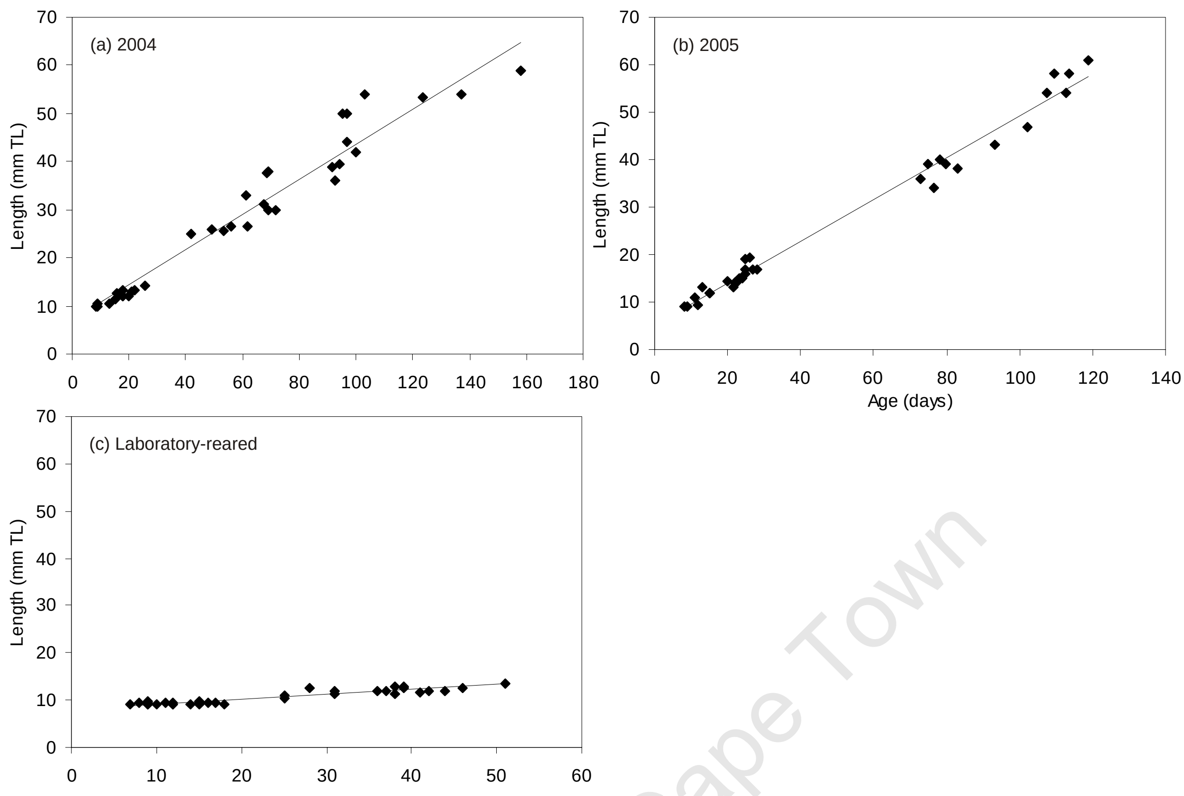

Figure 7.5 Age-length regressions for wild-caught and laboratory-reared larval and juvenile sawfin between 8-158 days old.

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Sawfin reared in the laboratory during 2006 were sampled between November 2006 and January 2007 (Section 7.2) and ranged in age from one week to 50 days. During this time they increased their length from 9 - 14 mm TL (Figure 7.5 c). Aging laboratory-reared fish older than 50 days presented significant challenges to counting because growth rates were very slow under laboratory conditions. Consequently, increment spacing was reduced and individual increments were difficult to distinguish. Other factors that led to poor estimates included: under- or over-polishing, blemishes or cracks in the otolith, or ambiguities close to the primordia or margins. The linear equations fitted to the growth in total length accounted for 95% (2004/5 cohort), 99% (2005/6 cohort) and 87% (laboratory-reared) of the variation in length (Figure 7.5) and the relationship was found to be significant for both wild-caught sawfin in both years as well as laboratory-reared sawfin (t-test; $p = 0.05$) (Table 7.4).

TABLE 7.4 Results of the regressions for age-length relationships for larval and juvenile wild-caught and laboratory-reared sawfin: $H_0\ \beta = 0$; $H_A\ \beta \neq 0$ and $H_0\ a = 0$; $H_A\ a > 0$.

	Statistic	*Coefficients*	*Std. Error*	*t-stat*	*P-value*	*Lower 95%*	*Upper 95%*
2004 wild-caught	Intercept (a)	7.0	1.14	6.17	0.05	4.69	9.31
	Regression coefficient (β)	0.37	0.01	24.52	0.05	0.33	0.4
2005 wild-caught	Intercept (a)	5.11	0.57	8.95	0.05	3.94	6.27
	Regression coefficient (β)	0.44	0.01	47.3	0.05	0.42	0.46
2006 laboratory-reared	Intercept (a)	0.1	0.19	41.97	0.05	7.74	8.53
	Regression coefficient (β)	8.13	0.01	14.44	0.05	0.09	0.12

Growth rate—Significant interannual variation in growth was evident between the two wild-caught sawfin cohorts. The 2005 wild-caught cohort exhibited a significantly faster growth rate (0.44 mm day^{-1}) than the

2004 cohort (0.37 mm day^{-1}) (Table 7.5). The laboratory-reared sawfin also exhibited a significantly slower growth rate (0.1 mm day^{-1}) than either of the wild-caught cohorts (Table 7.5).

TABLE 7.5 Two-tailed *t*-test comparisons of regression coefficients of linear models fitted to length *vs* age between (1) 2004 and 2005 cohorts and (2) between lumped 2004 and 2005 cohorts and laboratory-reared fish.

Comparison	*df*	*t-stat*	*P value*
2004 *vs* 2005 cohort	64	-6.92	0.05
2004/05 *vs* laboratory-reared	98	15.13	0.05

7.4 DISCUSSION

Validation of otolith increment deposition rate—This study verified that it is possible to estimate the age of wild-caught larval and juvenile sawfin between eight and 160 days (5 months) old (8-60 mm TL) using daily growth increments in otoliths. Regression of estimated age (increment counts) as a function of known age confirmed that the rate of increment deposition was equivalent to one day and that the onset of increment formation was between two and three days post-fertilisation, or upon hatching. Sagittae are generally the preferred otoliths for aging studies because of their larger size (Campana and Neilson 1985), whereas the use of lapilli is relatively uncommon (David *et al*. 1994). A number of studies, however, have noted that the atypical shape of some cyprinid sagittae precludes their usefulness for daily increment analysis and have used lapilli instead, e.g. carp (*Cyprinius carpio*) (Vilizzi 1998); sanjika (*Opsaridium microcephalum*) (Morioka and Matsumoto 2003); kabyabya (*Opsaridium tweddleorum*) (Morioka and Matsumoto 2007) and Colorado Pikeminnow (*Ptychocheilus lucius*) (Bestgen and Bundy 1998). In this study, sagittae of sawfin, particularly in older fish, were found to be unsuitable for growth increment analysis because of their convex-concave cross-sectional profile and the presence of numerous check marks on their surface. The shape of sawfin sagittae would have required the application of a transverse sectioning technique which is more time consuming than the sagittal sectioning applied in this study. It was found in sawfin that the first increment was laid down roughly at the time of hatching (two to three days post-fertilisation). Thus spawning dates should be calculated as the increment count plus three days.

Counting precision and accuracy—There were no significant differences between the mean of three counts by two separate readers of daily growth increments and the precision of the counts was therefore considered good. Underestimation of actual age in older specimens was common due to ambiguities in increment deposition towards the primordium or margins of the otolith, blemishes or cracks in the otoliths, or over- or under-polishing.

Effect of temperature on increment formation—One of the disadvantages of rearing fish in a laboratory is that environmental conditions and food regimes cannot simulate field conditions exactly. Campana and Nielsen (1984) suggested that while daily increment formation is endocrine driven and linked to an endogenous circadian rhythm, environmental variables can mask this rhythm. Cermeño *et al*. (2003) suggested that a loss of daily synchronisation among laboratory-reared European anchovy (*Engraulis encrasicolus*) was related to aquarium conditions. Campana (2001), however, proposed that although otolith microstructure may differ between wild-caught and laboratory-reared fish, the periodicity of increment formation is not affected.

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In this study, environmental conditions in the laboratory, i.e. temperature and photoperiod, were set to simulate conditions that the developing eggs and larvae would have experienced in the Driehoeks River over the growing season. Although conditions in the field could not be replicated exactly in the laboratory, it was possible to achieve an approximation of diel temperature cycles experienced by fish in the river. There were nevertheless several artefacts of the laboratory conditions that affected fish growth and increment deposition. Diel temperature fluctuations in the field hatchery were less than those in the temperature-control rooms and increments formed under the former conditions were difficult to discern, whereas larvae hatched in the laboratory exhibited well-defined increments. The clarity of increments laid down in the otoliths of wild-caught fish were intermediate between these extremes – reflecting the less extreme temperature variations in the wild compared with the laboratory, but more extreme than the field hatchery. The effects of temperature on increment formation have been widely reported for a number of species in the literature. Campana (1984) found that the increments of laboratory-reared starry flounder (*Platichthys stellatus*) under conditions of weak diel temperature fluctuations were low in contrast and irregularly spaced compared to those of wild fish. Other species for which this has been reported include: plainfin midshipman (*Porichthys notatus*) (Campana 1984); chinook salmon (*Oncorhynchus tshawytscha)* (Neilson and Geen 1985) and Colorado pikeminnow (*Ptychocheilus lucius*) (Bestgen and Bundy 1998). The findings of this study therefore support the evidence that constant temperatures reduce increment contrast in growing otoliths. The periodicity of increment deposition, however, appeared to be unaffected.

***Growth rate*—**The second artefact of laboratory conditions was a significantly slower growth rate among laboratory-reared sawfin compared with wild-caught larvae. Rearing fish at high stocking densities is known to negatively affect growth rate due to increased competition for food and space (Koebele 1985) and increased stress as a result of confinement and crowding (Fagurland *et al.* 1981; Ruane 2002). Temperatures were slightly lower in the laboratory than they were in the field and this may have had some effect on growth rates. In addition, larval fish in the field inhabit shallow marginal slackwaters (Chapter 4) where daily temperature ranges would be considerably higher than they were in the main channel. The feeding requirements may have been underestimated for the number of fish that were laboratory-reared. Although reduced growth rates in this study did not appear to affect increment deposition rate, they did reduce increment spacing, rendering otoliths from fish over 50 days old difficult to read.

In addition to differences in growth rates between wild-caught and laboratory-reared larvae, there were significant differences in growth rates of wild-caught sawfin between years: 2005/6 recruits grew significantly faster than 2004/5 recruits. This could not be easily explained in terms of temperature differences between the two years. Mean temperatures measured by sensors in the Driehoeks River set to record temperature at 30 minute intervals showed that temperatures were on average 0.67 °C higher during the 2004/5 growing season (November to March; $\bar{x}$ 20.85 °C) than the 2005/6 growing season ($\bar{x}$ 20.18 °C) and a *t*-test confirmed that these differences were significant (*t-test*; t = 18.6; p<0.05). In addition, temperatures during 2004/5 were considerably more stable than they were in 2005/6 (SD±1.71 and SD±2.51 respectively) and a greater proportion of the values were near the upper extremes of the range (Figure 7.6). During 2004/5, temperatures in the middle of the range were higher and prevailed for a much greater proportion of the time. The differences in growth rates between years could not therefore be related to temperature and may be related to the fact that larval densities in the Driehoeks River were higher during 2004/5 than 2005/6 (Chapter 3, this

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report) and so competition for space and food would therefore have been higher than in 2004/5 and growth rates lower (Jenkins *et al*. 1991; Bystrom and Garcia-Berthou 1999).

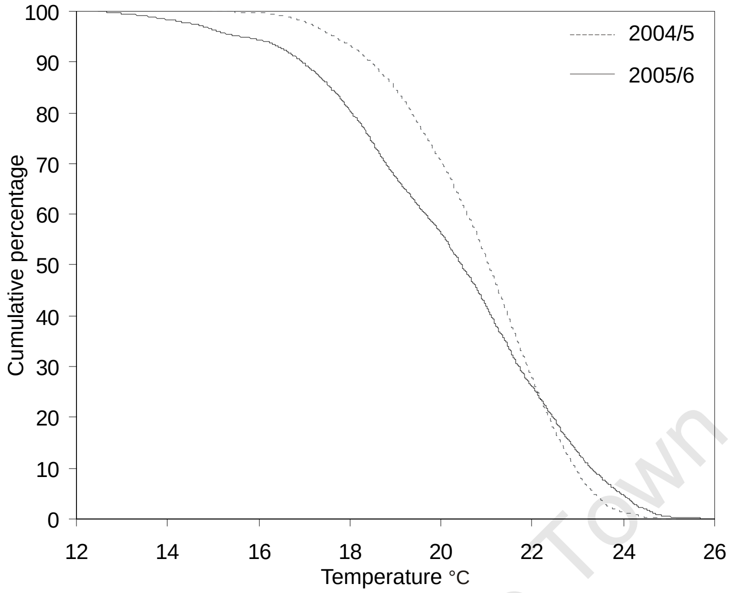

Figure 7.6 Temperature duration curves for the growth period: 2004/5 growth period (01/11/2004—21/03/2005, broken line) and the 2005/6 growth period (01/11/2005—21/03/2006, solid line).

7.4.1 Summary and conclusion

The results from the present study suggest that counts of daily growth increments in otoliths can be used to age sawfin larvae and juveniles up to an age of approximately five months. Validation of increment formation suggested that this occurred on a daily basis and accuracy was age-dependent. Onset of increment formation appeared to occur around hatching (2-3 days post-fertilisation). It is suggested that two separate relationships be used to estimate spawning dates because counts of otoliths in older fish underestimated age due to reader error. In the following chapter this information is used to estimate the spawning timing, duration and frequency of spawning by sawfin in the Driehoeks River in order to characterise the temperature and flow conditions that may promote recruitment and cues that may trigger spawning.

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CHAPTER 8 The effects of flow and temperature on spawning and recruitment of sawfin in the Driehoeks River

8.1 INTRODUCTION

River flow has been found havev a major influence of year-class strength in fish populations (Freeman *et al*. 2001; Marchetti and Moyle 2001; Propst and Gido 2004; Bonvechio and Allen 2005). Fish time the release of their eggs into the environment to coincide with the availability of suitable temperatures, habitats, and food sources that promote the growth and development of their progeny (Wootton 1990; Bye 1984; Cushing 1990; Jobling 1995). To ensure synchronisation with these conditions, fish have evolved physiological responses to a range of environmental cues (*zeitgebers*), which are regulated via the pituitary gland and secretion of the hormone Gonadotropin (Horváth 1985). These cues entrain or induce both gonadal recrudescence as well as the later stages of gametogenesis, i.e. maturation, ovulation and oviposition (Lam 1983). Temperature and photoperiod have been recognised as being the most important primary or 'proximate' cues for the early stages of gametogenesis (Lam 1983; Bromage *et al*. 2001; Bromage and Davies 2002). Once maturation is near completion, the eggs are kept in a state of readiness awaiting secondary or 'ultimate' cues that will induce ovulation and spawning. It is with these 'ultimate' cues that this chapter concerns itself, of which photoperiod (Bromage *et al*. 2001), temperature (Hilder and Pankhurst 2003) and fluctuating water levels in rivers (Nesler *et al*. 1998; Cambray *et al*. 1997; Durham and Wilde 2006), either individually or in combination are considered to be among the more important. In addition to these, however, a number of other factors may play a role in cueing the release of eggs into the environment including: social interactions (courtship behaviours and pheromones) (Stacey 1983), lunar phase (Middaugh 1981; Watanabe 2000), barometric pressure (Peterson 1972), energy status (food supply) (Wootton 1979) and the presence of a suitable substratum (e.g. gravel or vegetation) (Stacey 1984). Should any of these conditions not be met, fishes may in some cases resorb or retain their eggs and postpone spawning the next season (Rideout *et al*. 2005).

In freshwater environments (lakes and rivers), water level fluctuations and flow have been identified as important secondary cues for many fish species. Positive correlations have been found between river flow and gonad maturation (Merron *et al.* 1993), fish catches (Christensen 1993) and year-class strength (Ponton and Vauchel 1998). Junk *et al.* (1989) formulated the Flood Pulse Concept (FPC), proposing that pulses of high flow and optimal temperatures combine to increase primary productivity in floodplain habitats and that river fish have evolved to synchronise their reproduction with this period of increased productivity. Sparks *et al.* (1990) proposed that if floods fail or waters recede too rapidly after the high flow season, optimal flows and temperatures become 'decoupled', nursery habitats are lost and recruitment fails.

Much of the evidence in support of the FPC comes from rivers with extensive floodplains and where flooding is predictable – particularly tropical and sub-tropical rivers (Welcomme 1985) – but there are also indications that flooding plays a role in inducing spawning by fish in temperate rivers without extensive floodplains. Nesler *et al*. (1988) related spawning intensity to larval drift by Colorado pikeminnow (*Ptychocheilis lucius*) and showed that floods provided cues for spawning. Brouder (2001) showed that the catch per unit effort

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(*cpue*) of roundtail chub *Gila robusta* in the Verde River, Arizona increased significantly in years following late winter/early spring floods.

More recent views have suggested that the FPC is too simplistic to encompass all spawning strategies (King *et al*. 2003). Humphries *et al*. (1999) proposed the Low Flow Recruitment hypothesis (LFR), which suggests that recruitment is promoted by low-flow conditions in the main channel rather than flood pulses. The LFR proposes that, over the low-flow period, smaller volumes of water in the main channel increase the availability of littoral areas, backwaters and embayments. Increased water-retention times and higher productivity levels in these shallow habitats promote the production, and concentrate the densities, of larval fish prey items such as zooplankton. Higher temperatures from solar heating in these habitats also increase metabolic rates and enhance fish growth and survival (Bestgen 1996). Support for the LFR is provided by researchers who have noted that flooding can in fact have a negative impact on recruitment by disrupting these shallow nearshore habitats and washing larvae and young fish into areas where they may be exposed to higher levels of predation and lower food concentrations (Harvey 1987; Scheidegger and Bain 1995).

Both the FPC and LFR hypotheses underscore that the effect of hydrological variability on fish populations depends on the type of system and the species concerned (Bonvechio and Allen 2005; Zeug and Winemiller 2007). In tropical systems where annual photoperiod and temperatures cycles are less pronounced, flooding is likely to play a greater role in inducing spawning (Lam 1983), whereas in temperate systems, flooding may play a subsidiary role to the more pronounced photoperiod and temperature regimes in these regions. In temperate systems, spawning cues may be associated with spring and summer floods synchronised with rising temperatures such as occur in the summer rainfall areas of South Africa (Jackson 1982; Allanson and Jackson 1983), or with the end of winter floods such as occurs in the Western Cape and in parts of Murray-Darling Basin in Australia (King *et al*. 2003). King *et al*. (2003) suggested that in more variable systems where flooding is less predictable (such as may be found in parts of Australia and South Africa), floods are likely to play less of a role in cueing reproduction than in more predictable systems, and reproductive strategies therefore are likely to be more opportunistic and flexible. Evidence that physiological responses to environmental cues may be fairly flexible comes from carp (*Cyprinus carpio*), which are stimulated to spawn by a rise in temperature in temperate zones, whereas in the tropics, hydrological changes are responsible (Bardarch *et al*. 1972 cited in Horváth 1985).

Approaches to studying reproductive responses to flow among fish populations have been varied. Flood regimes and a range of hydrological indices have been related to year-class strength (Bonvechio and Allen 2005), *cpue* (Brouder 2001) and the functional organisation of fish communities (Poff and Allan 1995). Estimation of spawning or hatch-date frequencies from daily age data (Campana and Neilsen 1985) has also proved to be a useful method for investigating the effect of environmental variability on the timing, frequency and duration of spawning by fish. Hatch-date analysis involves the collection of a random fish sample from a population collected on a known date and the application of an age model to determine the frequency distribution of hatch dates (Campana and Jones 1992). The hatch-date distribution can then be assessed in terms of environmental variables to investigate which, if any, correlate with spawning frequency and recruitment levels. Although this technique has been applied to freshwater fish elsewhere in the world (e.g. Graham and Orth 1986; Humphries 2005; Koehn and Harrington 2006) and on marine fish in South Africa

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(Wilhelm *et al*. 2005), it has thus far not been applied in South Africa for studying spawning by freshwater fish species.

Circumstantial evidence suggests that flow provides a stimulus for spawning by native freshwater fish species in South African rivers, particularly those living in the summer rainfall region, including largemouth yellowfish (*Labeobarbus kimberleyensis*), smallmouth yellowfish (*L. aeneus*) (Allanson and Jackson 1983) and the moggel (*Labeo umbratus*) (Jackson 1982). In the winter rainfall region of the Western Cape, however, spawning period commences at the tail end of the high-flow season when temperatures are increasing and flows receding. This suggests that the LFR developed by Humphries *et al*. (1999) may be a more appropriate model for fish spawning in Western Cape rivers.

Sawfin deposit adhesive demersal eggs in moderate- to high-velocity riffle areas where they are incubated over a period of two to three days after which the larvae hatch out (Chapter 5 and Chapter 7, this document). The larvae remain photophobic for another 10-11 days before swim-up when they are dispersed into shallow nearshore nursery habitats in the main channel and begin feeding (Chapter 7 this document). Prior to this study, little information existed on the timing of spawning by sawfin. Van Rensburg (1966) showed that the gonado-somatic index (GSI) of sawfin sampled from the Olifants River began increasing in July before reaching a peak in October and then declining between November and January. The primary objectives of this component of the study was (1) to investigate spawning and recruitment patterns of sawfin in the Driehoeks River and (2) to investigate how these are influenced by environmental conditions in the river, particularly flow and water temperature. This was achieved by back-calculating spawning dates using the age-length models developed in Chapter 7 of random samples of fish collected from the Driehoeks River towards the end of the low-flow season in two consecutive years. Since Clanwilliam yellowfish did not spawn over the study period, it was not possible to include them in the study.

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8.2 METHODS

8.2.1 Collection of larval and juvenile sawfin

Key priorities of the sampling regime were to ensure that the entire year's cohort and all age-classes were represented in the samples and to ensure that the sample reflected the proportions of individuals in each age-class in the population. Sampling took place in the Driehoeks River over two consecutive reproductive seasons (2004/5 and 2005/6) at five sites: Lower Tafelberg, Sneeuberg, Driehoeks Cascade, Rietgat and Maalgat (Figure 3.4; Chapter 3). These were the only sites along the 6 km study segment where larval and juvenile sawfin were encountered throughout the study period (Chapter 4). Monthly and replicate sampling of larval and juvenile sawfin in the Driehoeks River was therefore not considered feasible because of their highly clumped distribution and the fact that their abundances at each site were relatively low (Chatper 4). A more intensive sampling regime may therefore have entailed a higher mortality rate than was considered acceptable for an endangered species and would also have contributed significantly to annual mortality rates that would have affected the outcome of the study. Only two samples were collected of the year's cohort - one early in the season (December – Sample A) and one at the end of the low-flow season (February/March – Sample B) in each season (2004/5 and 2005/6). Sample A was collected from downstream of the two main spawning sites: Lower Tafelberg and Sneeuberg (Figure 3.4; Chapter 3) in early and mid-December 2004 and 2005 respectively using a combination of hand netting (one ½ hour interval in each year at each site), quatrefoil light traps (two traps set over three nights at each site); and drift nets (two nets set over three nights at each site) (Table 8.1). Van Rensburg's (1966) monthly estimation of sawfin gonadosomatic indices suggested that spawning ended in January. Thus to ensure that the sampled population of 0^+ fish included individuals from the latest potential spawning, Sample B was collected in late February 2005 and March 2006. These juvenile 0^+ sawfin were collected from shallow water (< 0.5 m depth) by means of a 5 m seine net with a 6 mm mesh from three sites: Driehoeks Cascade, Rietgat and Maalgat (Figure 3.4; Chapter 3). In both years, two hauls with the seine net where schools were observed was considered sufficient to obtain a sample that was representative of all age-classes (Table 8.1). The total lengths of live fish were measured to the nearest 0.5 mm on a measuring board and returned to the river. A proportion of each sample was set aside for age determination (Chapter 7).

TABLE 8.1 Dates, gear types, effort and sites of sampling for larval (A) and juvenile (B) sawfin in the Driehoeks River between December 2004 and March 2006 (Refer to Figure 3.4 for map of sites).

Years	Sample ID.	Collection dates	Gear/effort	Sites
2004/5	A	3-6 Dec 2004	Hand net (½ hr) Light trap (2 × 3 nights) Drift nets (2 × 3 nights)	Lower Tafelberg Sneeuberg
	B	23-26 Feb 2005	Seine net (2 × 5 m)	Driehoeks Cascade Rietgat Maalgat
2005/6	A	10-13 Dec 2005	Hand net (½ hr) Light trap (2 × 3 nights) Drift nets (2 × 3 nights)	Lower Tafelberg Sneeuberg
	B	24-26 Mar 2006	Seine net (2 × 5 m)	Driehoeks Cascade Rietgat Maalgat

8.2.2 Environmental variables

Continuous records of temperature and river stage were obtained for the reproductive season between August 2004 and March 2006. Temperatures were monitored by means of two thermistor temperature sensors coupled to data loggers (HOBO® Water Temp Pro) accurate to ± 0.2°C at 25°C. Water surface elevations on the Driehoeks River were monitored continuously by means of a piezoresistive pressure sensor coupled to a data logger (STS® data logger DL/N 641) installed at the Driehoeks Cascade Site (Figure 3.4; Chapter 3). The STS® data logger measures depth (river height above a datum) in metres (m). The sampling rate was set at 30 min intervals. A discharge rating curve was developed from a site downstream of the data logger (Lower Tafelberg). The curve was not accurate at discharges > 5 $m^3 s^{-1}$ since flows over this value were not rated. Where flows are reported that exceed this value, therefore, river stage (water level above a datum) is used. Over the reproductive season, however, this value was not exceeded and flow is reported in cubic metres per second ($m^3 s^{-1}$).

8.2.3 Age estimation and back-calculation of spawning times

Linear models were fitted to the age-length data obtained from counts of daily increments deposited on the otoliths of larval and juvenile sawfin (Chapter 7). Back-calculation of spawning dates using these age-length models was applied to the random sample of larval and juvenile fish collected from the Driehoeks River

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between December 2004 and March 2006 (Section 8.2.1). The length-frequency distributions obtained from the samples were transformed to age-frequency distributions using inverse regression (Bolz and Lough 1988). Although this method ignores the variability in size-at-age and is therefore not the preferred means of back-calculation (Francis 1990; Campana and Jones 1992), there were insufficient fish sampled per age-class to use an age-length key. A separate age-length model was derived for each year-class due to differences in growth rates between the two years (Equations 1 and 2; Chapter 7) and these were fitted to the corresponding length-frequencies derived from fish collected in that year. Estimated spawning times could then be derived by back-calculating from larval ages. An additional two days were added to account for the two days prior to hatching before the first increment was laid down (Chapter 7) and thus the frequencies represent estimated spawning dates rather than hatch dates. Constant mortality was assumed and therefore the proportion of fish in each age class was assumed to represent the number of fish spawned (spawning frequency) on any particular date.

8.3 RESULTS

8.3.1 Temperature and flow

Temperatures in the Driehoeks River over the study period varied between a minimum of 5.7 °C in winter (Jun-Aug) to a maximum of 26.0 °C in summer (Dec-Feb) (Figure 8.1; APPENDIX F.1). Daily variations in minimum and maximum temperatures in the river ranged between 0.3 and 4.5 °C ($\bar{x}$ = 2.25 °C), with the highest daily variations occurring in autumn (April 2005: SD 2.17; April 2006 SD 2.12) and spring (Nov 2004: SD 1.56; Nov 2005: SD 2.53). The high-flow period extended from June to September with the last minor winter floods occurring towards the end of October/beginning of November in both years (Figure 8.1). Highest mean monthly flows occurred in the winter months: June – August 2005 and May – July 2006, i.e. the months corresponding to the lowest temperatures (APPENDIX F.2). Maximum discharges were not calculated for river stages exceeding 0.6 m (5.0 $m^3 s^{-1}$) since the discharge rating curve (APPENDIX F.3) could not be calibrated for flows higher than this. The low-flow period extended from November to May with the minimum flows occurring between February and April (< 0.01 $m^3 s^{-1}$). The discharge at which the Driehoeks River overtopped the active channel (identified as the maximum break in slope of the cross-sections of the sites modelled in Chapter 6) corresponded to a stage height of ~0.48 m (2.45 $m^3 s^{-1}$) or 20 % of the maximum recorded flood stage (2.6 m). Flows of this magnitude were exceeded for 3 % of the time between August 2004 – July 2005 and for 6.7 % of the time between August 2005 and July 2006 (APPENDIX F.4). The median discharge (Q_{50}) for the total period on record was 0.2 $m^3 s^{-1}$ (roughly half the discharge that overtopped the banks). The period 1 September to 31 January of both years is delimited as the 'spawning seasons' (Figure 8.1). Median discharges (Q_{50}) were lower over the 2004/5 spawning season (0.11 $m^3 s^{-1}$) than they were over the 2005/6 spawning season (0.28 $m^3 s^{-1}$). The discharge that overtopped the banks was exceeded 2.5 % of the time during September 2005, whereas they were never exceeded during the 2004/5 spawning season (Figure 8.2). A two-sample *t*-test showed that mean temperatures were significantly lower and discharges significantly higher during the 2005/6 spawning season than they were over the 2004/5 spawning season (Table 8.2).

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TABLE 8.2 Results of a two-sample t-test of differences in mean temperature ($T\bar{x}$) and mean discharge ($Q\bar{x}$) measured at half-hour intervals in the Driehoeks River over the reproductive season of both years (1 Sep – 31 Jan 2004/5 and 2005/6). * significant at p = 0.05.

			t-test	
	2004/5	2005/6	*t*	df
$T\bar{x}$ (°C)	18.2	17.6	8.3*	14686
$Q\bar{x}$ ($m^3 s^{-1}$)	0.17	0.43	-45.7*	14686

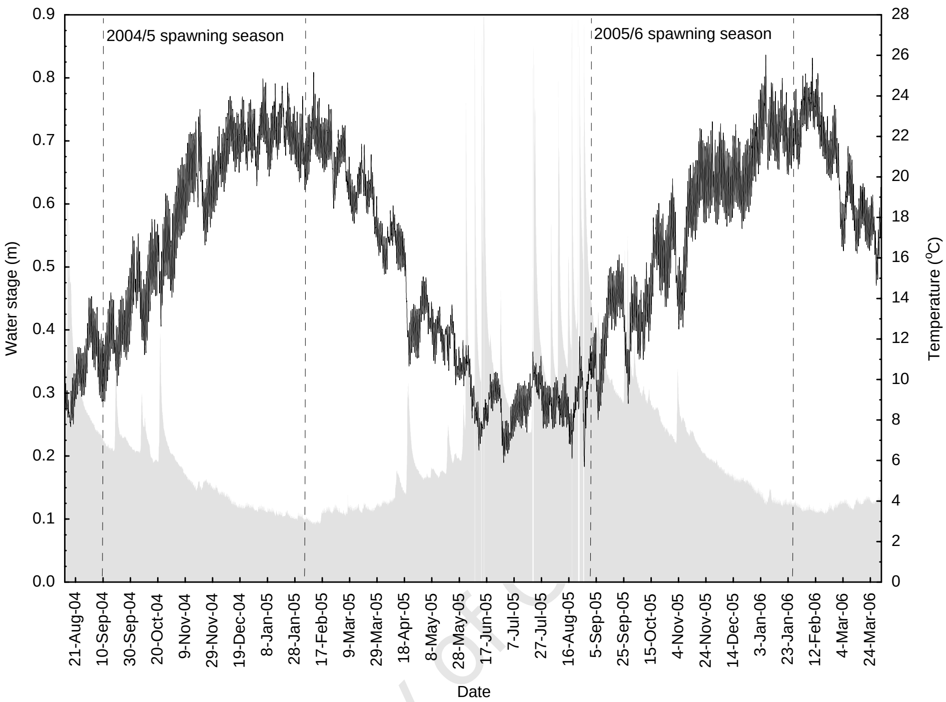

Figure 8.1 Temperature, river stage and spawning seasons for sawfin between 12 August 2004 and 31 March 2006 at three sites on the Driehoeks River. Water stage is depicted by the shaded grey area and temperature by the dark grey line. Flow is reported in river stage rather than discharge since the rating curve was only accurate to discharges < 5 $m^3 s^{-1}$.

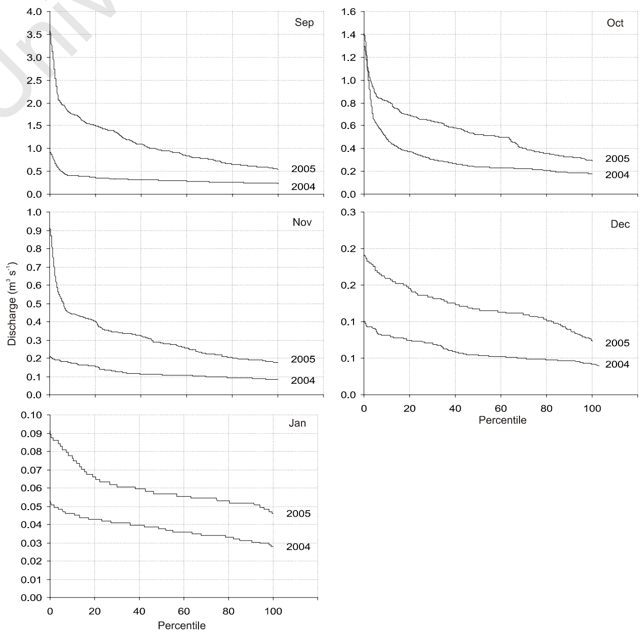

Figure 8.2 Comparison of monthly Flow Duration Curves for the 2004 and 2005 spawning seasons (Sep – Jan).

8.3.2 Length frequency distributions

Much higher numbers of larvae were collected in Sample 2004/5-A from the Lower Tafelberg Site (151) than in than in the following year's sample (2005/6-A) (29), whereas comparable numbers were caught at the Sneeuberg Site over the two seasons (8 and 12 respectively) (Figure 8.3 a(i) and b(i); APPENDIX F.5).

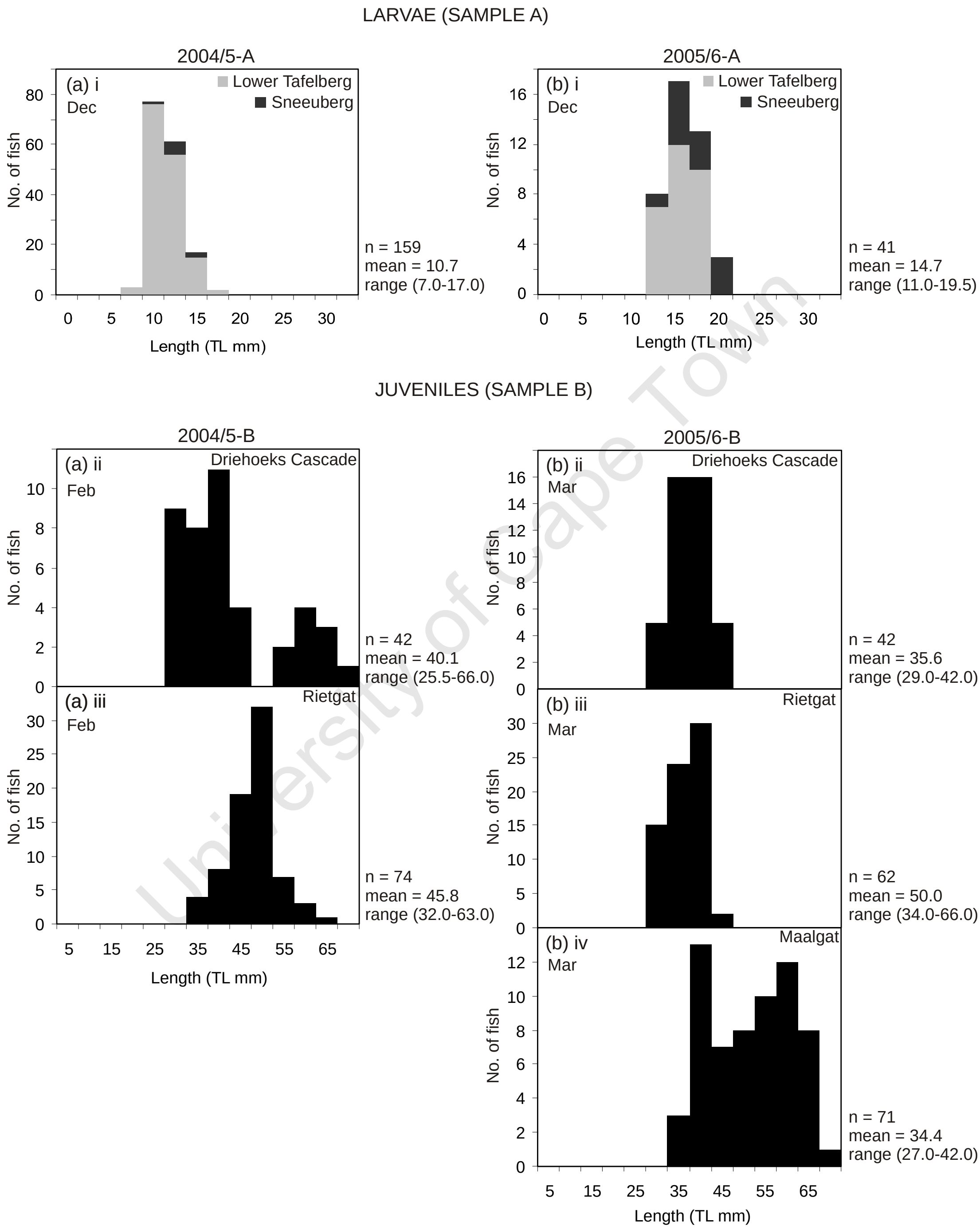

Figure 8.3 Stacked histograms showing the length frequency distributions of larval and juvenile sawfin collected from the Driehoeks River during the (a) 2004/5 season: December (A) and February (B) and (b) 2005/6 season: December (A) and March (B). Five sites on the Driehoeks River were sampled: (i) Lower Tafelberg and Sneeuberg, (ii) Driehoeks Cascade, (iii) Rietgat and (iv) Maalgat.

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In Chapter 4 it was pointed out that there were fewer larvae present in the water during 2005 and none of these were caught in the light traps as had happened in the previous year (2004). Due to differences in gear selectivity therefore (hand nets *vs* light traps), larval abundances are not comparable between years. The sizes of the larvae in the 2004/5 season ranged between 7 – 17 mm TL ($\bar{x}$=10.7 mm TL; n = 159) (APPENDIX F.6). Using equation (1) (Section 7.3.3) this translates to 3 – 30 days post-spawning.

Larvae collected in the 2005/6 season (A) were slightly larger, and ranged between 11 – 19.5 mm TL (16 – 36 days post-spawning) (Equation 2, Section 7.3.3). In the later sample (B) of both years, a total of 291 juveniles was collected from three sites on the Driehoeks River (Driehoeks Cascade, Rietgat and Maalgat) in February 2005 (Sample 2004/5-B) (116) and March 2006 (Sample 2005/6-B) (175). In the 2004/5-B sample, 42 juvenile sawfin ranging in size from 25.0 to 66.0 mm TL and representing two separate cohorts (25 – 45 and 55 – 66 mm TL respectively) were collected from Driehoeks Cascade site (Figure 8.3 a(ii)). This translates to post-spawning ages of 51 – 162 days. In March 2006 (Sample 2005/6-B), the same number of fish in a smaller size range: 29 – 42 mm TL (54 – 84 days post-spawning) representing a single cohort was collected from the Driehoeks Cascade site (Figure 8.3 b(ii)). In February 2005 (Sample 2004/5-A), 74 fish were sampled at Rietgat ($\bar{x}$=45.8 mm TL; 106 days) whereas 62 were collected from this site in 2006 (Sample 2005/6-A) ($\bar{x}$=50.0 mm TL; 102 days). Juvenile sawfin were sampled from the most downstream reaches of the study segment at Maalgat in 2006. This group were slightly larger ($\bar{x}$=34.4 mm TL; 66 days) than the fish caught at the two upstream sites.

8.3.3 Recruitment distributions

In Figure 8.4 the recruitment distributions produced from the December larval samples (2004/5-A and 2005/6-A) are distinguished from the distributions produced from the February and March samples of juvenile sawfin (2004/5-B and 2005/6-B). Since these two sample sets were collected using different gear, they are not comparable and are therefore considered separately. The juvenile fish collected in March (B) better represent the full year's cohort since they were sampled later in the year and they were much easier to locate and sample than the larval fish. Features such as the commencement and termination of spawning and responses to weekly environmental variability have therefore been based on these sample sets. Because of greater accuracy in aging the younger larvae, however, (Chapter 7) the earlier larval samples (A) were found to be more useful for examining daily responses to environmental variability.

The distribution produced from 2004/5-B suggests a much earlier commencement to spawning than is suggested by 2004/5-A, whereas in 2005 the commencement dates suggested by the two sample-sets are roughly equivalent – 2005/6-A suggests a slightly later start to spawning in this year (+4 days). Thus the distributions produced from the juvenile samples (B) in both years suggests that sawfin began spawning 53 days earlier in 2004 and ended 30 days earlier (12 Sep 2004 – 1 Jan 2005) than they did in 2005 (2 Nov 2005 – 31 Jan 2006) (Figure 8.4 (a) and (b)). In each season, the fish were spawned over a period lasting roughly 100 days (111 and 91 in 2004/5 and 2005/6 respectively) between the 1 September and 31 January. Spawning appeared to continue throughout the season, but recruitment peaked over certain periods (Figure 8.4). That these peaks are related to spawning activity is supported by observations in the field which suggested that sawfin were present on the spawning beds daily, but that larger numbers of fish and more spawning activity (release of eggs into the water by females) was evident on only some of these days.

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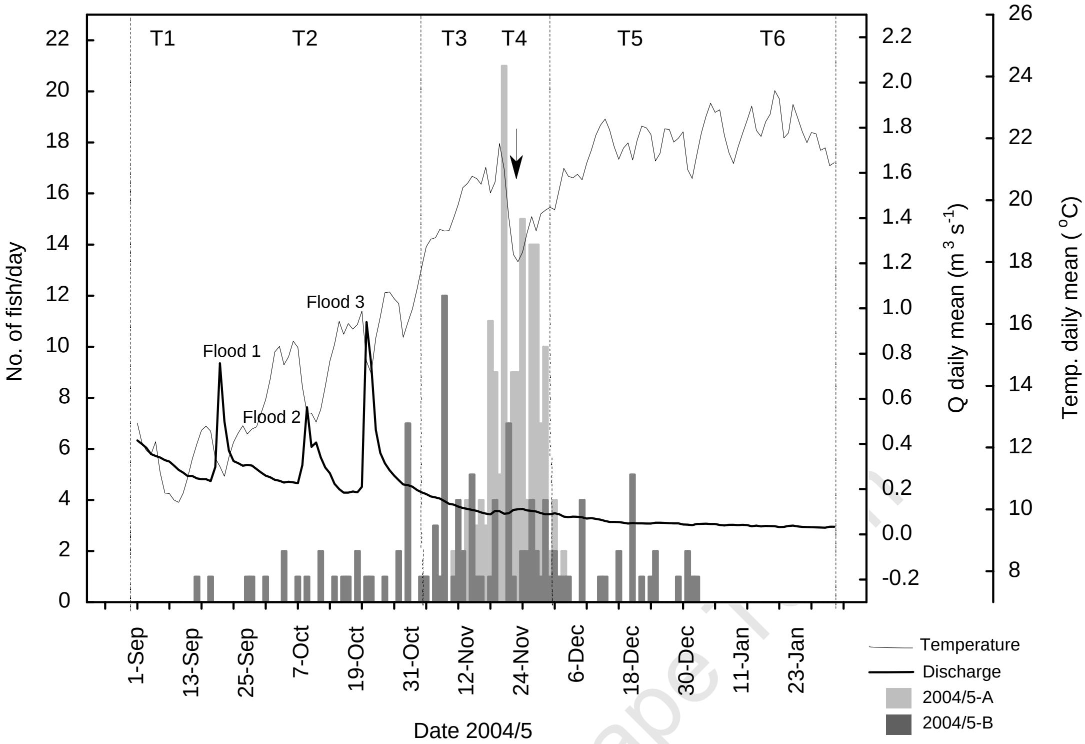
(a)



(b)

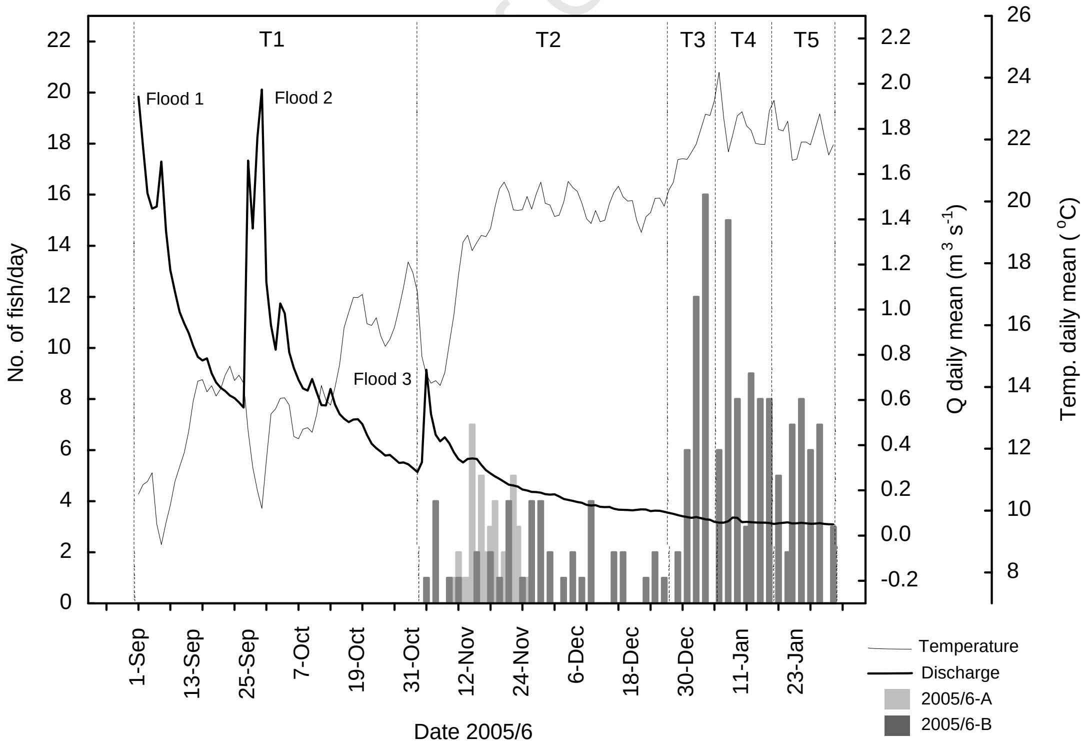


Figure 8.4 The number of sawfin collected per spawning-date in (a) 2004/5 and (b) 2005/6. Light grey bars = larval sawfin collected in December (2004/5-A and 2005/6 A); dark grey bars represent juvenile sawfin collected in February and March (2004/5-B and 2005/6-B). Number of individuals is represented on the primary *y*-axis. Daily mean temperature (°C) (fine line), and daily mean discharge ($m^3\ s^{-1}$) (bold line) for the periods 1 September – 31 January 2004/5 and 2005/6 are represented on the secondary *y*-axes. T1-T6 = time periods outlined in Table 8.3. The arrow in Figure (a) indicates the interruption in the continuity of spawning referred to in Section 8.3.3.

TABLE 8.3 The 2004/5 and 2005/6 spawning seasons divided into time intervals (T1-T6) based on 25% increments of the number of juvenile sawfin collected per spawning-date (from the B sample-set), as well as pre-spawning and post-spawning periods. Statistics have been derived from temperature and flows recorded at 30 min intervals over each time period. The table shows the mean (T $\bar{x}$ ±SD; °C), minimum (T_{min}) and maximum (T_{max}) temperatures for the time interval (T) and the mean daily rate of change in temperature (dT $\bar{x}$; °C day^{-1}) (the difference between temperatures recorded at 10h00 on each successive day), as well as the mean (Q $\bar{x}$ ±SD; m^3 s^{-1}), maximum (Qmax) and the minimum (Qmin) discharge for each time interval (T). Shaded cells show highest mean daily rates of change in temperature.

2004/5											
Time interval					**Temperature (°C)**			**Rate of change (°C day^{-1})**	**Discharge (m^3 s^{-1})**		
	Start	**End**	**No. of fish 25 % incr.**	**Days**	**T $\bar{x}$ ±SD**	**T*max***	**T*min***	**dT $\bar{x}$**	**Q $\bar{x}$ ±SD**	**Q*max***	**Q*min***
T1	1 Sep	11 Sep	0%	12	11.3 ±1.3	14.1	8.9	-0.30	0.33 ±0.05	0.43	0.25
T2	12 Sep	2 Nov	25%	50	14.4 ±2.1	19.6	9.7	0.14	0.31 ±0.16	1.40	0.18
T3	3 Nov	13 Nov	50%	11	19.5 ±1.4	22.2	16.5	0.29	0.14 ±0.02	0.18	0.10
T4	14 Nov	29 Nov	75%	16	19.8 ±1.5	23.3	16.6	-0.07	0.10 ±0.01	0.12	0.08
T5	30 Nov	1 Jan	100%	33	21.5 ±1.1	24.0	18.3	0.07	0.06 ±0.02	0.10	0.04
T6	2 Jan	31 Jan	0%	33	22.3 ±1.0	24.8	19.7	-0.02	0.04 ±0.01	0.05	0.03
				T1:T6	**18.1**	**24.8**	**8.9**	**0.05**	**0.17**	**1.40**	**0.03**

2005/6											
Time interval					**Temperature (°C)**			**Rate of change (°C day^{-1})**	**Discharge (m^3 s^{-1})**		
	Start	**End**	**No. of fish 25 % incr.**	**Days**	**T $\bar{x}$ ±SD**	**T*max***	**T*min***	**dT $\bar{x}$**	**Q $\bar{x}$ ±SD**	**Q*max***	**Q*min***
T1	1 Sep	2 Nov	0%	63	13.7 ±2.4	19.9	8.0	0.08	0.56 ±0.48	3.57	0.27
T2	3 Nov	25 Dec	25%	52	19.0 ±2.2	22.7	12.5	0.07	0.21 ±0.13	0.91	0.10
T3	26 Dec	6 Jan	50%	11	22.0 ±1.5	26.0	18.6	0.32	0.08 ±0.01	0.11	0.05
T4	7 Jan	15 Jan	75%	9	22.3 ±1.1	24.7	20.4	-0.28	0.06 ±0.01	0.09	0.05
T5	16 Jan	31 Jan	100%	16	22.1 ±1.0	24.9	20.1	0.01	0.05 ±0.00	0.07	0.05
				T1:T5	**17.6**	**26.0**	**8.0**	**0.07**	**0.33**	**3.57**	**0.05**

The shape of the distributions suggests continuous spawning, but this is probably a consequence of variability in the data set resulting either from counting errors (Chapter 7), from natural variability in age-at-length and/or the use of inverse regression in calculating ages rather than age-length keys.

The 2004/5 and 2005/6 seasons have been divided into a number of time intervals based on a delineation of pre-spawning and post-spawning periods as well as on 25% increments of the total number of sawfin collected per spawning-date of the juvenile samples (B) only. Based on these criteria therefore, the spawning seasons can be divided into six (2004/5) and five (2005/6) time intervals respectively (Table 8.3; Figure 8.4). Spawning commenced at the end of the high-flow season in both years on the recession limbs of the last winter floods (Floods 1-3 in 2004 and 2005, Figure 8.4). In 2004 the mean daily temperature on the days spawning commenced was 12.1 °C and the mean daily discharge was 0.2 m^3 s^{-1}.

In 2005 the mean daily temperature at the commencement of spawning was 14.4 °C and the discharge was 0.3 m^3 s^{-1}. Both the former discharge values closely approximate the Q_{50} discharge for the Driehoeks River over the study period (0.2 m^3 s^{-1}). The later start to spawning in 2005 (T1, Figure 8.4 (a)) was associated with higher daily mean discharges (daily $\bar{x}$=0.56 m^3 s^{-1}) and larger floods during the pre-spawning period (T1) (Table 8.3). There were three floods over the early part of the spawning season in 2004 (T1-T2) and 2005 (T1). In 2004, however, the instantaneous peak magnitudes of the floods were low – ranging between 0.9 (Flood 2) and 1.4 m^3 s^{-1} (Flood 3) – whereas in 2005 instantaneous peak magnitudes were higher – ranging between 0.9 (Flood 3) and 3.6 m^3 s^{-1} (Flood 2) – and their flood periods were longer. As a consequence, daily mean discharges between 1 September and 31 October were considerably lower in 2004 (T1: daily $\bar{x}$= 0.33

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±0.05 m^3 s^{-1}; T2: daily $\bar{x}$ = 0.31 ±0.16 m^3 s^{-1}) than they were in 2005 (T1: daily $\bar{x}$ = 0.56 ±0.48 m^3 s^{-1}).

Despite the earlier start to spawning in 2004 (12 September), the number of juvenile sawfin sampled per spawning-date (2004/5-B) suggested that spawning continued at very low levels throughout this first time period (T2), or that recruitment levels remained low. Only 25 % of total number of fish sampled were spawned over this 50 day period (T2). Thereafter (T3-T4), both the 2004/5-A and -B samples show a peak in number of fish that survived or were spawned per day. The 2004/5-A distribution shows a sharp decrease in numbers of fish per day corresponding to a sudden drop in temperature between 20-23 November from 21.8 to 18.1 °C (the point marked by the arrow in Figure 8.4). Spawning began much later in 2005 (2 November) following the last winter flood (Flood 3) and this was accompanied by a sharp rise in temperature from 14 to 19 °C between 8-13 November. Fish production nevertheless remained at low levels throughout T2 with only 25% of the season's cohort produced over a period of 52 days (Table 8.3). Discharges were identical (0.05 m^3 s^{-1}) on the day spawning ceased in both years (1 January 2005 and 31 of January 2006) and temperatures were similar 21.4 and 21.8 °C respectively.

In both years, the greatest proportion of the year class (50%) recruits were spawned over a relatively brief 20-30 day period (T3-T4 in 2004/5 and 2005/6). The environmental conditions over the time intervals that preceded the highest peaks in larval production (T3 in both years) were characterised by continuously increasing temperatures over a period of ~7 days (Figure 8.4) together with the highest mean daily rates of change in temperature over the entire spawning season (increases of 0.29 and 0.32 °C day^{-1} in 2004/5 and 2005/6 respectively; shaded cells in Table 8.3). In all other instances, mean daily rates of change in temperature were positive but small (0.01 – 0.14 °C day^{-1}) or negative (-0.02 – -0.3 °C day^{-1}) (Table 8.3). Mean water temperatures over these peak spawning periods were 19.5 and 22 °C in 2004/5 and 2005/6 respectively. At time intervals T5 and T6 in 2004/5 and T2 in 2005/6, sawfin continued spawning, but at a low levels. These time intervals were characterised by water temperatures that fluctuated over cycles that lasted between 3 and 5 days (Figure 8.4), but there was no trend of increasing temperatures over these periods and mean daily rates of change were relatively low (Table 8.3).

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8.4 DISCUSSION

One of the principal disadvantages of using age-frequency distributions to estimate spawning dates is that larvae hatched earlier in the season will experience greater cumulative mortality and therefore be under-represented in the population compared to those hatched later (Campana and Jones 1992). Spawning date distributions therefore tend to be skewed towards younger fish and may not accurately represent the spawning/hatch-date of survivors in each age-class. Campana and Jones (1992) pointed out, however, that spawning date distributions will most closely represent initial production if the fish are relatively old at the time of collection and the mortality differential between young and old fish has stabilised. The samples used to interpret the duration, frequency and intensity of fish production in this study (B sample-sets) were collected towards the end of the low-flow season (February/March) and the minimum age of these fish was 51 days. It has been assumed, therefore, that mortality rates would have stabilised before the onset of the high-flow season (June) and that the population structure was a close enough approximation of initial production to reflect spawning intensity.

A second drawback of using age-frequency distribution to estimate spawning dates is the effect that variable mortality resulting from environmental or biotic perturbations has on the shape of the distribution (Campana and Jones 1992). The fact that the age structure of the 0^+ sawfin cohort collected at the end of the reproductive season represents egg production (spawning) date frequencies is therefore based on the premise that mortality rates were constant throughout this period. In this study, mortality rates would have been difficult to estimate, firstly because gear selectivity differs between age/size classes and relative abundance estimates are not comparable between the first (A) and second (B) sample-sets; and secondly, the shorter sampling intervals required for mortality estimates would have had potentially detrimental effects on the populations of this endangered species (abundances in the Driehoeks River were so low that repeated sampling would have significantly depleted populations).

Although it is believed unlikely that levels of predation and food availability varied enough to give rise to the polymodality observed in the spawning date distributions, the effect of high flows and temperatures on the survival of embryos and larvae cannot be ruled out. The low recruitment towards the beginning of the 2004 reproductive season, for instance, may reflect the combined influence of low temperatures as well as reduced availability of littoral habitat on larval survival rather than reduced egg production. Assumptions regarding the effect of environmental variables on spawning (particularly their role as 'cues') should be made bearing these limitations in mind. Nevertheless, the assumption that the distributions reflect, to some degree, spawning frequencies rather than variable mortality rates is borne out by observations in the field that spawning was not continuous throughout the season. The low recruitment periods suggested by the spawning date distributions corresponded to observations in the field which indicated there were no fish on the spawning beds at the time (*pers. obs.*).

The effect of environmental variability (either natural or anthropogenic) on reproduction is complex and can impact on all stages of reproduction from recrudescence to oviposition. Humphries and Lake (2000) have suggested that temperature or flow changes that result from river regulation can affect fish populations either through (i) *reproductive effects*, by changing conditions for gonad maturation, migration, pre-spawning interactions, or spawning; or (ii) *recruitment effects*: by decoupling the appearance of eggs and larvae in the river from conditions that promote their growth and survival (e.g. flushing larvae from, or reducing the availability of nursery habitats, egg desiccation and thermal stress). As a result of uncertainties around differential and cumulative mortality and the effect of environmental variability, it was not possible in this study to determine unequivocally whether the polymodality evident in the spawning-date distributions was the result of reproductive (spawning intensity) or recruitment (egg and larval mortality) effects. Nevertheless, a number of premises regarding the conditions that promote recruitment in the Driehoeks River can be suggested.

Sawfin have a relatively protracted but discrete reproductive season extending over approximately 100 days. Despite the fact that spawning commenced 50 days later in 2005 than 2004, the length of the reproductive season in both years was similar – with spawning over the 2005/6 season ending later. As relatively long-lived fish with a predictable breeding season synchronised with favourable environmental conditions, sawfin fit the 'periodic strategist' model outlined by Winemiller (2005). It is likely that single sawfin females are able to spawn more than once in each season. Horváth (1985) suggests that partitioning spawning into several sub-spawnings and distributing these across different time intervals reduces egg mortality by reducing the risk

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of predation and infection by the *Saprolegnia* fungus. Fungal infection was noted to have caused mortality of large numbers of sawfin eggs in the Driehoeks River, especially where these were deposited in high densities. Egg cannibalism by adult sawfin as well as predation by Clanwilliam yellowfish and introduced largemouth bass juveniles was also noted.

There was no evidence that flood events (spring freshets) cued spawning as has been hypothesised for Clanwilliam yellowfish (Cambray *et al*. 1997; King *et al*. 1998). To the contrary, flows exceeding > 0.5 $m^3 s^{-1}$ in the Driehoeks River appeared to suppress spawning and/or reduce survival of larvae during the early part of the season. Only once flows reached 0.2-0.3 $m^3 s^{-1}$ did spawning commence. This conflicts with findings in Chapter 6 (Section 6.3.4) where hydraulic modelling predicted increased spawning habitat with increasing discharge. The Driehoeks River, together with other rivers in the Western Cape represent a situation in which the highest flows and floods do not coincide with the highest temperatures. Sawfin therefore commence spawning at the end of the high-flow season – in both years on the recession limbs of the very last flood of the season. Evidence for the spawning on receding flows has been reported for several fish species including: smallmouth bass (*Micropterus dolomieu*) (Graham and Orth 1986) and Murray cod (*Maccullochella peelii*) (Humphries 2005). Thus the findings of this study support the LFR proposed by Humphries *et al*. (1999) who contended that recruitment is promoted by low flow conditions in the main channel rather than flood pulses. The discrepancy in the onset of spawning between the two years does, however, suggest that although flow may not ‘cue’ spawning, high flows certainly play a role in delaying spawning and/or reducing recruitment. Later during the season, flows between 0.1-0.3 $m^3 s^{-1}$ on the falling limbs of the flood hydrograph provide sufficient circulation through riffle beds to incubate eggs, while at the same time supporting sufficient slackwater habitats that are critical for the growth and development of larvae. Flows exceeding the values reported here are likely to displace larvae into less favourable habitats and reduce the productivity of shallow water environments.

Mean temperatures ranging between 18-20 °C have been reported as a requirement for spawning for several of the large barbine cyprinids in South Africa including the smallmouth yellowfish (Le Roux 1968), largemouth yellowfish (Tómasson *et al*. 1984) and the Clanwilliam yellowfish (King *et al*. 1998). The evidence presented in this study suggests that sawfin commence spawning at temperatures that are considerably lower than this (daily $\bar{x}$ 12-14 °C). The only other indication that native cyprinids spawn at lower temperatures is provided by Wright and Coke (1975) who reported spawning by the Kwazulu-Natal Yellowfish (*Labeobarbus natalensis*) in the relatively cold water of a trout hatchery (minimum temperature 15.5 °C). It should be noted that at a mean altitude of 860 *amsl*, temperatures in the Driehoeks River begin rising considerably later than in the remainder of the catchment. Simultaneous temperature monitoring in the mainstem Doring River 20 km east of the Driehoeks River showed that maximum temperatures here were 22 °C in September 2004 whereas they did not exceed 16 °C over the same period in the Driehoeks River. It is therefore conceivable that sawfin in the Driehoeks, responding to invariable cues such as photoperiod, spawn at lower temperatures than do their conspecifics elsewhere in the catchment. From spawning date distributions, however, it is evident that spawning at these lower temperatures did not contribute significantly to year class strength and that most spawning took place when temperatures were between 18 and 20 °C. The earlier start to spawning may also have been attributable to errors in back-calculation. As pointed out in Chapter 7, older fish were more difficult to age because there were more blemishes and increment widths were more compressed in otoliths belonging to older fish. Nevertheless, recounts of these older fish

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confirmed that these early spawning dates were correct. Further studies will be required to establish the validity of this finding.

Although spawning appeared to continue throughout the season, periods lasting 20-30 days could be identified in both years that contributed disproportionately high numbers of recruits to the two year classes. In all instances, these peaks were preceded and/or accompanied by at least seven days of continuously increasing temperatures. These periods were also characterised by the highest mean daily rate of change in temperatures. The periods between these peaks were characterised by stable or variable temperatures. During one of these periods (T2 2005), for instance, hardly any spawning aggregations were observed in the field. This is reflected in the distributions which suggest low recruitment throughout this period.

Temperature has been found to be an cue for reproduction in freshwater fish (Graham and Orth 1986, Pankhurst and Porter 2003) and the importance of rising water temperatures for gonad maturation has been reported by Stacey (1984). Stable to rising water levels and temperatures, together with calm weather over the spawning season were associated with strong year classes of northern pike (*Esox lucius*). Bromage and Davies (2002) suggested that while photoperiod had a primary influence Rainbow trout (*O. mykiss*) were able to delay the timing of final maturation and ovulation if water temperatures were unfavourable.

The peaks in numbers of fish spawned per day in the present study, however, could also be explained by increased survival due to favourable post-spawning conditions, i.e. stable flows and elevated and stable temperature conditions that would have promoted the growth and development of young fish. A far more intensive (weekly) sampling programme would have been required to determine whether peak recruitment periods were the result of increased spawning intensity or reduced mortality. As pointed out initially, however, the populations could not have withstood such an intensive sampling regime.

Previous studies on spawning by native South African freshwater fish (e.g. Tómasson *et al*. 1984) have relied on incidental records of temperatures in the river at the time of spawning and these are presumed to be 'thresholds', i.e. minimum temperatures below which spawning will not occur – although King *et al*. (1998) hypothesised that Clanwilliam yellowfish spawned when temperatures were 'stable or rising'. The implication is that spawning will continue as long as temperatures remain within a suitable range. The results from this study suggest that although threshold temperatures may be important as primary cues early in the season, once suitable temperatures have been reached, the rate and duration of temperature increase may provide secondary cues.

8.4.1 Summary and Conclusion

Sawfin fall into the 'periodic strategist' model outlined by Winemiller (2005), i.e. a relatively long lived fish with a predictable breeding season synchronised with favourable environmental conditions. This suggests that they would be sensitive to changes in the flow or temperature regime over the reproductive season. Thus irrigation releases timed during the early summer may disrupt spawning and reduce recruitment, particularly if these are associated with hypolimnetic water.

This study has shown that spawning by sawfin can and does take place across a broad range of flow and temperature conditions, but that the periods which contributed a disproportionate number of recruits to the

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year class were characterised by stable flows and continuously increasing temperatures over several days. Mean daily temperatures over these periods were ~19.5 °C. Although there are undoubtedly specific cues that stimulate the various stages of gonad development in sawfin (e.g. temperature and photoperiod), it is likely to be the interaction of a number of variables closer to the spawning season that provide the ultimate cues that trigger ovulation and oviposition. These cues are likely to be maximum threshold temperatures (>10 °C) and minimum threshold flows (<0.5 m^3 s^{-1} in the Driehoeks River). The co-occurrence of peak recruitment periods with periods of increasing temperatures suggests that additional cues such as the rate and duration of increase in temperatures may be as important as a threshold temperature. This is supported by the fact that recruitment was low despite temperatures being well above the hypothesised threshold. Long term data sets with multiple combinations of variables would be required to isolate more specific cues. In addition, estimates of mortality rates at each life stage together with more frequent sampling would be required to more confidently link population age structure to spawning frequency.

8.4.2 Note on sawfin spawning

Large schools of between 70-100 adult sawfin were observed in spawning aggregations in the Driehoeks River from early November to late December 2005 and 2006. These schools arrived at high velocity riffle and run habitats (Chapter 5) at roughly 10h00 in the morning and remained there for most of the day. They did not appear to be disturbed by the presence of divers and could be observed at close range without interference. An ovipositing female would lie prostrate against the river bed and release eggs into the interstices between substratum particles (cobbles or boulders). Several attendant males, jostling for position beside her, would release milt to fertilise the eggs. These spawning aggregations could be observed on most days through the spawning season. Although they were not always actively engaged in spawning, they could be seen holding position in the current over the spawning site for most of the day. Oviposition therefore did not always appear to be associated with these aggregations.

8.4.3 Note on spawning by Clanwilliam yellowfish

One of the more significant results to emerge from this study was the failure to observe Clanwilliam yellowfish spawning or collect their eggs, larvae or 0^+ juvenile fish in the two year study period. No spawning related behaviour was observed in 2004 during the course of dive surveys (Chapter 4), however, during November 2005, staging by schools of between 15 and 20 adult Clanwilliam yellowfish was observed on the same spawning beds that the sawfin used. No oviposition by females was observed and no eggs could be found, despite the fact that ripe-and-running females had been caught several days prior to the observed behaviour. This suggests either that Clanwilliam yellowfish failed to spawn at all, or that spawning events were so infrequent or late in the year that sampling failed to detect them. The timing of gonad development among Clanwilliam yellowfish parallels that of sawfin (van Rensburg 1966) and therefore there is no reason to believe they spawn later than sawfin. If they had spawned, then schools of young fish should have been present in the river by March. Evidence that Clanwilliam yellowfish population are not as successful as sawfin in the Driehoeks River is supported by the fact that populations of the former were 50% of the latter. Also, 75 % of the sampled Clanwilliam yellowfish population were over 250 mm TL (3-4 years old), i.e. the population was dominated by older juvenile and adult fish, suggesting several years of low recruitment.

Spawning omission has been reported for a number of fish species and although most of the evidence comes from marine species (e.g. Fedorov 1971; Rideout *et al.* 2000; Engelhard and Heino 2004), there have been

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several examples of spawning omission by freshwater species, e.g. white suckers (*Catostomus commersoni*) due to heavy metal poisoning (McFarlane and Franzin 1978) and Australian grayling (*Prototroctes mareana*) as a consequence of low river discharge (O'Connor and Mahoney 2004). Rideout *et al*. (2005) has identified three types of spawning omission: (1) *retaining*; eggs ripen and may ovalute but are not released, (2) *reabsorbing*; gametogenesis is halted at the vitellogenic stage and (3) *resting*; eggs remain in a pre-vitellogenic state throughout the year. Rideout *et al*. (2005) suggests that (2) and (3) occur due to poor nutrition, low temperatures and pollution, whereas the first type (retaining) can occur as a result of, *inter alia*: lack of spawning sites, low dissolved oxygen and insufficient water movement. The fact that female Clanwilliam yellowfish in the Driehoeks River were ripe-and-running suggests that they had retained their eggs, possibly due to unfavourable environmental conditions. Clanwilliam yellowfish are a significantly larger-bodied species than sawfin and their eggs are also larger (~2.8 mm compared with ~1.8 mm for the sawfin). Thus a combination of larger bodies and egg size and greater fecundity could mean that greater depths, higher current speeds and/or spring freshets may be required before spawning will commence as Cambray *et al*. (1997) and King *et al*. (1998) have hypothesised. Thus, due to its considerably lower discharge than the mainstem, the Driehoeks River may be sub-optimal for Clanwilliam yellowfish production.

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CHAPTER 9 Conclusion: an appraisal of the key findings and the implications for environmental flow studies in South Africa

9.1 A LIFE CYCLE MODEL FOR THE SAWFIN

In Chapter 4 the seasonal distribution patterns of sawfin the Driehoeks River were examined by means of underwater visual survey techniques. The principal advantage of this approach was that it enabled the identification of key habitats at intermediate reach and river segment scales, as well as the ability to ascertain the seasonal distribution of larvae and juveniles. This chapter demonstrated that spawning habitat was a scarce resource in the Driehoeks River – the existing or potential spawning habitat for sawfin in the Driehoeks River comprised less than 1% of the total length of the study segment and a smaller proportion of that habitat was responsible for over 90% of fish production. Spawning habitat was more prevalent in shallower reaches (*Reach 3*) that were less habitable for sawfin towards the end of the summer when they became too shallow, and during winter when fish could hold position in the elevated velocities of these reaches.

The finding that larger abundances of sawfin occupied deeper pools and very few were found in shallower runs in early spring prior to spawning (October, Chapter 4) confirmed that the pools were being used as overwintering refugia. Thus, during spring, adult sawfin appeared to move from deeper, high volume overwintering pools to shallow riffles and runs for feeding and spawning. This movement took place as flows were subsiding on the descending limbs of winter floods. The recovery of tagged fish suggested that fish moved in an upstream direction with individual adult fish covering distances of up to 3 km in three days shortly before the commencement of spawning. The possibility that sawfin migrated from upstream pools to spawning habitat downstream, however, cannot be ruled out. Rather than a shift in the 'centre of gravity' of the population from a single downstream to a single upstream location, the movement of fish in October resulted in a more even and less clumped distribution throughout the river segment. Thus, the adaptive significance of the movement appears to be to ensure an even allocation of resources (particularly spawning habitat) to all individuals.

As important to cyclical movements to adult fish are habitat changes that occur over the entire life span of the fish – most evident in the downstream dispersal of young-of-the-year sawfin. This aspect of movement amongst fish species has generally been paid little regard in the literature (Koehn *et al*. 2004). Chapter 4 showed that over the summer, young-of-the-year sawfin undertake a gradual migration or are displaced several kilometres downstream. The adaptive significance of this downstream movement by young fish may include avoidance of cannibalism (Folkvard 1997) (observed on the spawning grounds during this study) and competition (McCarthy 1999), or dispersal to favourable rearing habitats further from the spawning areas (Schlosser 1991). In this case, juvenile sawfin were associated exclusively with the only two bedrock reaches in the study area (Reaches 1 and 7, Figure 3.4, Chapter 3) that had greater structure with large clasts and rocky overhangs, which could have provided the young fish with cover from high flows, cannibalism and/or predation. At no other time, other than the summer months immediately following the spawning season, were young fish found in the intervening reaches (Reaches 2 to 6, Figure 3.4, Chapter 3). Chapter 5 showed that, in addition to downstream movements, there was a diel migration of juvenile sawfin in the rearing habitats from

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shallow embayments where they spent the day to deeper areas in the main channel at night once temperatures in the shallows dropped below those in the main channel.

While Chapter 4 described the spatial context of the key habitats in the Driehoeks River, Chapter 5 described and quantified them. While spawning continued throughout the three months between October/November and December/January, spawning and/or recruitment is suppressed by high flows early in the season and promoted by stable flows combined with continuously rising temperatures of ~19 °C over seven days or more. While it could not be ascertained with certainty that these periods of increasing temperatures provided a cue for spawning, or that the ensuing stable temperatures promoted embryo growth and development. Adult sawfin held position in the current in schools of between 70-100 fish over gravel and cobble substrata with relatively shallow (0.13-0.36 m) fast-flowing water (0.3-0.8 m s^{-1}). While these schools were present on spawning beds for several days, actual nuptial behaviour was observed for only part of the time, as and when environmental conditions corresponded to those mentioned above.

Chapter 7 showed that sawfin eggs are adhesive and negatively buoyant, suggesting that they are well-adapted to being laid in fast-flowing water (Mills 1981). Once they are released in the gravel and cobble by the female, they settle into the substratum and hatch over a period lasting between 50 and 70 hours post-fertilisation at 20 °C. Fungal infection (*Saprolegnia* spp.) appeared to be a major source of mortality while the eggs were in the substratum, particularly where high densities of eggs accumulated in small interstices that had little circulation. The hatched larvae are initially photophobic and attach themselves to substratum particles by means of an adhesive pad on the head. After 10-11 days the swim bladder becomes prominent, the larvae become phototaxic and swim-up occurs. They are then washed into very shallow marginal slackwaters (< 0.15 m), gradually moving into deeper waters (never more than 0.5 m) as they grow through their first season.

No fecundity or reproductive development studies were planned for this study because of the vulnerability of existing populations. In retrospect, these could have been carried out on the Driehoeks River population since the population appears to be large enough to withstand sampling mortality, and should most certainly be incorporated as a component of future studies. Evidence from the minimum size of ripe-and-running males and females caught during the course of this study and the aging studies conducted by van Rensburg (1966), however, suggested that sawfin reach reproductive maturity at around two years for males and four years for females.

Chapter 5 provided evidence for habitat separation between juvenile sawfin and juvenile Clanwilliam yellowfish (75-150 mm TL), the latter being found in shallow, fast-flowing riffle habitats in those reaches where juvenile sawfin were absent (*Reaches 2* to *6*, Figure 3.4, Chapter 3). While little could be learnt about the spawning ecology of the Clanwilliam yellowfish in this study, the evidence, i.e. low overall abundances of adults and juveniles and the absence of any eggs or spawning activity, point to the fact that the Driehoeks River is marginal for this species – either due to insufficient or inadequate spawning habitat (insufficient velocities or depths), or due to the absence of flow and/or temperature related spawning cues. There are few other areas remaining in the catchment where viable, recruiting populations still occur and all except the Rondegat River are relatively inaccessible for study purposes. Future studies on this species should therefore focus on the Rondegat River.

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Putting the key findings of this study together, Figure 9.1 shows a schematic representation of important stages in sawfin life cycle compiled from information contained in Chapters 4, 5, 7 and 8 on their distribution, habitat requirements, growth and development. Five Critical Habitat Units (CHUs) are identified in this figure: spawning, rearing, nursery, feeding and overwintering refugial habitats. The distinction is made between *nursery* habitats – shallow (< 0.15 m deep) marginal slackwaters near the spawning sites that are critical for recently emerged larvae – and *rearing* habitats – deeper (< 0.5 m) embayments located in bedrock reaches occupied by 1^+ juveniles. Four types of movement between CHUs are discriminated: (1) dispersal by juvenile fish from nursery to rearing habitat, (2) seasonal migration of adult fish from overwintering refugia to spawning habitat, (3) diel movements by juvenile fish between shallow embayments during the day and deeper areas in the main channel at night and (4) daily movements for feeding by adults as the location of and movement by fish between these CHUs.

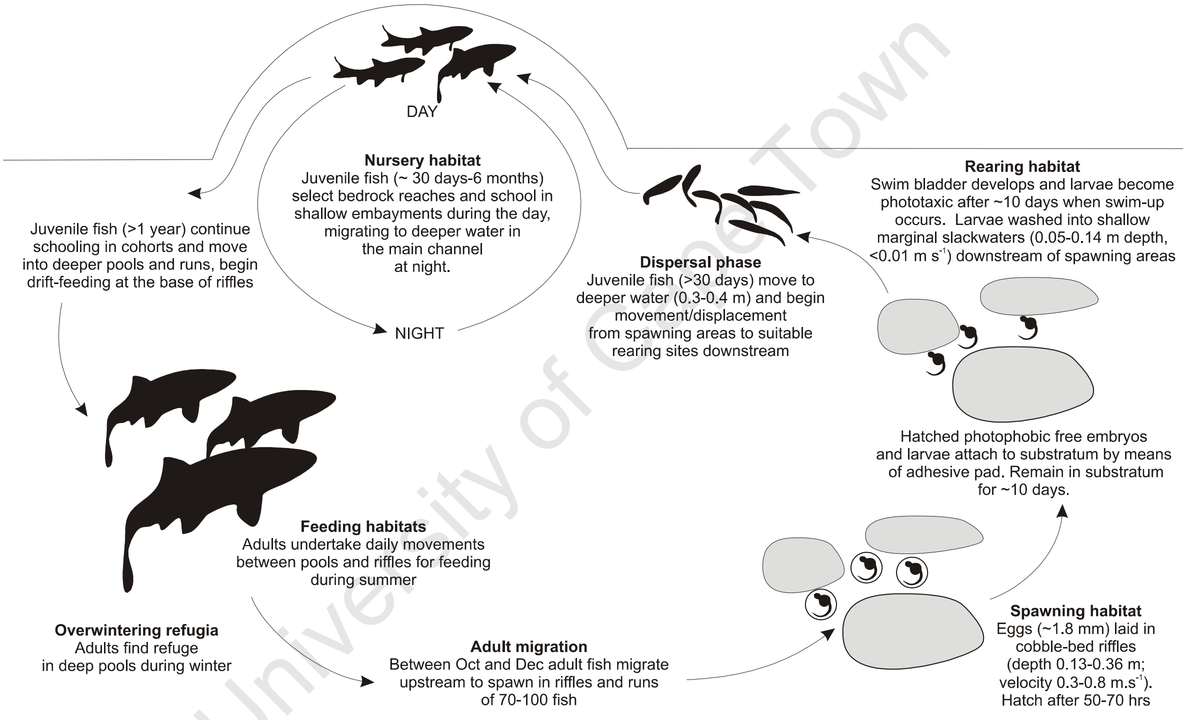

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Figure 9.1 Schematic representation of the life cycle of the sawfin showing Critical Habitat Units (CHUs) used during different stages of the life cycle, seasons and times of the day as suggested by the findings of this study. The location of these CHUs in the Driehoeks River are summarised in Figure 9.2.

Figure 9.2 shows the location of the CHUs in the Driehoeks River. A distinction should here be made between Kocik and Ferreri's (1998) use of the term Functional Habitat Unit (FHU) introduced in Secion 4.4, and CHU as it is used here. The FHU as used by Kocik and Ferreri (1998) refers to the full range of individual CHUs required by a species in a river segment to complete all stages of their life history. As such, the FHU encompasses the whole study segment including the five types of CHU contained within it. Within the study segment juvenile fish located at the most upstream nursery site were assumed to have dispersed from spawning sites further upstream since it was not considered likely that they ascended the Driehoeks Cascade separating *Reaches 1* and *2*. Key refuge habitats included the deepest pools (Pools 8 and 10) or pool complexes (Pools 3-5) in the study segment. The area identified as spawning habitat delineates the reaches that had the highest concentration of spawning sites – the actual area available for spawning is therefore a much small proportion of the area indicated.

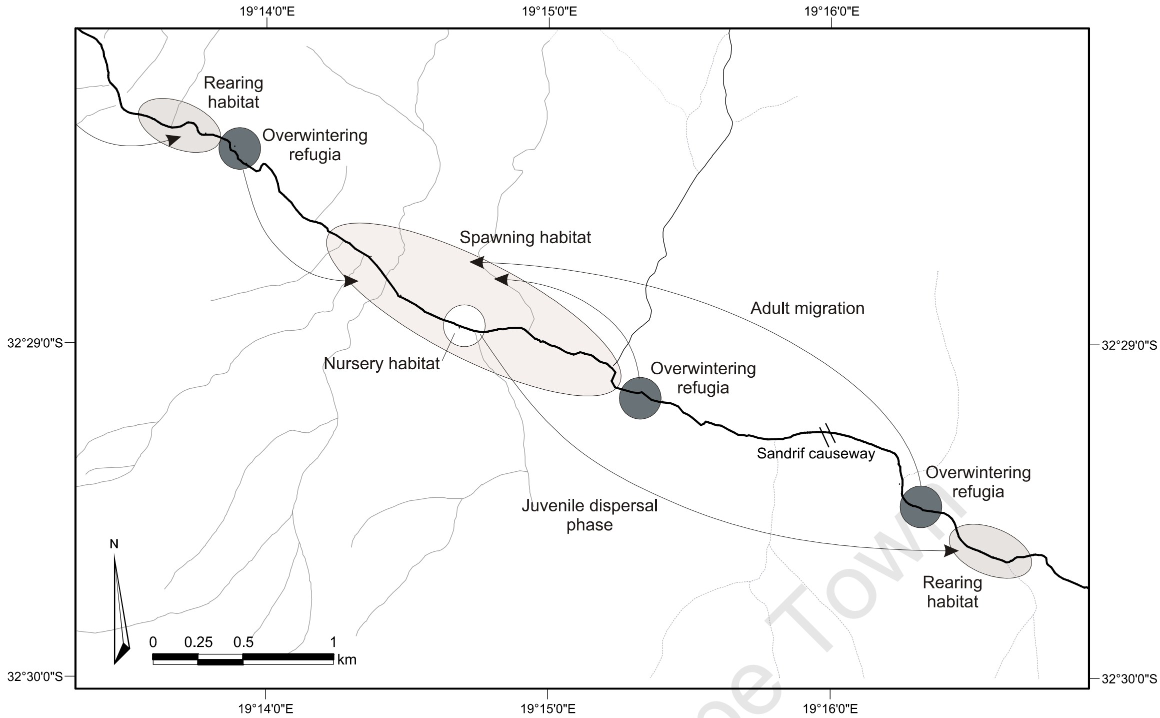

Figure 9.2 Location of sawfin CHUs (defined in Figure 9.1) identified in the Driehoeks River study area.

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9.2 DEFINING FISH HABITATS FOR ENVIRONMENTAL WATER REQUIREMENTS STUDIES IN SOUTH AFRICA

Arthington *et al*.'s (2003a: 58) call that environmental flow methodologies be improved 'by applying a wider range of quantitative techniques to relate flow alterations to ecological responses and by integrating models that facilitate prediction of the responses of river ecosystems to flow change' is reiterated here. Considerable effort has gone into developing appropriate methodologies for setting the water-quantity component of the Ecological Reserve for water resources in the South Africa. Several different approaches have been tested and either abandoned, or adopted and developed further (King and Louw 1998; Tharme and King 1998; O'Keeffe *et al*. 2002). Holistic methodologies, in particular the BBM (King and Louw 1998) and DRIFT (King *et al*. 2004), have attracted wide interest in South Africa and elsewhere because they are able to incorporate a range of ecosystem components – and the latter also incorporates socio-economic considerations – into planning scenarios. This study was conducted in part to address a common impediment to the successful application of all these approaches, i.e. irrespective of the relative merits of the different methodologies, there currently exists in South Africa a paucity of basic ecological knowledge on river ecosystem functioning and organismal responses to flow change. As a consequence, input to the various methodologies continues to rely on best-available-knowledge or expert-opinion estimates rather than on solid data from empirical studies.

In this study, the traditional approach of linking hydraulic models to HSC for water depth, velocity and substratum particle size (e.g. PHABSIM – Bovee 1982; RHYHABSIM – Jowett 1989; EVHA – Ginot 1998) was applied to Clanwilliam yellowfish and sawfin of the Driehoeks River. The complexity and cost of the aforementioned family of models notwithstanding, they offer the most effective means of quantifying and assessing changes to aquatic habitat resulting from flow regulation (Tharme 2003). With or without these models, HSC remain a useful method for interrogating habitat use by fish. HSC, however, have not been widely accepted in South Africa. In terms of current practice for defining fish-habitat associations for a Comprehensive Determination of the Ecological Reserve in this country, Kleynhans (1999) has suggested a modification of Oswood and Barber's semi-quantitative flow-depth (habitat) classes:

Slow (<0.3 m/s), Shallow (<0.5 m) (SS): shallow pools and backwaters
Slow (<0.3 m/s), Deep (>0.5 m) (SD): deep pools and backwaters
Fast (>0.3 m/s), Shallow (<0.3 m) (FS): shallow runs, rapids and riffles
Fast (>0.3 m/s), Deep (>0.3 m) (FD): deep runs, rapids and riffles

These categories have been assigned (with varying degrees of confidence) to each of the ~134 species of indigenous freshwater fish species found in South Africa and they have been widely applied in Reserve and Present Ecological Status assessments (Kleynhans 2003; Kleynhans and Louw 2007). Since fish surveys for Reserve Determinations are extremely limited in scope and extent due to time and budget constraints (usually between four and six sites are visited once only during the low-flow season) and flow-related data for fish species are often lacking, these pre-defined categories are useful surrogates.

But how accurately do the flow-depth categories reflect actual habitat selection and what implication does this have for estimating the flow parameters for any given species? It may be of some value therefore to examine how the data presented in this study compare with Kleynhan's (1999) flow-depth classes. Figure 9.3 (a) and (b) shows optimal habitats – flow-depth intervals for which suitability values are >0.85 (Chapter 5) – for sawfin and Clanwilliam yellowfish. These optimal habitats have been superimposed onto the flow-depth classes.

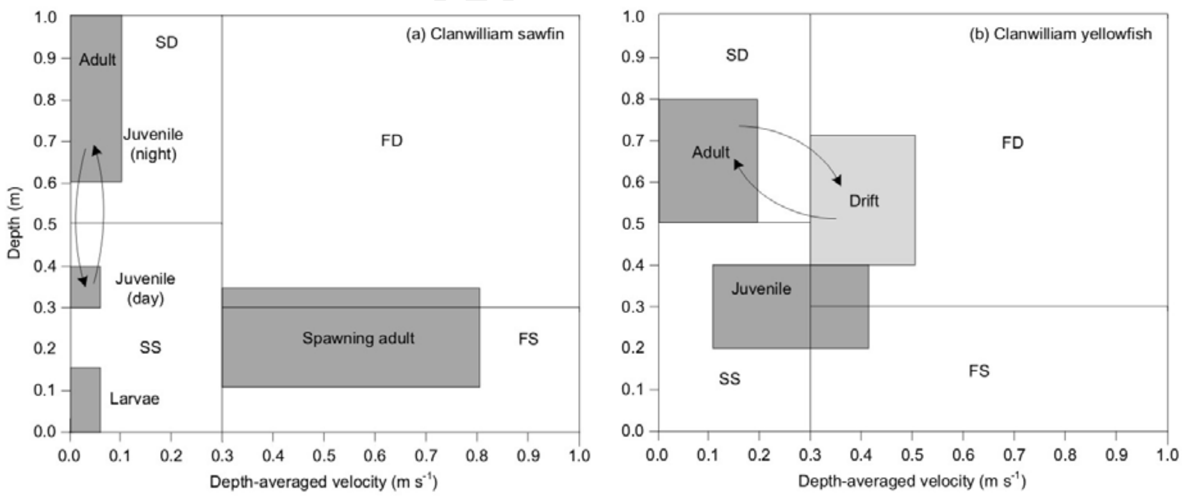

Figure 9.3 Flow classes adapted for use in South Africa by Kleynhans (1999). The centroids represent >0.85 suitability ranges derived in Chapter 5. The arrows indicate movement between two types of habitat: in the case of (a) movement of juvenile sawfin between daytime and night-time habitat and (b) movement of foraging Clanwilliam yellowfish between hydraulic cover and drift-feeding zones.

A number of issues are evident from this figure: (1) both sawfin and yellowfish use a much smaller subset of the habitat defined by each class; (2) there are considerable differences between life-stages – as well as differences between behaviours (e.g. feeding *vs* sawfin) and (3) connectivity between habitat patches is an important consideration – for juvenile sawfin this means connectivity between shallow daytime habitats and deeper night-time habitat and for yellowfish this means slow deep habitats in proximity to drift-feeding zones.

At first glance, the differences between flow classes and the centroids do not appear to be problematic because each centroid is accounted for by at least one of the classes. But flow classes are not preserved as wholes during EWR assessments; they are evaluated in terms of the proportion of each class remaining at a give discharge as predicted by an empirical frequency distribution or hydraulic model. For the purposes of this discussion, it is assumed that SD habitat will be the flow least vulnerable to modification, although connectivity between SD-SD and SD-FD habitats may be altered as already pointed out. The flow classes most vulnerable to flow change are therefore SS and FS and arguably the shallower component of SD (<0.4-0.5 m).

Depending on the channel cross-sectional profile, shallow marginal slackwaters (SS) and riffles (FS) can be inundated by very high flows, or dry out completely during low flows. From Figure 9.3 it is evident that preserving 90 % of SS habitat will not necessarily preserve the small proportion (10 %) of this habitat class actually used by larval sawfin – if current speeds exceed 0.1 m s^{-1} (i.e. 5-7 body lengths per second, Chapter 5) they are likely to be washed out or if depths exceed 0.15 m the larvae may become vulnerable to predators in the main channel. In the case of FS habitat, if it is assumed that velocities of 0.8-1.0 m s^{-1} are relatively rare in a river channel, then FS habitat corresponds well with sawfin spawning habitat, except if depths declined below 0.1 m.

Hydraulic habitats for adult and juvenile yellowfish (excluding spawning habitat that could not be evaluated in this study) are clustered between depths of 0.2-0.8 m and velocities between 0-0.5 m s^{-1} (Figure 9.3). For feeding yellowfish, the proximity of SD to FD habitats is important. In most cases, the velocity shears that provide drift-feeding opportunities may not change, but flows outside of the natural ranges may reduce optimal foraging efficiency within these habitats.

Both juvenile sawfin and yellowfish select similar depths (0.2-0.4 m), but yellowfish select these depths at higher velocities (0.1 – 0.4 m s^{-1}). The selection of these depths together with the selection of shallow depths by larvae mentioned above, suggests that an additional depth class in the region of 0.2-0.4 m may be required to better fit these trends. It should be noted that since Kleynhans' (1999) paper, several new classes have been added and applied if the information is available. These classes include: slow very shallow (<0.1 m deep), fast very shallow (<0.1 m deep) and fast intermediately deep (0.2-0.3 m deep). Future monitoring of the Reserve will take these classes into consideration (*pers. comm*. Dr. N. Kleynhans, Institute for Water Quality Studies, Pretoria).

In general, flow classes provide a useful alternative to HSC where these are not available. The risk of applying flow classes arbitrarily, however, is that habitat may not be perceived by a fish species in exactly the same way, leading to reduced availability or elimination of certain critical categories. The evidence presented here suggests that a greater number of flow classes may be required than the existing four (invertebrate habitats are currently defined by nine classes and these are under revision, Hirschowitz *et al*. 2007). While a revision of the intervals for each class may therefore be warranted, this should only be undertaken once more

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quantitative information is available on habitat use by a greater number of South Africa's indigenous freshwater fish. A start has been made here.

Collecting habitat information on a large number of species is not feasible given current research budgets and time frames. In addition, defining HSC with the accuracy presented in this study for large-bodied fish species in large river systems with turbid water is only possible by means of relatively expensive radio- or acoustic-telemetry methods (Scruton *et al*. 2002). Selecting target species on the basis of their representivity for a particular habitat or life history guild and on their socio-economic or conservation value is therefore advisable (see Chapter 2; Section 2.4).

Given the complexity of managing rivers for many different species and life stages, some authors have suggested that most habitat requirements for a diversity of species and life stages could be met simply by maintaining structural complexity and a diversity of 'hydraulic patches' (e.g. Azzellino and Vismara 2001; Dyer and Thoms 2006). Maintaining habitat diversity is a key objective of the hydraulic biotope approach used in this country and 2-D hydraulic models are also particularly suited to assessing habitat diversity. Although this seems like an attractive option when data are lacking, Dyer and Thoms (2006) warn of 'blindly managing for maximum diversity' without understanding the biotic response to hydraulic characteristics.

One of the most pertinent issues to emerge out of this study was the discrepancy between the discharges required for optimal spawning habitat as predicted by River2D (Chapter 7) and the conditions under which the sawfin actually spawned as suggested by spawning-date distributions (Chapter 8). At each of the three modelled sites, River2D predicted that spawning habitat would be available even at the lowest discharges (0.1 $m^3 s^{-1}$). This was supported by the fact that sawfin continued spawning until discharges in the Driehoeks River reached 0.05 $m^3 s^{-1}$ in both years (Section 8.3.3). Above these lower estimates of WUA, however, River2D predicted an increasing trend with increasing discharge. The evidence provided by the spawning-date distributions, however, showed that sawfin did not begin spawning before discharge reached 0.2-0.3 $m^3 s^{-1}$. These differences serve to highlight the limitations of hydraulic habitat modelling and the value of hydrological information for identifying flows of ecological importance.

Whatever approaches may be adopted towards the spatial aspect of habitat, the message throughout this document has been that an over-reliance on instantaneous measures of habitat is not advisable. In most instances, the immediate consequences of the loss of a particular habitat to particular species in terms of reduced fitness or increased mortality is usually not known (Rosenfeld 2003) and habitat may be limiting for only part of the time, for instance during spawning (Armstrong *et al*. 2003). For these reasons, habitat availability does not correlate well with biomass as pointed out in Chapter 2 (Section 2.3.5). Australian workers have also raised doubts about the appropriateness of methods that rely heavily on maintaining proportions of available habitat in a river – particularly for rivers in Australia that experience long periods of no-flow (Pusey 1998).

Early environmental flow methods such as the Montana method (Tenant 1976) focussed on historical flow records for estimating the amount of water for environmental allocation. Later methods shifted focus toward the relation between discharge and the availability of hydraulic habitat (e.g. IFIM; Bovee 1982). As levels of understanding grew, however, so did sophistication and complexity. In South Africa there has been a strong

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focus on habitat-based approaches in ecological research into species-flow relations (e.g. King and Tharme 1994; Kleynhans 1999; Pollard 2000) and the development of EWR methodologies (e.g. Birkhead 1999; Jordanova *et al*. 2004; Hirshowtiz *et al*. 2007). Stalnaker *et al*. (1998) cautioned, however, that the initial focus of river ecology studies – including habitat studies – should be on the hydrology. Armitage (1994) emphasised that it was only through retrospective analyses of flow change in aquatic ecosystems that future biological responses can be predicted. In recent years, as Souchon and Capra (2004) pointed out, the pendulum appears to have swung back towards hydrological approaches – a consequence perhaps of a growing awareness of the limitations of habitat-based approaches and an appreciation for the dynamic nature of river systems. Ideally, hydrology and hydraulic approaches are combined through habitat time series (Stalnaker *et al*. 1998), but this is not always feasible given data and manpower constraints.

Given these limitations, the *modus operandi* of this study from its conception has been to adopt a holistic approach to understanding the habitat needs of the target fish species – essentially it has been an attempt to put the 'ecology' back into Ecological Water Requirement studies. Rather than focussing purely on the quantity of available habitat at the reach scale therefore, the study incorporated: (1) the principles of landscape ecology and the seasonal distribution patterns of fish populations in relation to critical habitat units, (2) habitats for key life stages and behaviours and (3) spawning ecology and early life history in relation to annual flow and temperature regimes in order to achieve a broad understanding of the spatial as well as temporal dimensions of the fish's life history and its relation to its environment.

Pre-identifying potential bottlenecks to sustainable populations in terms of habitat availability was a key exercise early in the study. Abiotic variability has a strong influence on year-class strength and the early life stages of fish exert a disproportionate influence on their population dynamics (Gadomski and Barfoot 1998). The conditions post-spawning – during growth and development of larvae and juveniles – can have as much of an impact on year-class strength as spawning cues (Humphries 2005). Thus, a focus of this study was on the timing of early life-history events in relation to abiotic variability. It has shown that small floods towards the end of the high-flow season played a role in suppressing spawning and/or reducing recruitment. The evidence from the observed commencement of spawning in relation to the flow regime (Chapter 8) suggested that a discharge > 0.2-0.3 $m^3 s^{-1}$ in the Driehoeks River was an important threshold flow, above which spawning would not take place.

Some knowledge regarding the timing and duration of events in an organism's life cycle is essential for providing information to water resource managers, yet little research has thus far been undertaken on this topic in South Africa. A critical distinction between habitat assessments with only information on instantaneous measurements of habitat availability and those that include some form of time series, is that in the latter case, detailed recommendations can be provided regarding the timing of flows. With this information, water allocations can be planned around critical periods. For example, in this study it was determined that spawning lasts from late October to the end of January (depending on the prevailing flow and temperature conditions), and that the larvae are most vulnerable between the period beginning in December (when they first appear in the water) to the end of February. In addition, information can be provided to managers that will allow them to synchronise flows to coincide with optimal temperature conditions, for example with periods when weather conditions (in this case continuously increasing temperatures) are likely to trigger spawning.

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South Africa has recently entered an implementation phase of environmental water allocations. The next vital step will be to begin monitoring programmes to assess whether habitat-flow-response objectives are being met. In developing countries, financial, expertise and man-power constraints will continue to define the limits of what is possible and simple rapid methods of assessment are therefore required (*pers. comm*. Dr. N. Kleynhans, Institute for Water Quality Studies, Pretoria). Close cooperation between research and management institutions will ensure that monitoring data are collected in a way that feeds into research programmes and similarly, that research objectives remain relevant to the challenges faced by management. Bunn and Arthington (2002) have called for aquatic science to move into a more experimental phase and Poff *et al*. (2003) have called for EWRs to be treated as experiments in an adaptive management framework to be adjusted as new knowledge becomes available. With monitoring being a high priority in South Africa comes the opportunity for gathering information on ecosystem responses to managed flow releases. The call is made here for a coordinated approach to basic research into species, community and ecosystem-level responses to flow change that is closely tied to monitoring programmes. Without this information, the most sophisticated flow methodologies are destined to remain low confidence estimates at best.

Of critical importance to research in South Africa that supports EWRs is the collection of long term datasets. Current funding cycles in South Africa do not support research beyond three years and in some cases, budget constraints limit EWR ‘monitoring’ to a single year. This time period is inadequate for detecting the response of fish populations (or for that matter the response of any other ecological process) to hydrological change. A minimum of 5-10 years of data is required to do this effectively. In combination with extended monitoring programmes, FHUs need to be delineated in for a broader range of South African fish species, or groups of species.

9.3 RIVER FRAGMENTATION BY DAMS AND WEIRS

Fragmentation of rivers by instream barriers such as dams and weirs limit the dispersal of eggs, larvae (Agostinho *et al*. 2002) and juveniles (Raymond 1979; Spicer *et al*. 1995), obstruct or delay upstream and downstream migrations by adults (Baras and Lucas 2001), and disrupt emigration and immigration processes that encompass longer-term natural variations in spatial distributions (Schlosser and Angermeier 1995). Low structures such as road culverts may also present obstructions to certain species or size classes at critical times of the year.

Monitoring of fishways in South Africa has revealed that a significant proportion of freshwater fish species migrate on a regular basis (Meyer 1974; Cambray 1990; Kotze *et al*. 1998; Heath *et al*. 2005). Research into the functional significance of these movements, however, has been limited. The evidence presented in Chapter 4 and summarised in Figure 9.1 and 9.2, demonstrates that these movements are related to the patchiness of habitats in river and the need to access different CHUs at different times of the year. Downstream dispersal of young-of-the-year from rearing habitats to nursery habitats was shown to be as important as upstream movement of adult fish from winter refugia to spawning areas. Fortuitously, the river segment selected for this study corresponded to a complete Functional Habitat Unit (FHU), defined as being ‘natural partitions within the river system that contain all the necessary habitat elements to support all life history stages’ (Kocik and Ferreri 1998: 194) as pointed out in Section 4.4. Fragmentation of a FHU such as this one, either by a dam, weir, or even a poorly designed road culvert could disrupt movement between

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critical reaches and reduce recruitment levels in the segment – possibly to the point where populations could become locally extinct. FHUs in South African rivers need to be identified, mapped and their connectivities to other FHUs identified and efforts made to protect them in conservation and water allocation strategies.

The need for fish passage facilities to be built on existing instream structures in South Africa has been recognised by the DWAF. The criteria for the design of fishways and guidelines for the planning, design and operation have been dealt with by Bok (2004) and Heath *et al*. (2005).

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CHAPTER 10 Water resources and indigenous fish in the Olifants and Doring Rivers basin: management and conservation priorities

The threats to and current status of the populations of the larger-bodied cyprinids in the Olifants system have been documented in Chapter 1 of this document and by Paxton *et al*. (2002). The primary threats as stated at the outset of this document are invasion by alien fish species and habitat degradation. Although Clanwilliam yellowfish, sawfin and sandfish were harvested from the Olifants and Doring Rivers during the earlier part of the 20th century when pools were dynamited and the fish sold in local markets (Mr. Koos Greef, landowner Melkboom farm, *pers. comm*.), very little subsistence and no commercial harvesting has taken place in recent years due to their reduced abundances and the low human population densities in areas where the remaining fish populations still occur.

What follows here is a region-by-region basin-scale assessment of the catchment in terms of the current status of the aquatic habitats, the status of existing fish populations and key conservation and management actions required in each instance. Most of the threats and the measures required to mitigate them are well understood in general terms. The current study has, however, identified specific habitat and flow conditions that need to be met to ensure the success of management and conservation programmes. It has given special consideration to the movement, habitat and temperature requirements of sawfin (but some will apply to Clanwilliam yellowfish as well) and these are summarised in Section 10.6 (Table 10.2).

Several factors make Clanwilliam yellowfish and sawfin particularly vulnerable to environmental change. Firstly, they are long-lived species, they utilise a wide variety of habitats and they have relatively delayed maturation. Species that share these characteristics can take decades to recover from population declines (Rose 2000). Secondly, like many of the other large-bodied cyprinids in South Africa, they are periodic strategists. They are therefore adapted to the natural seasonal temperature and flow patterns in their native rivers and are for this reason particularly susceptible to flow regulation (Olden *et al*. 2006). There are little more than five known recruiting populations of Clanwilliam yellowfish and sawfin in the Olifants and Doring Rivers' basin that are reasonably secure from alien fish invasion and major water-resource infrastructure and utilisation. Although these populations are located in areas where impacts on the aquatic ecosystem are comparatively minor and localised, this is made up for by the fact that these areas are mostly headwater tributaries. Thus, because they are relatively small streams with low discharges, they are as susceptible to disturbances as the mainstem reaches although for different reasons. The populations are nevertheless relatively secure for the moment, however, a relatively minor incident such as a sewage spill or bulldozing could have serious consequences.

In the mainstem rivers, due to the existing demands for water and the fact that the Ecological Reserve of water for maintenance of the ecosystem has been agreed upon by the DWAF, but at the time of writing, it has not been implemented, the basic ecological requirements of the larger-bodied cyprinids are currently not being met and populations are on a negative trajectory. Occasional sightings of juvenile Clanwilliam yellowfish by

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farmers and fishermen in the area suggest that sporadic spawning continues to take place in the mainstems and therefore that they cannot be ignored in terms of their current and potential future contribution to overall recruitment levels. There exists considerable scope for improving habitat conditions and easing pressures on remaining populations in these areas.

The DWAF recognises six management sub-areas within the greater Olifants/Doring Water Management Area (DWAF 2005), of which four: the Upper and Lower Olifants, the Doring and Kouebokkeveld sub-areas are relevant to Clanwilliam yellowfish and sawfin conservation and management; there are few perennial rivers in the Sandveld or Knersvlakte sub-areas (Figure 10.1). The total yield balance for the WMA as a whole shows that water resources have been maximally or over-allocated (Table 10.1). Each of the four main sub-areas is dealt with separately in the sections that follow.

Water requirements outstrip availability by 34 Million $m^3 a^{-1}$ primarily due to over-allocation in the Lower Olifants sub-area. Although the environmental stressors affecting the fish populations in each of the sub-areas are generally comparable, each sub-area differs according to the present-day status of populations as well as the nature and degree of impact.

TABLE 10.1 Reconciliation of water requirements and availability for the year 2000 at 1:50 year assurance (million $m^3 a^{-1}$) from DWAF (2005) Olifants/Doring Water Management Area: internal strategic perspective

	Available yield			Water requirements			
Sub-area	**Local yield**	**Transfers in**	**Total**	**Local requirement**	**Transfers out**	**Total**	**Balance**
Upper Olifants	197	0	197	103	94	197	0
Kouebokkeveld	67	0	67	66	0	66	1
Doring	11	3	14	15	0	15	-1
Knersvlakte	4	4	8	7	0	7	1
Lower Olifants	25	94	119	144	4	148	-29
Sandveld	32	0	32	38	0	38	-6
Total for WMA	**336**	**101**	**437**	**373**		**471**	**-34**

10.1 UPPER OLIFANTS

Location and status of the aquatic habitat—The Upper Olifants management sub-area extends from the headwaters of the Olifants River on the Agterwitzenberg plateau at around 800 *amsl* to Clanwilliam Dam (Figure 10.1). It contributes the highest water yield in the region (Table 9.1). From the Agterwitzenberg plateau, the Olifants River flows through the Olifants River Gorge (a Natural Heritage Site) between the Groot Winterhoek and Skurweberg mountains before issuing into the wider Olifants River Valley a further 25 km downstream near Keerom.

Agricultural development on the Agterwitzenberg plateau (Figure 10.2) is intensive with irrigation fed primarily by farm dams. In terms of the National Water Resource Classification System (NWRCS: DWAF 2006; Kleynhans and Louw 2007) the Ecostatus category of the mainstem river in this area is a C (moderately modified). Due to the steepness of the valley sides, disturbance to the aquatic ecosystem in the Olifants River Gorge is limited to abstraction in the Agterwitzenberg and invasion of the riparian belt by black wattle *Acacia mearnsii*. The river here has therefore been assigned an ecostatus category of B (largely natural).

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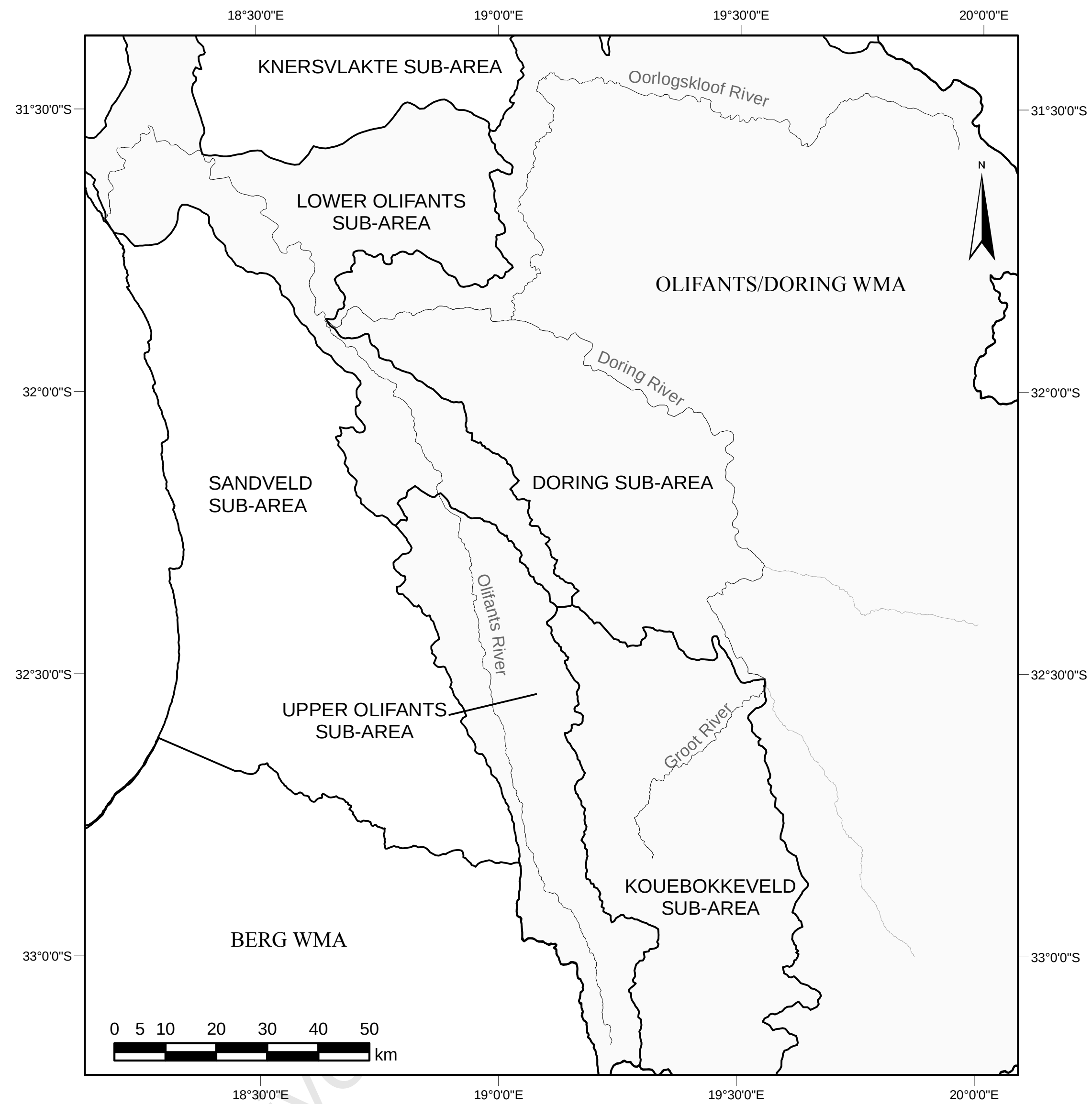

Figure 10.1 The six management sub-areas within the Olifants/Doring Water Management Area (WMA) as recognised by the DWAF (2005): Upper and Lower Olifants, Kouebokkeveld, Doring, Knersvlakte and Sandveld. The sub-areas that are important from a fish perspective are shaded in grey.

Downstream of Keerom to Citrusdal the valley slopes widen and agricultural activity (primarily citrus orchards) becomes more widespread. Habitat quality deteriorates to an E-category (seriously modified) due to extensive run-of-river abstraction over the low flow season and modification of the floodplains. Downstream of Citrusdal the river flows north in an alternately braided and single-thread channel before reaching Clanwilliam Dam reservoir. In this section of river, peak run-of-river abstractions of water occur during the agricultural growing season during spring. In recent years a combination of abstraction and unusually dry winters has reduced the normally perennial main channel to a series of standing pools by the end of summer (Plate 10.1). Under these conditions the duration of the no-flow period during the dry season has increased from 5% under natural conditions to 45% presently (Birkhead *et al*. 2005).

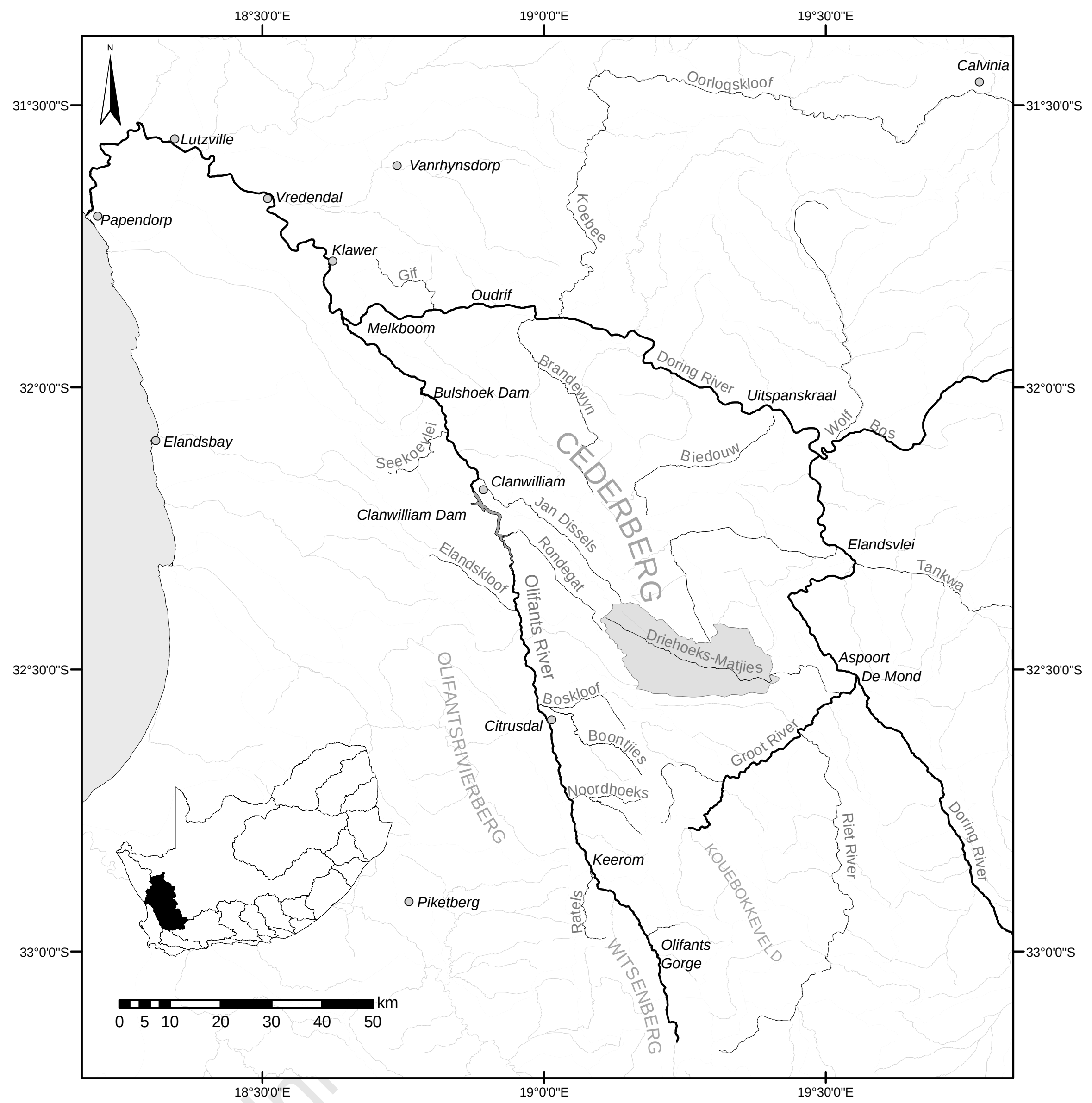

Figure 10.2 Olifants and Doring Rivers Basin showing the main tributaries, towns, dams and sites referred to in the text. The shaded area shows catchment E21K, the main study catchment.

The tributaries of the Olifants River flowing off the eastern flanks of the Cederberg into this section of the mainstem (notably the Rondegat, Jan Dissels and Noordhoeks) are still relatively undisturbed in their upper reaches, but habitat quality declines in the lower reaches where farming activities intensify. Invasion of the riparian zone by alien plants and failure to enforce a riparian buffer zone (resulting in bulldozing of the river channel and cultivation on the floodplains), together with unsustainable levels of abstraction, is primarily responsible for the low Ecostatus category in this region.

Status of the fish—Upstream of the confluence of the Boskloof River (Figure 10.2) the Olifants River mainstem supports some of the highest abundances of sawfin and Clanwilliam yellowfish to be found anywhere in the catchment (Paxton 2004).

Plate 10.1 The main channel of the Olifants River near Citrusdal showing the normally perennial river reduced to series of standing pools (photographed March 2006).

Downstream of the Boskloof River confluence to Keerom the status of sawfin and Clanwilliam yellowfish populations is unclear, but numbers probably decline with increasing distance from the source of the Olifants River. Populations of Clanwilliam yellowfish occur in the tributaries in this sub-area (notably the Ratels, Boontjies-Boskloof Rivers system and Noordhoeks Rivers). There are occasional records of sawfin in the mainstem of the Olifants River in recent times, but the only known reproducing populations of sawfin in this region are found in the Ratels River (Impson *et al*. 2007). Between Keerom and Clanwilliam Dam, populations of both sawfin and Clanwilliam yellowfish in the Olifants River are functionally extinct. No sawfin have been collected during the course of recent surveys and the few adult Clanwilliam yellowfish that have been collected are believed to be migrants from tributaries (Paxton *et al*. 2002; PGWC 2004; Birkhead *et al*. 2005). Although the mainstem of the Olifants River is likely to be a population sink for extant tributary populations, it is critical as a corridor facilitating genetic interchange between the otherwise isolated tributary populations.

Attenuated flows over the spawning season caused by farm dams in the tributaries and run-of-river abstraction in the mainstem would limit the success of any spawning should this still take place in the mainstem. Drying of riffle habitat over the summer would also likely result in juvenile Clanwilliam yellowfish that would normally find refuge from predation in these types of habitat being forced into the few isolated pools with little depth- or flow-cover from predation by alien fish species. In addition to flow manipulations in the

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mainstem, un-regulated bulldozing of the channel and abstraction by landowners in the tributaries is diminishing the remaining mainstem habitat supporting endemic fish populations.

Management and conservation priorities—The Olifants River upstream of Keerom should enjoy the highest conservation status in the catchment and every effort should be made to limit the downstream impacts on it of farming activities in the Agterwitzenberg. This means enforcing the Ecological Reserve and ensuring that water quality is not degraded by agricultural runoff. The presence of alien fish species such as bass and trout in farm dams should be assessed and they should be removed from dams where they occur.

The impact of invasive vegetation on the water yield in this region is estimated at 5 million m^3/a (DWAF 2005). Clearing would therefore substantially increase base flows and ensure that more water is available to meet both agricultural and ecological demand. Downstream of Keerom, conservation and management priorities include (1) increasing off-channel storage capacity in the mainstem during the winter high flows which would alleviate pressure on water resources during the low-flow period and (2) securing, reclaiming and/or rehabilitating degraded or invaded aquatic habitat in the tributaries. In some cases, however, over-abstraction in the foothill reaches of certain tributaries has benefitted endemic fish populations upstream by limiting migration of alien fish into the upper reaches. Restoring flow and habitat in the foothills reaches of these rivers could in some cases be detrimental to endemic fish populations and the re-establishment of riverine corridors should not be encouraged where the danger of invasion exists. The importance of isolating endemic fish populations from alien fish may override the necessity for genetic interchange between tributaries.

10.2 LOWER OLIFANTS

Location and status of the aquatic habitat—The lower Olifants management sub-area extends from Clanwilliam Dam to the mouth of the Olifants River (Figure 10.2). It has the highest water yield deficit in the catchment (29 million $m^3\ a^{-1}$, Table 10.1) despite receiving a sizeable transfer (94 million $m^3\ a^{-1}$) from the Upper Olifants for irrigation, primarily of table grapes and wine vineyards. The sub-area includes the Bulshoek Weir and canal system which assists in the transfer of this water from the Upper Olifants. Flow in the Olifants River between Clanwilliam Dam and Bulshoek Weir a further 35 km downstream is regulated by irrigation demands, as well as to control the level of the back-up water behind Bulshoek Weir.

There are no release structures on Bulshoek Weir and flows downstream are therefore substantially curtailed over the low-flow season. The attenuated flow regime together with the reduced sediment supply and cultivation on the flood terraces has transformed the river channel downstream of Bulshoek from a braided system to a single-thread channel. This channel comprises a series of deep pools connected by shallower bedrock-controlled rapids that have largely been terrestrialised by reed and palmiet encroachment. From the Doring River confluence to the estuary, intensive farming of the Olifants River floodplain has resulted in entrenchment of the river channel and water quality has been impacted by agricultural return flows, which have resulted in substantial increases in salinity (Dallas 1997). In terms of the National Water Resource Classification System (NWRCS; Kleynhans and Louw 2007) the Ecostatus category in this region is an F (critically modified).

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Status of the fish—As pointed out in Chapter 1, Clanwilliam Dam reservoir and the backup of water behind Bulshoek Weir have together inundated 30 km of river habitat that would have included spawning habitat for Clanwilliam yellowfish and sawfin and have restricted the movement of migrating fish. Although historical records confirm that sawfin once occurred in this area – a record from the Albany Museum in 1972 and a sawfin caught close to the mouth of the estuary in the 1980s (Day 1981) – recent surveys undertaken in 2001 and 2003 suggest that they have since become locally extinct (Paxton *et al*. 2002; PGWC 2004; Birkhead *et al*. 2005). Similarly, there are historical records of Clanwilliam yellowfish in this region from the aforementioned data sources, as well as numerous anecdotal accounts of large numbers of Clanwilliam yellowfish migrating up the lower Olifants River to spawn in the early half of the twentieth century (Chapter 1, Section 1.2). Recent surveys (Paxton *et al*. 2002; PGWC 2004; Birkhead *et al*. 2005) reported very low abundances of Clanwilliam yellowfish in the lower Olifants mainstem, with less than one adult yellowfish caught per night in overnight nets. Clanwilliam yellowfish populations in this part of the catchment are therefore believed to be functionally extinct. There are also no endemic cyprinid populations remaining throughout most of the lower Jan Dissels River (the only major tributary known to support endemic fish), although a population of sawfin has been reported in the uppermost reaches of this river.

Management and conservation priorities—No management or conservation actions aimed at conserving endemic fish populations are recommended downstream of the Bulshoek Weir since it is unlikely fish populations will recover here given the extensive nature of the habitat modification and high densities of predatory alien fish. The potential exists, however, to substantially improve instream habitat in the upstream mainstem Olifants River between Clanwilliam Dam and Bulshoek Weir, a reach of roughly 20 km. Proposals to raise the height of Clanwilliam Dam are currently being advanced and this represents an opportunity for implementing the Ecological Reserve in this reach (Birkhead *et al*. 2005). Particularly important in this regard is the incorporation of multiple release-structures in the dam wall for releasing flows of the correct temperatures and volume (see Section 9.2). There is an extant Clanwilliam yellowfish population in the reaches between the Clanwilliam Dam and Bulshoek Weir – possibly the last significant mainstem population – which will stand to benefit from the release of environmental flows. It is highly recommended that a comprehensive assessment of the status of this population be carried out and that pre- and post-construction monitoring of fish populations be implemented. On-site monitoring of impacts during the construction phase should also take place.

10.3 KOUEBOKKEVELD

Location and status of the aquatic habitat—The Kouebokkeveld management sub-area is situated in the upper Doring River catchment and includes the headwaters of the Riet and Groot Rivers – two of the largest tributaries that contribute water to the Doring River. It includes the Driehoeks-Matjies River where the current study was conducted. Water in this region is used primarily for growing deciduous fruit and vegetables, and this has resulted in a high concentration of farm dams located in the Kouebokkeveld region itself. The water yield shows a surplus of 1 million $m^3\ a^{-1}$ (Table 10.1), but it is likely that flows are substantially curtailed from natural in the Riet, which impacts flows in the Groot and mainstem Doring Rivers.

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Status of the fish—This part of the Olifants/Doring catchment has not been sampled as extensively as other parts. The status of sawfin populations in the upper Groot and Leeu Rivers system is unclear, but there are two records of sawfin in the Brandkraals and Twee Rivers respectively (collections database South African Institute for Aquatic Biodiversity – SAIAB 2006). Clanwilliam yellowfish have been translocated into the Twee River and pose a risk to the endemic Twee River minnow (*Barbus erubsescens*) (Impson *et al*. 2007). Limited numbers of adult sawfin have been recorded from the Groot River close to its confluence with the Doring River near De Mond (Figure 10.2) (Paxton *et al*. 2002). A significant population of sawfin occurs in the upper Driehoeks-Matjies river system (a tributary of the Groot River), and the study reported on here suggests that these rivers represent one of the most important refuges for both Clanwilliam yellowfish (despite the Driehoeks being marginal for this species) and sawfin anywhere in the catchment.

Management and conservation priorities—More surveys are required in this area to establish the conservation-worthiness of other rivers in the region, but the Driehoeks-Matjies River is amongst the highest priority rivers in the catchment for the conservation of Clanwilliam yellowfish and sawfin. Relatively localised impacts such as water abstraction, agricultural runoff and bulldozing of the river channel can have major implications for fish populations in these rivers and indeed, for continued existence of the species, and landowners should be sensitised to the consequences of their interventions.

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10.4 DORING RIVER

Location and status of the aquatic habitat—The Doring River sub-area extends from the confluence of the dry Doring River with the Groot River in the south to the confluence of the Doring with the Olifants River near Klawer in the north and includes tributaries entering from both the wetter Cederberg and drier Karoo. Major tributaries that support endemic fish populations in this region include those contributing water from the Cederberg – the Tra-tra and Biedouw Rivers – and those contributing from the Karoo such as the most northerly tributaries of the Koebee-Oorlogskloof River system. All of these support Clanwilliam yellowfish and sawfin populations.

While development along the Doring River is not as intensive as it is in the Olifants River, abstraction in the Kouebokkeveld region is believed to have a significant impact on flows in the Doring (DWAF 2005). Localised impacts are evident at Elandsvlei and Uitspanskraal where farming activities (particularly livestock and agricultural return flows) are having a negative impact on water quality in the downstream reaches. Over the summer when fish are concentrated in isolated pools this may contribute to mortality levels. A number of dam options on the Doring River has been put forward to meet the demand for increased agriculture in the region (DWAF 2005).

Status of the fish—As pointed out in Chapter 1, Clanwilliam yellowfish and sawfin occur in greater abundances in the Doring River system than they do in the Olifants River downstream of Keerom to the estuary. During preliminary dive surveys for the current study, abundances of adult Clanwilliam yellowfish were estimated on the mainstem of the Doring River between De Mond and Aspoort. Their frequency of occurrence and relative abundances, despite being higher than on the Olifants, were, nevertheless, still very low (~6 fish.river-km; Chapter 3, Section 3.4). Fyke and gill net sampling elsewhere on the Doring River suggests that this density is probably realistic for most of the Doring mainstem (Paxton *et al*. 2002). Sawfin appear to be a little more numerous in the lower Doring River between the confluence of the Brandewyn River with the Olifants and the Gif River (Paxton *et al*. 2002; Impson 1999). Recruiting populations of both species are found in the upper reaches of the Oorlogskloof-Koebee Rivers system that joins the Doring River 42 km from its confluence with Olifants (Paxton *et al*. 2002). This is the most northerly limit of their distribution.

Of most concern in the Doring sub-area is the absence of Clanwilliam yellowfish and sawfin less than 300 mm TL in the mainstem. Back-calculating from annual increment counts on scales of adult Clanwilliam yellowfish and sawfin caught in the Doring River (Paxton unpublished data), this suggests that successful recruitment has not taken place here for at least seven years and leads to speculations that populations may soon disappear from the mainstem Doring altogether.

Management and conservation priorities—Although abundances are low in the mainstem Doring River, the sawfin and Clanwilliam yellowfish are nevertheless still present. The possibility therefore exists that populations will recover in favourable years. Any further development of water-resource infrastructure on the Doring River, however, is likely to increase their trajectory of decline. The principal threats from additional dams or weirs include the inundation of spawning habitat upstream by the impounded waters, reduced access to habitat upstream of the dam wall and an increase in lentic habitats that would favour the proliferation of alien fish species. Environmental releases of water from dams would mitigate some of the negative effects downstream of any dam or weir, but the general status of endemic fish populations in the Olifants River does not augur well for their continued existence in the Doring River in the face of potential future water-resource developments. In all parts of the system, the tributaries are now the main refuge from predation by invasive fish and the impacts of flow change. Part of the Oorlogskloof River is situated within a nature reserve and fish populations are monitored by Northern Cape Nature Conservation on an infrequent basis. Some protection is therefore afforded these populations. Clanwilliam yellowfish and sawfin populations also occur in the Biedouw and Tra-tra Rivers where small-scale farming in localised area impacts on the riverine corridor. Interventions here should include education and awareness programmes.

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10.5 CONCLUDING REMARKS

Both the Clanwilliam yellowfish and sawfin depend for their continued existence on a number of disjunct populations isolated by artificial barriers such as dams and weirs and biological barriers such as invasive alien fish. The recovery of mainstem populations in the Olifants River – particularly downstream of Bulshoek Weir – is considered improbable, whereas populations in the Doring River may recover in years when flows favour the indigenous fish to the detriment of the alien fish. Effective management and conservation therefore depends on securing existing populations in the tributaries while ensuring that habitat and flow conditions do not further deteriorate in the Doring River. Chapter 4 demonstrated the extreme vulnerability of populations in the Driehoeks River – a typical tributary refuge. Destroying critical spawning and nursery habitat, or obstructing access to key habitats would likely result in population declines if not local extinctions.

The Olifants-Doring River system in the south-western Cape is a catchment of national and international biogeographic importance (Skelton *et al*. 1995; Impson 1999). Despite this there is very little awareness on the part of landowners and conservation or water-resource authorities in the region of the importance of aquatic ecosystem conservation. There are three organisations through which conservation and management objectives in the catchment can be achieved: the Western Cape Nature Conservation Board (WCNCB); the Department of Water Affairs and Forestry through the Olifants/Doring Catchment Management Agency (CMA), and local conservancies, of which there are several in the catchment. The principal legal apparatuses supporting conservation and management of objectives are the National Water Act (NWA; 1998) and the National Environmental Management: Biodiversity Act (NEMBA 2004). The NWA governs water use and management in South Africa and requires water users to ensure that there is enough runoff to meet the requirements of the ecosystem component of the Reserve. NEMBA provides for the drafting of Biodiversity Management Plans for Species (BMP-S) for indigenous or migratory species that warrant special conservation attention.

The capacity and awareness of the aforementioned bodies could be increased to ensure that these laws are enforced and that vigilance is maintained with regard to the potential impacts on aquatic ecosystems of existing or future agricultural or water-resource developments. Some of the more important management considerations need to be implemented at the conservancy level, including enhancing the efficiency of irrigation schemes, reducing the necessity for dry-season abstraction and creating riparian buffer zones to limit run-off of agro-chemicals. Management and conservation measures need to be aimed at broad-based whole-ecosystem approaches that incorporate the principles of Integrated Catchment Management without neglecting specific catchments for special interventions (e.g. clearing alien fish species and river rehabilitation) where these are necessary.

Nel *et al*. (2006) identified key spatial areas for conservation action based on a systematic assessment of the Olifants/Doring catchment. They called for an implementation strategy that includes key stakeholders and a management plan for each selected area. It is suggested here that BMP-S (using the guidelines in Table 10.2, Section 10.6) as a starting point) be drawn up for the endemic fish in the catchment that would feed in to this broader management plan. In addition to the specific measures listed in Table 10.2, a list of additional key ecosystem and community-level interventions appears below that overlaps with some of those proposed by Nel *et al*. (2006):

- ***Education and awareness***: landowners, conservation and water resource authorities sensitised to the importance of aquatic ecosystem management and their awareness increased with regards to the correct measures to protect important ecosystems
- ***Protection and rehabilitation***: securing and rehabilitating targeted tributary habitats is a direct, relatively cost-effective conservation intervention that has most chance of success in the short term
- ***Fish sanctuaries***: where practical, the establishment of fish sanctuaries in some areas (Rondegat, Driehoeks-Matjies, Noordhoeks, Olifants River Gorge) would provide additional protection and, where rivers are frequented by tourists, they would serve an additional educational purpose
- ***Enforcement***: in the broader Olifants/Doring catchment it is essential that the Ecological Reserve is met, particularly in important mainstem reaches such as downstream of Clanwilliam Dam where Clanwilliam yellowfish populations still persist, albeit tenuously. Vigilance on the part of the authorities with regard to habitat degradation and alien fish introductions should be exercised
- ***Monitoring***: monitoring the status of fish populations (relative abundances and population size structure) by trained DWAF and WCNCB personnel especially in key catchments, or where

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proposed water-resource developments may impact extant populations. The status of existing populations and trajectories of change could thereby be ascertained.

- ***Alien fish eradication***: efforts by CapeNature to reclaim tributary reaches by eradicating alien fish and re-introducing indigenous species are currently underway.

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10.6 THE FLOW-RELATED ECOLOGICAL REQUIREMENTS OF CLANWILLIAM YELLOWFISH AND SAWFIN

TABLE 10.2 The ecological requirements of the Clanwilliam yellowfish and sawfin as highlighted by the findings of this study together with the potential impacts, causes, effects, ecological significance and the relevant chapters that deal with the topic.

Ecological requirements	Potential impacts to the ecological requirements	Effects	Ecological significance	Recommendations	Relevant Chapters
Habitat quality and heterogeneity	Disturbance to the riparian belt by farming too close to the channel Trampling by livestock Bulldozing the river channel Invasion of the riparian belt by alien vegetation Reduced magnitude and frequency of flushing flows, i.e. wet season floods that have sufficient shear-stress to mobilise sediment in cobble bars	Increased sediment yield and mobilisation Reduced interstitial spaces between bed particles Processes of erosion and deposition that shape the natural morphology of the river channel are altered	Reduced quality and availability of spawning habitats Reduced availability of marginal slackwater and floodplain habitat for juvenile fish	Enforce a 35 m buffer zone on all rivers: no farming activities, bulldozing, livestock grazing should be permitted in and around the river channel. Eradicate alien vegetation along river banks Ensure flushing flows are released downstream of dams to maintain interstitial habitats	Chapter 5 and 8
Hydraulic habitat	Retention of base-flows over the low-flow season by mainstem dams and retention of run-off by off-channel farm dams Over-abstraction during low-flow season by run-of-river irrigation pumps	Reduced availability of suitable hydraulic habitat for eggs, larvae, juvenile, adult and spawning habitat	Spawning omission or reduced spawning intensity or frequency Reduced egg survival due to insufficient circulation through spawning beds – in some instances, habitat may dry up altogether Insufficient inundation of marginal slackwater habitats that are important rearing habitats – young fish impacted by adverse flow conditions and predation levels in the main channel Delivery of food to drift-feeding fishes reduced	Implementation of the Ecological Reserve Ensure that the Ecological Reserve accounts for all life stages – particularly early life stages and spawning requirements that are most sensitive to flow changes Increase off-channel storage capacity to reduce run-of-river low-flow season abstraction	Chapter 5*, 6 and 7

*While the HSC developed for sawfin and yellowfish in this study may be biased by being derived from a single tributary, they can be taken as a guide for habitat requirements for populations elsewhere in the catchment, particularly other tributary reaches.

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TABLE 10.2 (cont'd)

Ecological requirements	Potential impacts to the ecological requirements	Effects	Ecological significance	Recommendations	Relevant Chapters
Timing of flows	Retention of floods during the high flow season by dams High irrigation releases during the low flow season	Some degree of seasonal flow reversal (lower than normal high-flows, and higher than normal low-flows) resulting in a mismatch of flow and temperature regimes	Higher than normal flows over the low-flow season may suppress spawning and cause wash-out of eggs and larvae from nursery habitats. Juvenile fish may be flushed from littoral rearing habitats	Releases of flows need to be timed to match the annual life cycle requirements of the fish species Environmental flows need to strike a balance between the required depths and velocities over spawning beds and flows of a higher magnitude that may wash out marginal rearing habitat	Chapter 5, 6 and 8
Rate of change of flows	Irrigation or hydropower releases from dams	Higher rate of change in discharge	Sudden increases in flow: fish fail to orient themselves in the current and are washed downstream. Fish fail to find hydraulic cover (move onto floodplains and river margins) Sudden decreases in flow: young fish in rearing habitats become stranded in the shallows	Flows released that match the natural rate of change in discharge	Not dealt with in this study but identified as a potential threat
Temperature	Hypolimnial releases from dams	Lower than normal river temperatures	Fish fail to spawn, or spawn at low intensities, or later than natural and so juveniles not sufficiently mature to withstand the next winter's high flows.	Multiple release structures should be fitted to any dam or weir that is likely to cause stratification of water in its reservoir A continuous period of increasing temperatures (~7 days) is required for spawning to trigger major spawning events. Releases should be timed to coincide with optimal ambient temperatures for spawning	Chapter 8

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TABLE 10.2 (cont'd)

Ecological requirements	**Potential impacts**	**Effects**	**Ecological significance**	**Recommendations**	**Relevant Chapters**
Connectivity	Artificial barriers (e.g. dams, weirs and causeways) Flow regulation (drying of intervening shallows) Alien fish species: predators fragment river fish populations Irrigation canals and pumps	Reduced connectivity between river reaches	Adult fish unable to access over-wintering areas resulting in fish being washed downstream Adult fish unable to access spawning and feeding habitats during summer resulting in recruitment failure Juvenile fish unable to access suitable rearing habitat. Fish may end up in unfavourable rearing habitat with insufficient cover from predation and high flows Larval and juvenile fish may become trapped in irrigation canals and entrained in irrigation pumps	Detailed assessment of habitat conditions before the construction of dams or weirs and before the rehabilitation projects are carried out. Construction of bypass mechanisms such as fish ladders (not advisable where this will facilitate invasion by alien fish)	Chapter 4

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APPENDICES

APPENDIX A

APPENDIX A.1 Dates and duration of key fieldtrips undertaken during the course of the study.

From	To	Activities	No. of days
2004/5			
02 Jun 2004	07 Jun 2004	Site Selection	6
11 Aug 2004	15 Aug 2004	Installation of temperature and stage loggers	4
06 Oct 2004	21 Oct 2004	First sampling fieldtrip: Dive Surveys 01 (8/10/04 - 12/10/04)	16
27 Oct 2004	11 Nov 2004	Second sampling fieldtrip: Dive Survey 02 (28/10/04 - 31/10/04) and 03 (7/11/04 - 10/11/04). Identification of spawning sites	16
27 Nov 2004	12 Dec 2004	Third sampling fieldtrip: Dive Survey 04 (7/12/04 - 9/12/04) Monitoring spawning. Collection of eggs and larvae for aging.	16
22 Feb 2005	03 Mar 2005	Fourth sampling fieldtrip: Dive Survey 05 (23/02/05 - 27/02/05). Collection of juveniles for aging.	10
2005/6			
27 Jun 2005	11 Jul 2005	Survey spawning sites Collection of physical habitat information	14
11 Oct 2005	25 Oct 2005	Fifth sampling fieldtrip: Dive Survey 06 (13/10/05 - 16/10/05) and 07 (23/10/05 - 25/10/05). Collection physical habitat information	15
04 Nov 2005	28 Nov 2005	Sixth sampling fieldtrip: Dive Survey 08 (7/11/05 - 10/11/05). Monitoring spawning. Collection physical habitat information.	25
07 Dec 2005	16 Dec 2005	Seventh sampling fieldtrip: Dive Survey 09 (8/12/05 - 11/12/05). Monitoring spawning. Collection of eggs and larvae for aging. Collection physical habitat information.	10
17 Mar 2006	27 Mar 2006	Eighth sampling fieldtrip: Dive Survey 10 (19/03/05 - 22/03/05). Collection of juveniles for aging Collection physical habitat information.	12
10 Nov 2006	20 Nov 2006	Ninth sampling fieldtrip: Collecton of fertilised sawfin eggs for rearing experiments and age validation	10
		Total	**154**

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APPENDIX B

APPENDIX B.1 Location and classification of each of the 87 separate Habitat Units, as well as their upstream hydraulic controls (if these were present), identified along the study segment in terms of the length, width, distance along the river channel (Cum. Dist.); morphological unit type (Morph.); Biotope; width (WDT); Depth (DPT), dominant and sub-dominant flow type (FLW1 and FLW2) and dominant and sub-dominant substratum particle class (SUB1 and SUB2). The key to the categories used follow in APPENDIX B.2.

										Habitat Unit								Upstream control (if present)					
HU	LAT	LONG	HU No.	Reach	LNTH (m)	Cum. Dist. (m)	Morph.	Biotope	WDT (m)	DPT (m)	FLW1	FLW2	SUB1	SUB2	Morph	Biotope	W1	DPT1	FLW1	FLW2	SUB1	SUB_2	Comment
1	-32.4944	19.27961	1	7	9.00	9.00	BRPL	GL	4.6	1.2	RS	RS	BD	LB	CT	CH	4.6	0.2	CH	CH	BR	BR	Run u/s second maalgat waterfall below cascades
2	-32.4944	19.27953	2	7	9.31	18.31	BRPL	GL	5.2	1.1	RS	RS	BD	LB	CT	CH	4.9	0.23	CH	CH	BR	BR	2cnd cascade
3	-32.4943	19.27949	3	7	5.93	24.24	BRPL	GL	8.4	0.85	RS	RS	BD	LB	CT	CH	8.4	0.15	CH	CH	BR	BR	3rd cascade
4	-32.4943	19.27945	4	7	6.27	30.51	BRPL	GL	8.4	0.9	RS	RS	BD	LB	CT	CH	8.4	0.3	CH	CH	BR	BR	Upstream last caade
5	-32.494	19.27944	5	7	28.82	59.33	BP	RS	7	0.82	RS	RS	SB	SB	CT	CH	2.5	0.16	CH	CH	SB	SB	Boulder bed run downstream nursery pool
6	-32.4939	19.27929	6	7	18.76	78.09	PL	PL	12.5	1.9	SBT	SBT	BD	LB	CT	RS	0.7	0.14	RS	RS	BD	LB	Nursery pool
7	-32.4938	19.27865	7	7	60.57	138.65	PL	BPF	15.5	1.9	BPF	BPF	SA	BD	CT	CH	2.5	0.2	CH	CH	BR	SB	Sawfin pool with large boulders
8	-32.4939	19.27835	8	7	28.22	166.88	BRPL	RN	7.3	1.4	RS	RS	BD	CO	CT	CH	0.4	0.2	CH	CH	BD	BR	Run directly u/s of sawfin pool (u/s cascades control)
9	-32.4939	19.27774	9	7	57.11	223.98	CT	RN	8.9	1.4	SBT	RS	BR	BD	BP	CS	1.2	0.3	SW	SW	BR	SA	Glide upstream waterfall
10	-32.494	19.27759	10	7	15.90	239.88	CT	CS	1.2	0.3	CS	CS	BR	BR	BP	CS	1.2	0.3	SW	SW	BR	BR	Bredrock cascades
11	-32.4941	19.27736	11	7	27.26	267.14	BRPL	BR	11.7	1.4	SBT	SBT	BR	BR	BP	CS	1.6	0.25	RS	RS	BR	SB	Pool with deep shelf u/s bedrock cascades
12	-32.4942	19.27732	12	7	6.80	273.94	BP	CS	2.5	0.2	RS	BR	BR	BR	BP	CS	2.5	0.2	RS	RS	BR	BR	2cnd bedrock cascades with vegetation
13	-32.4942	19.27692	13	7	36.80	310.73	BP	RN	9.8	1.4	SBT	SBT	SA	SA	WF	CS	0.6	0.25	SBT	SBT	BR	SA	Last pool on lower reach survey
14	-32.4903	19.27073	14	6	0.00	310.73	X	X	0	0	X	X	X	X	X	X	0	0	X	X	X	X	Reed bed (no sample)
15	-32.489	19.27022	15	6	149.48	460.21	PL	PL	14	2.6	BPF	BPF	SA	SA	RN	RN	12	0.8	SBT	SBT	SA	SA	Wolfberg pool
16	-32.4888	19.2699	16	6	36.80	497.01	RN	R	12	0.5	SBT	SA	SA	SA	RN	R	12	0.5	SBT	SBT	SA	SA	Run u/s wolfberg pool to reeds
17	-32.488	19.2676	17	6	0.00	497.01	X	X	0	0	X	X	X	X	X	X	0	0	X	X	X	X	Begin reeds at sanddrif campsite - no sample
18	-32.4877	19.26655	18	5	103.99	601.00	RN	RN	24	0.3	BPF	SBT	SA	SA	RN	RN	17.3	0.2	BPF	BPF	SA	SA	Sandrif bridge, begin upper survey, yf, one metre, outside meander
19	-32.4877	19.26618	19	5	34.44	635.44	RN	RN	17.3	1.3	BPF	BPF	SA	SA	RN	RN	17.3	0.2	BPF	BPF	SA	SA	Meander bend refugia
20	-32.4881	19.26333	20	5	271.60	907.05	RN	RN	17.3	0.2	BPF	SBT	SA		RN	RN	17.3	0.2	BPF	BPF	SA	SA	Continuation of 18 (long shallow run)
21	-32.488	19.26251	21	5	78.00	985.05	RN	RN	8.2	1.8	BPF	BPF	SA	SA	RN	RN	9.5	0.5	BPF	BPF	SA	SA	Narrowing and deepening (meander COours) of shallow run
22	-32.4874	19.26009	22	5	236.31	1221.35	RN	RN	9.5	0.5	SBT	SBT	SA	SA	RN	RN	9.5	0.5	BPF	BPF	SA	SA	Shallow run
23	-32.4874	19.2599	23	5	19.27	1240.62	PL	PL	8.7	2	BPF	BPF	SA	SA	RN	RN	2.5	0.9	BPF	BPF	SA	SA	Pool just beyond sheds
24	-32.4873	19.25976	24	5	13.11	1253.73	RN	RN	2.5	0.9	BPF	SBT	SA	RW	RN	RN	2.5	0.9	BPF	BPF	SA	SA	Narrow run in reeds after shed pool, reeds
25	-32.4872	19.25934	25	5	41.00	1294.73	RN	RN	8	0.4	SBT	SBT	SA	SA	RN	RN	3	0.6	SBT	SBT	SA	SA	Short run
26	-32.4874	19.25907	26	5	29.87	1324.60	RN	RN	4.4	0.85	RS	RS	SA	GR	RN	RN	6.1	0.55	RS	RS	SA	SA	River bends and deepens
27	-32.4871	19.25852	27	5	59.25	1383.85	PB	RN	8	0.6	SBT	RS	CO	CO	PB	RN	2.2	0.6	SBT	RS	CO	CO	Long open run no canopy
28	-32.4869	19.25837	28	5	23.00	1406.84	RN	RN	2	0.7	SBT	RS	CO	CO	RN	RN	2	0.7	SBT	RS	CO	CO	Channel very braided, 1st sawfin spawning site, canopy
29	-32.4869	19.25799	29	5	36.94	1443.78	RN	RN	2.7	1.1	SBT	RS	CO	CO	RN	RN	4.9	1	SBT	RS	CO	CO	Sawfin spawning site
30	-32.4867	19.2578	30	5	26.91	1470.69	RN	RN	4.9	1	SBT	RS	CO	GR	ST	CH	0.5	0.18	CH	CH	CO	CO	Second spawning site, also yellowfish, chute upstream
31	-32.4865	19.25776	31	5	16.00	1486.69	RN	RN	2.1	1.2	SBT	SBT	SA	CO	RN	RN	2.1	1.2	SBT	SBT	SA	CO	Reeds
32	-32.4864	19.25758	32	5	22.49	1509.18	RN	RN	7.7	0.7	SBT	RS	SA	SA	CT	CS	7.7	0.7	CS	RS	BR	BR	Bedrock, open canopy, spawning pothole
33	-32.4862	19.25674	33	5	82.28	1591.46	PL	PL	13.5	1.7	BPF	BPF	SA	GR	RN	RN	5.2	0.3	SBT	RS	SA	SA	Pool
34			34	5	13.60	1605.06	RN	RN	5.2	1.2	SBT	SBT	BD	BD	RN	RN	6	0.9	SBT	SBT	SA	SA	2 channels
35	-32.4862	19.25641	35	5	17.62	1622.68	RN	RN	6	0.9	SBT	SBT	SA	SA	BP	CS	1.4	0.4	SW	SW	BR	BR	
36	-32.4862	19.25622	36	5	18.97	1641.65	BP	CS	1.4	0.4	SW	SW	BR	BR	RN	RN	6.7	0.8	SBT	SBT	BD	BD	
37	-32.4859	19.25573	37	5	55.72	1697.37	RN	RN	6.7	0.8	SBT	SBT	BD	BD	RN	RN	5.1	1.3	SBT	SBT	SA	SA	
38	-32.4858	19.25552	38	5	21.97	1719.34	RN	RN	5.1	1.3	SBT	SBT	SA	SA	RN	RN	6.6	1.2	BPF	BPF	BR	BR	
39	-32.4857	19.25505	39	5	45.14	1764.48	RN	RN	2	0.6	RS	RS	BR	BR	RN	RN	2	0.6	BPF	BPF	SA	SA	Braided through shrubs and reeds
40	-32.4855	19.25389	40	5	111.36	1875.84	RN	RN	6.6	1.2	BPF	BPF	SA	SA	CS	CS	1	0.2	CS	CS	BR	BR	
41	-32.4851	19.2537	41	5	51.05	1926.89	CS	CS	1	0.2	CS	CS	BR	BR	RN	RN	4.5	1.3	RS	RS	BR	BR	Bedrock cascades
42	-32.4849	19.25387	42	5	27.99	1954.88	RN	RN	4.5	1.3	RS	RS	BR	BR	PL	PL	19	2.8	BPF	BPF	SA	SA	
43	-32.4838	19.2521	43	4	202.70	2157.58	PL	PL	19	2.8	BPF	BPF	SA	SA	RN	RN	4.5	2.3	SBT	SBT	SA	SA	Start of oak tree pool
44	-32.4837	19.2519	44	4	21.80	2179.38	RN	RN	4.5	2.3	SBT	SBT	SA	SA	RN	RN	3	0.8	SBT	RS	CO	CO	End oak tree pool - deep vegetated run
45	-32.4839	19.25146	45	4	44.06	2223.44	RN	RN	3	0.8	RS	RS	CO	CO	RN	RN	3	0.8	RS	RS	CO	CO	Sawfin spawning site
46	-32.4837	19.25095	46	4	50.12	2273.56	RN	RN	3	0.8	RS	RS	CO	CO	RN	RN	3	1	BPF	BPF	BR	BR	
47	-32.4836	19.25059	47	4	38.16	2311.72	RN	RN	3	1	BPF	BPF	BR	BR	PL	PL	8.1	1.7	BPF	BPF	SA	SA	
48	-32.4834	19.25023	48	4	36.39	2348.11	PL	PL	8.1	1.7	BPF	BPF	SA	SA	RN	RN	8.2	1.8	SBT	SBT	CO	CO	
49	-32.4833	19.24976	49	4	47.56	2395.66	RN	RN	8.2	1.8	SBT	SBT	CO	CO	RN	RN	0	1	RS	RS	BR	BR	
50	-32.4833	19.24955	50	4	20.77	2416.43	RN	RN	1.3	1	RS	RS	BR	BR	CS	CH	0.8	0.15	CH	RS	CO	CO	Spawning site
			51	4	14.30	2430.73	RN	RN	13.5	1.2	BPF	BPF	SA	SA	RN	RN	13.5	1.2	BPF	BPF	SA	SA	Deeper area ds wolfberg run
51	-32.4832	19.24942	52	4	69.96	2500.69	RN	RN	14.5	1.3	BPF	RS	BR	SA	CS	CH	0.3	0.2	CH	RS	CO	CO	Wolfberg run
52	-32.4829	19.24878	53	4	19.88	2520.57	X	X	0	0	X	X	X	X	X	X	0	0	X	X	X	X	No sample, end of bedrock spawning pool, braided riffles
53	-32.4827	19.24864	54	4	20.14	2540.70	RN	RN	2	0.8	RS	RS	CO	CO	RS	RS	2.3	0.15	CH	CH	CO	GR	Run, spawning site, eggs collected at 839
54	-32.4826	19.24849	55	4	35.52	2576.23	PL	PL	16.4	2.7	BPF	BPF	SA	SA	RN	RN	12.7	1.7	SBT	SBT	SA	SA	Evening pool
55	-32.4825	19.24814	56	4	30.42	2606.64	RN	RN	2	2	BPF	BPF	SA	SA	RN	RN	2	2	BPF	BPF	SA	SA	Run flowing into evening pool
56	-32.4825	19.24782	57	3	127.82	2734.46	RN	RN	12.4	0.7	SBT	SBT	SA	SA	RN	RN	8.25	0.5	SBT	SBT	SA	SA	Begin long sandy run
57	-32.4825	19.24646	58	3	18.85	2753.31	RN	RN	8.25	1.43	SBT	SBT	SA	SA	RS	RS	5.9	0.26	RS	RS	CO	SA	Deeper pool/run

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APPENDIX B.1 (cont'd)

							Habitat Unit								Upstream control								
HU	LAT	LONG	HU No.	Reach	LNTH (m)	Cum. Dist. (m)	Morph.	Biotope	WDT (m)	DPT (m)	FLW1	FLW2	SUB1	SUB2	Morph	Biotope	W1	DPT1	FLW1	FLW2	SUB1	SUB_2	Comment_ha
58	-32.4826	19.24628	59	3	37.80	2791.11	RS	RS	5.9	0.26	RS	SA	CO	SA	RN	RN	9.6	1.25	SBT	GR	GR		Shallower riffle
59	-32.4827	19.24589	60	3	110.52	2901.63	RN	RN	9.6	0.35	SBT	SBT	SA	SA	RN	RN	9.6	0.35	SBT	SBT	SA	SA	Begin very long open shallow run
60	-32.4825	19.24473	61	3	64.59	2966.21	RN	RN	9	1.3	SBT	SBT	GR	GR	RS	RS	7	0.3	RS	RS	GR	CO	Deeper section of long shallow run
61	-32.4822	19.24414	62	3	41.75	3007.96	RN	RN	6	0.38	SBT	SBT	CO	SA	RS	RS	4.5	0.47	RS	RS	CO	GR	Run upstream of discharge riffle
62	-32.4821	19.24373	63	3	94.48	3102.44	RS	RS	4.5	0.47	RS	RS	CO	CO	RS	RS	4.5	0.47	RS	RS	CO	GR	Sneeuberg
63	-32.4818	19.2428	64	3	131.71	3234.15	PL	PL	12.5	1.1	BPF	BPF	SA	SA	CS	CS	0.5	0.15	CH	CH	SA	SA	Upstream sneeuberg
64	-32.4811	19.24166	65	3	40.31	3274.46	RN	RN	3.3	0.9	SBT	SBT	SA	SA	RN	RN	3.3	0.9	SBT	SBT	SA	SA	Run immediately downstream tafelberg pool
65	-32.4809	19.24127	66	3	270.85	3545.32	RN	RN	18.3	1.09	BPF	BPF	SA	SA	RS	RS	7.9	0.15	RS	RS	CO	GR	Tafelberg pool
66	-32.479	19.23951	67	3	23.09	3568.41	RS	RS	7.9	0.15	RS	RS	CO	GR	RS	RS	7.9	0.15	RS	RS	CO	GR	Lower tafelberg riffle, spawning
67	-32.4789	19.23931	68	3	89.63	3658.04	RN	RN	6.5	0.85	BPF	BPF	SA	SA	RS	RS	6.2	0.15	RS	RS	CO	GR	Run upstream of lower tafelberg
68	-32.4785	19.23847	69	3	25.93	3683.98	RS	RS	6.2	0.8	RS	RS	CO	GR	RS	RS	5.6	0.6	RS	RS	CO	GR	Short run between tafelberg and upper tafelberg
69	-32.4783	19.23826	70	3	29.75	3713.73	RS	RS	5.6	0.6	RS	RS	CO	GR	RS	RS	5.6	0.6	RS	RS	CO	GR	Upper tafelberg spawning site
70	-32.4783	19.23796	71	3	112.00	3825.73	RN	RN	12.1	0.61	BPF	BPF	SA	SA	RS	RS	3	0.28	RS	RS	GR	GR	Run upstream upper tafelberg spawning site
71	-32.4776	19.23705	72	3	29.72	3855.45	RS	RS	3	0.28	RS	RS	GR	GR	RS	RS	3	0.28	RS	RS	GR	GR	Last sawfin spawning site
72	-32.4776	19.23674	73	3	158.82	4014.27	RN	RN	6.75	0.77	BPF	BPF	CO	CO	RN	RN	6.35	0.66	SBT	SBT	GR	GR	
73	-32.4768	19.23529	74	3	110.50	4124.77	RN	RN	6.35	0.66	SBT	SBT	GR	GR	PL	PL	18.7	0.82	BPF	BPF	SA	SA	
74	-32.4761	19.23444	75	3	77.35	4202.13	PL	PL	18.7	0.82	BPF	BPF	SA	SA	RN	RN	8.25	0.67	SBT	SBT	SA	SA	
75	-32.4755	19.23411	76	3	91.55	4293.68	RN	RN	8.25	0.67	SBT	SBT	SA	SA	RN	RN	5.3	0.65	SBT	SBT	CO	SA	
76	-32.4747	19.2337	77	3	69.09	4362.76	RN	RN	5.3	0.65	SBT	SBT	CO	SA	RN	RN	1.35	0.45	RS	RS	GR	GR	
77	-32.4743	19.23316	78	3	40.16	4402.92	RN	RN	1.35	0.45	RS	RS	GR	GR	RN	RN	4.35	1.16	SBT	GR	GR	GR	Very braided
78	-32.4746	19.23295	79	3	81.09	4484.02	RN	RN	6.5	0.9	BPF	BPF	GR	CO	PL	PL	17.6	1.7	BPF	BPF	SA	SA	
79	-32.4744	19.23214	80	2	100.78	4584.80	PL	PL	17.6	1.7	BPF	BPF	SA	SA	RS	RS	6.6	0.4	RS	RS	BR	BR	1st pool
80	-32.4736	19.23155	81	2	15.32	4600.12	RS	RS	6.6	0.4	RS	RS	BR	BR	RS	RS	6.6	0.4	RS	RS	BR	BR	Bedrock riffle
81	-32.4735	19.23145	82	2	68.25	4668.38	PL	PL	22.6	2	BPF	BPF	SA	SA	RS	RS	5.6	0.3	RS	RS	BR	BR	2cnd pool
82	-32.4732	19.23084	83	2	109.08	4777.45	PL	PL	15.5	2.7	BPF	BPF	SA	SA	BP	CS	1.6	0.2	SW	SW	BR	BR	3rd pool
83	-32.4728	19.22974	84	2	12.84	4790.29	BP	CS	1.6	0.2	SW	SW	BR	BR	BP	CS	1.6	0.2	SW	SW	BR	BR	Driehoeks cascades, spawning observed in potholes 2005 Nov
84	-32.4728	19.22963	85	1	50.91	4841.20	PL	PL	15.4	2.5	BPF	BPF	BR	BR	CS	CS	3.08	0.55	CS	CS	BR	BR	Bedrock pool upstream Driehoeks cascades
85	-32.4725	19.22917	86	1	19.46	4860.66	CS	CS	3.08	0.55	CS	CS	BR	BR	CS	CS	3.08	0.55	CS	CS	BR	BR	Small cascades u/s Driehoeks cascades
86	-32.4724	19.229	87	1	33.97	4894.63	PL	PL	12.12	1.45	BPF	BPF	BR	BR	CS	CS	1.3	0.15	CS	CS	BR	BR	Short pool upstream final cascades
87	-32.4725	19.22865	88	1			X	X	0	0	X	X	X	X	X	X	0	0	X	X	X	X	End dive survey

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APPENDIX B.2 Categories used to classify Habitat units in Table 3, according to Rowntree and Wadeson (1999).

SUBSTRATUM CLASS	KEY	Description
Sand	SA	<2mm
Gravel	GR	2-64 mm
Cobble	CO	64-256 mm
Boulder	BD	256-1000 mm
Bedrock	BR	>1000 mm
FLOW TYPE		
No flow	NF	no water movement
Barely perceptible flow	BPF	smooth surface flow, perceptible through floating objects
Smooth boundary turbulent flow	SBT	water surface smooth, streaming flow
Rippled surface	RS	transverse ripples across flow direction
Standing waves	SW	undular or broken standing waves
Cascade	CS	bed has a stepped structure due to cobble
Chute	CH	water channeled between large bed elements
MORPHOLOGICAL UNIT		
Alluvial Pool	PL	topographical low point caused by scour
Bedrock Pool	BRPL	deeper flow behind resistant strata
Bedrock Pavement	BP	horizontal area of exposed rock
Cataract	CT	step-like succession of small waterfalls
Step	ST	step-like features formed by large cobbles or boulders
HYDRAULIC BIOTOPE		
Pool	PL	deep, slow flowing
Run	RN	transition between pool and riffle, low relative roughness
Riffle	RF	topographic high points, high relative roughness
Glide	GL	uniform flow, no convergence or divergence
Chute	CH	Water channeled between large bed elements

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APPENDIX B.3 Estimates of the abundance of adult sawfin (>150 mm TL) recorded during the course of dive surveys between October 2004 and March 2006. Summary statistics are reported for each reach: total, mean no. of fish per morphological unit, Standard Deviation (SD) and Coefficient of Variation (CV). Reaches are numbered from upstream (Reach 01) to downstream (Reach 07) for presentation purposes. Dives took place from downstream to upstream and morphological units are therefore listed in that order.

	Morph Unit	Dive 01 Oct 2004	Dive 02 Oct 2004	Dive 03 Nov 2004	Dive 04 Dec 2004	Dive 05 Mar 2005	Dive 06 Oct 2005	Dive 07 Oct 2005	Dive 08 Nov 2005	Dive 09 Dec 2005	Dive 10 Mar 2006
Reach 01	85								1		1
	86										
	87										
	Total	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*1*	*0*	*1*
	Mean	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*0.33*	*0.00*	*0.33*
	SD	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*0.58*	*0.00*	*0.58*
	CV	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*1.73*	*0.00*	*1.73*
Reach 02	80			12	68	18			2	12	85
	81										
	82		1	60	25	20			1	11	32
	83				21				100	40	
	84									15	
	Total	*0*	*1*	*72*	*114*	*38*	*0*	*0*	*103*	*78*	*117*
	Mean	*0.00*	*0.20*	*14.40*	*22.80*	*7.60*	*0.00*	*0.00*	*20.60*	*15.60*	*23.40*
	SD	*0.00*	*0.45*	*26.02*	*27.80*	*10.43*	*0.00*	*0.00*	*44.39*	*14.77*	*37.12*
	CV	*0.00*	*2.24*	*1.81*	*1.22*	*1.37*	*0.00*	*0.00*	*2.16*	*0.95*	*1.59*
Reach 03	57		2	28					3		
	58								1	2	23
	59								7		
	60										
	61				1					60	34
	62					1			40		
	63			11	83				7		
	64			3	23	25			7	35	8
	65										2
	66				12	55				60	26
	67			92	25				10		
	68								8		
	69				2				5		
	70			68						60	
	71								1	1	
	72										
	73				40	43				30	
	74				50	20			2		7
	75					8				5	12
	76										
	77					4					2
	78										
	79			5	40	10				7	54
	Total	*0*	*2*	*207*	*276*	*166*	*0*	*0*	*91*	*260*	*168*
	Mean	*0.00*	*0.09*	*9.00*	*12.00*	*7.22*	*0.00*	*0.00*	*4.23*	*11.82*	*7.30*
	SD	*0.00*	*0.42*	*23.51*	*21.93*	*14.90*	*0.00*	*0.00*	*8.71*	*21.75*	*14.00*
	CV	*0.00*	*4.80*	*2.61*	*1.83*	*2.06*	*0.00*	*0.00*	*2.06*	*1.84*	*1.92*
Reach 04	43			9	18	20		9		1	
	44		12	2	38	2				27	2
	45		2					2			
	46		17	6	1	6		6	31		
	47		25	35		8		6			
	48			23							
	49				60				13	48	
	50							5		4	
	51		28			1					
	52			75	40				60		
	54			17		2			24		
	55		15	70				27			65
	56		2						5		1
	Total	*0*	*101*	*237*	*157*	*39*	*0*	*55*	*133*	*80*	*68*
	Mean	*0.00*	*7.77*	*18.23*	*12.08*	*3.00*	*0.00*	*4.23*	*10.23*	*6.15*	*5.23*
	SD	*0.00*	*10.37*	*26.41*	*20.56*	*5.72*	*0.00*	*7.52*	*18.19*	*14.60*	*17.97*
	CV	*0.00*	*1.33*	*1.45*	*1.70*	*1.91*	*0.00*	*1.78*	*1.78*	*2.37*	*3.44*

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APPENDIX B.3 (cont'd)

	Morph Unit	Dive 01 Oct 2004	Dive 02 Oct 2004	Dive 03 Nov 2004	Dive 04 Dec 2004	Dive 05 Mar 2005	Dive 06 Oct 2005	Dive 07 Oct 2005	Dive 08 Nov 2005	Dive 09 Dec 2005	Dive 10 Mar 2006
Reach 05	18									3	
	19	40	60	6			56	70	30		
	20										
	21	4	25	7	8	23	5	40	33		36
	22										4
	23		1					1			
	24										
	25										
	26	1									
	27										
	28			20							
	29				60					1	
	30			3		1					
	31										
	32							5		2	
	33		20		30	30			36	17	43
	34							15			
	35								9		
	36									5	
	37								1		20
	38									2	
	39									2	
	40				3	6			25		
	41									1	
	42										
	Total	*45*	*106*	*36*	*101*	*60*	*61*	*131*	*134*	*33*	*103*
	Mean	*1.80*	*4.24*	*1.44*	*4.04*	*2.40*	*2.44*	*5.24*	*5.36*	*1.32*	*4.12*
	SD	*8.00*	*13.19*	*4.29*	*13.17*	*7.42*	*11.20*	*15.90*	*11.68*	*3.50*	*11.43*
	CV	*4.44*	*3.11*	*2.98*	*3.26*	*3.09*	*4.59*	*3.03*	*2.18*	*2.65*	*2.77*
Reach 06	15		~200	8			80	5	42		
	16										
	Total	*0*	*200*	*8*	*0*	*0*	*80*	*5*	*42*	*0*	*0*
	Mean	*0.00*	*100.00*	*4.00*	*0.00*	*0.00*	*40.00*	*2.50*	*21.00*	*0.00*	*0.00*
	SD	*0.00*	*141.42*	*5.66*	*0.00*	*0.00*	*56.57*	*3.54*	*29.70*	*0.00*	*0.00*
	CV	*0.00*	*1.41*	*1.41*	*0.00*	*0.00*	*1.41*	*1.41*	*1.41*	*0.00*	*0.00*
Reach 07	01	1									
	02										
	03										
	04										
	05					1	1		6		
	06										
	07	5	21	55	57	12	1	12	39	38	
	08			20			3	1	3	2	5
	09					3	2	13	35	10	
	10					23		1	11		1
	11	8	21	34			2			20	
	12				30				6		
	13	2							5	2	
	Total	*16*	*42*	*109*	*87*	*39*	*9*	*27*	*105*	*72*	*6*
	Mean	*1.23*	*3.23*	*8.38*	*6.69*	*3.00*	*0.69*	*2.08*	*8.08*	*5.54*	*0.46*
	SD	*2.49*	*7.89*	*17.48*	*17.24*	*6.87*	*1.03*	*4.65*	*13.31*	*11.38*	*1.39*
	CV	*2.02*	*2.44*	*2.08*	*2.58*	*2.29*	*1.49*	*2.24*	*1.65*	*2.05*	*3.01*
	Grand Total	*61*	*452*	*669*	*735*	*342*	*150*	*218*	*611*	*523*	*463*
	Mean	*0.73*	*5.38*	*7.96*	*8.75*	*4.07*	*1.79*	*2.60*	*7.36*	*6.30*	*5.51*
	SD	*4.26*	*21.88*	*18.80*	*18.39*	*9.49*	*9.86*	*8.95*	*15.79*	*14.03*	*14.20*
	CV	*5.87*	*4.07*	*2.36*	*2.10*	*2.33*	*5.52*	*3.45*	*2.14*	*2.23*	*2.58*

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APPENDIX B.4 Estimates of abundance of juvenile sawfin (20-150 mm TL) and larval (5-20 mm TL – in parentheses) recorded during the course of dive surveys between October 2004 and March 2006. Summary statistics are reported for each reach (Total, Mean, Standard Deviation (SD) and Coefficient of Variation (CV)). Reaches are numbered from upstream (Reach 01) to downstream (Reach 07) for presentation purposes. Dives took place from downstream to upstream and Habitat Units are therefore listed in that order.

	Habitat Unit	Dive 01 Oct 2004	Dive 02 Oct 2004	Dive 03 Nov 2004	Dive 04 Dec 2004	Dive 05 Mar 2005	Dive 06 Oct 2005	Dive 07 Oct 2005	Dive 08 Nov 2005	Dive 09 Dec 2005	Dive 10 Mar 2006
Reach 01	85						21			100	213
	86				77	118					
	87					3	70				3
	Total	*0*	*0*	*0*	*77*	*121*	*91*	*0*	*0*	*100*	*216*
	Mean	*0.00*	*0.00*	*0.00*	*25.67*	*40.33*	*30.33*	*0.00*	*0.00*	*33.33*	*72.00*
	SD	*0.00*	*0.00*	*0.00*	*44.46*	*67.28*	*35.92*	*0.00*	*0.00*	*57.74*	*122.12*
	CV	*0.00*	*0.00*	*0.00*	*1.73*	*1.67*	*1.18*	*0.00*	*0.00*	*1.73*	*1.70*
Reach 02	80										
	81										
	82										
	83				8						
	84										
	Total	*0*	*0*	*0*	*8*	*0*	*0*	*0*	*0*	*0*	*0*
	Mean	*0.00*	*0.00*	*0.00*	*1.60*	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*
	SD	*0.00*	*0.00*	*0.00*	*3.58*	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*
	CV	*0.00*	*0.00*	*0.00*	*2.24*	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*
Reach 03	57										
	58										
	59										
	60									(10)	
	61									(5)	
	62				(28)						
	63										
	64				(3)						
	65				(306)						
	66				(3)					(67)	
	67										
	68									(2)	
	69										
	70										
	71								1		
	72										
	73										
	74										
	75										
	76										
	77										
	78										
	79										
	Total	*0*	*0*	*0*	*(340)*	*0*	*0*	*0*	*1*	*(84)*	*0*
	Mean	*0.00*	*0.00*	*0.00*	*(17.00)*	*0.00*	*0.00*	*0.00*	*0.04*	*(4.42)*	*0.00*
	SD	*0.00*	*0.00*	*0.00*	*(91.61)*	*0.00*	*0.00*	*0.00*	*0.21*	*(21.13)*	*0.00*
	CV	*0.00*	*0.00*	*0.00*	*(5.39)*	*0.00*	*0.00*	*0.00*	*4.80*	*(4.77)*	*0.00*
Reach 04	*43*										
	44										
	45										
	46										
	47										
	48										
	49										
	50										
	51										
	52									*(7)*	
	54										
	55										
	56										
	Total	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*7*	*0*
	Mean	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*0.30*	*0.00*
	SD	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*1.40*	*0.00*
	CV	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*4.60*	*0.00*

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APPENDIX B.4 (cont'd)

	Morph Unit	Dive 01 Oct 2004	Dive 02 Oct 2004	Dive 03 Nov 2004	Dive 04 Dec 2004	Dive 05 Mar 2005	Dive 06 Oct 2005	Dive 07 Oct 2005	Dive 08 Nov 2005	Dive 09 Dec 2005	Dive 10 Mar 2006
Reach 05	18										
	19										
	20				2 (6)						
	21				(7)	15					
	22					407					41
	23										
	24				(1)						38
	25										
	26				(1)	18					
	27					3					23
	28				(1)						
	29					16					
	30										
	31										
	32				3						5
	33										
	34										
	35										
	36					1					
	37										
	38										
	39										2
	40										17
	41										
	42										
Total		*0*	*0*	*0*	*5 (16)*	*460*	*0*	*0*	*0*	*0*	*126*
Mean		*0.00*	*0.00*	*0.00*	*0.20 (0.8)*	*18.40*	*0.00*	*0.00*	*0.00*	*0.00*	*5.04*
SD		*0.00*	*0.00*	*0.00*	*0.71 (1.9)*	*81.14*	*0.00*	*0.00*	*0.00*	*0.00*	*11.79*
CV		*0.00*	*0.00*	*0.00*	*3.54 (2.38)*	*4.41*	*0.00*	*0.00*	*0.00*	*0.00*	*2.34*
Reach 06	15										
	16										
Total		0	0	0	0	0	0	0	0	0	0
Mean		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SD		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CV		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Reach 07	01			8			3		3		33
	02					2			4		23
	03				8	9					
	04					12					66
	05	3		13	145						35
	06			29		60					23
	07		100	106	160		1		1		
	08			64	65			65			37
	09				24						56
	10										55
	11					80	1				
	12								26		14
	13						26			26	11
Total		*3*	*100*	*220*	*402*	*163*	*31*	*65*	*34*	*26*	*353*
Mean		*0.23*	*7.69*	*16.92*	*30.92*	*12.54*	*2.38*	*5.00*	*2.62*	*2.00*	*27.15*
SD		*0.83*	*27.74*	*32.51*	*57.05*	*26.12*	*7.15*	*18.03*	*7.15*	*7.21*	*22.34*
CV		*3.61*	*3.61*	*1.92*	*1.84*	*2.08*	*3.00*	*3.61*	*2.73*	*3.61*	*0.82*
Grand Total		***3***	***100***	***220***	***492 (356)***	***744***	***122***	***65***	***35***	***126 (91)***	***695***
Mean		***0.04***	***1.19***	***2.62***	***5.86 (8.28)***	***8.86***	***1.45***	***0.77***	***0.42***	***1.50 (2.11)***	***8.27***
SD		***0.43***	***14.28***	***17.92***	***32.40 (33.28)***	***44.76***	***8.21***	***9.28***	***3.76***	***10.76 (7.37)***	***26.84***
CV		***12.00***	***12.00***	***6.84***	***5.53 (4.02)***	***5.05***	***5.65***	***12.00***	***9.02***	***7.17 (3.49)***	***3.24***

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APPENDIX B.5 Complete list of Clanwilliam yellowfish and sawfin tagged in the Driehoeks River between October 2004 and November 2005, showing the tag no., Total Length (TL mm); Fork Length (TL mm); mass (g); girth (mm), sex, gonad development stage (Gon. Dev.) when these were measured or could be ascertained. Recap = recapture fish (marked with asterisk), LF = Large Fyke, RR = ripe-and-running.

Year	Mon	Day	Gear	Samp. no.	Samp. Code	Site name	Genus	Species	Tag No.	Recap	TL (mm)	FL (mm)	SL (mm)	Mass (g)	Girth (mm)	Sex	God Dev
2004	10	9	LF	01	DH-9102004-LF01	Driehoeks Pool	*Barbus*	*serra*	P03		337			102	110		
2004	10	9	LF	01	DH-9102004-LF01	Driehoeks Pool	*Barbus*	*serra*	P04		292			218.5	146		
2004	10	9	LF	01	DH-9102004-LF01	Driehoeks Pool	*Barbus*	*serra*	P05		295			226.5	148		
2004	10	9	LF	01	DH-9102004-LF01	Driehoeks Pool	*Barbus*	*serra*	P23		306			241.5	148		
2004	10	9	LF	01	DH-9102004-LF01	Driehoeks Pool	*Barbus*	*serra*	P24		225			83.3	102		
2004	10	9	LF	01	DH-9102004-LF01	Driehoeks Pool	*Barbus*	*serra*	P43		247			120.5	115		
2004	10	9	LF	01	DH-9102004-LF01	Driehoeks Pool	*Barbus*	*serra*	P45		224			94	110		
2004	10	9	LF	01	DH-9102004-LF01	Driehoeks Pool	*Barbus*	*serra*	P65		215			80.3	101		
2004	10	9	LF	01	DH-9102004-LF01	Driehoeks Pool	*Barbus*	*serra*	S16		258			141.5	122		
2004	10	9	LF	01	DH-9102004-LF01	Driehoeks Pool	*Barbus*	*serra*	S17		265			151.3	122		
2004	10	9	LF	01	DH-9102004-LF01	Driehoeks Pool	*Barbus*	*serra*	S19		236			109.5	112		
2004	10	9	LF	01	DH-9102004-LF01	Driehoeks Pool	*Barbus*	*serra*	S36		271			171.5	132		
2004	10	9	LF	01	DH-9102004-LF01	Driehoeks Pool	*Barbus*	*serra*	S37		234			114.5	112		
2004	10	9	LF	01	DH-9102004-LF01	Driehoeks Pool	*Barbus*	*serra*	S38		243			110.5	110		
2004	10	9	LF	01	DH-9102004-LF01	Driehoeks Pool	*Barbus*	*serra*	S39		283			200.5	138		
2004	10	9	LF	01	DH-9102004-LF01	Driehoeks Pool	*Barbus*	*serra*	S55		290			185.5	133		
2004	10	9	LF	01	DH-9102004-LF01	Driehoeks Pool	*Barbus*	*serra*	S56		352			410.4	178		
2004	10	9	LF	01	DH-9102004-LF01	Driehoeks Pool	*Barbus*	*serra*	S57		294			214	140		
2004	10	9	LF	01	DH-9102004-LF01	Driehoeks Pool	*Barbus*	*serra*	S58		299			239.3	148		
2004	10	9	LF	01	DH-9102004-LF01	Driehoeks Pool	*Barbus*	*serra*	S75		263			151.1	125		
2004	10	9	LF	01	DH-9102004-LF01	Driehoeks Pool	*Barbus*	*serra*	S78		252			134.8	120		
2004	10	9	LF	01	DH-9102004-LF01	Driehoeks Pool	*Barbus*	*serra*	S79		275			160	128		
2004	10	9	LF	01	DH-9102004-LF01	Driehoeks Pool	*Barbus*	*serra*	S98		258			143.7	125		
2004	10	9	LF	01	DH-9102004-LF01	Driehoeks Pool	*Barbus*	*serra*	S99		296			191.5	138		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P02		228			103	114		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P11		455			867	224		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P12		253			149.3	125		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P14		263			145.9	122		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P15		214			81.2	103		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P21		244			124	119		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P22		282			194.2	136		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P31		289			196.5	136		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P32		227			98.9	109		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Labeobarbus*	*capensis*	P33		320			265.5	153		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P34		275			169.5	130		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P35		221			90.5	109		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P40		278			189.2	135		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Labeobarbus*	*capensis*	P41		315			269.5	156		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P42		197			66.3	96		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P44		192			56.1	92		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P51		256			143.2	123		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P53		281			189.2	133		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P54		258			141.5	122		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P55		244			114	112		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P60		252			127.5	116		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P61		271			159.5	130		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P62		199			85.5	93		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P63		320			267.1	151		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P64		294			208.9	142		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P71		248			117.9	114		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Labeobarbus*	*capensis*	P72		327			283.5	156		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P73		242			110.5	114		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P74		219			91.5	110		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P75		310			263.5	154		

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APPENDIX B.5 (cont'd)

Year	Mon	Day	Gear	Samp. no.	Samp. Code	Site name	*Genus*	*Species*	Tag No.	Recap	TL (mm)	FL (mm)	SL (mm)	Mass (g)	Girth (mm)	Sex	God Dev
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P80		211			75.5	102		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P81		227			100.5	110		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P82		281			196.5	138		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P83		233			101.4	111		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P91		239			116.5	120		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P92		243			122	118		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Labeobarbus*	*capensis*	P93		302			226.1	142		
2004	10	13	LF	01	DH-13102004-LF01	Driehoeks camp	*Barbus*	*serra*	P95		252			143.5	126		
2004	11	30	SF	01	DH-30112004-SF01		*Barbus*	*serra*	P16		276			176	129	M	RR
2004	11	30	SF	01	DH-30112004-SF01		*Barbus*	*serra*	P17		266			135.5	124	-	
2004	11	30	SF	01	DH-30112004-SF01		*Barbus*	*serra*	P18		222			92	105	-	
2004	11	30	SF	01	DH-30112004-SF01		*Barbus*	*serra*	P19		236			103	109	-	
2004	11	30	SF	01	DH-30112004-SF01		*Labeobarbus*	*capensis*	S05		427			733.4	212	F	RR
2004	11	30	SF	01	DH-30112004-SF01		*Barbus*	*serra*	S25		270			144.8	119	F	RR
2004	11	30	SF	01	DH-30112004-SF01		*Barbus*	*serra*	S26		276			165.3	126	-	
2004	11	30	SF	01	DH-30112004-SF01		*Barbus*	*serra*	S27		277			164	127	M	RR
2004	11	30	SF	01	DH-30112004-SF01		*Barbus*	*serra*	S28		281			178.5	134	-	
2004	11	30	SF	01	DH-30112004-SF01		*Labeobarbus*	*capensis*	S29		394			498.3	186	M	RR
2004	11	30	SF	01	DH-30112004-SF01		*Barbus*	*serra*	S45		286			181	128	F	RR
2004	11	30	SF	01	DH-30112004-SF01		*Barbus*	*serra*	S46		345			360.1	163	F	RR
2004	11	30	SF	01	DH-30112004-SF01		*Barbus*	*serra*	S47		264			141.6	116	F	SP
2004	11	30	SF	01	DH-30112004-SF01		*Barbus*	*serra*	S48		255			130.9	118	F	SP
2004	11	30	SF	01	DH-30112004-SF01		*Barbus*	*serra*	S49		288			196	137	M	RR
2004	11	30	SF	01	DH-30112004-SF01		*Barbus*	*serra*	S65		250			127	118	M	RR
2004	11	30	SF	01	DH-30112004-SF01		*Barbus*	*serra*	S67		271			169.3	126	M	RR
2004	11	30	SF	01	DH-30112004-SF01		*Barbus*	*serra*	S68		239			177.9	114	M	RR
2004	11	30	SF	01	DH-30112004-SF01		*Barbus*	*serra*	S69		259			140.8	120	M	RR
2004	11	30	SF	01	DH-30112004-SF01		*Labeobarbus*	*capensis*	S85		286			193.7	133	M	RR
2004	11	30	SF	01	DH-30112004-SF01		*Barbus*	*serra*	S86		279			174.5	127	-	
2004	11	30	SF	01	DH-30112004-SF01		*Barbus*	*serra*	S89		293			207	136	M	RR
2004	12	4	SF	01	DH-4122004-SF01	Nursery Pool	*Barbus*	*serra*	P36		228			87.95	100		
2004	12	4	SF	01	DH-4122004-SF01	Nursery Pool	*Barbus*	*serra*	P37		191			58.14	86		
2004	12	4	SF	01	DH-4122004-SF01	Nursery Pool	*Barbus*	*serra*	P38		274.5			174.5	124		
2004	12	4	SF	01	DH-4122004-SF01	Nursery Pool	*Barbus*	*serra*	P39		218			79.06	98		
2004	12	4	SF	01	DH-4122004-SF01	Nursery Pool	*Barbus*	*serra*	P56		225			84.1	90		
2004	12	4	SF	01	DH-4122004-SF01	Nursery Pool	*Barbus*	*serra*	P76		250			130.9	114		
2005	02	24	LF	01	DH-24022005-LF01	Driehoeks Pool	*Barbus*	*serra*	P77		182						
2005	02	24	LF	01	DH-24022005-LF01	Driehoeks Pool	*Barbus*	*serra*	P79		200						
2005	02	24	LF	01	DH-24022005-LF01	Driehoeks Pool	*Barbus*	*serra*	P98		217						
2005	02	24	LF	01	DH-24022005-LF01	Driehoeks Pool	*Barbus*	*serra*	S62		184						
2005	02	24	LF	01	DH-24022005-LF01	Driehoeks Pool	*Barbus*	*serra*	S84		159						
2005	02	25	LF	01	DH-25022005-LF01	Driehoeks camp	*Barbus*	*serra*	P99		252						
2005	02	25	LF	01	DH-25022005-LF01	Driehoeks camp	*Labeobarbus*	*capensis*	S23		257						
2005	02	25	LF	01	DH-25022005-LF01	Driehoeks camp	*Barbus*	*serra*	S24		220						
2005	02	25	LF	01	DH-25022005-LF01	Driehoeks camp	*Barbus*	*serra*	S40		284						
2005	02	25	LF	01	DH-25022005-LF01	Driehoeks camp	*Barbus*	*serra*	S41		256						
2005	02	25	LF	01	DH-25022005-LF01	Driehoeks camp	*Barbus*	*serra*	S42		280						
2005	02	25	LF	01	DH-25022005-LF01	Driehoeks camp	*Barbus*	*serra*	S43		246						
2005	02	25	LF	01	DH-25022005-LF01	Driehoeks camp	*Barbus*	*serra*	S44		144						
2005	02	25	LF	01	DH-25022005-LF01	Driehoeks camp	*Barbus*	*serra*	S60		258						
2005	02	25	LF	01	DH-25022005-LF01	Driehoeks camp	*Barbus*	*serra*	S61		221						
2005	02	26	LF	01	DH-26022005-LF01	Driehoeks camp	*Barbus*	*serra*	S21		263						
2005	02	26	LF	01	DH-26022005-LF01	Driehoeks camp	*Barbus*	*serra*	S22		250						
2005	02	26	LF	01	DH-26022005-LF01	Driehoeks camp	*Barbus*	*serra*	S24R								
2005	02	27	SF	01	DH-27022005-SF01	Tafelberg Pool	*Barbus*	*serra*	S01		286						
2005	02	27	SF	01	DH-27022005-SF01	Tafelberg Pool	*Barbus*	*serra*	S02		307						

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APPENDIX B.5 (cont'd)

Year	Mon	Day	Gear	Samp. no.	Samp. Code	Site name	*Genus*	*Species*	Tag No.	Recap	TL (mm)	FL (mm)	SL (mm)	Mass (g)	Girth (mm)	Sex	God Dev
2005	02	27	SF	01	DH-27022005-SF01	Tafelberg Pool	*Barbus*	*serra*	S20		313						
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	G07		259	208	216	178	140		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	G08		255	207	130	152	132		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	G09		250	221	207	149	121		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	G18		220	182	180	95.3	112		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	P06		275	241	222	184	140		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	P07		255	221	203	131	122		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	P08		272	241	225	196	144		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	P09		280	145	230	198	146		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	P10		300	263	245	258.3	154		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	P26		225	194	178	88.1	108		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	P27		280	248	232	204	122		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	P28		264	231	216	170	138		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	P29		255	223	207	155	138		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	P30		240	213	198	126	126		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	P46		265	235	218	165	136		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	P47		246	217	202	137	125		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	P48		248	217	202	137.5	130		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	P49		242	208	193	123.5	126		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	P50		281	248	230	190	140		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	P58		282	247	235	213.3	148		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	P59		254	221	212	150	129		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	P66		239	208	193	137.5	132		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	P67		322	285	270	313	176		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	P68		233	205	190	73.3	126		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	P69		261	227	211	160.8	138		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	P70		255	224	210	150	132		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	P86		268	237	224	186	140		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	P87		258	225	213	158	140		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	P88		219	189	179	94.5	111		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	P89		288	247	230	195	142		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	P90		270	236	223	170	135		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	P96		220	197	185	101.5	108		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	S03		268	237	223	177.8	138		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	S04		334	290	276	350.6	180		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	S82		270	239	226	178.5	135		
2005	10	15	LF	01	DH-15102005-LF01	Sanddrif Pool	*Barbus*	*serra*	S83		253	223	211	155	130		
2005	10	21	LF	01	DH-21102005-LF01	Piero's Pool	*Barbus*	*serra*	S53		312					M	RR
2005	10	21	LF	01	DH-21102005-LF01	Piero's Pool	*Barbus*	*serra*	S72		265					M	RR
2005	10	21	LF	01	DH-21102005-LF01	Piero's Pool	*Barbus*	*serra*	S73		350						
2005	10	21	LF	01	DH-21102005-LF01	Piero's Pool	*Barbus*	*serra*	S74		273						
2005	10	21	LF	01	DH-21102005-LF01	Piero's Pool	*Barbus*	*serra*	S90		298						
2005	10	21	LF	01	DH-21102005-LF01	Piero's Pool	*Barbus*	*serra*	S91		278					M	RR
2005	10	21	LF	01	DH-21102005-LF01	Piero's Pool	*Barbus*	*serra*	S92		319						
2005	10	21	LF	01	DH-21102005-LF01	Piero's Pool	*Labeobarbus*	*capensis*	S93		305						
2005	10	21	LF	01	DH-21102005-LF01	Piero's Pool	*Barbus*	*serra*	S94	*	311						
2005	11	06	LF	01	DH-06112005-LF01	Piero's Pool	*Barbus*	*serra*	G19		265	231	219				
2005	11	08	LF	01	DH-08112005-LF01	Piero's Pool	*Barbus*	*serra*	D40	*	230	202	190			M	RR
2005	11	08	LF	01	DH-08112005-LF01	Piero's Pool	*Barbus*	*serra*	D41	*	246	217	204			M	RR
2005	11	08	LF	01	DH-08112005-LF01	Piero's Pool	*Barbus*	*serra*	D42		266	235	211			M	RR
2005	11	08	LF	01	DH-08112005-LF01	Piero's Pool	*Barbus*	*serra*	D43		242	211	198			M	RR
2005	11	08	LF	01	DH-08112005-LF01	Piero's Pool	*Barbus*	*serra*	D44		296	259	243				
2005	11	08	LF	01	DH-08112005-LF01	Piero's Pool	*Barbus*	*serra*	D45		274	241	227			M	RR
2005	11	08	LF	01	DH-08112005-LF01	Piero's Pool	*Barbus*	*serra*	D46		308	270	255			M	RR
2005	11	08	LF	01	DH-08112005-LF01	Piero's Pool	*Barbus*	*serra*	D60		299	260	246				
2005	11	08	LF	01	DH-08112005-LF01	Piero's Pool	*Barbus*	*serra*	D61	*	319	286	270				

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APPENDIX B.5 (cont'd)

Year	Mon	Day	Gear	Samp. no.	Samp. Code	Site name	*Genus*	*Species*	Tag No.	Recap	TL (mm)	FL (mm)	SL (mm)	Mass (g)	Girth (mm)	Sex	God Dev
2005	11	08	LF	01	DH-08112005-LF01	Piero's Pool	*Barbus*	*serra*	D62		287	254	240				
2005	11	08	LF	01	DH-08112005-LF01	Piero's Pool	*Barbus*	*serra*	D63	*	275	242	227			M	RR
2005	11	08	LF	01	DH-08112005-LF01	Piero's Pool	*Barbus*	*serra*	D64		280	247	230				
2005	11	08	LF	01	DH-08112005-LF01	Piero's Pool	*Barbus*	*serra*	D65		306	272	257			M	RR
2005	11	08	LF	01	DH-08112005-LF01	Piero's Pool	*Barbus*	*serra*	D66		302	269	254				
2005	11	08	LF	01	DH-08112005-LF01	Piero's Pool	*Barbus*	*serra*	D67		330	293	271				
2005	11	08	LF	01	DH-08112005-LF01	Piero's Pool	*Barbus*	*serra*	D68	*	299	261	247				
2005	11	08	LF	01	DH-08112005-LF01	Piero's Pool	*Barbus*	*serra*	D69		282	249	234				
2005	11	08	LF	01	DH-08112005-LF01	Piero's Pool	*Barbus*	*serra*	D80		262	230	217			M	RR
2005	11	08	LF	01	DH-08112005-LF01	Piero's Pool	*Barbus*	*serra*	D81	*	258	225	210			M	RR
2005	11	08	LF	01	DH-08112005-LF01	Piero's Pool	*Labeobarbus*	*capensis*	D82		239	210	196				
2005	11	08	LF	01	DH-08112005-LF01	Piero's Pool	*Barbus*	*serra*	D83		252	223	207			M	RR
2005	11	08	LF	01	DH-08112005-LF01	Piero's Pool	*Barbus*	*serra*	D84		264	232	220			M	RR
2005	11	08	LF	01	DH-08112005-LF01	Piero's Pool	*Barbus*	*serra*	D85	*	310	275	260				
2005	11	08	LF	01	DH-08112005-LF01	Piero's Pool	*Barbus*	*serra*	D86		268	237	223			M	RR
2005	11	08	LF	01	DH-08112005-LF01	Piero's Pool	*Barbus*	*serra*	D87		290	255	240				
2005	11	08	LF	01	DH-08112005-LF01	Piero's Pool	*Barbus*	*serra*	D88		280	250	235			M	RR
2005	11	08	LF	01	DH-08112005-LF01	Piero's Pool	*Barbus*	*serra*	D89	*	287	257	242				
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D06		196					M	RR
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D07		280					M	RR
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D08		293						
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D09		308						
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Labeobarbus*	*capensis*	D10		229						
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D11		230					M	RR
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D12		338						
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D13		283						
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D14		285					M	RR
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D15		270					M	RR
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D18		368					F	RR
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D19		301						
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D20		199						
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D21		296						
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D22		296						
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D23		265						
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D24		314						
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D25		281						
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D26		307						
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D27		342					F	RR
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D28		348					F	RR
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D29	*	300					M	RR
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D30		289					M	RR
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D31		281					F	RR
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D32		266					M	RR
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D33		293						
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D34		301					F	RR
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D35		336						
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D36		303						
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D37		296						
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D38		312					M	RR
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D39		291						
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D48		269					M	RR
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D49		347						
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D50		274						
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Labeobarbus*	*capensis*	D51		236						
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D52		304						
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D55		293						

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APPENDIX B.5 (cont'd)

Year	Mon	Day	Gear	Samp. no.	Samp. Code	Site name	*Genus*	*Species*	Tag No.	Recap	TL (mm)	FL (mm)	SL (mm)	Mass (g)	Girth (mm)	Sex	God Dev
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D56		306					M	RR
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D57		344						
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D58		171						
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D59		250					M	RR
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D63	*							
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D70		284					M	RR
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D71		315					F	RR
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D72		307					M	RR
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Labeobarbus*	*capensis*	D73		326						
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Labeobarbus*	*capensis*	D74		350					M	RR
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D81	*							
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D85	*							
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	D89	*							
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	G11	*							
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Labeobarbus*	*capensis*	G14	*							
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	S13	*							
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	S30	*							
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Barbus*	*serra*	S93	*							
2005	11	09	LF	01	DH-09112005-LF01	Piero's Pool	*Labeobarbus*	*capensis*	S93	*							
2005	11	10	LF	01	DH-10112005-LF01	Driehoeks Waterfall	*Barbus*	*serra*	D61	*							
2005	11	10	LF	01	DH-10112005-LF01	Driehoeks Waterfall	*Barbus*	*serra*	S94	*							
2005	11	10	SF	01	DH-10112005-SF01	Lower Sneeuberg	*Barbus*	*serra*	D29	*	302						
2005	11	10	SF	01	DH-10112005-SF01	Lower Sneeuberg	*Barbus*	*serra*	D41	*	246						
2005	11	11	LF	01	DH-11112005-LF01	Driehoeks Pool	*Barbus*	*serra*	D40	*	233					M	RR
2005	11	11	LF	01	DH-11112005-LF01	Driehoeks Pool	*Barbus*	*serra*	D68	*							
2005	11	11	LF	01	DH-11112005-LF01	Driehoeks Pool	*Barbus*	*serra*	S94	*							

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APPENDIX B.6 Two way contingency table of frequency of occurrence of adult sawfin in depth, substratum and flow categories

	Depth (m)							Substratum				Flow		
	0.3	0.6	0.9	1.2	1.8	2.4	2.8	Sand-gravel	Cobble	Boulder	Bedrock	Slow	Intermediate	Fast
Oct 04	0	0	22	54	206	16	215	413	19	27	54	421	45	47
Nov 04	92	171	76	41	212	82	87	253	217	55	144	333	87	249
Dec 04	55	138	133	98	264	63	39	336	271	57	70	328	209	198
Mar 05	23	24	94	96	86	22	20	238	57	13	34	267	31	44
Oct 05	1	1	14	26	201	5	121	302	8	29	29	303	37	28
Nov 05	34	81	92	32	254	9	143	315	137	46	113	356	109	146
Dec 05	19	86	45	100	211	40	41	229	139	38	57	224	174	125
Mar 06	1	5	97	34	221	40	65	405	2	20	1	367	94	1

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APPENDIX C

APPENDIX C.1 Depth, velocity and substratum (subs.) measurements used to compile habitat utilisation curves. Substratum codes: S = Sand; BR = Bedrock or the length of the substratum particle along the beta (intermediate) axis, C = Cobble.

Larval sawfin (5-20 mm TL)

Date	Site	Depth (m)	Velocity ($m^3 s^{-1}$)	Subs.
2005/12/13	Lower Tafelberg	0.18	-0.03	S
2005/12/13	Lower Tafelberg	0.11	-0.02	S/BR
2005/12/13	Lower Tafelberg	0.07	0.01	S/BR
2005/12/13	Lower Tafelberg	0.09	0.02	S/BR
2005/12/13	Lower Tafelberg	0.07	0.02	S/BR
2005/12/13	Lower Tafelberg	0.12	0.06	S/BR
2005/12/13	Lower Tafelberg	0.14	-0.01	S/BR
2005/12/13	Lower Tafelberg	0.09	-0.01	S/BR
2005/12/13	Lower Tafelberg	0.08	-0.01	S/BR
2005/12/13	Lower Tafelberg	0.06	0.00	S/BR
2005/12/13	Lower Tafelberg	0.04	-0.01	S/BR
2005/12/13	Lower Tafelberg	0.12	-0.02	BR
2005/12/13	Lower Tafelberg	0.14	0.01	S/BR
2005/12/13	Lower Tafelberg	0.20	-0.01	S/BR
2005/12/13	Lower Tafelberg	0.06	-0.03	S/BR
2005/12/13	Lower Tafelberg	0.09	-0.01	S/BR
2005/12/13	Lower Tafelberg	0.08	-0.03	BR
2005/12/13	Lower Tafelberg	0.04	0.00	S
2005/12/13	Lower Tafelberg	0.28	0.00	S
2005/12/13	Lower Tafelberg	0.38	0.00	S/BR
2005/12/13	Lower Tafelberg	0.12	-0.01	S/BR
2005/12/13	Lower Tafelberg	0.18	0.01	BR
2005/12/13	Lower Tafelberg	0.04	0.00	BR
2005/12/13	Lower Tafelberg	0.20	0.05	BR
2005/12/13	Lower Tafelberg	0.20	0.03	BR
2005/12/13	Lower Tafelberg	0.27	0.02	BR
2005/12/13	Lower Tafelberg	0.17	0.00	S/BR
2005/12/13	Lower Tafelberg	0.18	0.00	S/BR
2005/12/13	Lower Tafelberg	0.14	0.00	BR
2005/12/13	Lower Tafelberg	0.20	-0.02	S/BR
2005/12/13	Lower Tafelberg	0.19	-0.01	S/BR
2005/12/13	Lower Tafelberg	0.08	0.01	S/BR
2005/12/13	Lower Tafelberg	0.36	-0.01	S/BR
2005/12/13	Lower Tafelberg	0.11	0.00	BR
2005/12/13	Lower Tafelberg	0.43	-0.01	S
2005/12/13	Lower Tafelberg	0.52	-0.02	S
2005/12/13	Lower Tafelberg	0.38	0.01	S/BR
2005/12/13	Lower Tafelberg	0.12	0.00	S/BR
2005/12/13	Lower Tafelberg	0.05	0.00	S/BR
2005/12/13	Lower Tafelberg	0.08	0.03	S/BR
2005/12/13	Lower Tafelberg	0.53	0.00	S/BR
2005/12/13	Lower Tafelberg	0.10	0.00	BR
2005/12/13	Lower Tafelberg	0.05	0.02	S/BR
2005/12/13	Lower Tafelberg	0.03	0.00	S/BR
2005/12/13	Lower Tafelberg	0.09	0.00	S/BR
2005/12/13	Lower Tafelberg	0.06	-0.01	S/BR
2005/12/13	Lower Tafelberg	0.08	-0.01	S/BR
2005/12/13	Lower Tafelberg	0.45	0.02	C
2005/12/13	Lower Tafelberg	0.35	0.01	S
2005/12/14	Sneeuberg	0.09	-0.01	S
2005/12/14	Sneeuberg	0.06	-0.02	S
2005/12/14	Sneeuberg	0.11	-0.01	S
2005/12/14	Sneeuberg	0.12	-0.01	S
2005/12/14	Sneeuberg	0.04	-0.01	S
2005/12/14	Sneeuberg	0.10	0.04	S
2005/12/14	Sneeuberg	0.04	0.01	S
2005/12/14	Sneeuberg	0.08	-0.03	S
2005/12/14	Sneeuberg	0.29	-0.02	S
2005/12/14	Wolfberg	0.13	0.01	S
2005/12/14	Wolfberg	0.07	0.01	S
2005/12/14	Wolfberg	0.06	0.00	S
2005/12/14	Wolfberg	0.07	0.01	S
	Mean	**0.15**	**0.00**	
	SD	**0.12**	**0.02**	

0+ Juvenile sawfin (21-75 mm TL)

Date	Site	Depth (m)	Velocity ($m^3 s^{-1}$)	Subs.
2005/12/14	Driehoeks Waterfall	0.54	-0.01	S/BR
2005/12/14	Driehoeks Waterfall	0.35	-0.02	S
2005/12/14	Driehoeks Waterfall	0.33	0.00	BR
2005/12/14	Driehoeks Waterfall	0.13	-0.03	BR
2005/12/14	Driehoeks Waterfall	0.35	-0.01	BR
2005/12/14	Driehoeks Waterfall	0.29	0.02	BR
2005/12/14	Driehoeks Waterfall	0.72	-0.02	BR
2005/12/14	Driehoeks Waterfall	0.43	-0.02	BR
2005/12/14	Driehoeks Waterfall	0.40	-0.06	BR
2005/12/14	Driehoeks Waterfall	0.33	-0.01	BR
2005/12/18	Maalgat	0.38	0.00	BR
2005/12/09	Maalgat	0.40	0.00	BR
2005/12/26	Maalgat	0.28	0.00	BR
2005/12/15	Wolfberg	0.16	0.00	
	Mean	**0.36**	**-0.01**	
	SD	**0.15**	**0.02**	

1+ Juvenile sawfin (76-150 mm TL)

Date	Site	Depth (m)	Velocity ($m^3 s^{-1}$)	Subs.
2005/12/10	Maalgat	0.82	0.24	BR/S
2005/12/15	Maalgat	0.97	-0.02	BR
2005/12/06	Maalgat	0.85	-0.01	BR
2005/12/04	Maalgat	0.79	0.04	BR/S
2005/12/19	Maalgat	0.74	0.05	BR
2005/12/23	Maalgat	1.16	0.01	0.82
2005/12/23	Maalgat	1.00	0.05	0.4
2005/12/23	Maalgat	0.82	0.24	BR/S
2005/12/23	Maalgat	0.82	0.24	BR/S
2005/12/23	Maalgat	0.90	0.13	BR
2005/12/23	Maalgat	0.97	-0.02	BR
2005/12/23	Maalgat	0.79	0.04	BR/S
2005/12/21	Maalgat	0.76	0.08	BR
2005/12/21	Maalgat	1.12	-0.03	S
2005/12/21	Maalgat	0.66	0.19	BR
2005/12/21	Maalgat	1.13	0.22	0.6
2005/12/21	Maalgat	1.10	0.14	0.2
2005/12/21	Maalgat	0.68	0.25	0.4
2005/12/21	Maalgat	0.54	0.00	S
2005/12/21	Maalgat	0.56	0.17	BR
2005/12/21	Maalgat	1.22	0.03	S
2005/12/21	Maalgat	1.24	0.05	S
2005/12/21	Maalgat	1.82	0.05	S
2005/12/21	Maalgat	1.27	0.11	BR/S
2005/12/21	Maalgat	0.17	0.02	BR
2005/12/21	Maalgat	0.70	0.21	BR
2005/12/21	Maalgat	0.91	0.10	BR/S
2005/12/21	Maalgat	0.31	0.10	BR
	Mean	**0.89**	**0.10**	
	SD	**0.32**	**0.09**	

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APPENDIX C.1 (cont'd)

Adult sawfin (>150 mm TL) - spawning

Date	Site	Depth (m)	Velocity ($m^3 s^{-1}$)	Subs.
2005/11/11	Piero's Pool	0.54	0.66	0.2
2005/11/11	Piero's Pool	0.52	0.67	0.32
2005/11/11	Piero's Pool	0.44	0.15	0.12
2005/11/11	Piero's Pool	0.48	0.97	0.07
2005/11/11	Piero's Pool	0.50	0.39	0.08
2005/11/11	Wolfberg	1.04	0.33	0.09
2005/11/11	Wolfberg	0.98	0.36	0.18
2005/11/11	Wolfberg	1.04	0.40	0.22
2005/11/11	Wolfberg	1.04	0.34	0.1
2005/11/25	Rietgat	1.24	0.40	0.02
2005/11/25	Rietgat	1.27	0.20	0.09
2005/11/25	Rietgat	1.16	0.27	0.05
2005/11/25	Rietgat	1.11	0.18	0.06
2005/11/25	Rietgat	1.32	0.46	0.05
2005/11/24	Wolfberg 1	0.64	0.43	0.06
2005/11/25	Wolfberg 1	0.96	0.15	0.01
2005/11/25	Wolfberg 1	0.66	0.25	0.1
2005/11/25	Wolfberg 1	0.86	0.17	0.11
2005/11/25	Wolfberg 1	0.14	1.32	0.3
2005/11/25	Wolfberg 1	0.22	1.37	0.07
2005/11/25	Upper Tafelberg	0.42	0.22	0.24
2005/11/25	Upper Tafelberg	0.36	0.07	0.03
2005/11/25	Upper Tafelberg	0.46	0.36	0.55
2005/11/25	Upper Tafelberg	0.56	0.25	0.03
2005/11/25	Upper Tafelberg	0.50	0.30	0.25
2005/11/25	Upper Tafelberg	0.34	0.23	0.01
2005/11/27	Upper Tafelberg	0.38	0.02	0.2
2005/11/27	Tafelberg	0.40	0.12	0.01
2005/11/27	Tafelberg	0.24	0.33	0.18
2005/11/27	Lower Tafelberg	0.34	0.27	0.05
2005/11/27	Sneeuberg 1	0.64	0.26	0.1
2005/11/27	Sneeuberg 2	0.92	0.20	0.17
2005/11/27	Rietgat 2	1.21	0.38	0.2
2005/11/27	Rietgat 3	0.50	-0.04	0.13
2005/11/27	Piero's Pool	0.46	0.48	0.45
2005/11/27	Wolfberg 2	0.96	0.11	0.1
2005/11/27	Wolfberg 3	0.92	0.21	0.04
2005/11/27	Wolfberg 4	0.66	0.29	0.04
2005/11/27	Evening Pool	0.64	0.41	0.6
2005/11/27	Maalgat	0.30	0.85	0.03
2005/11/15	Wolfberg 3	0.52	0.12	0.32
2005/11/15	Wolfberg 3	0.48	0.40	0.07
2005/11/15	Wolfberg 3	0.52	0.43	0.22
2005/11/15	Wolfberg 3	0.49	0.17	0.06
	Mean	**0.67**	**0.36**	
	SD	**0.32**	**0.29**	

Juvenile Clanwilliam yellowfish (75-150 mm TL)

Date	Site	Depth (m)	Velocity ($m^3 s^{-1}$)	Subs.
2005/11/15	Wolfberg	0.52	-0.01	0.06
2005/11/15	Sneeuberg	0.46	0.52	0.2
2005/11/16	Tafelberg lower	0.46	0.2	0.22
2005/11/16	Tafelberg lower	0.29	0.32	0.11
2005/11/16	Sneeuberg	0.30	0.25	0.09
2005/11/17	Tafelberg upper	0.32	0.36	0.25
2005/11/17	Tafelberg upper	0.46	0.15	0.11
2005/11/17	Tafelberg lower	0.80	0.04	BR
2005/11/17	Tafelberg lower	0.52	0.11	0.16
2005/11/17	Tafelberg lower	0.42	0.04	0.16
2005/11/19	Wolfberg	0.56	0.1	0.18
2005/11/20	Tafelberg	0.53	0.12	0.16
2005/11/20	Tafelberg	0.22	0.42	0.08
2005/11/20	Tafelberg	0.24	0.57	0.12
2005/11/24	Tafelberg	0.34	0.13	0.2
2005/11/24	Tafelberg	0.22	0.49	0.08
2005/11/24	Tafelberg	0.34	0.86	0.09
2005/11/24	Tafelberg	0.22	0.36	0.12
2005/11/24	Tafelberg	0.36	0.24	0.12
2005/11/24	Tafelberg	0.22	0.33	0.12
2005/11/24	Tafelberg	0.24	0.61	0.06
2005/11/24	Tafelberg	0.23	0.67	0.06
2005/11/25	Tafelberg upper	0.26	0.46	0.06
2005/11/25	Tafelberg upper	0.54	0.18	BR
2005/11/25	Tafelberg upper	0.42	0.54	0.05
2005/11/25	Sneeuberg	0.26	0.61	0.06
2005/11/25	Sneeuberg	0.20	0.05	0.12
2005/11/25	Wolfberg	0.36	0.22	0.09
2005/11/25	Tafelberg	0.42	0.13	0.08
2005/11/15	Wolfberg	0.38	0.01	S
	Mean	**0.37**	**0.30**	
	SD	**0.14**	**0.23**	

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APPENDIX C.1 (cont'd)

* For. = measurements taken from the area in which fish were foraging (drift feeding).

Clanwilliam yellowfish (>150 mm TL)

Date	Site	Depth (m)	Velocity ($m^3 s^{-1}$)	Subs.
2005/11/13	Sneeuberg	0.6	0.40	0.013
2005/11/13	Sneeuberg	0.7	0.00	S
2005/11/13	Sneeuberg	1.04	0.04	S
2005/11/13	Sneeuberg	0.5	0.21	S
2005/11/13	Sneeuberg	0.88	0.02	0.08
2005/11/13	Sneeuberg	0.5	0.18	S
2005/11/13	Sneeuberg	0.62	0.32	BR
2005/11/13	Sneeuberg	0.6	0.24	BR
2005/11/13	Sneeuberg	0.6	0.41	BR
2005/11/13	Sneeuberg	1.68	0.06	S
2005/11/13	Sneeuberg	0.68	0.15	S
2005/11/15	Wolfberg	0.84	0.24	BR
2005/11/15	Wolfberg	0.64	0.27	S
2005/11/15	Wolfberg	0.92	0.01	BR
2005/11/15	Wolfberg	0.47	0.12	S
2005/11/16	Sneeuberg	0.4	0.77	0.03
2005/11/16	Sneeuberg	0.6	0.28	0.02
2005/11/16	Sneeuberg	0.74	0.40	0.01
2005/11/16	Tafelberg	0.71	0.08	BR
2005/11/16	Sneeuberg	0.38	0.41	0.02
2005/11/16	Sneeuberg	0.84	0.04	S
2005/11/16	Sneeuberg	0.96	-0.01	S
2005/11/16	Sneeuberg	0.69	0.11	0.08
2005/11/16	Sneeuberg	0.94	0.06	0.06
2005/11/16	Sneeuberg	0.5	0.91	0.04
2005/11/16	Sneeuberg	0.84	0.04	S
2005/11/16	Sneeuberg	0.62	0.05	S
2005/11/16	Tafelberg	0.58	0.10	BR
2005/11/17	Tafelberg	0.84	0.03	S
2005/11/17	Tafelberg	0.44	0.23	0.11
2005/11/17	Tafelberg	0.26	0.61	0.06
2005/11/17	Tafelberg	0.48	0.36	0.16
2005/11/17	Tafelberg	0.42	0.13	0.08
2005/11/19	Wolfberg	0.4	0.33	S
2005/11/19	Wolfberg	1	0.23	0.04
2005/11/19	Wolfberg	1.22	0.16	0.11
2005/11/19	Wolfberg	1.16	0.02	S
2005/11/19	Sneeuberg	0.62	0.13	S
2005/11/19	Wolfberg	1.07	0.09	S
2005/11/19	Wolfberg	1.44	0.07	S
2005/11/20	Tafelberg	0.99	0.02	BR
2005/11/20	Tafelberg	0.64	0.07	0.2
2005/11/20	Tafelberg	0.64	0.08	BR
2005/11/21	Sneeuberg	0.82	0.01	S
2005/11/21	Sneeuberg	0.48	0.02	0.01
2005/11/21	Sneeuberg	0.67	0.04	S
2005/11/21	Sneeuberg	0.8	0.00	S
2005/11/21	Sneeuberg	0.42	0.13	0.01
2005/11/21	Sneeuberg	0.72	0.04	0.01
2005/11/25	Wolfberg	0.54	0.18	BR
2005/11/25	Wolfberg	0.78	-0.05	S
	Mean	**0.72**	**0.17**	
	SD	**0.28**	**0.20**	

Clanwilliam yellowfish (>150 mm TL) - drift-feeding

Date	Site	Depth (m)	For.* Dep. (m)	Velocity ($m^3 s^{-1}$)	For.* Vel ($m^3 s^{-1}$)	Subs.
2005/11/16	Sneeuberg	0.88		0.08		0.15
2005/11/16	Sneeuberg	0.34		0.61		0.08
2005/11/16	Sneeuberg	0.84		-0.05		0.12
2005/11/17	Tafelberg	0.60		0.64		0.14
2005/11/15	Wolfberg	1.17		0.20		0.15
2005/11/15	wolfberg	0.99		0.01		S
2005/11/15	Wolfberg	0.70		0.53		BR
2005/11/16	Sneeuberg	0.52		0.43		0.08
2005/11/16	Sneeuberg	0.58		0.32		BR
2005/11/16	Sneeuberg	0.56		0.28		BR
2005/11/16	Sneeuberg	0.52		0.11		0.16
2005/11/16	Sneeuberg	0.34		0.71		0.14
2005/11/17	Tafelberg	0.58		0.21		0.1
2005/11/17	Tafelberg	0.30		0.43		0.08
2005/11/17	Tafelberg	0.16	0.24	0.44	0.96	S
2005/11/17	Tafelberg	0.80		0.38		BR
2005/11/19	Sneeuberg	0.68	0.68	0.16	0.3	0.11
2005/11/19	Sneeuberg	0.66	0.68	0.14	0.35	0.09
2005/11/19	Sneeuberg	0.64	0.68	0.15	0.31	0.14
2005/11/20	Tafelberg upper	0.40	0.36	0.23	0.4	BR
2005/11/20	Tafelberg upper	0.54	0.46	0.17	0.32	BR
2005/11/20	Tafelberg upper	0.78	0.79	0.22	0.27	0.18
2005/11/20	Tafelberg upper	0.44	0.50	0.33	0.41	0.12
2005/11/20	Tafelberg upper	0.58	0.52	0.29	0.62	0.06
2005/11/20	Tafelberg upper	0.46	0.46	0.34	0.39	0.08
2005/11/21	Sneeuberg	0.64	0.64	0.12	0.25	0.08
2005/11/22	Sneeuberg	0.58	0.58	0.21	0.23	0.008
2005/11/22	Sneeuberg	0.61	0.61	-0.02	0.32	S on BR
2005/11/22	Sneeuberg	0.63	0.63	0.24	0.33	BR
2005/11/22	Sneeuberg	0.56	0.56	0.26	0.41	BR
2005/11/22	Sneeuberg	0.55	0.55	-0.06	0.27	BR
2005/11/22	Sneeuberg	0.59	0.59	0.23	0.34	BR
2005/11/22	Sneeuberg	0.62	0.62	0.17	0.33	BR
2005/11/22	Sneeuberg	0.52	0.52	0.15	0.52	BR
2005/11/22	Sneeuberg	0.57	0.57	-0.03	0.28	0.05
2005/11/22	Sneeuberg	0.63	0.63	0.00	0.14	0.15
2005/11/22	Sneeuberg	0.79	0.79	0.02	0.14	0.05
2005/11/22	Sneeuberg	0.80	0.76	0.08	0.26	S on BR
2005/11/22	Sneeuberg	0.80	0.80	0.01	0.13	0.04
2005/11/24	Tafelberg	0.22	0.30	0.24	0.55	0.2
2005/11/24	Tafelberg	0.34	0.33	0.16	0.39	0.18
2005/11/24	Tafelberg	0.64	0.58	0.19	0.47	0.11
2005/11/24	Tafelberg	0.80	0.58	0.11	0.47	BR
2005/11/24	Tafelberg	0.29	0.23	0.17	0.38	C
2005/11/24	Tafelberg	0.24	0.18	0.10	0.46	0.35
2005/11/24	Tafelberg	0.22	0.08	0.05	0.53	0.12
2005/11/24	Tafelberg	0.72	0.58	0.18	0.47	0.32
2005/11/24	Tafelberg	0.24	0.37	0.29	0.54	0.12
2005/11/24	Tafelberg	0.43	0.39	0.00	0.51	0.55
2005/11/25	Tafelberg	0.33		0.43		0.08
2005/11/25	Tafelberg	0.42	0.40	0.07	0.38	0.04
2005/11/25	Wolfberg	0.86	0.72	0.10	0.42	BR
2005/11/25	Wolfberg	0.84		0.15		BR
2005/11/25	Wolfberg	0.79		0.33		0.08
2005/11/25	Wolfberg	0.58		0.54		0.3
2005/11/25	Wolfberg	0.58	0.64	-0.12	0.55	S
2005/11/25	Wolfberg	0.62	0.64	0.16	0.49	S
2005/11/25	Wolfberg	0.44		0.43		0.04
2005/11/25	Wolfberg	0.54		0.68		BR
2005/11/25	Wolfberg	0.40		0.70		0.04
2005/11/25	Tafelberg	0.48		0.30		0.07
2005/11/25	Sneeuberg	0.30	0.35	0.22	0.6	0.05
2005/11/25	Sneeuberg	0.48	0.46	0.17	0.49	0.14
2005/11/25	Sneeuberg	0.46		0.50		0.1
2005/11/25	Sneeuberg	0.46	0.40	-0.05	0.49	S
2005/11/25	Sneeuberg	0.39		0.64		0.09
2005/11/25	Wolfberg	0.82	0.76	-0.02	0.47	BR
2005/11/25	Wolfberg	0.49		0.34		0.02
2005/11/25	Tafelberg	0.60	0.48	0.26	0.3	0.2
2005/11/25	Wolfberg	0.89	0.38	0.02	0.33	BR
	Mean	**0.57**	**0.52**	**0.23**	**0.40**	
	SD	**0.20**	**0.17**	**0.20**	**0.15**	

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APPENDIX D

APPENDIX D.1 Table showing surveyed fish postions for the three modelling sites: Upper Tafelberg, Lower Tafelberg and Sneeuberg. MB = Marker Bouy number. Size class reported in mm, x- and y-axes refer to the surveyed coordinates of each fish.

Site	Date	MB	x-axis	y-axis	Species	Size class/behaviour
Lower Tafelberg	2005/12/12	27	152.18	-1.09	*B. serra*	5-20
Lower Tafelberg	2005/12/12	51	153.66	-0.92	*B. serra*	5-20
Lower Tafelberg	2005/12/12	34	160.10	-3.14	*B. serra*	5-20
Lower Tafelberg	2005/12/12	16	161.36	-3.78	*B. serra*	5-20
Lower Tafelberg	2005/12/12	48	166.12	-5.33	*B. serra*	5-20
Lower Tafelberg	2005/12/12	36	167.02	-5.50	*B. serra*	5-20
Lower Tafelberg	2005/12/12	23	167.18	-7.27	*B. serra*	5-20
Lower Tafelberg	2005/12/12	8	151.82	6.42	*B. serra*	5-20
Lower Tafelberg	2005/12/12	6	159.95	1.50	*B. serra*	5-20
Lower Tafelberg	2005/12/12	41	166.10	-0.85	*B. serra*	5-20
Lower Tafelberg	2005/11/19	18	140.89	1.45	*B. serra*	spawning
Sneeuberg	2005/11/19	2	667.64	-103.47	*L. capensis*	>150
Sneeuberg	2005/11/19	1	663.57	-104.39	*L. capensis*	>150
Sneeuberg	2005/11/19	8	663.20	-105.17	*L. capensis*	>150
Sneeuberg	2005/11/19	5	662.24	-105.81	*L. capensis*	>150
Sneeuberg	2005/11/19	53	655.60	-111.82	*L. capensis*	>150
Sneeuberg	2005/11/19	25	652.06	-112.91	*L. capensis*	>150
Sneeuberg	2005/11/19	12	629.61	-114.95	*L. capensis*	>150
Sneeuberg	2005/11/19	23	628.43	-114.01	*L. capensis*	>150
Sneeuberg	2005/11/19	43	627.88	-113.96	*L. capensis*	>150
Sneeuberg	2005/11/19	17	627.36	-114.19	*L. capensis*	>150
Sneeuberg	2005/11/19	51	623.55	-116.20	*L. capensis*	>150
Sneeuberg	2005/11/19	24	620.89	-116.31	*L. capensis*	>150
Sneeuberg	2005/11/23	19	663.74	-105.29	*L. capensis*	>150
Sneeuberg	2005/11/23	50	663.58	-105.46	*L. capensis*	>150
Sneeuberg	2005/11/23	20	663.26	-105.30	*L. capensis*	>150
Sneeuberg	2005/11/23	35	663.03	-105.54	*L. capensis*	>150
Sneeuberg	2005/11/23	28	662.89	-105.71	*L. capensis*	>150
Sneeuberg	2005/11/23	30	662.76	-105.25	*L. capensis*	>150
Sneeuberg	2005/11/23	17	661.22	-105.94	*L. capensis*	>150
Sneeuberg	2005/11/23	21	661.02	-105.72	*L. capensis*	>150
Sneeuberg	2005/11/23	43	631.47	-114.14	*L. capensis*	>150
Sneeuberg	2005/11/23	34	630.55	-114.24	*L. capensis*	>150
Sneeuberg	2005/11/23	47	631.27	-113.55	*L. capensis*	>150
Sneeuberg	2005/11/23	3	630.94	-112.92	*L. capensis*	>150
Sneeuberg	2005/11/23	56	626.25	-115.55	*L. capensis*	>150
Sneeuberg	2005/11/27	30	659.08	-107.25	*L. capensis*	>150
Sneeuberg	2005/11/27	21	651.98	-112.73	*L. capensis*	>150
Sneeuberg	2005/11/27	28	649.45	-113.43	*L. capensis*	>150
Sneeuberg	2005/11/27	36	623.33	-116.42	*L. capensis*	>150
Sneeuberg	2005/11/27	16	622.64	-116.18	*L. capensis*	>150
Sneeuberg	2005/11/27	35	622.44	-116.76	*L. capensis*	>150
Sneeuberg	2005/11/27	17	621.76	-116.17	*L. capensis*	>150
Sneeuberg	2005/11/19	8	663.20	-105.17	*L. capensis*	>150
Sneeuberg	2005/11/19	5	662.24	-105.81	*L. capensis*	>150
Sneeuberg	2005/11/19	53	655.60	-111.82	*L. capensis*	>150
Sneeuberg	2005/11/19	25	652.06	-112.91	*L. capensis*	>150
Sneeuberg	2005/11/19	12	629.61	-114.95	*L. capensis*	>150
Sneeuberg	2005/11/19	23	628.43	-114.01	*L. capensis*	>150
Sneeuberg	2005/11/19	43	627.88	-113.96	*L. capensis*	>150
Sneeuberg	2005/11/19	17	627.36	-114.19	*L. capensis*	>150
Sneeuberg	2005/11/19	51	623.55	-116.20	*L. capensis*	>150
Sneeuberg	2005/11/19	24	620.89	-116.31	*L. capensis*	>150
Sneeuberg	2005/11/23	35	663.03	-105.54	*L. capensis*	>150
Sneeuberg	2005/11/23	17	661.22	-105.94	*L. capensis*	>150
Sneeuberg	2005/11/23	21	661.02	-105.72	*L. capensis*	>150
Sneeuberg	2005/11/23	43	631.47	-114.14	*L. capensis*	>150
Sneeuberg	2005/11/23	24	630.55	-114.24	*L. capensis*	>150

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APPENDIX D.1 (cont'd)

Site	Date	MB	x-axis	y-axis	*Species*	Size class/behaviour
Sneeuberg	2005/11/23	47	631.27	-113.55	*L. capensis*	>150
Sneeuberg	2005/11/23	3	630.94	-112.92	*L. capensis*	>150
Sneeuberg	2005/11/23	56	626.25	-115.55	*L. capensis*	>150
Sneeuberg	2005/11/19	2	667.64	-103.47	*L. capensis*	75-150
Sneeuberg	2005/11/19	1	663.71	-104.41	*L. capensis*	75-150
Sneeuberg	2005/11/23	19	663.74	-105.29	*L. capensis*	75-150
Sneeuberg	2005/11/23	50	663.58	-105.46	*L. capensis*	75-150
Sneeuberg	2005/11/23	20	663.26	-105.30	*L. capensis*	75-150
Sneeuberg	2005/11/23	28	662.89	-105.71	*L. capensis*	75-150
Sneeuberg	2005/11/23	30	662.76	-105.25	*L. capensis*	75-150
Sneeuberg	2005/11/19	13	652.57	-112.14	*B. serra*	spawning
Sneeuberg	2005/11/19	21	663.48	-104.27	*B. serra*	spawning
Upper Tafelberg	2005/11/21	23	1.16	1.90	*L. capensis*	>150
Upper Tafelberg	2005/11/21	17	1.91	1.53	*L. capensis*	>150
Upper Tafelberg	2005/11/21	29	2.07	2.26	*L. capensis*	>150
Upper Tafelberg	2005/11/21	18	16.24	8.13	*L. capensis*	>150
Upper Tafelberg	2006/03/23	13	17.76	6.21	*L. capensis*	>150
Upper Tafelberg	2005/11/21	26	2.98	2.19	*L. capensis*	75-150
Upper Tafelberg	2005/11/21	36	3.83	1.85	*L. capensis*	75-150
Upper Tafelberg	2005/11/21	52	5.04	3.39	*L. capensis*	75-150
Upper Tafelberg	2005/11/21	34	5.89	3.41	*L. capensis*	75-150
Upper Tafelberg	2005/11/21	31	9.98	4.99	*L. capensis*	75-150
Upper Tafelberg	2005/11/21	28	12.30	5.78	*L. capensis*	75-150
Upper Tafelberg	2005/11/26	6	12.16	5.79	*L. capensis*	75-150
Upper Tafelberg	2005/11/26	29	11.93	5.29	*L. capensis*	75-150
Upper Tafelberg	2005/11/19	28	0.35	1.13	*B. serra*	spawning
Upper Tafelberg & Tafelberg	2005/11/21	43	158.43	1.18	*L. capensis*	75-150
Upper Tafelberg & Tafelberg	2005/11/21	19	145.15	3.01	*L. capensis*	75-150
Upper Tafelberg & Tafelberg	2005/11/21	55	145.76	4.98	*L. capensis*	75-150
Upper Tafelberg & Tafelberg	2005/11/21	47	145.32	4.99	*L. capensis*	75-150
Upper Tafelberg & Tafelberg	2005/11/21	20	144.84	4.51	*L. capensis*	75-150
Upper Tafelberg & Tafelberg	2005/11/21	30	139.86	1.06	*L. capensis*	75-150
Upper Tafelberg & Tafelberg	2005/11/21	56	139.74	1.31	*L. capensis*	75-150
Upper Tafelberg & Tafelberg	2005/11/21	49	139.37	1.30	*L. capensis*	75-150
Upper Tafelberg & Tafelberg	2005/11/21	50	138.92	1.53	*L. capensis*	75-150
Upper Tafelberg & Tafelberg	2005/11/21	35	138.44	1.90	*L. capensis*	75-150

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APPENDIX D.2 WUA values (m^2) for the three modelling sites: Upper Tafelberg, Lower Tafelberg and Sneeuberg for spawning and three size-classes of sawfin and two size classes of Clanwilliam yellowfish.

Upper Tafelberg	Sawfin				Yellowfish	
Discharge ($m^3 s^{-1}$)	Spawning	5-20 (mm TL)	21-75 (mm TL)	>75 (mm TL)	75-150 (mm TL)	150 (mm TL)
	WUA	WUA	WUA	WUA	WUA	WUA
0.1	32.2	13.5	4.28	18.5	15.6	16.4
0.2	38.33	14.9	4.3	25.2	22.5	20.5
0.3	41.5	13.59	4	26.6	24	21.3
0.4	53.5	12	3.7	30.1	27.1	23
0.5	58.1	28.9	3.58	42.5	29.8	25.02
0.6	61.9	35.6	4.35	46.4	32.1	26.9
0.7	64.6	39.37	4.9	50.8	33.7	28.7
0.8	67.2	39.5	5.47	54.5	35.7	30.4
0.9	69	35	5.56	58.1	37.5	31.7
1.0	70.9	31	5.31	61.2	39.7	33.7
1.2	73.6	27.6	4.3	67.1	42.4	33.5

Lower Tafelberg	Sawfin				Yellowfish	
	Spawning	5-20 (mm TL)	21-75 (mm TL)	>75 (mm TL)	75-150 (mm TL)	150 (mm TL)
	WUA	WUA	WUA	WUA	WUA	WUA
0.1	39.2	22.9	6.07	34.4	19.01	14.3
0.2	50.33	25.2	6.66	46.6	22.06	18.6
0.3	57.03	20.04	5.81	38.7	23.7	17.9
0.4	60.9	18.43	5.5	35.4	23.9	17.46
0.5	63.07	20.6	5.8	43.5	23.6	16.55
0.6	62.63	19.36	5.38	37.6	22.19	17.9
0.7	64.69	17.4	5.47	29.37	21.34	15.03
0.8	65	19.7	5.7	28.17	19.7	13.9
0.9	64.6	19.38	5.8	29.59	19.38	14.1
1.0	63.6	18.8	5.7	29	18.36	13.7
1.1	63.17	18.9	5.85	25.6	17.6	13.1
1.2	62.05	17.49	5.78	28.6	16.8	12.5

Sneeuberg	Sawfin				Yellowfish	
	Spawning	5-20 (mm TL)	21-75 (mm TL)	>75 (mm TL)	75-150 (mm TL)	150 (mm TL)
	WUA	WUA	WUA	WUA	WUA	WUA
0.1	71.6	39.3	7.14	53.9	29.2	35.7
0.2	88.2	28.1	5.07	71.8	40.39	41.3
0.3	97.5	27.15	3.2	64	46	45.5
0.4	103	28.9	3.4	64	48.3	45.7
0.5	109.2	28.48	2.7	66.03	50	50
0.6	109.8	28.13	2.38	67.1	49.3	45.9
0.7	110.7	27.7	2.4	69.8	49.6	45
0.8	109.4	28.1	2.8	75.8	49.6	47.9
0.9	107.6	28.7	3.3	83.2	49.9	50.1
1.0	104.7	27.5	3.6	91.3	50.3	52.4
1.1	96.5	23.8	2.9	110.3	51.8	58.4
1.2	96.5	20.7	2.7	108.8	51	56.6

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APPENDIX E

APPENDIX E.1 Dates on which sawfin laboratory-reared sawfin were fertilised, hatched, and commenced swim-up and the date on which they were sacrificed (Sample date). The length (mm TL), count of the number increments (Incr. count) actual age (Act. age), and the difference betweeen these two figures (Diff.) are also reported. The tray and slot letters and numbers are the collection identifier codes.

Fertilisation date	Hatch date	Swim-up date	Sample date	Tray	Slot	Length (mm TL)	Incr. count	Act. Age (days)	Diff
13-Nov-06	15/16 Nov 06	23/24 Nov 06	08-Jan-07	C	50	13.5	51	56	5
13-Nov-06	15/16 Nov 06	23/24 Nov 06	04-Jan-07	C	29	12	44	52	8
13-Nov-06	15/16 Nov 06	23/24 Nov 06	04-Jan-07	C	30	12.5	46	52	6
20-Nov-06	22/23 Nov 06	1/2 Dec 2006	08-Jan-07	C	45	12	36	49	13
20-Nov-06	22/23 Nov 06	1/2 Dec 2006	08-Jan-07	C	46	11.5	41	49	8
20-Nov-06	22/23 Nov 06	1/2 Dec 2006	08-Jan-07	C	47	11.2	38	49	11
20-Nov-06	22/23 Nov 06	1/2 Dec 2006	08-Jan-07	C	48	12.5	39	49	10
20-Nov-06	22/23 Nov 06	1/2 Dec 2006	04-Jan-07	C	31	13	38	45	7
20-Nov-06	22/23 Nov 06	1/2 Dec 2006	04-Jan-07	C	32	13	39	45	6
13-Nov-06	15/16 Nov 06	23/24 Nov 06	27-Dec-06	C	17	12	42	44	2
13-Nov-06	15/16 Nov 06	23/24 Nov 06	27-Dec-06	C	18	12	37	44	7
13-Nov-06	15/16 Nov 06	23/24 Nov 06	27-Dec-06	C	44	-	35	44	9
20-Nov-06	22/23 Nov 06	1/2 Dec 2006	27-Dec-06	C	19	12	31	37	6
20-Nov-06	22/23 Nov 06	1/2 Dec 2006	27-Dec-06	C	20	12.5	28	37	9
13-Nov-06	15/16 Nov 06	23/24 Nov 06	19-Dec-06	C	14	11.16	31	36	5
20-Nov-06	22/23 Nov 06	1/2 Dec 2006	20-Dec-06	C	15	11	25	30	5
20-Nov-06	22/23 Nov 06	1/2 Dec 2006	20-Dec-06	C	16	10.5	25	30	5
13-Nov-06	15/16 Nov 06	23/24 Nov 06	05-Dec-06	C	24	9	18	22	4
13-Nov-06	15/16 Nov 06	23/24 Nov 06	05-Dec-06	C	25	9.5	16	22	6
13-Nov-06	15/16 Nov 06	23/24 Nov 06	02-Dec-06	C	40	9.1	12	19	7
13-Nov-06	15/16 Nov 06	23/24 Nov 06	02-Dec-06	C	41	9.5	15	19	4
13-Nov-06	15/16 Nov 06	23/24 Nov 06	02-Dec-06	C	42	9.5	17	19	2
13-Nov-06	15/16 Nov 06	23/24 Nov 06	02-Dec-06	C	43	9	14	19	5
13-Nov-06	15/16 Nov 06	23/24 Nov 06	02-Dec-06	D	47	12.5	16.5	19	2.5
13-Nov-06	15/16 Nov 06	23/24 Nov 06	01-Dec-06	D	45	9.1	13	18	5
13-Nov-06	15/16 Nov 06	23/24 Nov 06	01-Dec-06	D	46	12.5	16	18	2
13-Nov-06	15/16 Nov 06	23/24 Nov 06	30-Nov-06	C	23	9	15	17	2
13-Nov-06	15/16 Nov 06	23/24 Nov 06	29-Nov-06	D	43	-	13	16	3
13-Nov-06	15/16 Nov 06	23/24 Nov 06	28-Nov-06	C	22	9.6	15	15	0
13-Nov-06	15/16 Nov 06	23/24 Nov 06	28-Nov-06	C	37	9.4	11	15	4
13-Nov-06	15/16 Nov 06	23/24 Nov 06	28-Nov-06	C	38	9.1	12	15	3
13-Nov-06	15/16 Nov 06	23/24 Nov 06	27-Nov-06	C	39	9.5	12	14	2
13-Nov-06	15/16 Nov 06	23/24 Nov 06	25-Nov-06	D	40	-	8	12	4
13-Nov-06	15/16 Nov 06	23/24 Nov 06	24-Nov-06	D	39	-	7	11	4
20-Nov-06	15/16 Nov 06	23/24 Nov 06	1-Dec-06	D	44	9.1	9	11	2
13-Nov-06	15/16 Nov 06	23/24 Nov 06	23-Nov-06	D	38	-	6	10	4
13-Nov-06	15/16 Nov 06	23/24 Nov 06	23-Nov-06	C	33	9	9	10	1
13-Nov-06	15/16 Nov 06	23/24 Nov 06	23-Nov-06	C	35	9	7	10	3
13-Nov-06	15/16 Nov 06	23/24 Nov 06	23-Nov-06	C	34	9	8	10	2
13-Nov-06	15/16 Nov 06	23/24 Nov 06	23-Nov-06	C	36	9.1	8	10	2
13-Nov-06	15/16 Nov 06	23/24 Nov 06	21-Nov-06	C	21	9.5	9	8	-1

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APPENDIX E.2 Length (mm TL) and otolith increment counts (number) for sawfin larvae collected over the 2004/5 and 2005/6 spawning season. The tray and slot letters and numbers are the collection identifier codes.

Date collected	Tray No.	Slot No.	Length in mm TL	Count 1	Count 2	Mean
29-Oct-04	B	009	25	42	-	42
3-Dec-04	B	017	12.1	-	18	18
3-Dec-04	B	018	12.1	18	-	18
3-Dec-04	C	28	10	9	-	9
4-Dec-04	A	016	11.55	16	15	15
4-Dec-04	A	018	13.2	18	17	18
4-Dec-04	A	019	12.65	17	15	16
4-Dec-04	B	003	44	107	86	97
4-Dec-04	B	004	53.35	130	117	124
4-Dec-04	B	019	13.2	20	22	21
4-Dec-04	B	020	10.45	12	13	13
5-Dec-04	A	009	9.9	9	8	9
5-Dec-04	A	013	14.19	26	26	26
5-Dec-04	A	014	10.45	9	9	9
5-Dec-04	B	041	13	19	22	20
6-Dec-04	C	27	12	20	-	20
23-Feb-05	B	013	26.5	54	57	56
23-Feb-05	B	031	25.5	54	53	54
23-Feb-05	B	032	26	50	49	50
23-Feb-05	B	033	30	68	73	70
23-Feb-05	B	035	26.5	60	63	62
23-Feb-05	B	036	31	67	-	67
23-Feb-05	B	042	39.5	92	97	94
23-Feb-05	B	043	36	89	94	92
23-Feb-05	D	37	39	91	-	91
26-Feb-05	B	038	37.5	68	69	69
26-Feb-05	B	039	38	75	67	71
26-Feb-05	B	040	42	100	-	100
23-Mar-05	D	25	59	158	-	158
23-Mar-05	D	26	54	137	-	137
23-Mar-05	D	27	50	98	96	97
23-Mar-05	D	28	54	-	103	103
23-Mar-05	D	29	59	-	158	158
26-Mar-05	A	035	50	95	96	95
26-Mar-05	D	006	33	61	-	61
27-Mar-05	A	031	30	69	-	69
11-Dec-05	B	022	14	22	22	22
11-Dec-05	B	023	15	24	24	24
11-Dec-05	B	024	14.3	20	20	20
11-Dec-05	B	025	16	25	25	25
11-Dec-05	C	26	15	23	23	23
11-Dec-05	D	5	12	13	13	13
11-Dec-05	D	14	12	15	15	15
11-Dec-05	D	15	12	15	15	15
11-Dec-05	D	16	14	22	23	23
11-Dec-05	D	16	14	22	22	22
11-Dec-05	D	19	12	15	15	15
11-Dec-05	D	32	13	21	22	22
12-Dec-05	D	04	9	8	8	8
12-Dec-05	D	10	9.5	12	12	12
12-Dec-05	D	12	11	11	11	11
13-Dec-05	B	026	19	25	25	25
13-Dec-05	B	027	19.5	26	26	26
13-Dec-05	B	028	17	28	28	28
13-Dec-05	B	029	17	27	27	27
13-Dec-05	B	030	17	25	25	25
13-Dec-05	D	01	9	9	9	9
24-Mar-06	D	07	34	74	79	77
24-Mar-06	D	08	36	75	71	73

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APPENDIX E.2 (cont'd)

Date collected	Tray No.	Slot No.	Length in mm TL	Count 1	Count 2	Mean
24-Mar-06	D	09	38	83	83	83
24-Mar-06	D	11	39	75	75	75
24-Mar-06	D	13	43	93	93	93
24-Mar-06	D	18	40	78	77	78
24-Mar-06	D	20	47	102	102	102
24-Mar-06	D	21	54	111	106	107
24-Mar-06	D	22	54	111	114	113
24-Mar-06	D	23	58	118	111	114
24-Mar-06	D	24	39	81	77	80
24-Mar-06	D	30	61	118	118	119
24-Mar-06	D	31	58	107	110	109

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APPENDIX F

APPENDIX F.1 Summary statistics of water temperatures in the Driehoeks River from August 2004 to July 2006 measured at 30 min intervals by means of a HOBO® Water Temp Pro logger.

Mon		Aug 2004 - Jul 2005 (°C)	Aug 2005 - Jul 2006 (°C)
Aug	*Mean*	9.96	8.86
	Max	14.03	12.12
	Min	7.67	5.69
	SD	1.44	1.09
Sep	*Mean*	11.95	12.24
	Max	16.18	16.15
	Min	8.92	8.02
	SD	1.40	1.96
Oct	*Mean*	15.28	14.93
	Max	19.18	19.91
	Min	11.22	10.98
	SD	1.64	2.03
Nov	*Mean*	19.52	18.17
	Max	23.33	22.73
	Min	14.98	12.49
	SD	1.56	2.53
Dec	*Mean*	21.55	20.09
	Max	23.98	23.14
	Min	18.58	17.44
	SD	1.09	1.30
Jan	*Mean*	22.26	22.32
	Max	24.85	26.01
	Min	19.75	20.10
	SD	1.02	1.15
Feb	*Mean*	21.53	22.51
	Max	25.16	25.87
	Min	18.44	19.84
	SD	1.16	1.34
Mar	*Mean*	19.42	17.99
	Max	22.56	21.51
	Min	16.11	14.65
	SD	1.39	1.27
Apr	*Mean*	15.05	15.44
	Max	18.58	20.44
	Min	10.66	11.39
	SD	2.17	2.12
May	*Mean*	12.17	10.58
	Max	15.08	14.36
	Min	9.68	7.75
	SD	1.21	1.47
Jun	*Mean*	8.84	8.66
	Max	11.69	11.37
	Min	5.90	6.33
	SD	1.19	0.88
Jul	*Mean*	8.81	8.73
	Max	11.37	10.44
	Min	6.36	6.51
	SD	1.07	0.85

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APPENDIX F.2 Summary statistics of river stage and discharge in the Driehoeks River from August 2004 to July 2006 measured at 30 min intervals by means of data logger (STS® datalogger DL/N 641). Discharges exceeding 0.6 m river stage were not calculated since the rating curve (APPENDIX F.3) was not calibrated for values exceeding this.

Mon		Aug 2004 - Jul 2005 Stage (m)	Discharge ($m^3 s^{-1}$)	Aug 2005 - Jul 2006 Stage (m)	Discharge ($m^3 s^{-1}$)
Aug	*Mean*	0.35	0.97	0.51	2.90
	Max	0.72	-	2.06	-
	Min	0.26	0.43	0.30	0.66
	SD	0.08	0.02	0.25	0.38
Sep	*Mean*	0.23	0.32	0.35	1.04
	Max	0.34	0.91	0.55	3.57
	Min	0.21	0.23	0.28	0.55
	SD	0.02	0.00	0.05	0.01
Oct	*Mean*	0.22	0.29	0.28	0.53
	Max	0.39	1.40	0.38	1.30
	Min	0.19	0.18	0.23	0.29
	SD	0.04	0.00	0.03	0.00
Nov	*Mean*	0.16	0.12	0.23	0.30
	Max	0.20	0.21	0.34	0.91
	Min	0.15	0.08	0.19	0.18
	SD	0.01	0.00	0.03	0.00
Dec	*Mean*	0.13	0.06	0.16	0.12
	Max	0.16	0.10	0.19	0.19
	Min	0.11	0.04	0.14	0.07
	SD	0.01	0.00	0.01	0.00
Jan	*Mean*	0.11	0.04	0.13	0.06
	Max	0.12	0.05	0.15	0.09
	Min	0.10	0.03	0.12	0.05
	SD	0.01	0.00	0.01	0.00
Feb	*Mean*	0.10	0.03	0.11	0.04
	Max	0.12	0.05	0.13	0.06
	Min	0.09	0.02	0.11	0.04
	SD	0.01	0.00	0.00	0.00
Mar	*Mean*	0.12	0.04	0.13	0.06
	Max	0.14	0.07	0.14	0.07
	Min	0.11	0.03	0.11	0.04
	SD	0.00	0.00	0.00	0.00
Apr	*Mean*	0.17	0.12	0.16	0.11
	Max	0.32	0.75	0.26	0.43
	Min	0.12	0.05	0.13	0.06
	SD	0.04	0.00	0.03	0.00
May	*Mean*	0.19	0.17	0.37	1.20
	Max	0.28	0.55	1.72	-
	Min	0.16	0.12	0.17	0.14
	SD	0.02	0.00	0.24	0.35
Jun	*Mean*	0.41	1.56	0.44	1.97
	Max	1.23	-	2.63	-
	Min	0.24	0.35	0.28	0.51
	SD	0.16	0.12	0.29	0.61
Jul	*Mean*	0.34	0.96	0.34	0.97
	Max	1.59	-	0.52	2.98
	Min	0.24	0.33	0.31	0.69
	SD	0.19	0.19	0.04	0.00

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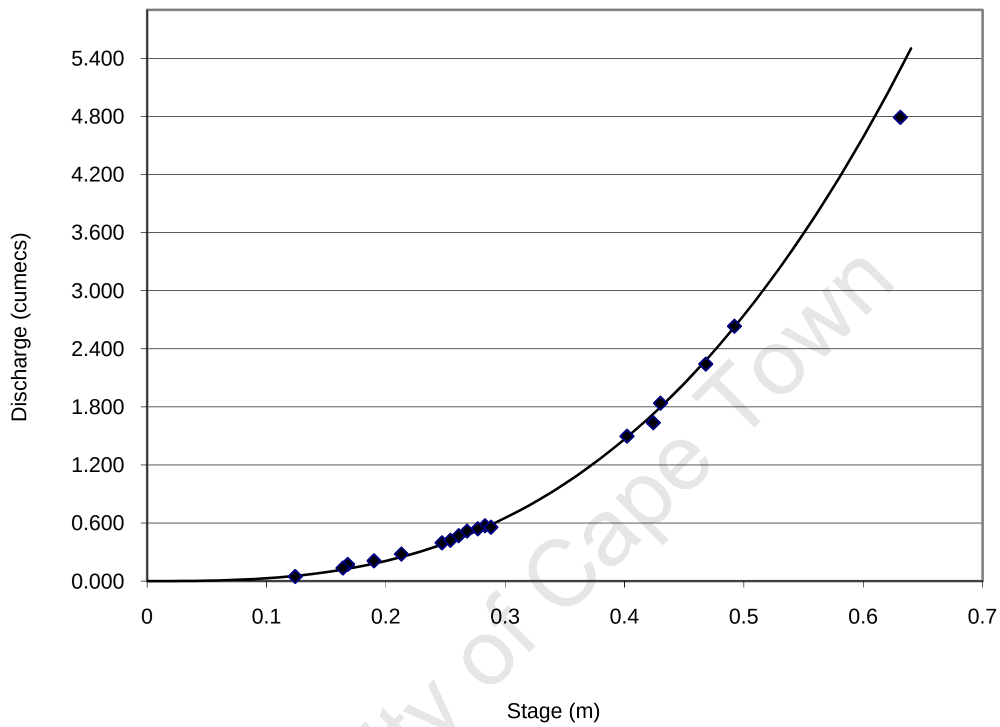
APPENDIX F.3 Stage-discharge curve developed for the Driehoeks River at Lower Tafelberg Site: $Q = 19.32(h)^{2.81}$. The discharge that overtopped the banks of the active channel approximates 2.5 $m^3\ s^{-1}$ or stage 0.48 m.



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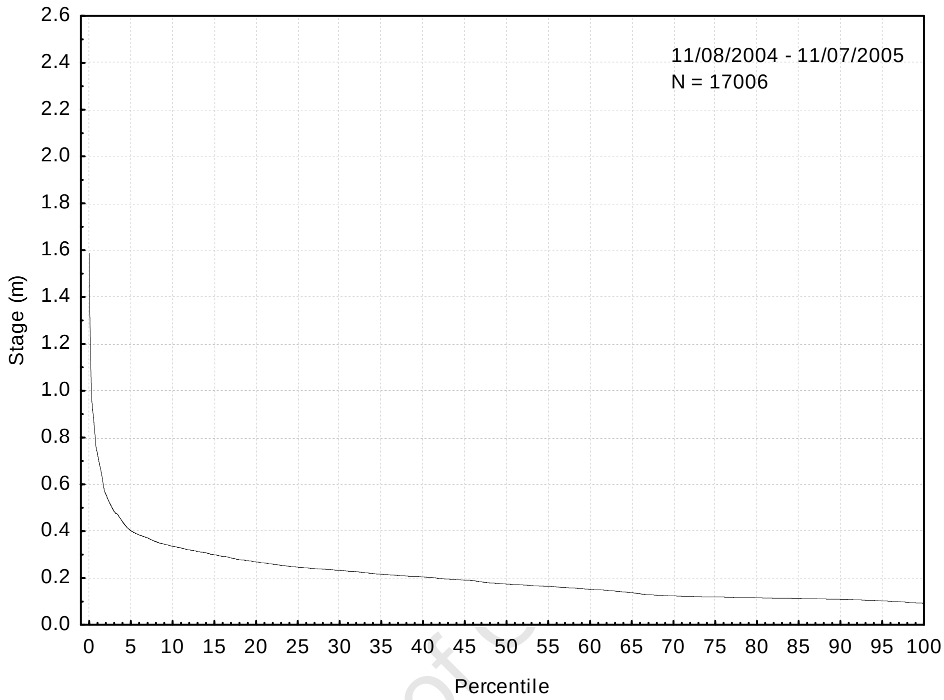
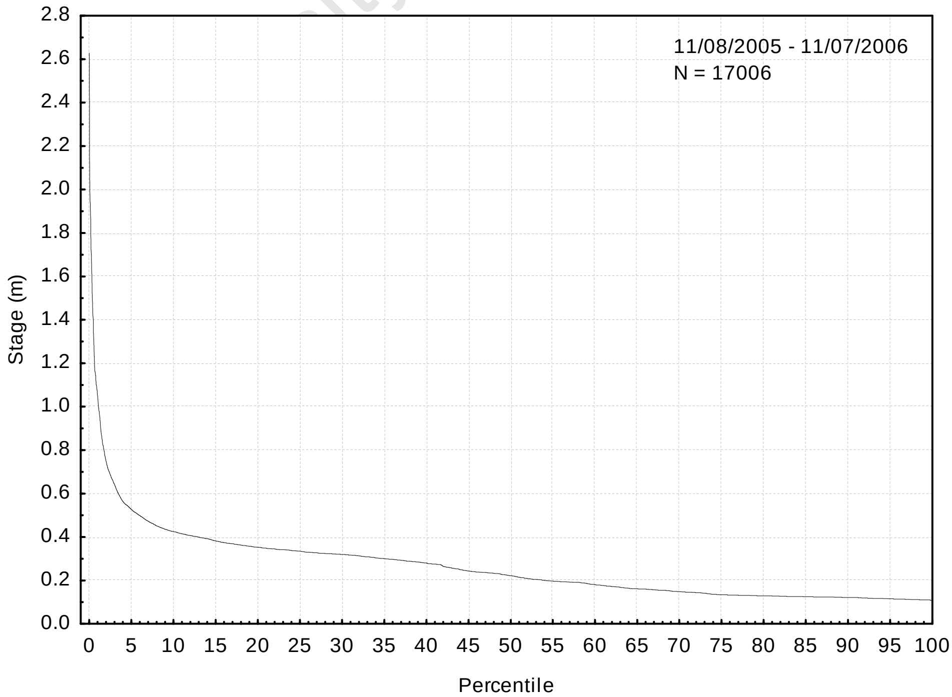
APPENDIX F.4 Flow Duration Curves of river stage (m) from the beginning of the study period (a) August 2004 – July 2005 and (b) August 2005 – August 2006.

(a)



(b)



APPENDIX F.5 Number of larval and juvenile sawfin sampled from the Driehoeks River between December 2004 and March 2006 (dash indicates no sample).

Larvae		Drift Net	Hand Net	Light Trap	Seine Net	*Total*
03-06 Dec 2004	Lower Tafelberg	11	9	131	-	*151*
	Sneeuberg	0	8	0	-	*8*
					Total	***159***
10-13 Dec 2005	Lower Tafelberg	0	29	0	-	*29*
	Sneeuberg	0	12	0	-	*12*
					Total	***41***
Juveniles						
23-26 Feb 2005	Driehoeks Cascade	-	-	-	42	*42*
	Rietgat	-	-	-	74	*74*
	Maalgat	-	-	-	0	*0*
					Total	***116***
24-26 Mar 2006	Driehoeks Cascade	-	-	-	42	*42*
	Rietgat	-	-	-	62	*62*
	Maalgat	-	-	-	71	*71*
					Total	***175***

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APPENDIX F.6 Larval and juvenile sawfin lengths (mm TL) of fish collected from the Driehoeks River between December 2004 and March 2006 by means of Drift Nets (DN), Hand Nets (HN), Quatrefoil Light Traps (LT) and Seine Net (SN).

3-6 Dec 2004	Lower Tafelberg																		Sneeuberg
	DN		HN	LT															HN
	9	9.5	17	15	12	11.5	10	15	14	12	12	10.5	11.5	10	9.5	9.5	9	8.5	14
	9	9.5	16	14	12	11	10	15	14	11.5	12	10.5	11	10	9.5	8	9	8	13
	9		15	13	12	11	10	14	13	11.5	12	10	11	10	9.5	9.5	9	8	12
	9		11.3	12.5	12	11	9.8	7	8.5	8.5	12	10	11	10	9.5	9.5	9	7	12
	9		11	12	11.5	11	9.5	14	12.5	11	12	10	11	10	9.5	9	9	8	11.5
	8.5		11	12	11.5	11	8	14	8.5	11	8.5	10	10	10	9.5	9	8.5		11
	8		11	12	11.5	11	12	13	12	11	12	10	10	9.5	9.5	9	8.5		12
	8		11	12	8	10.5	10	13	12	11	12	10	10	9.5	9.5	9	8.5		9.5
	10		10	12	11.5	10.5	14.5	12	7	10.5	11.5	10	10	9.5	9	9	8.5		

10-13 Dec 2005	Lower Tafelberg				Sneeuberg	
	HN				HN	
	11	13.5	15	17	12	18
	11.5	14	15.5	17	13	19
	12	14	15.5		13	19.5
	12	14	16		15	
	12	14.5	16		15	
	12	15	16		15	
	12	15	16		16	
	13	15	16		17	
	13	15	16		17.5	

23-26 Feb 2005	Driehoeks Cascade					Rietgat								
	SN					SN								
	25.5	31	37	40.5	59	63	51	49	47	46.5	45	42	39.5	33
	26	31	38	41	60.5	59	51	48.5	47	46	45	42	39	32
	26.5	31	38	41	61.5	57	50	48	47	46	45	42	39	
	26.5	31	38.5	42	65	56	50	48	47	46	44.5	42	38.5	
	27	33	38.5	53	66	55	50	48	47	46	44	42	38	
	29	35	39	54	37	54	50	47.5	47	45.5	43.5	41	37.5	
	29	35	39	56		53.5	50	47	47	45.5	43	41	36	
	29.5	35	39	57		53	50	47	47	45	43	40.5	34.5	
	30	36	39.5	59		52	50	47	47	45	43	40	33	

24-26 Mar 2006	Driehoeks Cascade					Rietgat							Maalgat							
	SN					SN							SN							
	35	31	42	40	30	34	39	42	50	54	57	61	39	42	35	29	36	27	30	37
	36	34	30	42	37	35	40	43	50	55	58	63	39	35	40	39	30	36	31	31
	30	31	40	38	36	35	40	44	50	55	58	64	39	34	38	34	30	33	37	37
	41	34	34	38	35	36	40	44	50	55	58	65	34	39	32	37	37	28	33	30
	32	32	40	34	29	36	40	45	51	55	58	65	38	38	35	37	35	28	40	29
	34	33	42	40		38	40	47	52	56	59	65	31	40	37	28	36	31	28	32
	30	40	38	38		38	40	47	52	56	60	65	34	32	31	35	28	36	35	41
	31	31	38	38		39	41	48	53	56	60	66	37	27	31	31	34	35	37	38
	36	33	34	41		39	41	48	54	56	61		40	39	28	36	39	27	39	

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