POST-IMPOUNDMENT POPULATION DYNAMICS OF NON-NATIVE COMMON CARP *CYPRINUS CARPIO* IN RELATION TO TWO LARGE NATIVE CYPRINIDS IN LAKE GARIEP, SOUTH AFRICA

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Dedicated to my mother

Monika Winker

ABSTRACT

To contribute to the understanding of the invasion biology of common carp *Cyprinus carpio* in southern Africa, this thesis investigated the life history, relative abundance, long-term population demographics and trophic niche utilisations of non-native common carp *C. carpio* in relation to two endemic cyprinids, Orange River mudfish *Labeo capensis* and smallmouth yellowfish *Labeobarbus aeneus* in South Africa's largest impoundment, Lake Gariep.

The growth zone deposition rates in astericus otoliths of the three species were validated as biannual for *C. carpio* and as annual for *L. capensis* and *L. aeneus*, which allowed for reliable estimation of lengths-at-age upon which growth, age-at-maturity and mortality rates could be estimated. *Cyprinus carpio* exhibited fast growth, matured relatively early at two years of age and attained a maximum age of seven years. *Labeo capensis* grew significantly slower, but attained older ages of up to 12 years. Females showed notably delayed maturation at approximately six years of age. The life history parameter estimates for *L. aeneus* were similar to those of *L. capensis*. These species-specific life history characteristics contributed to a substantially higher population growth potential of *C. carpio* compared to *L. capensis* and *L. aeneus*.

Delta-lognormal and delta-gamma Generalized Linear Models (GLMs) were used to analyse patterns of relative abundance of *L. capensis*, *L. aeneus* and *C. carpio*. The application of these GLMs was necessary to account for large proportions of zeros and strong skewness in the catch-per-unit-effort (CPUE) from experimental gillnet and fisheries-dependent angler surveys. Confidence intervals around predicted

abundance indices were obtained through the development of a generalised parametric bootstrap procedure. The resulting standardised abundance indices were coupled with results from analysis of stable isotope ratios of fish tissues and potential food resources and revealed that *C. carpio* was mainly confined to soft-bottom habitats, where it predominantly foraged on benthic invertebrates. *Labeo capensis* was abundant in a wide range of benthic habitats and was consumed basal food resources such as detritus. *Labeobarbus aeneus* was found to feed mostly on pelagic zooplankton. There were no significant interspecific differences in trophic niche space, suggesting limited resource competition among the three species.

Standardised historical and contemporary gillnet CPUE data indicated slow population growth rates of *L. capensis* and *L. aeneus* during the first ten years post-impoundment, but showed high biomass levels some four decades after impoundment. These results could be corroborated by stochastic age-structured production model (ASPM) simulations. In contrast to the two endemic species, the gillnet CPUE of *C. carpio* showed a clear 'boom and bust' pattern, which, based on ASPM simulations, could be best explained by increased food availability during the first five years post-impoundment, followed by suboptimal conditions thereafter. Together, these results provided evidence that the establishment of the *C. carpio* population did not prevent the slow but successful long-term establishment of the two large endemic cyprinids. Both endemic fishes revealed specialised feeding within the impoundment.

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Contents

CHAPTER 1

General introduction

1.1 INTRODUCTION

Globally, freshwater ecosystems are among the most susceptible to invasions by populations of non-native species (Dudgeon *et al.*, 2006). The introduction and spread of non-native species is now recognised as a major threat to native freshwater biodiversity (Rahel, 2002; Dudgeon *et al.*, 2006; Johnson *et al.*, 2008). The terms 'non-native' or 'alien' are normally used interchangeably and generally refer to those species that are introduced outside their natural range by human activity (Kolar & Lodge, 2001; Gozlan *et al.*, 2010). These introduced species may then subsequently establish by forming a self-sustaining population in their new environment (Gozlan *et al.*, 2010). However, the presence or even the establishment of a non-native population is not necessarily equivalent to this population being invasive in that it poses a threat to the native fauna or rapidly expands its range (Baltz & Moyle, 1993; Moyle & Light, 1996; Kolar & Lodge, 2002; Britton *et al.*, 2007; Gozlan *et al.*, 2010). The invasion of alien species can be viewed as a complex process consisting of several transitions, each with different levels of risks and impacts on the integrity of the native fauna (Kolar & Lodge, 2002; Marchetti *et al.*, 2004; Vander Zanden & Olden, 2008). Given that species invasions are a leading contributor to the increasing numbers of threatened, endangered and extinct freshwater species (Dudgeon *et al.*, 2006), it is not surprising that the understanding of the underlying processes that determine whether or not, and if, to which extent non-native species become invasive has been a long-standing goal of freshwater ecologists (Baltz & Moyle, 1993; de Moor, 1996; Moyle & Light, 1996;

Bøhn *et al.*, 2004; Gido *et al.*, 2004; Olden *et al.*, 2006; Britton *et al.*, 2007; Johnson *et al.*, 2008; Britton *et al.*, 2010; Gozlan *et al.*, 2010).

1.2 NON-NATIVE COMMON CARP

Common carp *Cyprinus carpio* is a species of world-wide importance and concern. Native to eastern Europe and central Asia, *C. carpio* is the most widely translocated freshwater fish species globally (Casal, 2006) and is established in all continents except Antarctica (Koehn, 2004). *Cyprinus carpio* is considered to be one of the eight most invasive freshwater fishes (Lowe *et al.*, 2000) and, world-wide, accounts for most of the records of successful establishments and adverse ecological effects (Casal, 2006; Kulhanek *et al.*, in press). Its potential to rapidly establish in newly invaded ecosystems has been linked to its life history characteristics, which typically include fast growth, early maturity and high reproductive capacity, in combination with high levels of phenotypic plasticity (2004; Koehn, 2004; Zambrano *et al.*, 2006; Britton *et al.*, 2007; Weber & Brown, 2009). Potential impacts on aquatic ecosystems as a result of *C. carpio* introductions have been studied and recently reviewed (Zambrano & Hinojosa, 1999; Zambrano *et al.*, 2001; Khan, 2003; Khan *et al.*, 2003; Parkos *et al.*, 2003; Hinojosa-Garro & Zambrano, 2004; Koehn, 2004; Chumchal *et al.*, 2005; Casal, 2006; Britton *et al.*, 2007; Ojuok *et al.*, 2008; Weber & Brown, 2009; Zambrano *et al.*, 2010; Kulhanek *et al.*, in press). Several of these impacts have been associated with its benthic foraging behaviour. *Cyprinus carpio* has the ability to effectively separate food items, such as benthic invertebrates and seeds, from sediment mixtures with the remainder being resuspended in the water column (Sibbing, 1988). As a result, high densities of *C. carpio* can cause increases in turbidity, nitrogen, ammonia and phosphorus within the water column (Lougheed *et al.*, 1998; Zambrano & Hinojosa, 1999; Chumchal *et al.*, 2005) and may therefore mediate eutrophication, algal blooms

and environmental degradation (Zambrano *et al.*, 2001; Khan *et al.*, 2003; Parkos *et al.*, 2003; Weber & Brown, 2009). Direct effects of competition with native fishes have been studied to a lesser extent (Zambrano *et al.*, 2010). However, with regard to its invasion success in new aquatic environments, there seems to be little doubt that *C. carpio* is often more efficient in exploiting certain food sources than many native species (Sibbing, 1988; Weber & Brown, 2009; Zambrano *et al.*, 2010). In some instances, this may lead to extremely high *C. carpio* densities that can dominate the invaded fish community (Pimentel *et al.*, 2000; Zambrano *et al.*, 2001; Egertson & Downing, 2004; Koehn, 2004; Britton *et al.*, 2007).

Cyprinus carpio was first introduced into southern Africa in the 18th century. According to a newspaper article in the Cape Argus from the 15th September, 1859, Mr Fairbridge imported six *C. carpio* from England and released them into the reservoir at the Cape Town Botanical Gardens (Anon, 1959). *Cyprinus carpio* is widely distributed throughout southern Africa with established populations in many major river systems (de Moor & Bruton, 1988; Scott *et al.*, 2006). Currently, *C. carpio* has the status of a nuisance species in southern Africa (de Moor & Bruton, 1988), which is, however, predominantly based on casual observations of habitat degradation and possible impacts on native biota (de Moor & Bruton, 1988). Despite the invasive history of *C. carpio*, which has been found to be a strong predictor for the likelihood of future invasions and the severity of associated impacts (Kolar & Lodge, 2002; Marchetti *et al.*, 2004; Kulhanek *et al.*, in press), there have been no studies on its impacts on southern African freshwater biota (de Moor & Bruton, 1988). This lack of knowledge therefore emphasises the need of understanding its biology, population dynamics and impact on the native fish communities in a southern African context.

1.3 FISH FAUNA OF THE UPPER ORANGE RIVER

The westward flowing Orange River ranks as the most turbid river system in Africa and the fourth most turbid globally (Bremner *et al.*, 1990). One of the most striking features of the system is its depauperate ichthyofauna, which comprises only 16 indigenous fishes, and is dominated by cyprinids. Lake Gariep falls within the distributional region of the upper Orange and Caledon Rivers, excluding the headwater tributaries of Drakensberg Mountains (Skelton, 1986). Fish collections from this region include eight indigenous species (Jubb, 1972; Skelton, 1986), of which seven were recorded during the current study in Lake Gariep (Table 1.1).

Table 1.1. Native (a) and non-native (b) fishes recorded within the distributional region of the upper Orange and Caledon River, excluding the headwater tributaries of the Drakensberg Mountains (Skelton, 1986; Skelton, 2001). *) Species recorded during the present study (2007 – 2008) in Lake Gariep.

Family and Species	Common name	Species authority
(a)	Native species	
Austroglanididae		
*Austroglanis sclateri**	Rock catfish	Boulenger, 1901
Cichlidae		
Tilapia sparmanii	Banded tilapia	Smith, 1840
Clariidae		
*Clarias gariepinus**	Sharptooth catfish	Burchel, 1822
Cyprinidae		
*Barbus anoplus**	Chubbyhead barb	Weber, 1897
*Labeobarbus aeneus**	Smallmouth yellowfish	Burchel, 1822
*Labeobarbus kimberleyensis**	Largemouth yellowfish	Gilchrist & Thompson, 1913
*Labeo capensis**	Orange River mudfish	Smith, 1841
*Labeo umbratus**	Moggel	Smith, 1841
(b)	Nonnative	
Centrarchidae		
*Micropterus salmoides**	Largemouth bass	Lacepède, 1802
Cyprinidae		
*Cyprinus carpio**	Common carp	Linnaeus, 1758
Salmonidae		
*Oncorhyncus mykiss**	Rainbow trout	Walbaum, 1792
Salmo trutta	Brown trout	Linnaeus, 1758

Of the four recorded introduced species (Table 1.1), only *C. carpio* occurs in notable abundance in Lake Gariep. The two salmonids, brown trout *Salmo trutta* and rainbow trout *Oncorhyncus mykiss*, have been widely introduced in the headwater tributaries, but are only occasionally caught further downstream (Jubb & Farquharson, 1965; Hamman, 1980; Tómasson *et al.*, 1985). Largemouth bass *Micropterus salmoides* is generally extremely scarce in the upper Orange River system (Skelton, 1986; Skelton, 2001).

Two large endemic cyprinids, Orange River mudfish *Labeo capensis* and smallmouth yellowfish *Labeobarbus aeneus* dominate assemblages of larger fishes in the wider river stretches of the Orange and Caledon Rivers (Jubb & Farquharson, 1965; Jubb, 1972; Skelton, 1986). During fish surveys conducted in the upper Orange River, both species together typically contributed to more than 80% the experimental gillnet catches by numbers (Skelton, 1986). Moggel, *Labeo umbratus*, was less abundant in the main streams and seems to prefer smaller secondary tributaries with slow flowing or standing water (Skelton, 1986). A large piscivoures cyprinid, largemouth yellowfish *Labeobarbus kimberleyensis*, is widespread but, being an apex predator within the system, does generally not occur in high densities (Jubb, 1972; Hamman, 1980; Ellender, 2008). The banded tilapia naturally only occurs in the Vaal and the lower Orange River, however, as a result of translocations is established in Vander Kloof Dam, a large impoundment downstream of Lake Gariep (Tómasson *et al.*, 1985). The rock catfish *Austroglanis sclateri* is a relatively small rock-dwelling catfish that prefers flowing-water. The relative abundance of this species is largely unknown as it is regarded as difficult to sample with standard gear (Skelton, 1986). The African sharptooth catfish *Clarias gariepinus* has the largest natural distribution within the

native ichthyofauna, which extends from the Orange River in the south northwards into Turkey, where it occurs in both riverine and lacustrine environments (Skelton, 2001; Cambray, 2003).

1.4 IMPOUNDMENTS AND INVASIONS

Dam construction creates major hydrological perturbations within river ecosystems (Rosenberg *et al.*, 2000). Commensurate with these perturbations is the increasing evidence that newly created impoundments may facilitate secondary invasion processes into aquatic landscapes (Havel *et al.*, 2005; Johnson *et al.*, 2008). It has been shown that indigenous riverine species often appear to be less adapted to impoundment conditions than invasive generalists, particularly those that have a history of successful establishments in a wide range of freshwater systems (Baltz & Moyle, 1993; Havel *et al.*, 2005; Olden *et al.*, 2006; Johnson *et al.*, 2008). Although it can be argued that ecological studies on impoundment populations have a low conservation priority because of the highly perturbed nature of these man-made habitats, from a research perspective, these altered ecosystems provide an opportunity to investigate colonisation and establishment processes of both non-native and indigenous species long after the initial invasion occurred.

The initial post-impoundment fish assemblage composition within the first 3 - 15 years after filling was relatively well-studied (e.g. Vanderpuye, 1981; Bodaly & Lesack, 1984; Tómasson *et al.*, 1985; Jackson, 1989; Cowx & Kapasa, 1995; Okada *et al.*, 2005). However, it has been recognised that few studies re-assess these population dynamics some three to four decades after impoundment, despite evidence that ecological succession may continue long after the initial monitoring programmes are terminated (Gido, 2000). In Lake Gariep, like in many other impoundments, initial

monitoring of the larger fish species commenced soon after the impoundment was filled in 1970 and continued for a decade afterwards (Hamman, 1980; 1981). The availability of this data source, therefore, provided a unique opportunity to examine the underlying processes that may explain long-term population patterns of *C. carpio* in comparison to native fishes.

1.5 THESIS OUTLINE

The overall aim of this thesis was to use Lake Gariep as a case study to improve the understanding of the invasion biology of *C. carpio* in southern Africa by investigating its life history, long-term population dynamics, and resource utilisation in relation to two abundant native cyprinids, *L. capensis* and *L. aeneus*.

To achieve this, the thesis has been divided into eight Chapters. After the general introduction (Chapter 1), Chapter 2 describes the study area, the sampling strategy and the data sources used in this thesis. To obtain reliable estimates of life history parameters, the growth zone deposition rate in otoliths first had to be validated for non-native *C. carpio* (Chapter 3) and the two native cyprinids, *L. capensis* and *L. aeneus* (Winker *et al.*, 2010; Appendix I). Aspects on the biology of *C. carpio* and *L. capensis* in Lake Gariep are presented in the Chapters 4 & 5, respectively. The specific objective of these chapters was to obtain robust life history parameters that were required as input parameters for developing the age-structured production model (ASPM) to simulate their long-term post-impoundment population demographics in Chapter 7. The objective of Chapter 6 was to identify predictor variables that explain temporal and spatial differences in catch rates of *L. capensis*, *L. aeneus* and *C. carpio*, as these could provide implications for potential habitat segregation among the three species. For this purpose, spatial and seasonal patterns in relative abundance trends of *C. carpio*, *L.*

capensis and *L. aeneus* were analysed using a delta-lognormal and delta-gamma Generalized Linear Modelling (GLMs). The aim of Chapter 7 was to examine underlying processes of the long-term population dynamics by integrating the findings from the previous with results from stable isotope analysis and historical and present gillnet catch data in conjunction with stochastic age-structured population model simulations. Finally, a synthesis of the findings is provided in Chapter 8.

CHAPTER 2

Study area and sampling

2.1 STUDY AREA

Lake Gariep (30°38' S; 25°46' E; 1250 m above mean sea level), an impoundment on the upper Orange River constructed for the purpose of hydropower generation, is situated between the Eastern Cape, Northern Cape and Free State provinces (Fig. 2.1). It is South Africa's largest inland water body with a surface area of about 360 km^2 (Hamman, 1981).

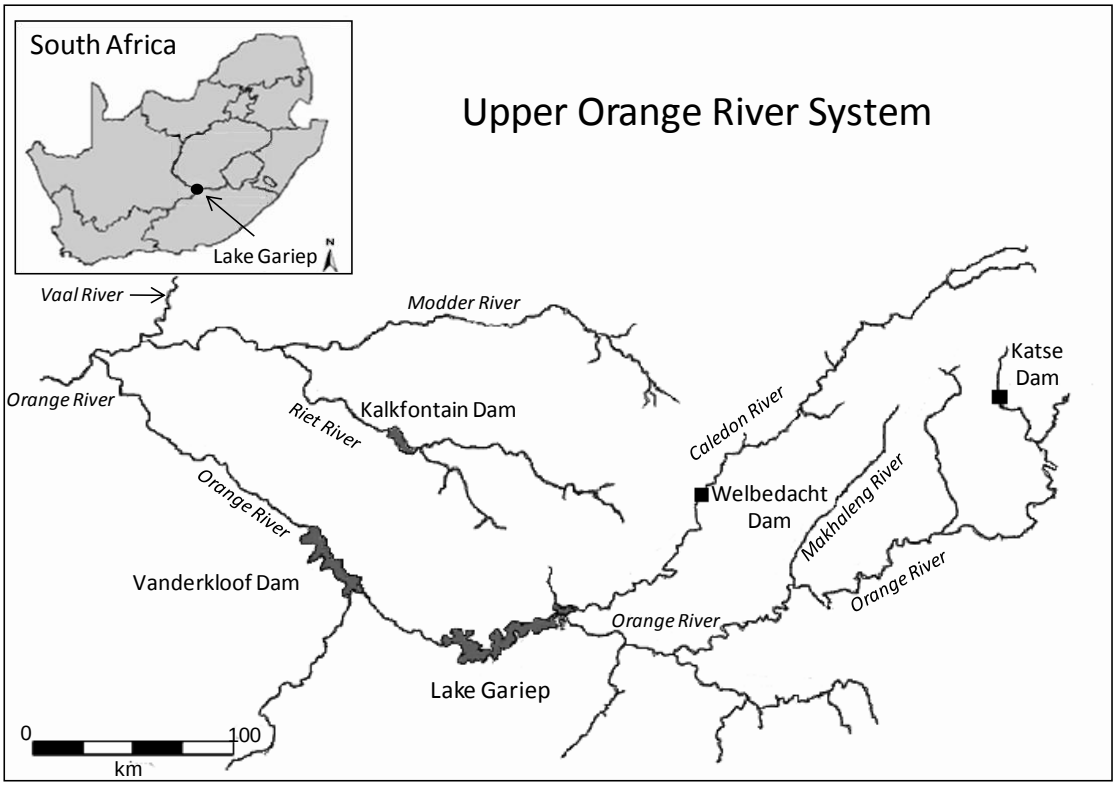

Fig. 2.1. Map illustrating the westward flowing upper Orange River from its catchment area to its confluence with the Vaal River, including major tributaries and impoundments.

The impoundment has a mean depth of 16.3 m and a maximum depth of about 50 m at full water level (Hamman, 1981). The approximately 400 km shoreline is primarily comprised of extensive, gradually sloping shores that are largely devoid of vegetation

(Hamman, 1981). Approximately 10% of the shoreline is steep and rocky (Cambray *et al.*, 1978). During spring and summer, exposed portions of the drawdown zone are colonised by an annual plant community (Cambray *et al.*, 1978). The region's climate is considered to be semi-arid. Rainfall is seasonal with most of the approximately 400 mm annual precipitation falling in summer (Keulder, 1979). The impoundment's water level fluctuates considerably and is generally a function of the seasonal inflow of the Orange River, usually during either spring or summer, and water release for power and water supply demands (Fig. 2.2).

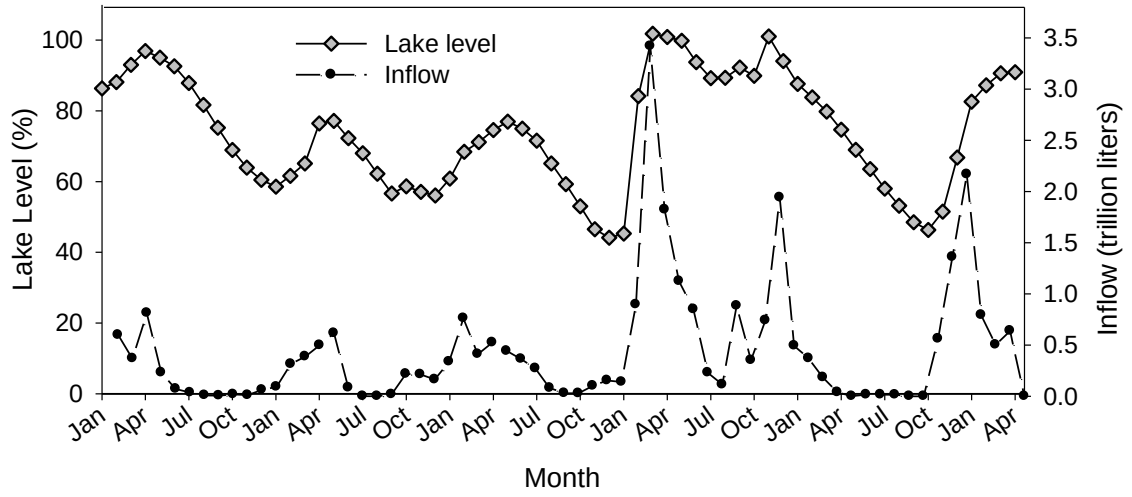

Fig. 2.2. Mean monthly lake levels (%) and water inflow of the Orange River for Lake Gariep between January 2003 and April 2008. The source data were obtained from the Department of Water Affairs and Forestry (DWAF) long-term monitoring data (DWAF, unpublished data).

Lake Gariep has been characterised as an oligo-mesotrophic impoundment that is highly turbid due to high levels of silt from the Orange River (Keulder, 1979). It was estimated that 0.6% of the volume of the upper Orange River comprises sediment, of which 90% is deposited in Lake Gariep (Keulder, 1979). This high sediment load can be mainly attributed to the naturally unstable river beds of the Orange and Caledon River (Keulder, 1979; Compton & Maake, 2007). Turbidity levels in Lake Gariep are positively correlated with seasonal inflow of the Orange River and are therefore

typically higher during spring and summer months (Keulder, 1979). During the present study, Secchi depth from offshore areas ranged from 5 cm to 34 cm (mean = 14.6 cm, *n* = 40). Annual average surface water temperature between May 2007 and May 2008 was 15.9 °C. The mean surface water temperature was 21.4 °C (range: 16.6 °C - 26 °C) in summer and 10.2 °C (8.7 °C - 11.3 °C) in winter.

2.2 GENERAL SAMPLING AND DATA SOURCES

The data used in this study were obtained from a variety of sources (Table 2.1). Field sampling was conducted from November 2006 until May 2008 and mainly consisted of experimental gillnetting and surveys of angling competitions. The gillnetting experiments and biological field sampling was conducted in close collaboration with Bruce Ellender who used a large portion of the same data sources for independent analyses published in his master thesis (Ellender, 2008).

Table 2.1 Sources of data used in this study

Data	Type	Source
Experimental gillnet surveys (2007 - 2008)	*Biological samples* (Chapters 3, 4 & 5) *Length frequency data* (Chapters 5 & 7) *Relative biomass indices* (Chapters 6 & 7)	This study
Angling competition surveys (2006 - 2007)	*Biological samples* (Chapters 3, 4 & 5) *Length frequency data* (Chapters 3 & 4)	This study
Experimental gillnet surveys (1971 - 1980)	*Relative biomass indices* (Chapter 7) *Length frequency data* (Chapter 7)	Hamman (1980)
Angler roving creel surveys (2007 - 2008)	*Relative biomass indices* (Chapter 6)	Ellender *et al.* (2008)
Biological data for *Labeobarbus aeneus*	*Life history parameters* (Chapter 7)	Ellender, (2008)

EXPERIMENTAL GILLNETTING

Gillnet surveys were conducted bi-monthly between March 2007 and May 2008. The experimental gillnet fleet comprised five multifilament nets (45 m × 3 m) constructed of green, knotted nylon netting. Each net consisted of five randomly positioned panels (9 m long × 3 m deep) with stretched mesh sizes ranging from 47 mm to 153 mm (Table 2.2).

Table 2.2. Manufacturer-quoted stretched mesh sizes (MQSM) and measured wet stretched mesh sizes of the experimental gillnet fleet

MQSM (mm)	Mean mesh size ± St Dev (mm)
44	46.6 ± 0.9
60	64.9 ± 0.8
75	77.2 ± 0.6
100	105.8 ± 0.8
144	152.6 ± 1.6

All gillnets were deployed parallel to the shore along the 2.5 – 3 m depth contour and were set between 17h00 and 19h00 in the evening and lifted between 05h00 and 07h00 the following morning. During bi-monthly routine gillnet surveys, five gillnet fleets were set on two nights within 10 km of the launch site located in close proximity to the small settlement Oviston (Fig. 2.3). During winter (June 2007) and summer (January 2008), sampling was intensified and extended to other lake areas (Fig. 2.3) to allow for spatial and seasonal comparisons of fish abundance (Chapter 6). Each seasonal gillnet survey comprised eight net nights during which five gill net fleets were deployed each night according to a randomised stratified sampling protocol described in Chapter 6. This resulted in a total sample size of 40 net nights per season.

All gillnet catches were separated by species and mesh size. Each catch was counted, and specimens weighed to the nearest 0.1 kg and measured to the nearest millimetre fork length (mm F_L).

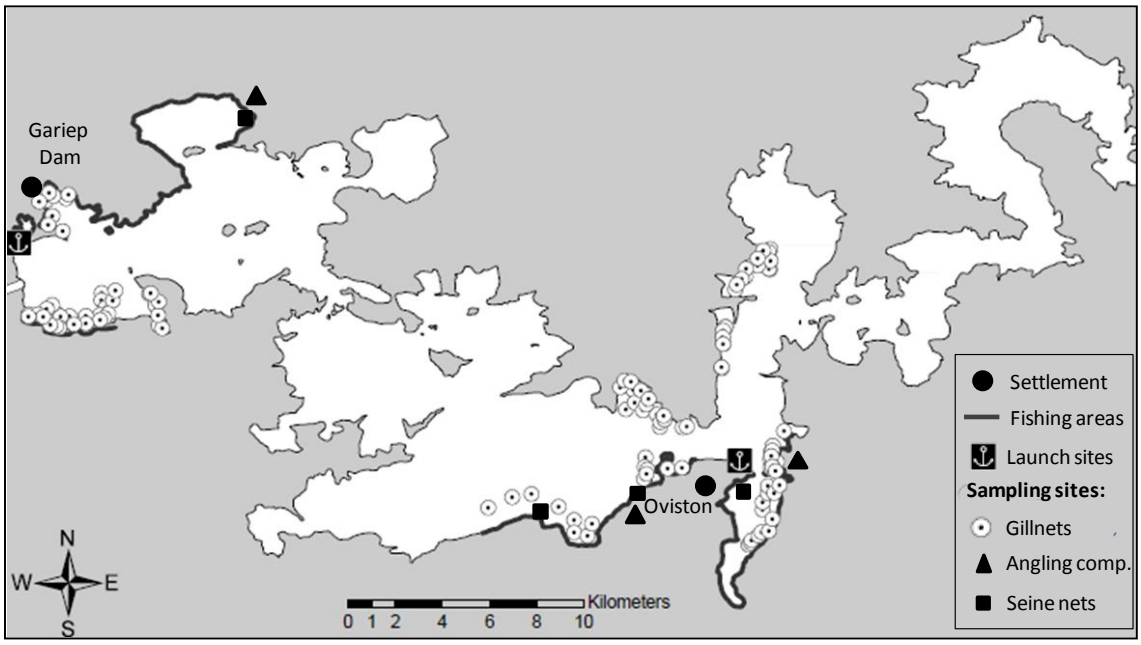

Fig. 2.3. Map of Lake Gariep showing gillnetting sites, locations of sampled angling competitions and areas used for seine netting

ANGLING COMPETITIONS

Shore angling competition events were held in November 2006, January 2007, April 2007 and October 2007 in different areas of Lake Gariep (Fig. 2.3). Participant numbers of these events ranged from 10 anglers during a one-day trial competition to 120 anglers who fished over three consecutive days. During competitions, teams (consisting of two anglers) fished a randomly assigned 25-m fixed section along the shoreline within a larger demarcated fishing area. Each angler fished with two rods for the same strictly controlled eight-hour competition period. Hook sizes used by competition anglers were fairly small (Size 6 – 12) and typically were baited with maize kernels, flour or maize dough, or earth-worms. After the official competition weigh-in was completed, specimens were collected by the research team for biological analysis from randomly selected weigh-in stations. All collected fish were separated by

species and were measured by the research team to the nearest mm L_F. According to sampling demands and feasibility, sub-samples of measured specimens were selected at random for further biological examination.

BIOLOGICAL SAMPLING

Most biological samples used in this study were collected during bi-monthly gillnet surveys and angling competition surveys. On occasion, samples were supplemented using seine nets of varying types and sizes (April 2007, January 2008 and May 2008) in different areas of Lake Gariep (Fig. 2.3) and by purchases from shore anglers.

Table 2.3. Macroscopic criteria used to determine gonadal development stages in *Cyprinus carpio* and *Labeo capensis* from Lake Gariep, South Africa (modified from Weyl & Booth, 1999; Smith & Walker, 2004).

Stage	Macroscopic appearance
Juvenile	Not possible to visibly distinguish the sex. Gonads appear as very thin transluscent strips
Immature	Sex distinguishable. Ovary visible as translucent strip. Testes form thin, but opaque white strips.
Resting	Ovary increased in size and translucent. Testis visible as a white and straight strip.
Developing	Enlarged ovary becomes opaque and is orange-red. Oocytes are visible. Testis increased in size and becomes lobular in shape.
Ripe	Ovaries turgid with oocytes filling the entire abdominal cavity. Oocytes are olive-green in colour. Blood capillaries are abundant. Testes creamy white, enlarged and fill more than a third of the body cavity. Sperm can be extruded from testes.
Spent	Ovary and testis flaccid and reddish in appearance. Ovary occasionally with a few vitellogenic oocytes present.

For biological analysis, fish were measured to the nearest mm F_L and weighed to the nearest gram. Specimens were then dissected and sexed, and the developmental stage of gonads was determined macroscopically according to the criteria summarised in

Table 2.3. Asteriscus otoliths were removed, dried and stored in 1.5 ml Eppendorf tubes for later age determination.

CHAPTER 3

Validating and corroborating the deposition of two annual growth zones in astericus otoliths of common carp *Cyprinus carpio* from South Africa's largest impoundment

3.1 INTRODUCTION

Accurate ageing is crucial for determining growth, age at sexual maturity and mortality (Campana & Thorrold, 2000) and other life history traits regarded as directly related to the fitness of a species (Roff, 1984). Structures that have been used for ageing *C. carpio* include scales, opercula bones, vertebrae, dorsal spines, pectoral fin rays and otoliths (Vilizzi & Walker, 1999; Britton *et al.*, 2007; Jackson & Quist, 2007; Phelps *et al.*, 2007). These studies have varied in their success, and there is a lack of consensus about the most appropriate structure. In recent studies, dorsal spines and astericus otoliths have been considered the most reliable in terms of accuracy and precision (Vilizzi & Walker, 1999; Brown *et al.*, 2004; Jackson & Quist, 2007; Phelps *et al.*, 2007).

Although *C. carpio* is one of the better studied cyprinids, detailed ageing studies based on formal validation of growth zone deposition are rare, and to date, astericus otoliths represent the only hard structure that has been validated using fluorochrome marking (Brown *et al.*, 2004). Only one study applied marginal increment and edge analysis to determine growth increment formation in scales, opercular bones and astericus otoliths (Vilizzi & Walker, 1999). Both studies were conducted on carp populations of the Murray-Darling Basin, Australia, and provided evidence that one growth zone was deposited annually.

In Africa, published literature on ageing *C. carpio* is virtually non-existent. In a recent study, Britton *et al.* (2007) collected scales to derive age estimates for *C. carpio* from Lake Naivasha, Kenya, but were confronted with a lack of consistency even within the same specimen, and in some cases, a complete absence of growth checks. In two South African studies, scales (Hamman, 1981) and vertebrae (Cochrane, 1985) were used for determining age and growth.

To contribute to the knowledge on accurate ageing of one of the most prominent invasive and widely distributed freshwater fishes, this Chapter validated the rate of growth zone deposition in astericus otoliths of *C. carpio* from Lake Gariep, South Africa. The validation approach included a mark-recapture experiment of chemically tagged carp that was conducted in large earthen ponds under ambient conditions in the vicinity of Lake Gariep. The validation results were then corroborated for the wild population using edge analysis and by applying a length-based age-structured model. For both methods, the hypotheses that growth zone deposition is annual and that growth zone deposition occurs biannually were tested. The findings of this Chapter represent the first validation of growth increments in otoliths of an African *C. carpio* population.

3.2 MATERIALS AND METHODS

Field sampling is described in Chapter 2. Most *C. carpio* samples were donated by anglers during bank angling competitions held in November 2006, January 2007, April 2007 and October 2007. Additional samples were obtained between March 2007 and March 2008 during bi-monthly gillnet surveys, from seine netting experiments (April 2007, January 2008 and May 2008) and from occasional purchases from shore anglers.

OTOLITH INTERPRETATION

As different ageing procedures have been used for different populations of the same species (Jackson & Quist, 2007; Richardson *et al.*, 2009), various approaches were assessed to determine the most suitable method for interpreting growth. These approaches included: (1) using the ventral lobe of 0.4 mm thick otolith sections, cut transversely through the nucleus and viewed under transmitted light (Brown *et al.*, 2004), (2) using whole otoliths submerged in water and viewed under reflected light with a dark background (Vilizzi & Walker, 1999) and (3) examining whole otoliths submerged in methyl salicylate and viewed under transmitted light using varying magnifications (×10 – 40). Highest confidence in the optical interpretation of growth zones was achieved by using the third method, which has also been suggested for determining age in astericus otoliths of other cyprinid species in South Africa (Potts *et al.*, 2006a; Weyl *et al.*, 2009). This method was therefore accepted as the standard protocol for this study.

Growth zones were visible as alternating translucent (light) and opaque (dark) zones (Fig. 3.1). The number of growth zones were determined by counting the numbers of opaque zones along an antero-dorsal ageing transect situated on the otolith rostrum (Fig. 3.1). All otoliths (n = 816) were read at least twice by the first author, at random, at least two weeks apart and without knowledge of the date of capture or length of the fish. If the two readings were identical, the count of growth zones was accepted. If the two readings differed, a third reading was conducted. If this resulted in two identical readings, the counts were accepted. If the three readings differed at most by two growth zones (e.g. 2, 3, 4), the median estimate was accepted, otherwise the otolith was rejected.

Fig. 3.1. Microphotograph showing alternating translucent (light) and opaque (dark) zones of a whole astericus otolith of *Cyprinus carpio* that was submerged in methyl salicylate and viewed under transmitted light. White circles indicate the antero-dorsal aging transect along the rostrum used for counting the opaque zones.

ACCURACY AND PRECISION

The precision of growth zone counts of the primary reader was assessed using the average percent error (APE) method (Beamish & Fournier, 1981) and by estimating the coefficient of variation (CV) suggested by Chang (1982). An experiment was conducted to account for systematic biases that may affect the accuracy of growth zone counts. For this purpose, 100 otoliths were randomly selected from the data set and read once by three secondary readers (Olaf Weyl, Anthony Booth and Bruce Ellender). The results were compared to the accepted counts that were conducted by the primary reader. All secondary readers were experienced in the interpretation of otoliths but unfamiliar with *C. carpio* otoliths. Each reading was therefore conducted without any prior knowledge of criteria applied by the primary reader, date of collection or size of the fish. Age-bias plots (Campana *et al.*, 1995) were used to assess the level of bias between primary and secondary readers. The assumption of a 1:1 relationship was

assessed by linear regression t-tests to test if the slope and the intercept were significantly different from one and zero, respectively (Roff, 1984; Weyl & Booth, 2008).

FLUOROCHROME MARKING EXPERIMENT

Oxytetracycline hydrochloride (OTC) was used to validate the frequency of otolith growth zone deposition. OTC rapidly chelates in otoliths and produces a fluorescent mark when viewed with ultraviolet light (Campana, 1999). Mark-recapture of OTC marked wild fish was suggested to be one of the most suitable methods available to validate growth zone periodicity (Campana, 2001). The vast surface area of the dam and the limitation of subsistence and recreational angling to less than 20% of the shoreline (Ellender *et al.*, 2009) precluded the use of mark-recapture of OTC marked wild fish as a suitable method because recapture probabilities were low. OTC marked wild caught *C. carpio* from Lake Gariep were, therefore, released into a large earthen pond under ambient conditions situated at the Lake Gariep State Fish Hatchery located 3.2 km below the dam wall on the banks of the Orange River (30°37’584 S; 25°28’229 E). The pond was 50 m long x 25 m wide x 1.5 m deep and stocked with 21 wild carp ranging from 295 mm L_F to 460 mm L_F caught by angling during March 2007. On capture, fish were placed in a water-filled canvas bag and carried to an oxygenated holding tank that contained 0.2 ml/L of the anaesthetic 2-Phenoxyethanol (Sigma-Aldrich Chemicals, Steinheim, Germany) to minimise post-capture stress until transported to the pond. On site, fish were injected with 60 mg/kg fish mass OTC solution (HiTet 120; Bayer, Leverkusen, Germany) prior to release into the pond. As a control and to monitor the growth rates during the course of the experiment, all fish were tagged with T-bar anchor tags (Hallprint; TBA-2). Stocking density was kept below one fish per 90 m^3 and there was no supplementary feeding. Fish were re-

captured after 14 months at liberty (in May 2008), sacrificed, measured to nearest mm L_F, and weighed to the nearest gram (g). Sex was determined macroscopically, and the astericus otoliths were removed and stored dry in 1.5 ml Eppendorf tubes. Otoliths were stored in the dark to prevent the degrading effect that UV light has on OTC.

Results from the only other study that used mark-recapture of OTC marked adult *C. carpio* for age validation purposes were based on thin otolith sections (Brown *et al.*, 2004). To allow for comparison, OTC marked otoliths were, therefore, not only examined whole, but also sectioned. One astericus otolith per specimen was embedded in clear polyester casting resin, sectioned transversely through the nucleus to a thickness of 0.4 mm and mounted on a microscope slide using DPX mounting agent. Whole and sectioned otoliths were viewed under reflected fluorescent (460 - 490 nm and 510-550 nm) and transmitted white light to determine the position of fluorescent mark and to count the number of opaque zones distal to the mark. To count the total number of growth zones, otoliths were also assessed under transmitted white light using varying magnifications (×10 – 40).

EDGE- AND LENGTH FREQUENCY ANALYSIS

To corroborate the results from the OTC marking experiment for the wild population, two indirect validation methods were applied: (1) edge analysis and (2) length frequency analysis (LFA). For both methods, the null hypotheses that growth zone deposition is annual (H_0^1) and that growth zone deposition occurs biannually (H_0^2) were tested. A significance level of $p < 0.05$ was used for all tests.

A total of 607 otolith pairs were used for the edge analysis. Otoliths with less than two growth zones were excluded from the analysis (Vilizzi & Walker, 1999). The optical

appearance of the edge of each whole otolith was assessed and categorised as either optically opaque (1) or translucent (0). Edge analysis is based on the assumption that the relative frequency of opaque edges was periodic when plotted against time (Campana, 2001). Otolith samples collected between November 2006 and May 2008 were assigned to 24 monthly periods of any given year M_i (with beginning of January being assigned 0 and end of December 23). The binary results were then expressed as the proportion of otoliths with an opaque zone present during M_i and modelled using a periodic logistic regression (Flury & Levri, 1999) of the form:

$$logit(\hat{O}_i) = \beta_0 + \beta_1 \sin(2\pi\frac{M_i}{P}) + \beta_2 \cos(2\pi\frac{M_i}{P}),$$

where *logit* is the link function for the binomial regression, $\hat{O}_i$ is the expected proportion of otoliths with an opaque zone present at the margin for each M_i, P is the assumed periodicity of growth deposition (i.e. here 24 and 12 for an annual and biannual cycle, respectively) and β_0, β_1, β_2 the regression coefficients (Beamish *et al.*, 2005).

Regression parameters were estimated by minimising the negated binomial log-likelihood function of the form:

$$-LL = -\sum_i \left[m_i \ln\left(\hat{O}_i\right) + (n_i - m_i)\ln(1-\hat{O}_i)\right],$$

where n_i is the number of otoliths examined in sample i and m_i represents the number of otoliths with an opaque zone present on the margin. To test H_0^1 and H_0^2, a Likelihood

Ratio Test $\chi_k^2 = 2(LL_{full} - LL_{reduced})$ was conducted, where $LL_{reduced}$ is the log-likelihood for the reduced model with the constraint that *P* is fixed (at either 24 or 12), LL_{full} is the log-likelihood for the full model where *P* is estimated, and *k* denotes the difference between the number of parameters estimated for the full model and the reduced model.

Length frequency analysis was conducted based on a length-based age-structured model suggested by MacDonald & Pitcher (1979). Three large length frequency (LF) samples were used that were collected during angling competition events in November 2006 (*n* = 692), January 2007 (*n* = 297) and April 2007 (*n* = 979). Sub-samples of otoliths were available for all three LF samples. For each sample, results from LFA were compared to the assumed mean length-at-age (according to H_0^1 and H_0^2) from otolith data.

For each of the samples, length data were regrouped into 10 mm L_F classes *i*. The resulting LF histograms showed several discernable modes and were therefore considered as suitable. The number of identifiable modes A_s for each LF sample *s* was graphically determined. For each sample *s*, it was assumed that the relative proportion of fish observed in length class $i, q_{i,s}$, was equal to the sum of all identifiable modes at length i. If each mode a in sample *s* can be described by a normal distribution function $\theta(\hat{\mu}_{a,s}, {\sigma_{a,s}}^2)$, where $\hat{\mu}_{a,s}$ and ${\sigma_{a,s}}^2$ are the mean and the variance, respectively, then the predicted proportion for length class i in sample *s* can be estimated as:

$$\hat{q}_{i,s} = \sum_{a=1}^{A_s} \hat{p}_{a,s}\theta(\hat{\mu}_{a,s}, {\sigma_{a,s}}^2),$$

where A_s is the maximum number of modes in sample s and $\hat{p}_{a,s}$ is the predicted relative abundance of fish in mode a from sample s, such that $\sum_{a=1}^{A} \hat{p}_{a,s} = 1$. The maximum likelihood for the parameters of interest, $\hat{p}_{a,s}$, $\hat{\mu}_{a,s}$ and $\hat{\sigma}_{a,s}$, were obtained for each LF sample by minimising the robust log-likelihood function (Fournier *et al.*, 1990; Simon & Booth, 2007) of the form:

$$LL = \sum_{i=1}^{L_s} \left[\ln(\sqrt{\xi_{i,s}}) + 2{\xi_{i,s}}^{-1} \left(q_{i,s} - \hat{q}_{i,s}\right)^2 \right],$$

where $\xi_{i,s} = \hat{q}_{i,s}(1 - \hat{q}_{i,s})\, n_s^{-1}$ is the relative binomial variance of $\hat{q}_{i,s}$, n_s is the number of observations in sample s and L_s is the maximum number of length classes in sample s.

To test ${H_0}^1$, mean length-at-age from otolith sub-samples, assuming annual growth zone deposition (e.g. 3 years = 3 opaque zones), was pair-wise regressed against predicted mean length-at-age from LFA. This regression was repeated based on the ${H_0}^2$ assumption that growth zone deposition occurs biannually (e.g. 3 years = 5 or 6 opaque zones, i.e., this hypothesis implies that a second opaque zone is deposited at some point during the course of the year and that this year class may therefore include fish with either five or six opaque zones). The assumption of a 1:1 relationship for each of the two regressions was tested using linear regression t-tests previously described. Age-bias plots (Campana *et al.*, 1995) were used for each LF sample for further graphical interpretation.

3.3 RESULTS

Throughout the study period more than 2500 carp were measured and 816 otolith pairs were removed. Angling competition surveys were the most effective sampling method, and resultant data accounted for more than 86% of measured fish and 81% of collected otoliths.

ACCURACY AND PRECISION OF OTOLITH INTERPRETATION

Of the 816 otolith pairs analysed, 34 (4.16%) were rejected as unreadable. Estimated APE index for the primary reader was 5.54% and the mean CV was calculated as 7.03%. Discontinuities, short and narrow opaque zones, also referred to as "pseudo-annulli" (Vilizzi & Walker, 1999), were clearly distinguishable from the usual thick and continuous "true" opaque zones and therefore excluded from growth zone counts. The maximum number of growth zones counted was 14. Due to a progressive decrease in the width of the translucent zones, interpretations of otoliths with more than eight growth zones became increasingly difficult.

There was no systematic bias between the primary reader and the three secondary readers for the first 0 to 9 growth zones (Fig. 3.2), which is the range of growth zones that accounted for 95% of the total sample (n = 816).

Only the oldest fish in the sample differed between the primary and two of the secondary readers by more than two growth zones. Secondary reader 3 tended to overestimate growth zones compared to the other readers (Fig. 3.2). The null hypothesis that the slope of the regression = 1 failed to be rejected ($p > 0.05$) for all t-tests between the primary reader and secondary readers, and none of the intercept estimates was significantly different from zero ($p > 0.05$).

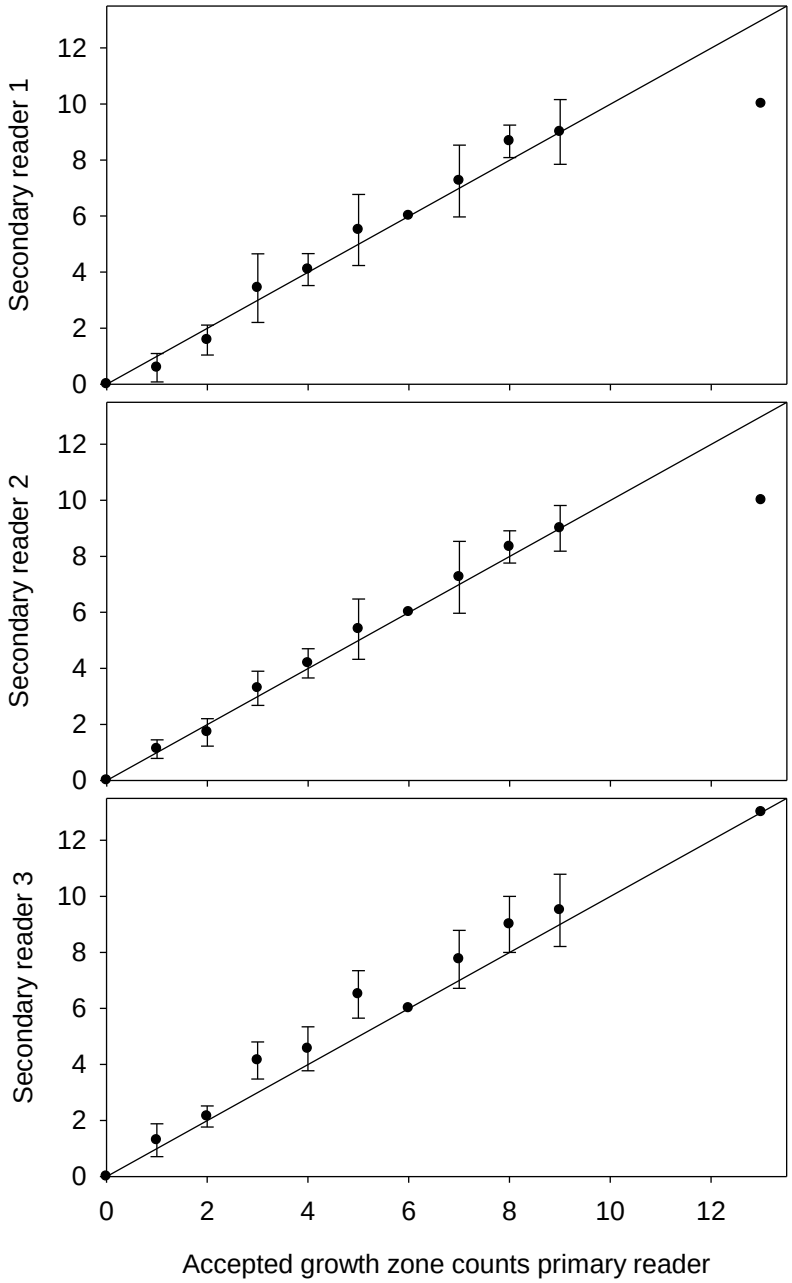

Fig. 3.2. Age-bias plots showing pair-wise comparison between the growth zone counts accepted by the primary reader and the results from the three secondary readers for whole astericus otoliths of *Cyprinus carpio* from Lake Gariep, South Africa. Error bars denote standard deviations from the mean. The solid line in each plot represents a 1:1 relationship. (*n* = 100).

FLUOROCHROME MARKING EXPERIMENT

Of the 21 *C. carpio* that were tagged, injected with OTC and released into the pond in March 2007, 19 were recaptured in May 2008 and only seven (37%) retained the T-bar tag. During the 14 months of the experiment, these specimens grew in length by an average of 176 mm F_L [95% CL = 141 - 202 mm] (Table 3.1). Average increase in weight was 1.68 kg [1.37 – 2.19 kg]. The fastest growth was recorded for a specimen that grew 220 mm L_F, from 345 mm to 565 mm L_F, corresponding to an increase in weight by 2.19 kg. One of each of the extracted 19 otolith pairs was sectioned and the other one was left whole. During the course of the analysis, two of the whole otoliths broke and had to be excluded (N/A). A fluorescent mark was visible in all 17 remaining whole otoliths and in 15 (78%) of the otolith sections (Fig. 3.3), of which two were classified as unreadable (U/R) due to the absence of clearly discernable opaque zones (Table 3.1).

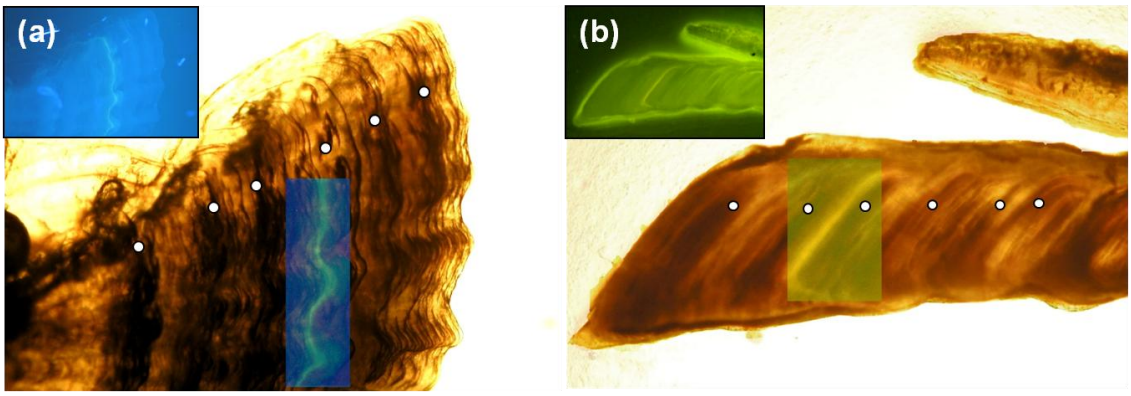

Fig. 3.3. Photomicrographs using of whole (a) and sectioned (b) astericus otoliths of *Cyprinus carpio* injected with oxytetracycline 14 months prior to the recapture. The base images show the otoliths under transmitted light with positions of opaque zones (○) indicated. The overlaid portions were viewed with transmitted fluorescent light highlighting the fluorescent mark. Inserts show the same images using fluorescent light only.

Growth zone counts at the time of recapture ranged from five to ten. If an opaque zone coincided with the fluorescent mark, it was counted as prior to the mark. All but one of the whole otoliths and all of the sectioned otoliths showed two growth zones distal to

the OTC mark. The optical appearance of the edge was categorised as translucent for 94% and 82% of the whole and sectioned otoliths, respectively. The results from this experiment suggested that two opaque zones were deposited during the 14 month period in the ponds. The presence of a translucent zone on the edge of the majority of otolith samples at the time of recapture indicated the commencement of a new growth zone.

Table 3.1 Summary of *Cyprinus carpio* that were injected with oxytetracycline hydrochloride (OTC) and recaptured after 14 months in large earthen ponds under ambient conditions. The summary includes length-at-capture (L_{CA}), length-at-recapture (L_{RE}), increase in length (ΔL), the total number of observed growth increments and those that were deposited prior (F_{PRE}) and posterior (F_{POST}) to the fluorescent mark. Edge appearance was categorised as translucent (T) or opaque (O)

	Length (mm F_L)			whole otolith				sectioned otolith			
Tag	L_{CA}	L_{RE}	ΔL	Pre-F	Post-F	Total	Edge	Pre-F	Post-F	Total	Edge
yes	345	530	185	4	2	6	T	4	2	6	T
yes	345	565	220	5*	2	7	O	5*	2	7	O
yes	340	536	196	4*	2	6	T	4	2	6	T
yes	460	575	115	6	2	8	T	6	2	8	O
yes	295	435	140	N/A	N/A	N/A	N/A	6*	2	8	O
yes	388	576	188	4	2	6	T	N/F	N/F	6	T
yes	335	520	185	4	2	6	T	N/F	N/F	N/D	N/D
no	-	586	-	N/A	N/A	N/A	N/A	5	2	7	T
no	-	592	-	6	2	8	T	6	2	8	T
no	-	514	-	4	2	6	T	4	2	6	T
no	-	584	-	4	2	6	T	4	2	6	T
no	-	632	-	8	2	10	T	7	2	9	T
no	-	626	-	6	2	8	T	8	2	10	T
no	-	619	-	4*	1	5	T	N/F	N/F	5	T
no	-	610	-	4	2	6	T	4	2	6	T
no	-	570	-	6	2	8	T	5	2	7	T
no	-	582	-	4	2	6	T	N/F	N/F	N/D	N/D
no	-	520	-	4	2	6	T	4*	2	6	T
no	-	601	-	6	2	8	T	6	2	8	T

N/A, otolith not available; N/F, no fluorescent mark discernable; U/R, unreadable; *), opaque zone coincided with the fluorescent mark

EDGE- AND LENGTH-FREQUENCY ANALYSIS

A biannual periodic regression model best described the temporal frequency distribution of opaque zone deposition on the edge of otoliths over a one year period (Table 3.2).

Table 3.2. Parameter estimates from the logistic periodic regression analysis predicting the temporal proportion of opaque zone deposition over a one-year period for *Cyprinus carpio* in Lake Gariep, South Africa. The periodicity (*P)* was estimated for the full model and fixed for the unimodal and bimodal model.

Parameter	periodic regression model		
	annual	biannual	full
β_0	-0.61	0.15	0.14
β_1	1.41	1.01	0.83
β_2	1.42	0.96	1.08
PE	24	12	12.2
df	3	3	4
LL	-354.55	-337.57	-337.49

Observed and predicted data indicated that the first mode peaked in summer (Dec-Mar) and a second mode in winter (Jun-Sep) (Fig. 3.4). A Likelihood Ratio Test revealed that there was no significant difference between the full model, where the yearly periodicity was estimated, and a model with a hypothesised deposition of two growth zones per year (H_0^2; $\chi^2 = 0.15$, df = 1, $p = 0.69$). The null hypothesis that growth zone deposition follows a unimodal annual cycle was, however, rejected (H_0^1; $\chi^2 = 34.12$, df = 1, $p < 0.05$).

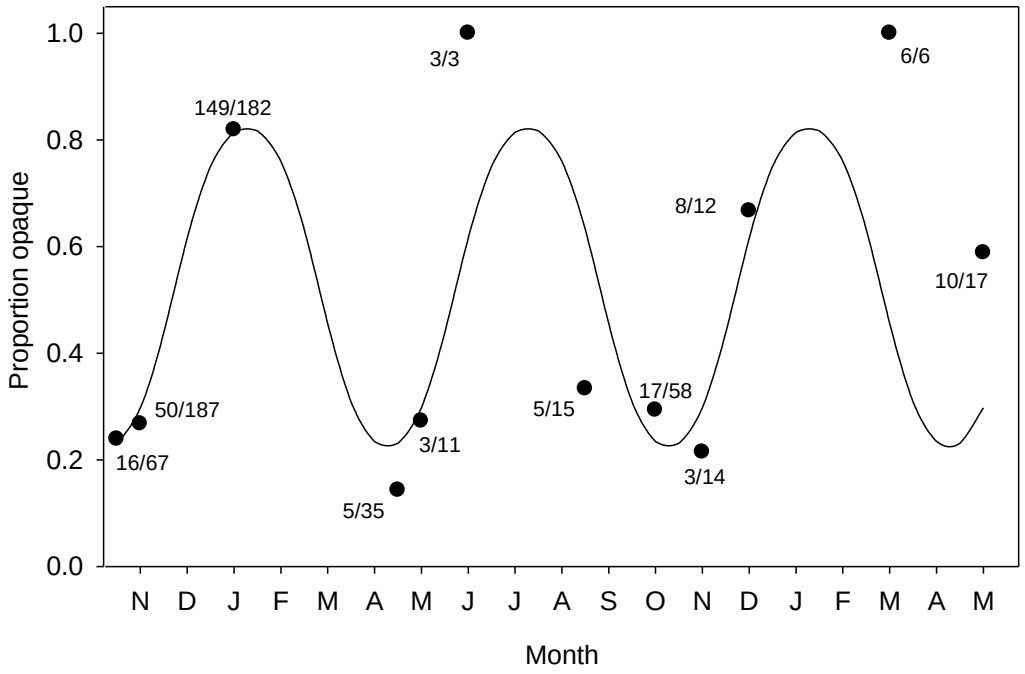

Fig. 3.4. Proportion of otoliths with an opaque zone on the margin for *Cyprinus carpio* based on data collected between November 2006 and May 2008 from Lake Gariep, South Africa. The solid line represents the predicted bimodal annual cycle of opaque zone deposition using a Binomial periodic regression. Opaque margins and total number of otoliths examined are denoted as numerator and denominator, respectively.

Results from LFA are illustrated in Fig. 3.5. The November LF sample consisted of a range of larger size classes (Fig. 3.5 a). Smaller size classes were absent in this sample and only recruited into angling competition catches during subsequent events in January and April (Fig. 3.5 b, c). Hence, the first discernable mode observed in the November sample was assigned to age class two (Fig. 3.5 a).

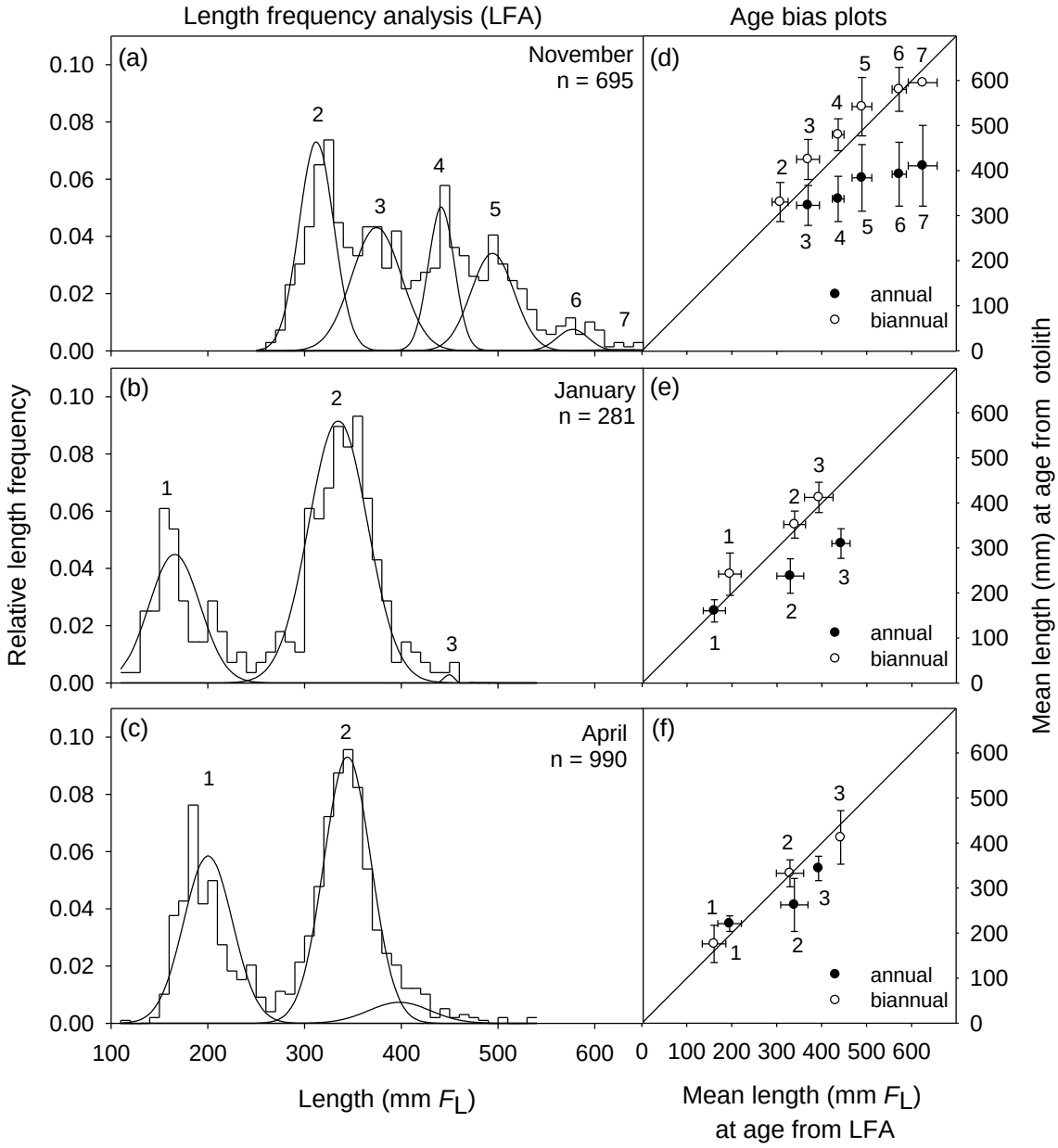

Fig. 3.5. Length frequency analysis (LFA) applied to *Cyprinus carpio* angling competition samples from November 2006 (a), January 2007 (b) and April 2007 (c). Solid curves show maximum likelihood fits of mixture distributions with numbers denoting the estimated age-groups. Age-bias plots (d)-(f) show corresponding pair-wise comparisons between mean length-at-age from LFA and otolith data assuming either annual (●) or biannual (○) growth zone deposition rates. Linear lines represent a 1:1 relationship. Error bars represent one standard deviation.

Based on the number of discernable modes, mean length-at-age could be estimated for five (November), three (January) and three (April) sequential age classes, respectively. If growth zone deposition rate was assumed biannual (H_0^2), this finding was identical with the estimated age classes from otolith samples, with the only exception of an

estimated six-year old specimen from the January sample. In contrast, the annual growth zone deposition hypothesis (H_0^1) resulted in wider ranges of age estimates (3 - 14 years for November, 1 - 11 years for January and 1 - 6 years for April).

A graphical inspection using age bias plots showed that mean length-at-age estimates based on H_0^2 approximated a 1:1 relationship when compared with the results from LFA, whereas estimates based on H_0^1 tended to underestimate the predicted mean length-at-age from LFA (Fig. 3.5 d - f). The first age class predicted by the LFA for January and April (Fig. 3.5 b, c) exclusively corresponded to length groups of carp that had otoliths with one or two opaque zones. While only 20% of these fish showed a second opaque zone by January, 50% of fish were recorded with a second opaque zone by April. This means that the results from the LFA provide corroborative evidence that the predicted age-1 group deposited two opaque zones during the course of one year and that fish with one or two opaque zones were part of the same age group. This also implies that not all fish in this age group had deposited the second opaque zone by the time of the April sampling event. The assumptions of a 1:1 relationship (slope = 1, intercept = 0) across all three samples were rejected for H_0^1 (t-test; $p < 0.05$) and were failed to be rejected for H_0^2 (t-test; $p > 0.05$) (Fig. 3.6).

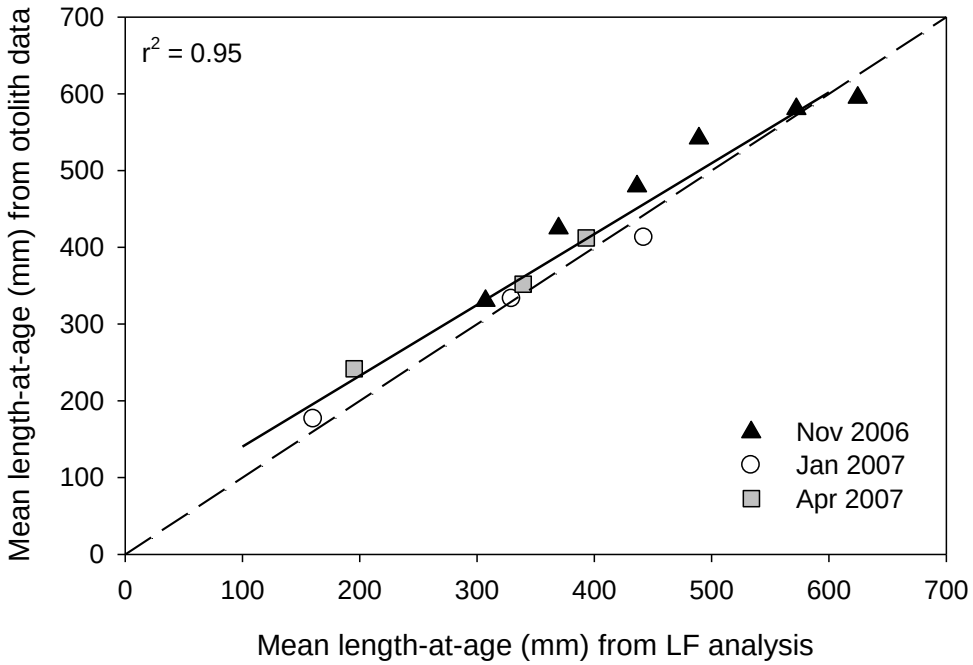

Fig. 3.6. Pair-wise comparison of mean length-at-age from the length frequency analysis (LFA) and mean length-at-age from otolith based on the null hypothesis that growth zone deposition occurs biannually. Linear regression: $F_{1,10}$; slope = 0.92; intercept = 47.8 mm; r^2 = 0.95). The solid line represents the fit of the linear regression and dashed line a 1:1 relationship.

GROWTH ZONES

Growth zone counts based on the number of observed opaque zones were plotted against L_F and grouped according to an assumed biannual growth zone deposition rate that was supported by the redundant results from the three validation approaches (Fig. 3.7). The number of opaque zones revealed an alternating growth pattern. While larger increases in length were observed between even and odd numbers of opaque zones, growth appeared to be reduced between odd and even numbers (Fig. 3.7). The most apparent transition in the proportion of odd to even numbers was observed in large otolith sub-samples available for November 2006 and January 2007. When both samples were combined, fish with three and four growth zones formed a dominant group that accounted for 58% of the sample (n = 450). While 83% of otoliths sampled in November (n = 99) were observed with three opaque zones, this proportion changed

to 91% of this group (n = 162) having four opaque zones when sampled in January, suggesting that these carp were likely to be part of the same age group.

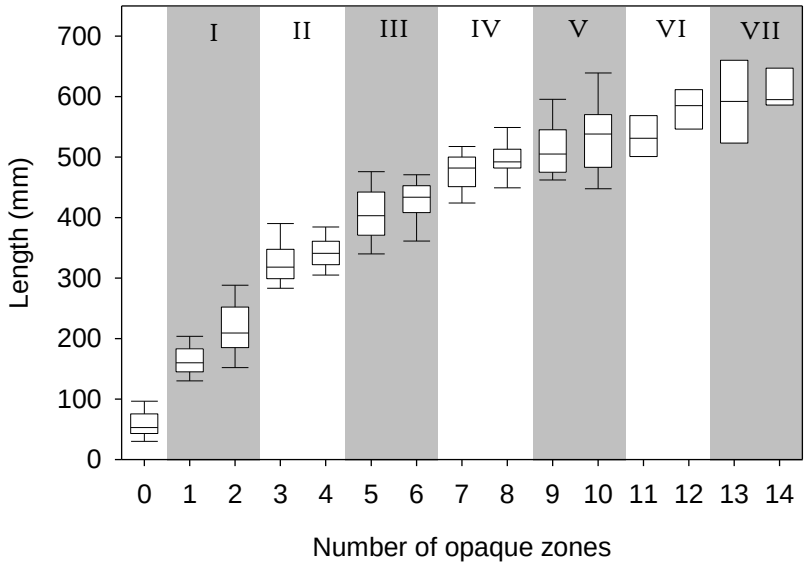

Fig. 3.7. Box and whisker plots derived from observed lengths at opaque zones. The alternating white and grey columns highlight the grouping in age classes according an assumed biannual deposition of growth zones with roman numbers denotes the age groups (n = 782).

3.4 DISCUSSION

Fish otoliths have been described as metabolically inert environmental recorders, with their microstructure being controlled by a suite of physical, chemical, environmental and physiological factors (Campana, 1999). This may result in regional differences of growth zone deposition rates and can therefore influence ageing precision or the choice of otolith preparation technique. Additional complications arise from the effect of reader subjectivity, which might be reduced and quantitatively determined, but not eliminated (Campana *et al.*, 1995). Therefore, the findings of this study should be interpreted as system- or region-specific.

In a comprehensive study on ageing *Cyprinus carpio* in the Murray-Darling Basin, Australia, Vilizzi & Walker (1999) found comparable interpretabilities between whole

and sectioned astericus otoliths, which they related to the specific morphological characteristics of these otoliths in cyprinids. Moreover, they noted that underestimation of the ages of older carp using whole otoliths instead of sections, a phenomenon often demonstrated for sagittal otoliths (Dwyer *et al.*, 2003), was not evident, and that sectioning otoliths even obscured the visibility of opaque zones close to the margin. Similar problems with sectioned otoliths were encountered during exploratory otolith preparation for the present study and the highest confidence in the optical interpretation of astericus otoliths was achieved by reading them whole under transmitted light while submerged in methyl salicylate. In some instances, however, sectioned otoliths may be more suitable or convenient. Brown *et al.* (2004), for example, reported higher within reader precision for sectioned otoliths (APE = 4.04 - 4.56%; CV = 5.55 - 6.41%) than found in this study (APE = 5.54% and CV = 7.03%), which were similar to those reported by Vilizzi & Walker (1999) for whole otoliths (APE = 5.64%; CV = 7.97%). While some of the differences in precision and choice of ageing structures may be a result of the experience and preference of the interpreter (Brown *et al.*, 2004), others are likely to be caused by differences in the optical properties among populations (Jackson & Quist, 2007).

The between-reader comparison experiment was conducted to test for the statistical significance of potential systematic biases that may have been related to false ageing criteria. The requirement for such an approach is that the secondary reader needs to be naïve about the species-specific hard structure of interest, but should also be experienced in ageing other fish species. A disadvantage is that this experiment is not suitable for determining between-reader precision, particularly when considering that *C. carpio* was described as a difficult species to age that requires extensive training and experience (Vilizzi *et al.*, 1998). The results suggest that all three secondary readers

independently applied similar interpretation criteria to those established by the primary reader after several preliminary reading trials and a study of available literature. This indicates that accepted otolith readings in the range between zero and nine growth zones are likely to have a high degree of reproducibility.

Among the three validation approaches applied in this study, chemical marking of wild fish is considered most powerful (Campana, 2001; Dwyer *et al.*, 2003; Brown *et al.*, 2004; Egger *et al.*, 2004). Although it was not possible to conduct this experiment in the lake itself, the results are considered to have strong implications, in particular since the wild caught carp were subject to the same seasonal changes in ambient temperatures, rainfall and day length regimes during the 14 months at liberty in the large ponds.

Although edge and marginal increment analysis belong to the most frequently used validation methods, they have been criticised for their lack of objectivity concerning the graphical interpretation of the results (Campana, 2001). The logistic periodic regression approach (Flury & Levri, 1999; Beamish *et al.*, 2005) allows modelling an assumed sinusoidal periodicity. As the parameter estimates are based on the minimisation of the negative binomial log-likelihood function, monthly observations of proportions of opaque zones on the margin are weighed according to sample sizes, a factor which is extremely difficult to quantify and incorporate into a graphical assessment. Furthermore, the likelihood approach provides the opportunity to objectively test the null hypotheses of whether the deposition rate follows a unimodal or bimodal yearly cycle. As the choice of distributions and related log-likelihood functions (e.g. binomial, normal, lognormal, gamma, Poisson) is in principle flexible,

this approach also has the potential to be applied to measurement results from marginal increment analysis.

A prerequisite for using length frequency analysis to corroborate results from other validation methods is that length modes should be discernable, which therefore limits the range of applications to relatively fast growing fish or younger age groups (Campana, 2001). Given that the data are suitable, inferences from subsequent comparisons, for example, of monthly length modes in juvenile fish or with estimates obtained from ageing structures may add valuable supporting or contradicting information (Jensen, 1970; Cochrane, 1985; Campana, 2001; Dwyer *et al.*, 2003; Brown *et al.*, 2004). The maximum likelihood estimation procedure (Fournier *et al.*, 1990; Simon & Booth, 2007) is able to provide a unique and statistically robust solution for a single length frequency distribution. Any comparison with otolith-derived length-at-age data should, however, be based on length-frequency data and corresponding sub-samples of otoliths that were collected at random from the same sampling event, so that factors such as catchability, size-selectivity, changes in spatial distributions and modal growth progression are more likely to be minimised.

All three applied validation approaches suggest that the deposition of growth zone increments occurs biannually. Supporting evidence for the possibility of a biannual growth zone deposition rate in the Lake Gariep population comes from a study by Cochrane (1985), which was conducted in Hartebeespoort Dam, a South African hypertrophic impoundment situated about 580 km north-east of Lake Gariep. Cochrane (1985) inferred a formation of two growth zones per year in vertebrae of *C. carpio* by comparing mean length-at-age estimates derived from available length-frequency samples using the Petersen (1891) method to calculate time of growth zone formation.

The predicted increase in the proportion of opaque zones in whole otoliths between October and January (Fig. 3.4) was also noted by Vilizzi & Walker (1999) and is in accordance with the time of growth check formation in vertebrae that was reported for the *C. carpio* population from Hartebeespoort Dam (Cochrane, 1985). This period of late-spring and early-summer usually coincides with peak spawning events of *C. carpio* (Cochrane, 1985; Fernàndez-Delgado, 1990; Sivakumaran *et al.*, 2003; Smith & Walker, 2004; Brown *et al.*, 2005). This was noticeable in the present study as a large proportion of reproductively active carp were recorded during November 2006 (Chapter 4). Fernàndez-Delgado (1990) also noted a sharp decrease in the somatic condition of *C. carpio* during this period, which they ascribed to high energy requirements for spawning.

The second opaque zone formation was predicted to occur during mid-winter (Fig. 3.5) when surface temperatures were at a minimum (8.7 °C - 11.3 °C). This also agrees with the timing of the annual opaque formation found in whole astericus otoliths of two large endemic cyprinids, *Labeo capensis* and *Labeobarbus aeneus*, which co-occur with *C. carpio* in Lake Gariep (Winker *et al.*, 2010; Appendix I). In Southern Africa, Hecht (1980) and Weyl & Booth (1999) observed biannual formation patterns similar to this study in sagittae otoliths of the tilapia species *Oreochromis mossambicus* and on scales of the cyprinid *Labeo cylindricus*, respectively, with one formation evident by the end of the peak spawning period and a second in winter when temperatures were low.

While the underlying processes of opaque zone depositions remain largely unclear and can be influenced by environmental variability, protracted spawning or a error in the

optical recognition of opaque material (Francis *et al.*, 1992; Vilizzi & Walker, 1999; Smith & Deguara, 2003; Egger *et al.*, 2004; Bwanika *et al.*, 2007), it appears to be a reasonable explanation that the biannual growth zone deposition in otoliths of adult *C. carpio* from Lake Gariep is related to high investment in reproduction during early summer and to low water temperatures in winter.

Uncertainty remains over the formation of the first two opaque zones because their deposition rate was not validated by fluorescent marking. Vilizzi & Walker (1999) found that otoliths with one and two increments showed almost exclusively translucent margins throughout the year, which they explained by a rapid development of the otolith structure in young fish in combination with relatively thin first opaque zones. This is similar to observations from the present study. Otoliths with one growth zone, for example, were excluded from edge analysis because they obscured the periodic pattern observed for older fish due to their high proportions of translucent margins. A weakly defined periodic pattern (not shown here) indicated that a first opaque zone was primarily formed between May and June, presumably signifying the end of the first growing season, whereas hardly any otoliths were noted with a single opaque zone on the margin of otoliths sampled between October and April. Otoliths with two opaque zones were generally scarce in all samples. In contrast to otoliths with a single increment, however, this two opaque zone group was predominantly found with opaque zone margins during the summer months, which agreed with the predicted periodicity of opaque zone deposition for older fish (Fig. 3.4). Under the assumptions that growth slows down as fish become older and that the initial somatic growth of immature fish is fastest because no energy needs to be allocated to reproduction (Roff, 1984; Shuter *et al.*, 2005), the presented results favour the hypothesis that growth zone deposition during the first year of life also occurs biannually. This is supported by the following

corroborative evidence: (1) specimens with one and two growth zones were both part of the first LF modes observed in January and April 2007, which was clearly distinct by a wide gap from subsequent LF modes (Fig. 3.5) and (2) the relative increase in L_F between the first and the second increment was smaller than the increase between the second and third (Fig. 3.7).

Although the data provide some support for a biannual growth zone deposition rate, the argument that one of these growth zones is formed as a result of energy reallocation towards reproduction is obviously not valid for immature fish. Thus the possibility of an annual deposition rate cannot be excluded. However, the formation of a growth increment in immature specimens during the spawning season could be linked to the reported size-dependent seasonal habitat shift of *C. carpio* (García-Berthou, 2001; Penne & Pierce, 2008). In a recent telemetry study on the movement of *C. carpio* in Lake Crescent, Iowa, Penne and Pierce (2008) showed that larger *C. carpio* (> 400 mm L_F) mainly aggregate in deeper waters (> 2 m) during Autumn and Winter and only move into the shallow littoral zone (< 2 m) before and during spawning, whereas smaller specimens (220 - 300 mm L_F) predominantly resided in the shallow littoral zone (0.5 - 1.5 m) throughout the year. This behaviour of larger specimens may therefore result in an increased competition for food in this habitat and cause a nutritional bottleneck for smaller specimens, in particular when foraging behaviour of mature specimens is potentially intensified between spawning events. However, further research is required to investigate the processes associated with the timing of increment formation and in particular that of the first two opaque zones.

In summary, this Chapter provides sufficient evidence that growth zone formation is biannual in astericus otoliths of age-2+ carp from Lake Gariep and represents the first

validation of growth zones in otoliths conducted on an African *C. carpio* population. Given that increments in the same ageing structure were validated as annual for carp populations of the Murray-Darling Basin, Australia (Vilizzi & Walker, 1999; Brown *et al.*, 2004), these findings demonstrate that growth zone deposition rates can vary among populations of the same fish species and exemplifies the importance of age validation as a prerequisite for understanding the life history of *C. carpio* in different geographical localities.

CHAPTER 4

The life history of non-native common carp *Cyprinus carpio* in South Africa's largest impoundment

4.1 INTRODUCTION

The life history of a species can be described as a trade-off between growth, reproduction and survival that are adjusted to optimise its fitness within different environments and constrained by natural selection and an underlying genetic system (Stearns, 1976; Adams, 1980; Roff, 1984; Winemiller, 2005). Life history theory suggests that these trade-offs reflect the result of evolutionary pressure that has (sub)optimised the life time reproductive success, which can be expressed as the number of offspring that are produced per female that survive to reproduce (Myers *et al.*, 1999). Life history strategies vary remarkably among fishes (Winemiller & Rose, 1992) and may even exhibit considerable adaptations among different intraspecific populations (Olsen *et al.*, 2004; Shuter *et al.*, 2005; Ormseth & Norcross, 2009).

Common carp, *Cyprinus carpio*, is one of the world's most widely introduced and established freshwater fishes (Casal, 2006). This suggests that this species is equipped with a set of adaptable life history attributes that allow it to successfully colonise a wide range of habitats (Fernàndez-Delgado, 1990; Koehn, 2004; Zambrano *et al.*, 2006; Britton *et al.*, 2007). In South-East Australia, for example, where feral[1] *C. carpio* is perceived as an invasive pest species (Sivakumaran *et al.*, 2003; Koehn, 2004), it accounts for the largest proportion of the ichthyobiomass in the continent's largest river

[1] Feral carp refers to *Cyprinus carpio* that intentionally or accidentally escaped domestification and returned, partly or wholly, to a wild state

system, the Murray-Darling Basin (Gehrke *et al.*, 1995). The serious concerns that have been raised about the threat that *C. carpio* poses to endemic freshwater species (Koehn, 2004) prompted several investigations into its life history (Vilizzi & Walker, 1999; Sivakumaran *et al.*, 2003; Brown *et al.*, 2004; Brown & Walker, 2004; Smith & Walker, 2004; Brown *et al.*, 2005). As a result, the life history of the population of *C. carpio* in the Murray-Darling has been comprehensively assessed with validated otolith-derived estimates of age, growth, age-at-maturity and mortality rates (Vilizzi & Walker, 1999; Brown *et al.*, 2004).

In Europe, more recent life history studies on *C. carpio* are surprisingly rare and published age and growth parameters were exclusively derived from scales (Crivelli, 1981; Fernàndez-Delgado, 1990; Balon, 1995; Ahmet & Sűleyman, 2000; Treer *et al.*, 2003). Scales, however, have never been validated as an ageing structure for any European population of *C. carpio* and have been shown to be less accurate when compared to astericus otoliths, dorsal spines and vertebrae (Vilizzi & Walker, 1999; Jackson & Quist, 2007; Phelps *et al.*, 2007).

In South Africa, *C. carpio* forms the basis of a directed recreational fishery, as a large proportion of the estimated 1.5 million freshwater anglers are considered to practice bank angling which mainly targets *C. carpio* (van Rensburg *et al.*, in press). The species is also an important target species of subsistence anglers and has been shown to have the potential to contribute to food security and livelihoods of previously disadvantaged rural communities (Ellender *et al.*, 2009; Ellender *et al.*, 2010a; Ellender *et al.*, 2010b). Conversely, *C. carpio* is widely perceived as highly invasive in South Africa and, as a result of intentional introductions by anglers, breeding populations are now found in parts of every major river system in the country (Laurenson & Hocutt,

1985; de Moor & Bruton, 1988; de Moor, 1996; Scott *et al.*, 2006). Despite reports on loss of water transparency caused by its bottom feeding behaviour, severe changes in benthic and macrophyte communities, impact on endemic fishes and loss of habitat heterogeneity and biodiversity elsewhere (e.g. Zambrano & Hinojosa, 1999; Zambrano *et al.*, 2001; Khan *et al.*, 2003; Koehn, 2004), impacts of *C. carpio* within the southern African region remain poorly studied (de Moor & Bruton, 1988). Understanding the role of *C. carpio* in South African ecosystems, assessing the species' potential ecological impacts and managing fisheries based on it are therefore issues of national and regional importance. All of these require information on the life history of this species. The aim of this chapter is to contribute to the knowledge of *C. carpio* in South African freshwater systems by undertaking a comprehensive life history study on this species in the largest impoundment of the Orange River system, Lake Gariep. The specific objective of this chapter was to estimate robust life history parameters, which were a not only crucial for the understanding the species' biology in Lake Gariep, but were also required as input parameters for developing the age-structured production model (ASPM) to simulate their long-term post-impoundment population demographics in Chapter 7.

4.2 MATERIALS AND METHODS

SAMPLING

The largest samples for the biological analyses of *C. carpio* were collected during shore angling competition events held in November 2006, January 2007, April 2007 and October 2007 (Chapter 2). Additional samples were obtained during bi-monthly gillnet surveys conducted between March 2007 and May 2008, from seine netting experiments

(April 2007, January 2008 and May 2008) and from occasional purchases from shore anglers (Chapter 2).

AGE AND GROWTH

A total of 816 whole astericus otoliths were examined by submerging them in methyl salicylate and viewing them under transmitted light according to the procedures outlined in Chapter 3. Of the total sample, growth zone counts from 782 otoliths were accepted for age determination. Mark-recapture of chemically tagged adult *C. carpio* using oxytetracycline hydrochloride along with edge analysis and corroboration by a length-based age structured model, suggested that two growth zones are deposited each year, one in early summer and one during winter (Chapter 3). To minimise potential biases caused by variability in the timing of biannual growth zone depositions, spawning periodicity or differences in gear selectivity, only the two largest otolith samples, collected during angling competitions in November 2006 (n = 325) and January 2007 (n = 241), were used for modelling length-at-age. As age-0 fish were absent from these samples, otolith samples from young of the year fish (YOY) were also added. The YOY fish were collected from small meshed seine net catches (8 m long × 1 m deep; 2 mm stretched mesh size) in January 2008 (n = 8), March 2008 (n = 12) and May 2008 (n = 4). To allow for back-calculation of monthly age estimates, November was set as the nominal hatching month, as this period coincided with a major spawning event (see Fig. 4.3).

Length-at-age was described by the four-parameter Schnute (1981) growth function of the form:

$$L_t = \left[{L_1}^b + ({L_2}^b - {L_1}^b) \frac{1-\exp(-a(t-t_1))}{1-\exp(-a(t_2-t_1))} \right]^{\frac{1}{b}},$$

where t_1 is the smallest age in the sample; t_2 is the oldest fish in the sample; L_1 the estimated mean length at t_1 old fish; L_2 the estimated mean length at t_2 and *a* and *b* are growth parameters of the Schnute model (Schnute, 1981). The Schnute (1981) model reduces to a three-parameter von Bertalanffy growth curve if the parameter *b* is fixed at one. This means that the two models are nested, which is a statistical requirement for model comparison using Likelihood Ratio Test approach (e.g. Quinn & Deriso, 1999). If *b* is fixed at one, transforming the Schnute parameters results in the von Bertalanffy growth function parameters of the form:

$$L_t = L_\infty (1-\exp(-K(t-t_0))),$$

with

$$L_\infty = \left(\frac{\exp(at_2)L_2 - \exp(at_1)L_1}{\exp(at_2) - \exp(at_1)} \right)$$

$$K = b$$

$$t_0 = t_1 + t_2 - \frac{1}{a} \ln \left(\frac{\exp(at_2)L_2 - \exp(at_1)L_1}{L_2 - L_1} \right),$$

where L_∞ is the predicted asymptotic length of the fish, *K* is the Brody growth coefficient and t_0 is the theoretical age of a zero-length fish. These von Bertalanffy parameters can then be used for comparisons with other growth studies on *C. carpio*.

The Schnute (1981) model can also describe a curve that has an inflection point. The age t' of growth inflection can then be calculated as (Schnute, 1981):

$$t' = t_1 + t_2 - \frac{1}{a}\ln\left(\frac{b^{at_2}L_2^{\,b} - e^{at_1}L_1^{\,b}}{L_2^{\,b} - L_1^{\,b}}\right) \qquad \text{with } a \neq 0, b \neq 0.$$

As there was less variation in length-at-age in younger fish than in older fish, a log-normal error structure was assumed for both models. Parameters were estimated by minimising the negative log-likelihood function of the form

$$-LL = n\ln(\hat{\sigma}) + \frac{n}{2},$$

with $\hat{\sigma}$ denoting the maximum likelihood estimate of model standard deviation as

$$\hat{\sigma} = \sqrt{\frac{\sum_i \ln(\hat{L}_i / L_i)^2}{n}},$$

where $\hat{L}_i$ is the predicted length-at-age, L_i is the observed length-at-age and n is the total number of observations. Likelihood Ratio Tests were used to test the null hypotheses that both models equally describe the length-at-age data and that growth was equal between sexes.

Parameter variability was estimated using the conditioned parametric bootstrap resampling technique described by Efron (1982). The percentile method (Buckland, 1984) was applied to estimate 95% confidence intervals from resulting bootstrap

vectors, where the 2.5% and 97.5% percentiles were chosen to obtain the lower and upper 95% confidence intervals, respectively.

REPRODUCTION

The sex and the developmental stage of gonads were determined macroscopically according to the criteria summarised in Table 2.3 (Chapter 2). Length-at-(50%)-sexual maturity (Lm_{50}) was determined based on 436 male and 467 female fish collected during peak reproduction periods. The proportion of reproductively active fish (developing, ripe or spent) was calculated by grouping specimens into 10-mm size classes and fitting a two-parameter logistic model of the form:

$$P(L) = \frac{1}{1+e^{-(L-Lm_{50})/\delta_L}},$$

where $P(L)$ is the percentage of mature fish at length L and δ_L the width of the ogive. Age-at-maturity was described as the fraction of mature fish per age class using age estimates from otoliths. Maximum likelihood estimates of these parameters were obtained by minimising the negated binomial log-likelihood function of the form:

$$-LL = -\sum_i \left[m_i \ln\left(\hat{P}_i\right) + (n_i - m_i)\ln(1-\hat{P}_i) \right],$$

where $\hat{P}_i$ is the expected proportion of mature fish in length class i, n_i is the number of individuals and m_i represents the number of these individuals that are mature.

Temporal patterns of spawning activity were assessed on the basis of the proportion of maturity stages per sampling month for adult fish (> female Lm_{50}), which were plotted against lake water levels. Only those sampling months where the sample size exceeded ten adult fish were considered in the analysis. The sex ratio of adult fish was determined and then compared to a 1:1 ratio using a contingency table.

POPULATION STRUCTURE

Due to the standardised sampling design and large sample sizes, the length frequency data collected during angling competitions were considered as being most suitable to represent the size structure of the *C. carpio* population. The corresponding age structures of these samples were estimated by transforming the length frequencies into age frequencies using an age-length-key based on length-at-age data of 737 individuals. Age-0 fish were not included in the analysis as these were absent from angler catches. The catchability of larger *C. carpio* may be strongly influenced by a size-dependent shift in seasonal habitat use (García-Berthou, 2001; Penne & Pierce, 2008). Therefore, size and age distributions from angling competitions were graphically assessed and related to season and spawning activity. To estimate total mortality rates, the derived results were then used to choose the age distributions, as these were assumed to closely resemble the population structure.

MORTALITY

Estimates of the instantaneous total mortality (Z) were obtained from normalised age-frequencies by means of a catch curve analysis (e.g. Ricker, 1975) and the maximum likelihood method described by Chapman and Robson (1960). As the *C. carpio* population in Lake Gariep can be assumed to be only lightly exploited (~ 2.kg.ha^{-1}.yr^{-1};

Ellender *et al*., 2010b), the empirical equation described by Hoenig (1983) was considered as suitable to obtain a first estimate of the instantaneous rate of natural mortality (*M*). Fishing mortality (*F*) was then calculated by subtraction, as $F = Z - M$.

A non-parametric bootstrap procedure (Efron & Tibshirani, 1986) was applied to estimate standard error (SE), coefficient of variation (CV) and confidence intervals for Z. For this purpose, random data sets were generated by resampling the length measurements and length-at-age data with replacement using a dynamic length-frequency table and a dynamic age-length-key, respectively. The Ricker (1975) and the Chapman and Robson (1960) model was executed 1000 times, and the percentile method (Buckland 1984) was used to estimate 95% confidence intervals from resulting bootstrap vectors.

4.3 RESULTS

Throughout the study period, more than 2500 specimens were measured, of which 1500 were sexed and staged, and otolith pairs were removed from more than 800 specimens. Angling competitions contributed significantly to the dataset (i.e. 86% of all *C. carpio* measured; 75% of all sexed and staged individuals; and 81% of otoliths). The weight-length relationship was described as Weight (g) = 0.000053 x F_L (mm) $^{2.829}$ (n = 275; r^2 = 0.97).

AGE AND GROWTH

The relationships between length and age are summarised in Table 4.1. The Likelihood Ratio Test showed that the growth curves for males (n = 222) and females (n = 257) differed significantly (χ^2 = 10.33, df = 3, $p < 0.05$). In order to select the most suitable growth model, unsexed juveniles (n = 81) were combined with female and male data,

respectively. Likelihood ratio tests showed that the full (Schnute) models and the reduced (von Bertalanffy type with $b = 1$) models differed significantly for males ($\chi^2 = 84.88$, df = 1, $p < 0.05$), females ($\chi^2 = 76.95$, df = 1, $p < 0.05$) and combined sexes ($\chi^2 = 112.28$, df = 1, $p < 0.05$).

Table 4.1. Parameter estimates [95% C.I.] of length-at-age data using both the von Bertalanffy and the Schnute growth model with a log-normal error structure for *Cyprinus carpio*, sampled at Lake Gariep, South Africa.

	von Bertalanffy growth model					
Parameter	Juv. + Males (n = 310)		Juv. + Females (n = 345)		Combined (n = 566)	
L_∞ (mm F_L)	839.3	[699.3, 979.94]	880.8	[757.3, 1021.7]	754.7	[682.6, 800.19]
K (yr^{-1})	0.21	[0.17, 0.27]	0.21	[0.16, 0.24]	0.26	[0.23, 0.29]
t_0 (yrs)	-0.02	[-0.05, 0.00]	-0.02	[-0.05, 0.00]	0.00	[-0.02, 0.02]
	Schnute growth model					
Parameter	Juv. + Males (n = 310)		Juv. + Females (n = 345)		Combined (n = 566)	
L_1 (mm F_L)	39.9	[36.1, 42.6]	39.4	[35.4, 41.8]	38.9	[35.23, 41.15]
L_2 (mm F_L)	473.3	[450.0, 478.7]	545.7	[507.5, 552.5]	529.7	[501.5, 537.9]
a (yr^{-1})	1.12	[0.90, 1.36]	0.90	[0.75, 1.10]	0.91	[0.78, 1.04]
b	-0.32	[-0.63, -0.03]	-0.10	[-0.38, 0.13]	-0.06	[-0.26, 0.13]
t_1 (yrs)	0.17		0.17		0.17	
t_2 (yrs)	7.00		6.17		7.00	

The Schnute (1981) model was therefore chosen, as the inclusion of the additional parameter described the relationship between length and age significantly better (Fig. 4.1). The inflection point of the Schnute (1981) growth curve indicates the change from an exponential to an asymptotic growth pattern, which was estimated at 1.38 years for males and 1.39 years for females.

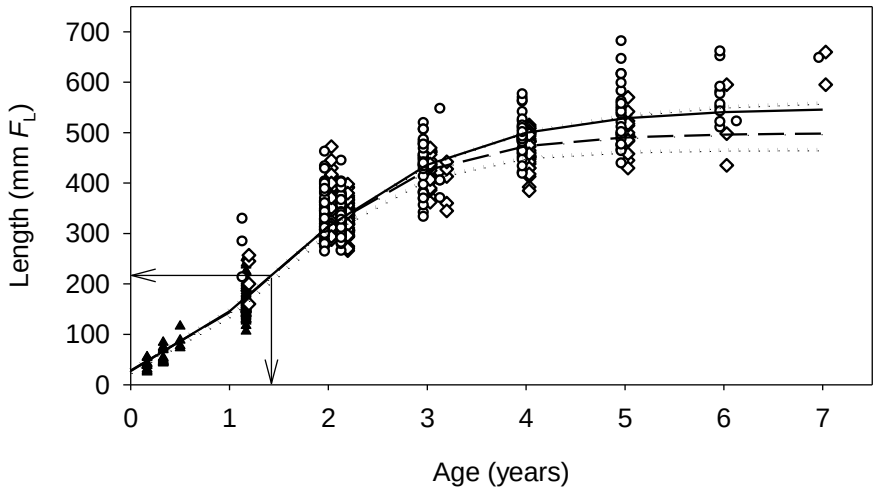

Fig. 4.1. Length-at-age data for *Cyprinus carpio* using whole otoliths (n = 474) sampled in Lake Gariep, South Africa. Growth was best described by the Schnute (1981) growth model assuming a log-normal error distribution. Growth curve fit for females (○; *n* =257) and juveniles (▲; *n* = 87) is indicated by a solid line, and that for males (◊; *n* = 222) and juveniles (▲) by a dashed line. Thin dotted lines indicate upper (females) and lower (males) 95% confidence intervals. The arrows indicate the age and size at which growth inflects.

REPRODUCTION

Length-at-(50%)-maturity was estimated at 295.9 mm F_L (δ_L = 37.7 mm) for males and 334.8 mm F_L (δ_L = 45.6 mm) for females (Fig. 4.2). The smallest mature male and female in the sample was 258 mm F_L and 276 mm F_L, respectively. The proportion of mature males (*n* = 136) and females (*n* = 187) per age class was based on the age estimates available from otolith samples obtained from the peak spawning period in November 2006 (Fig. 4.3). The results showed that the onset of maturity proceeded relatively quickly.

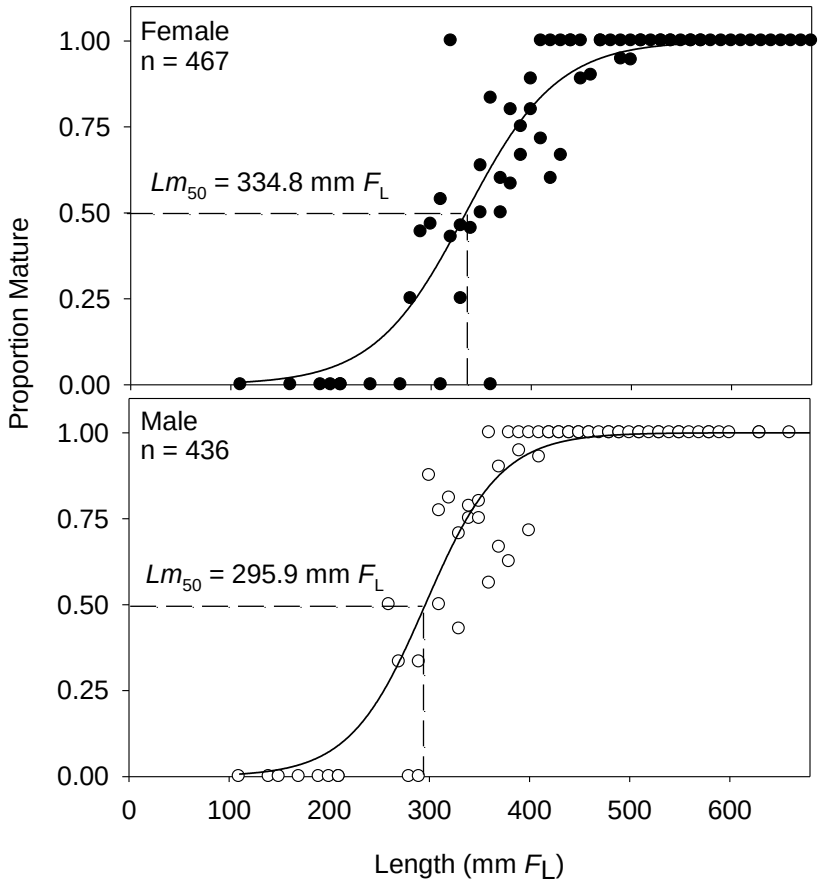

Fig. 4.2. Logistic ogives fitted to the proportion of mature female and male *Cyprinus carpio* from Lake Gariep, South Africa. Lm_{50} = length-at-50% maturity.

While none of the age-1 fish were mature, 75% of the age-2 males and 58% of the age-2 females were categorised as reproductively active (Table 4.2). By age-3, over 80% of the females and close to 100% of the males attained sexual maturity (Table 4.2). The adult population was slightly female dominated with a ratio of 1.1 females : 1 male (length bins 330 – 680 mm F_L), differing significantly from unity using length frequency data ($\chi^2 = 37.4$, df = 20, $p < 0.05$).

Table 4.2. Observed proportion of mature *Cyprinus carpio* per age class calculated from otolith sub-samples collected at Lake Gariep during a peak spawning period (November 2006).

Age class (years)		1	2	3	4	5	6	7
Female	Fraction mature	0.00	0.58	0.83	0.95	0.96	1.00	1.00
	Sample size (n)	8	69	35	39	25	10	1
Male	Fraction mature	0.00	0.75	0.96	1.00	1.00	1.00	1.00
	Sample size (n)	5	56	23	34	13	3	2

The interpretation of spawning dynamics on a seasonal level was restricted by the inherent difficulty of consistently obtaining sufficiently large adult *C. carpio* during routine gillnets surveys. Nevertheless, a rough but pronounced seasonal trend could be derived from the six sampling events considered (Fig. 4.3). November 2006 marked a peak spawning event with more than 90% of the adult population (> 335 mm F_L) categorised as reproductively active and more than 60% staged as either ripe or spent (Fig. 4.3).

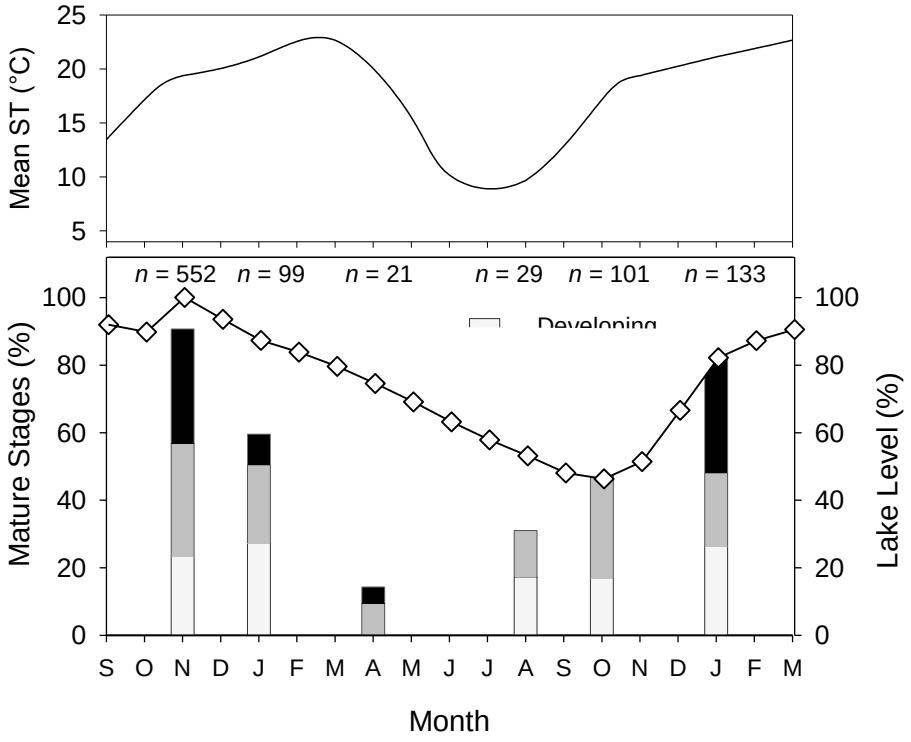

Fig. 4.3. Proportion of reproductively active adult *Cyprinus carpio* (combined bar height) from Lake Gariep and the lake's water levels expressed as percent of the full capacity (◊, solid line) for the period September 2006 to March 2008. The proportion of adult reproductive stages is illustrated within each bar. The upper graph illustrates general trends in mean surface water temperature in °C (ST) based on measurements taken during bi-monthly gillnet surveys (May 2007 – March 2008), which were then interpolated across the study period.

Spawning activity had decreased slightly in January 2007 and the proportion of spent specimens was small (9%). However, 23% of the adult population was still in ripe condition and an increase in the developing stage (38%) indicated the potential for subsequent spawning events. By April 2007, the proportion of reproductively active

individuals reached a minimum, with no gonads found to be in a developing stage and more than 85% of gonads categorised as resting. Gonadal development had increased by August 2007 (17%), when the first ripe gonads (12%) were also observed. By October 2007 this trend was amplified with 35% of gonads found in a ripe stage. By January 2007, more than 80% of the gonads examined were categorised as reproductively active, indicating a peak spawning period. Water level fluctuations, surface water temperatures and gonadal development showed similar trends with a small lag between changes in the proportion of gonad stages and the two environmental variables (Fig. 4.3).

POPULATION STRUCTURE

The largest proportion of fish > 400 mm F_L and older than two years (3+ group) were caught during shore angling competitions in November 2006 (Fig. 4.4 a), which coincided with a peak spawning event (Fig. 4.3). Smaller size classes were virtually absent from this sample and only recruited into angling competition catches during subsequent events in January and April 2007, whereas the age-3+ group became rare during these periods (Fig. 4.4 b, c). By October 2007, the proportion of the age-3+ group had increased again (Fig. 4.4 d), accompanied by a relative increase in spawning activity (Fig. 4.3). Length- and age-frequencies still appeared to be truncated with respect to larger and older fish when compared to November 2006, when spawning activity reached a relative maximum (Fig. 4.3). As a result, it was assumed that the large November sample (n = 695) best resembled the population structure of age-2+ fish, whereas length-frequency data collected during other periods appeared to be negatively biased towards larger specimens and were therefore not considered for deriving total mortality estimates.

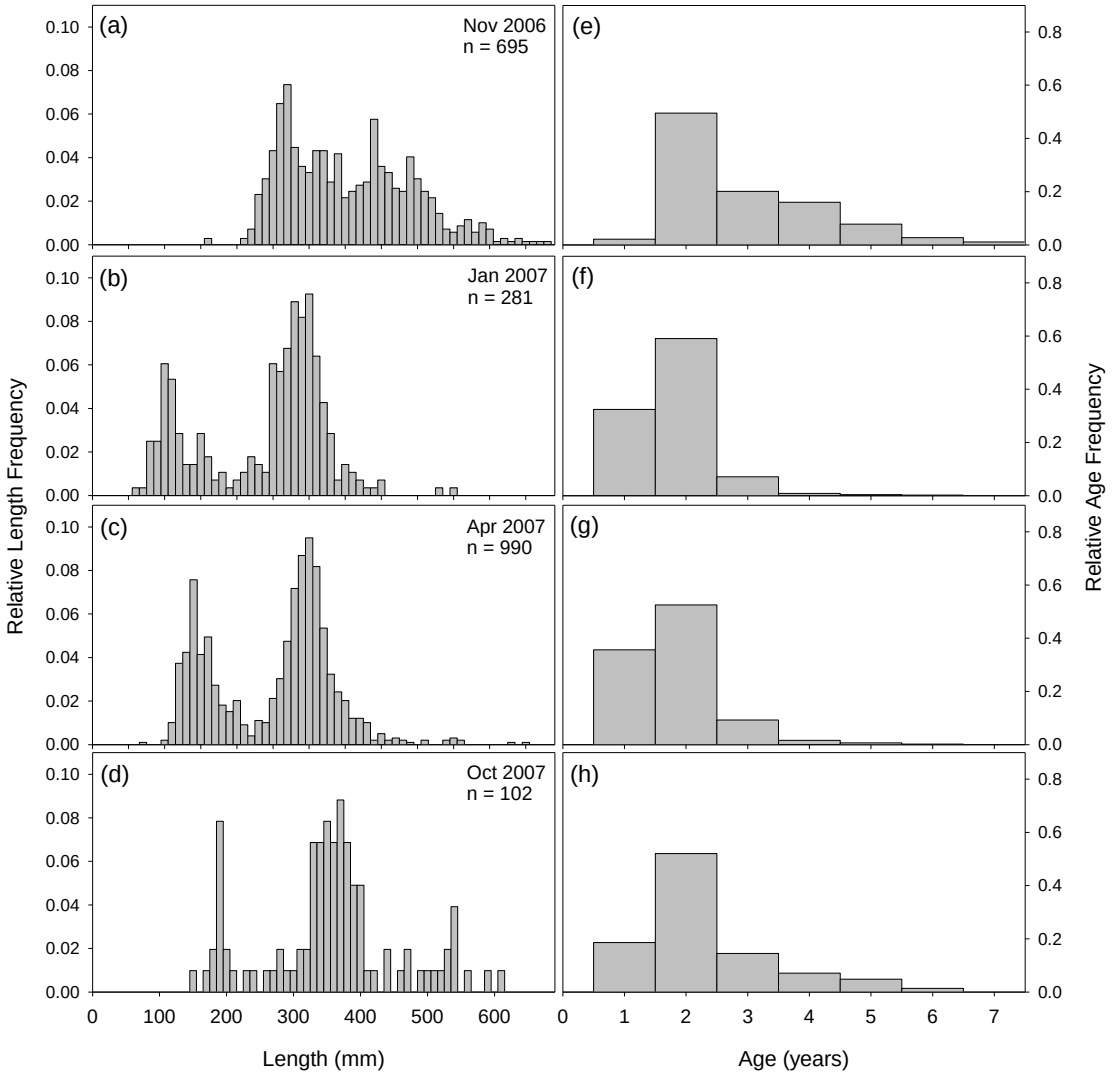

Fig. 4.4. Relative length-frequency distributions (a) - (d) and corresponding transformed age-frequencies (e) - (h) of *Cyprinus carpio* derived from data collected during four angling completion surveys (2006-2007) at Lake Gariep, South Africa.

MORTALITY RATES

The age-frequency histogram and the corresponding catch curve for the November 2006 angling competition is illustrated in Fig. 4.5. Although the catch curve analysis provided a relatively good fit of the linear regression (r^2 = 0.97), the non-parametric bootstrapping procedure showed that the Chapman and Robson (1960) estimate was less variable with a CV of 4.0% compared to 12.7% from catch curve analysis (Table 4.3) and was therefore considered the more precise estimate. Natural mortality was

estimated at $M = 0.60$ yr^{-1} based on a maximum observed age of seven years. Fishing mortality was relatively low and estimated at $F = 0.12$ yr^{-1}.

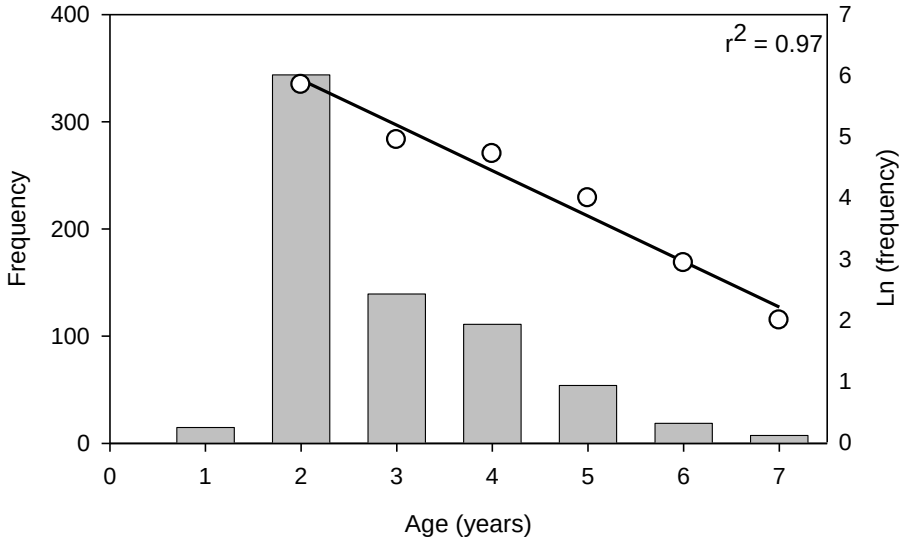

Fig. 4.5. *Cyprinus carpio* age-frequency histogram and catch curve generated from an age-length key (n = 737) and transformed length-frequency (*n* = 695) data obtained from an angling competition held at Lake Gariep, South Africa, in November 2006.

Table 4.3. Estimates of the instantaneous rates of total mortality (*Z*) for the *Cyprinus carpio* population from Lake Gariep, South Africa, including standard errors (SE), coefficient of variation (CV) and estimated 95% confidence intervals.

Method	Estimate	S.E	CV (%)	95% CI
Chapman and Robson (1960)	0.72	0.03	4.01	[0.67, 0.77]
Catch Curve Analysis	0.74	0.09	12.67	[0.63, 1.00]

4.4 DISCUSSION

Schnute (1981) proposed a comprehensive growth model that, as he pointed out, is not based on any "esoteric principle", but allows for concise biological interpretation. The statistically better fit of the Schnute (1981) model suggests that the population of *C. carpio* in Lake Gariep exhibited a distinct biphasic growth pattern. The initially slow

somatic growth gradually quickened before it slowed down during the second year of growth, just prior to the onset of maturity at age two.

A pronounced change in growth rate with the onset of maturation is common in many fishes and is usually ascribed to the reallocation of energy towards reproduction (Roff, 1984; Charnov *et al.*, 2001; Lester *et al.*, 2004). Therefore, biphasic growth models, in which adult somatic growth is modelled separately from juvenile growth, have been proposed to explicitly account for this effect (Charnov *et al.*, 2001; Lester *et al.*, 2004; Shuter *et al.*, 2005). Indirect support for the observed biphasic growth pattern also comes from a study by Villizi and Walker (1999) who found that a log-log quadratic function was statistically the better estimator of the growth of *C. carpio* in the lower Murray River than the von Bertalanffy model, although they detected no difference in the quality of the fit between the two models when juveniles were excluded from the data set. It is therefore likely that the observed biphasic growth is not unusual for this species, so that the Schnute (1981) growth model provides a valuable alternative to the commonly used von Bertalanffy model.

For ease of comparison between this study and growth studies conducted on other populations of *C. carpio*, the growth performance index $\Phi' = \log K + 2 \log L_\infty$ (cm) (Pauly & Munro, 1984) was used. This index was proposed to account for the interaction and dependence of the von Bertalanffy parameters L_∞ and K, and it has been found that similar populations, species or families often have similar Φ' estimates although their growth parameters may differ. The comparison among *C. carpio* populations indicated that feral *C. carpio* populations in Australia, the USA and South Africa tend to grow faster than their European counterparts, with the Barmah Forrest *C. carpio* population in Australia being the only exception (Table 4.4). The interpretation of this result, however, is limited by the uncertainty about the annual frequency of

growth zone deposition for the majority of *C. carpio* populations, which can differ among populations (Chapter 3). The population of *C. carpio* in Lake Gariep, for example, showed strong evidence for a biannual growth zone deposition rate (Chapter 3), whereas a commonly assumed annual growth zone deposition rate would have resulted in a severe underestimation of the growth performance as well as different age-at-maturity, longevity and mortality estimates. Furthermore, the relatively slow growth of two European *C. carpio* populations from the Carmargue (France) and the Guadalquivir River (Spain) has been attributed to suboptimal growth conditions in brackish waters, in spite of a perceived favourable location in low northern latitudes (Crivelli, 1981; Fernàndez-Delgado, 1990).

From the compiled records in Table 4.4, it appears that age-at-maturity estimates among populations of feral and koi forms are similar. Although males generally mature slightly earlier than females, with larger proportions of mature individuals at age-2 (Crivelli, 1981; Brown *et al.*, 2005; Tempero *et al.*, 2006), and therefore relatively smaller lengths-at-(50%) maturity, the difference between sexes seems to be less pronounced when compared to the wild form of *C. carpio* (Balon, 1995).

Balon (1995) described the wild form of *C. carpio* as an elongated, torpedo-shaped fish with large regular scales that is adapted to spawn on flooded grass flats within the inundation areas of rivers. He ascribed the most likely origin of most domesticated and feral populations of *C. carpio* to the floodplains of Danube basin. In the Danube, female wild *C. carpio* were observed to release their eggs in 10 - 14 day intervals and spawning was interrupted when water temperature dropped below 17°C (Balon, 1995). Comparable spawning behaviour has been documented for feral *C. carpio* populations (Crivelli, 1981; Fernàndez-Delgado, 1990; Sivakumaran *et al.*, 2003; Smith & Walker,

2004; Brown *et al.*, 2005) and the population in Lake Gariep also followed a similar spawning pattern, with an apparent relationship between spawning activity, increasing water temperatures in spring and the availability of recently inundated areas. In contrast to the wild form, however, feral *C. carpio* are also known to be able to spawn in the vegetated littoral zone of static water bodies (Balon, 1995).

The delayed age-at-maturity of female wild *C. carpio* is a commonly observed trait in intermediate- to large-bodied, highly fecund floodplain spawners, which is considered to be an adaptation to habitats that are influenced by strong periodic or seasonal changes (Winemiller, 1992; Olden *et al.*, 2006; Tedesco *et al.*, 2008). As no energy is allocated towards reproduction during the early years of life, the competitive advantage of such an adaptation would be that larger clutch sizes can be produced over an extended spawning period by the time of maturation, while adult survival is likely to be increased during suboptimal environmental conditions to allow spawning over several years (Gaigher *et al.*, 1980; Winemiller & Rose, 1992; Vila-Gispert & Moreno-Amich, 2002; Olden *et al.*, 2006). These fishes are categorised as 'periodic strategists' (Winemiller & Rose, 1992) and are considered to be the least adapted to present-day anthropogenic habitat alterations, including the loss of floodplain habitat and the creation of temporarily stable environments (Olden *et al.*, 2006). This has been documented by the decline of native *C. carpio* in the Danube, which was mainly attributed to the loss of floodplain habitat as a consequence of damming and river regulations (Balon, 1995). The wild form of *C. carpio* is even IUCN Red Listed as critically endangered (IUCN, 2010). As the feral form represents, to date, one of the most widely-established freshwater fishes (Casal, 2006), it is likely that part of its success is related to its earlier maturation and the reduced requirement for inundated flood plains for reproduction. Maturation at a younger age implies a shorter generation

time and therefore a shift towards a more opportunistic life history strategy when compared to the wild form (Winemiller, 1992), thus improving its ability to rapidly colonise and establish itself in new freshwater systems (Koehn, 2004; Zambrano *et al.*, 2006; Weber & Brown, 2009). However, these results also suggest that the invasive attributes of *C. carpio* are likely the product of human domestication, as initial fast growth rates, early sexual maturity and short generation times are traits that were probably selected for during centuries of extensive pond culture (Balon, 1995). Other attributes of feral *C. carpio* that were likely selected for include high levels in phenotypic plasticity, a wide environmental tolerance and a broad diet spectrum (Balon, 1995; Koehn, 2004; Matsuzak *et al.*, 2009; Weber & Brown, 2009).

Comparative life history studies of fishes have shown that their life history traits are interrelated and constrained among themselves (e.g. Pauly, 1980; Roff, 1984). The timing of maturation, for example, strongly influences growth and mortality (and *vice versa*) because energy that is allocated to reproduction is no longer available for either somatic growth or somatic tissue maintenance (Roff, 1984; Partridge & Sibly, 1991; Charnov *et al.*, 2001; Shuter *et al.*, 2005). As age-at-maturity was similar among feral and koi populations, it could be hypothesised that the relatively short life span (t_{max}) of the two South African populations of *C. carpio* (Table 4.4) is to some degree a trade-off between fast growth and higher mortality rates, given that mortality and longevity are correlated (Hoenig, 1983). By the same token, the oldest aged wild *C. carpio* was observed in the Barmah Forrest *C. carpio* population (Brown *et al.*, 2005), which also showed the lowest growth performance (Table 4.4). Although this hypothesis may explain some of the differences in longevity among populations of *C. carpio*, it can be assumed that the underlying processes are more complex.

Table 4.4. Ageing method, maximum observed age (t_{max}) and length (L_{max}), von Bertalanffy growth parameters, growth performance Φ' = 2log(L_∞/10)+log(K) (Pauly & Munro, 1984), length-at-maturity (L_m) and age-at-maturity (T_m) for *Cyprinus carpio* from different localities. For comparison, total length (L_T mm) and standard length (L_S mm) were converted to fork length (F_L mm) by T_L = 18.22 + 1.064 L_F and L_S = 35.24 + 1.117 L_S (n = 436; Treer *et al.* 2003)

Sex	Method	Variant	t_{max}	L_{max}	L_∞	K	t_0	Φ'	L_m	T_m	Region / Source
Male	otoliths*	Feral	24	570	489	0.25	-0.52	2.77	307	2-3	Barmah Forrest[1], Australia
Female	otoliths*	Feral	28	623	594	0.18	-0.61	2.80	328	2-3	Barmah Forrest[1], Australia
Combined	scales	Feral	13	554	550	0.20	-0.93	2.79	-	2-3	Carmargue[2], France
Combined	scales	Feral	11	632	752	0.12	-0.81	2.84	-	-	Vrasko Lake[3], Croatia
Female	scales	Feral	5	494	767	0.15	-0.62	2.94	-	-	Gölhisar Lake[4], Turkey
Male	scales	Feral	6	460	728	0.17	-0.45	2.96	-	-	Gölhisar Lake[4], Turkey
Combined	scales	Feral	6	438	796	0.14	0.03	2.96	-	2-3	Guadalquivir River[5], Spain
Combined	scales	Koi	12	700	675	0.21	0.15	2.98	-	2-3	Waikato region[6], New Zealand***
Male	scales	Wild	15	-	694	0.14	-1.10	2.82	316	3+	Danube[7], Slowakia
Female	scales	Wild	9	-	615	0.30	0.03	3.06	347	5+	Danube[7], Slowakia
Female	otoliths*	Feral	17	680	538	0.38	-0.39	3.04	273	2-3	Campaspe channels[8], Australia
Male	otoliths*	Feral	17	570	495	0.48	-0.29	3.07	287	2-3	Campaspe channels[8], Australia
Combined	**	Feral	8	-	679	0.28	0.01	3.12	-	-	41 populations[9], USA
Male	otoliths*	Feral	12	649	600	0.35	0.17	3.10	-	-	lower Murray River[10], Australia
Female	otoliths*	Feral	15	688	639	0.35	0.17	3.16	-	-	lower Murray River[10], Australia
Combined	otoliths*	Feral	7	550	475	0.64	-0.52	3.16			Lake Crescent[11], Tasmania, Australia
Male	otoliths*	Feral	7	661	839	0.21	-0.02	3.18	296	2-3	Lake Gariep[12], South Africa
Female	otoliths*	Feral	7	680	881	0.21	-0.02	3.20	335	2-3	Lake Gariep[12], South Africa
Male	vertebrae*	Feral	6	729	619	0.56	-0.15	3.33	-	2-3	Hartebeespoort Dam[12], South Africa
Female	vertebrae*	Feral	6	729	639	0.69	0.14	3.45	403	2-3	Hartebeespoort Dam[12], South Africa

[1]Brown *et al*. (2005); [2]Crivelli (1981); [3]Treer *et al.* (2003); [4]Ahmet and Sűleyman (2000); [5]Fernàndez-Delgado (1990); [6]Tempero *et al.* (2006); [7]Balon (1995); [8]Brown and Walker (2004); [9]Jackson *et al.* (2008); [10]Vilizzi and Walker (1999); [11]Present study; [12]Cochrane (1985). *studies where age and growth is based on validation or corroboration of growth zone deposition rates; ** various aging methods, t_{max} observed 75% of the 41 investigated populations and corresponding standardised von Bertalanffy growth parameters

Reduced longevity can also be caused by heavy fishing pressure. In Hartbeespoort Dam, for example, Cochrane (1987) estimated that recreational anglers harvested 500.tons.yr^{-1} (250 kg.ha^{-1}.yr^{-1}) of *C. carpio* in 1984, which may have resulted in a severe truncation of the population structure and could therefore explain the low observed maximum age in the population (Table 4.4). Similarly, Fernàndez-Delgado (1990) did not exclude the effect of fishing mortality as a possible cause for the small number of age groups observed in the Guadalquivir River (Table 4.4). By contrast, the impact of fishing mortality is considered minimal for most Australian populations of *C. carpio* (Brown *et al.*, 2005), as well as the population in the Carmarque, France (Crivelli, 1981). The fisheries resource of Lake Gariep is exclusively used by subsistence and recreational anglers (Ellender *et al.*, 2009; Ellender *et al.*, 2010a), and annual harvest in 2007 was estimated at 71.4 tons.yr^{-1}, of which, *C. carpio* accounted for 78.5% (Ellender *et al.*, 2010b). Given the large surface area of the impoundment (~ 360 km^2), the annual exploitation is low, only approximating 2.kg.ha^{-1}.yr^{-1}. It can therefore be assumed that fishing pressure has a minor effect on the age structure and population dynamics of *C. carpio*. These data are corroborated by the low estimated fishing mortality (F = 0.12 yr^{-1}). When considering that none of the ~ 1600 specimens measured during a shore angler roving creel survey (Ellender *et al.*, 2010b) exceeded the maximum observed length (680 mm F_L) of the present study (n > 2500) and that a representative subsample of ~ 800 specimens were aged, it appears unlikely that a significant proportion of the Lake Gariep population exceeds the maximum observed age of seven years. Therefore, Hoenig's (1983) empirical equation derived from longevity data of unexploited and lightly exploited populations is considered to provide a relatively accurate indication of the natural mortality rate (M = 0.6 yr^{-1}) of this population.

One factor that may greatly influence mortality estimates and the observed maximum age is the effect of sampling bias. *Cyprinus carpio* appears to be a species that is difficult to sample, particularly when attempts are made to obtain a "representative" sample of the population structure. This may largely be due to its seine net and gillnet avoidance behaviour (Hunter & Wisby, 1964; Barthelmes & Doering, 1996) and observed size-dependent seasonal habitat use (García-Berthou, 2001; Penne & Pierce, 2008). The species' net-avoidance behaviour was evident in the low catch efficiency of the multi-filament gillnet fleet, even when nets were set in areas that produced consistently high shore angling catches.

In a study on movement of *C. carpio* in Lake Crescent, Iowa, Penne and Pierce (2008) implanted radio transmitter into fish of various size classes and demonstrated that *C. carpio* exhibited size-dependent seasonal habitat shifts. Larger specimens (> 400 mm F_L) aggregated in deeper waters (> 2 m) during fall and winter. They only moved close to shore into the shallow littoral zone (< 2 m) before and during spawning, and subsequently moved further offshore again after spawning. In contrast, smaller specimens (220 - 300 mm F_L) were predominantly located in the shallow littoral zone (0.5 - 1.5 m) throughout the year (Penne & Pierce, 2008). This behaviour was also reflected in the shore angling competition catches at Lake Gariep, where representative proportions of larger specimens (> 400 mm F_L) were only observed during peak spawning periods.

The length- and age-frequency samples collected from angling competitions during spawning periods were assumed to be the least selective against larger specimens, whereas samples obtained during other periods would have resulted in unrealistically truncated population structures and excessively high total mortality estimates (Fig. 4.4).

Moreover, Rapp *et al.* (2008) found that small hook sizes, unlike in many other fish species, are most effective in catching large *C. carpio*, suggesting that the relatively small hook sizes used by the competition anglers are likely to further reduce sampling bias against larger specimens. As a result, angling competition surveys can provide a suitable sampling alternative in the absence of sophisticated boat-based electro-fishing equipment or sufficient man-power necessary to frequently employ large seine nets. However, irrespective of the sampling gear, the effect of the size-dependent seasonal habitat shift has general implications for developing accurate sampling protocols for *C. carpio* in larger water bodies, as it may result in constant systematic sampling biases when not accounted for.

In summary, the life history of the non-native *C. carpio* population in Lake Gariep is characterised by a fast growth rate, early maturation and a relatively short generation time. Although the shoreline is largely devoid of vegetation throughout most the year, flood cycles in association with floodplains and recently inundated terrestrial vegetation, likely provide a suitable spawning habitat. Hence, this species should be capable of rapidly colonising and saturating newly created impoundments like Gariep. This expectation is evaluated in Chapter 7.

CHAPTER 5

On the life history characteristics and population dynamics of an unexploited riverine cyprinid *Labeo capensis* in Lake Gariep

5.1 INTRODUCTION

The Orange River mudfish *Labeo capensis* is a cyprinid fish that is widely distributed throughout the Orange-Vaal River system and, together with smallmouth yellowfish *Labeobarbus aeneus*, it has been reported to dominate the larger ichthyofauna in most of the wider river stretches of the Orange, Vaal and Caledon Rivers (Jubb & Farquharson, 1965; 1973; Skelton, 1986). The life history of this species evolved under the harsh and unpredictable environmental conditions of the Orange River system, which is characterised by variations of considerable magnitude in such physical parameters as flow, turbidity and temperature (Keulder, 1979; Tómasson *et al.*, 1984; Skelton, 1986; Chapter 2).

Morphologically, *L. capensis* is characterised by a complex ventral mouth and a long coiled intestine, features suited for specialised feeding on benthic detritus and periphyton (Skelton, 1986). Breeding generally occurs in seasonal floodplain habitats during the summer months (Mulder, 1973; Gaigher *et al.*, 1980; Tómasson *et al.*, 1984). Like many of its congeners, *L. capensis* has relatively high fecundity is relatively high, with a large female of 400 mm F_L (~ 1 kg) able to produce in excess of 100 000 eggs (Baird, 1976; Gaigher *et al.*, 1980; Tómasson *et al.*, 1984).

Aspects of the age, growth and reproduction of *L. capensis* were first studied in the Vaal (Mulder, 1973) and Caledon Rivers (Baird, 1976). Following the construction of

Lake Gariep in 1970 and Vanderkloof Dam in 1976, both impoundments were subject to extensive experimental gillnet surveys in the periods 1971-1978 and 1976-1982, respectively. These surveys were designed to assess the commercial fisheries potential of large cyprinids and also initiated several studies on the life history and population dynamics of post-impoundment *L. capensis* populations in these two reservoirs (Fairall & Hamann, 1977; Gaigher *et al.*, 1980; Hamman, 1980; 1981; Tómasson, 1983; Tómasson *et al.*, 1984; Tómasson *et al.*, 1985). Both populations exhibited considerable fluctuations in abundance and recruitment during the first six years after the construction of the impoundments (Hamman, 1980; Tómasson *et al.*, 1985), with a large portion of the spawner biomass suggested to consist of individuals from the pre-impoundment riverine population (Fairall & Hamann, 1977). It was therefore postulated that the post-impoundment *L. capensis* populations would need to undergo large-scale demographic changes before stable populations could establish themselves in the newly created impoundments (Fairall & Hamann, 1977; Hamman, 1980). As a result, fisheries recommendations suggested that the implementation of a large gillnet fishery at that time, just a few years post-impoundment, would have had detrimental effects on the *L. capensis* population (Fairall & Hamann, 1977; Tómasson *et al.*, 1985). Tómasson *et al.* (1985) questioned the potential of *L. capensis* to sustain a large directed gillnet fishery, whereas Fairall & Hamann (1977) expected that targeted harvesting of this species would be feasible after it had established.

A large commercial fishery was never successfully implemented on either dam and, to date, the fisheries resource of Lake Gariep is exclusively used by subsistence and recreational anglers who mainly target common carp, *Cyprinus carpio* (Ellender *et al.*, 2009; Ellender *et al.*, 2010a), with *L. capensis* being a by-catch species (Ellender *et al.*, 2010b). The estimated annual harvest rate of approximately 0.16 $kg.ha^{-1}.yr^{-1}$ is low and

accounts for less than 8% of the estimated 79 tons.yr^{-1} of the total fish harvest from the impoundment (Ellender *et al.*, 2010b).

In this Chapter, the life history adaptation and important aspects on the biology of *L. capensis* in Lake Gariep are reassessed some four decades post-impoundment. The specific objective of this chapter was to estimate robust life history including sex-specific growth, length- and age-at-maturity and mortality rates that were required as input parameters for developing the age-structured production model (ASPM) to simulate their long-term post-impoundment population demographics in Chapter 7.

5.2 MATERIALS AND METHODS

GENERAL SAMPLING

The majority of data used in this Chapter were obtained from bi-monthly gillnet surveys conducted between May 2007 and March 2008. Additional samples were collected during shore angling competitions held in November 2006, January 2007, April 2007 and October 2007. Details of the field sampling methods are described in Chapter 2.

AGE AND GROWTH

A total of 512 astericus otolith pairs were used for age determination. To enhance the visibility of opaque (dark) and translucent (light) growth zones, whole otoliths were submerged whole in methyl salicylate and examined under transmitted light using varying magnifications (×10 – 40) using the same procedure as outlined for *C. carpio* in Chapter 3 and used in a validation study on this species (see Winker *et al.*, 2010; Appendix I). The growth zone deposition rate in astericus otoliths of *L. capensis* was

validated as annual in Lake Gariep (Winker *et al.*, 2010; Appendix I) and, therefore, the number of observed opaque zones in the otolith represented the age of *L. capensis*.

The consistency of growth zone counts was assessed using the average percent error (APE) method (Beamish & Fournier, 1981) and by calculating the average coefficient of variation (CV), as suggested by Chang (1982). The otolith readings were undertaken twice without reference to the length of the specimen, at random and at least two weeks apart. In cases where the two readings differed, a third reading was conducted. If this resulted in two identical readings, then the counts were accepted. If the three readings differed by no more than two growth zones (e.g. 2, 3, 4), then the median was accepted, otherwise the otolith was excluded from the analysis.

To avoid false year class identification, monthly age estimates were back-calculated by assuming that all fish were born in November (peak spawning) and that opaque zone formation occurred between June and August (Winker *et al.*, 2010; Appendix I). If otoliths of *L. capensis* captured during this transition period were categorised as opaque, the number of months between November (spawning) and the date of capture was either subtracted or added, depending on whether the fish were sampled prior or after the period of growth zone deposition.

Length-at-age was modelled by using both the four-parameter and three-parameter (b=1) Schnute (1981) growth model. In its reduced functional form, the Schnute (1980) model is mathematically identical to the von Bertalanffy growth model, which was described in detail in Chapter 4. For *L. capensis*, both models were fitted by minimising the negated normal log-likelihood function, as it was assumed that the residuals were homoscedastic.

REPRODUCTION

The sex and the developmental stage of gonads were determined macroscopically according to the criteria summarised in Table 2.3 (Chapter 2). Length-at-maturity was expressed as the proportion of reproductively active fish (developing, ripe and spent) in each 10-mm size class for each sex separately. The length-at-(50%) maturity (Lm_{50}) was estimated by fitting the data to a logistic model of the form

$$\psi(L) = \frac{m_\infty}{1 + \exp(-(L - Lm_{50})/\delta_L)},$$

where $\psi(L)$ is the predicted proportion of reproductively active fish in size class L and Lm_{50}, δ_L is the steepness parameter of the ogive and m_∞ is the asymptotic maturity as $L \rightarrow \infty$. For species where all mature individuals are in reproductively active condition at the same time, it is conventional to set $m_\infty = 1$ (see Chapter 4). However, if smaller proportions of the adult population mature at different times over an extended period, as has been reported for *L. capensis* (Gaigher *et al.*, 1980; Tómasson *et al.*, 1984), it may be desirable to estimate m_∞ as an additional parameter (Quinn & Deriso, 1999). Mathematically, Lm_{50} then denotes the size at which half the sampled population attained m_∞. Based on the results by Gaigher *et al.* (1980), the spawning season of *L. capensis* in Lake Gariep was assumed to occur mainly from October until March. However, monthly samples from this period were only considered if at least 50% of adult fish (> female Lm_{50}) were in reproductively active stages.

Length-at-maturity was converted to age-at-maturity using the reformulation of the von Bertalanffy equation

$$tm_{50} = t_0 - \frac{1}{K}\ln(1 - \frac{Lm_{50}}{L_\infty}).$$

According to Booth and Weyl (2004), the steepness parameter of the logistic ogive for age *t*, δ_t, can then be calculated as:

$$\delta_t = \frac{1}{2K\ln(3)}\ln\left(\frac{L_\infty - Lm_{50}}{L_\infty - Lm_{50} - \delta_L \ln(3)}\right).$$

The proportion of mature fish at age (*t*) was then calculated as:

$$\psi_t = \frac{1}{1 + \exp(-(t - tm_{50})/\delta_t)} \quad .$$

Temporal patterns of spawning activity were assessed by calculating the proportion of maturity stages per sampling month for both sexes.

POPULATION STRUCTURE

To assess size and age structure of the *L. capensis* population, it was necessary to first determine the gillnet selectivity such that sampled length frequencies from gillnet fleets, the most effective capture method, could be corrected to provide an unbiased estimate of the length structure in the population.

Gillnet Selectivity

The SELECT method of Miller and Holst (1997) was employed to estimate the gillnet selectivity of *L. capensis*. All individuals caught in the experimental multifilament

gillnet fleet were grouped into 10-mm F_L size classes L for any given mesh size m_i. The fundamental assumption of the SELECT approach is that for a given size class L, the number of fish that theoretically encounter (contact) mesh size m_i, $Y_{L,i}$, can be described by a Poisson distribution of the form:

$$Y_{L,i} \sim P(p_i \lambda_L),$$

where the expected count, $p_i \lambda_L$, is the product of the abundance of fish in length class L, λ_L, and the fishing intensity p_i of mesh size m_i (Millar & Holst, 1997; Booth & Potts, 2006). The number of length L fish that are actually caught by mesh m_i, $C_{L,i}$, can then be expressed as an independent random Poisson variable by multiplying $S_i(L)$ as a function of mesh size retention probability, such that:

$$C_{L,i} \sim P(p_i \lambda_L S_i(L)).$$

Assuming that the retention probability is normally distributed, the selectivity of mesh m_i is given by

$$S_i(L) = \exp\left(-\frac{(L-\mu_i)^2}{\sigma_i^2}\right).$$

The mean μ_i was expressed as a linear function of mesh size m_i and the spread σ_i was assumed to be proportional to m_i such that $\mu_i = m_i k_1$ and $\sigma_i = m_i \sqrt{k_2}$, where k_1 and k_2 are the scaling parameters for the selectivity curves. The scaling parameters were estimated using a log-linear model of the form

$$C_{L,i} = \ln(p_i) + \ln(\lambda_L) + \ln(S_i(L)),$$

where $S_i(L)$ can be rewritten such that

$$C_{L,i} = \ln(p_i) + \ln(\lambda_L) + \beta_0 + \beta_1 x_{L,i} + \beta_2 x_{L,i}^2,$$

with $\beta_0 = -k_1^2 / 2k_2$, $\beta_1 = k_1 / k_2$, $\beta_2 = -1/2k_2$ and $x_{L,i} = L / m_i$ (Millar & Holst, 1997; Booth & Potts, 2006). The parameters p_i, λ_L, β_0, β_1 and β_2 were estimated by minimising the negative log-likelihood function of the form

$$-LL = \sum_L \sum_i (\hat{C}_{L,i} - C_{L,i} \ln(\hat{C}_{L,i})),$$

where $C_{L,i}$ and $\hat{C}_{L,i}$ are the observed and expected number of fish caught in mesh size m_i, respectively. The scaling parameters were then calculated as $k_1 = \beta_2 / 2\beta_1$ and $k_2 = -1/2\beta_2$. The pseudo-coefficient of determination (r^2) was used to assess how much the variance in the gillnet catch data could be explained by the SELECT model and was calculated as

$$r^2 = 1 - \frac{\text{Residual deviance}}{\text{Null deviance}}.$$

As each gillnet had the same five mesh sizes with equal surface areas, it was assumed that the fishing intensity of each mesh size was equal (Millar & Fryer, 1999) and that the selectivity of a multi-mesh gillnet catching a fish of length L can therefore be calculated as

$$S_{GN}(L) = \sum_i S_i(L).$$

Population age structure

The size structure of the *L. capensis* population was determined from the bi-monthly gillnet length frequency samples. Gillnet length frequencies were pooled and corrected for gillnet selectivity. The expected frequency of fish in length class *L*, $\hat{f}_L$, was calculated as $\hat{f}_L = f_L / S_{GN}(L)$, where f_L is the observed length frequency. To obtain sex-specific mortality estimates, the selectivity-corrected length frequencies were multiplied by the observed proportion of females and males in each size class *L* and converted into age-frequencies by means of normalised age-length keys for each sex. Estimates of the instantaneous total mortality (*Z*) were obtained from catch curve analysis (e.g. Ricker, 1975) and by applying the maximum likelihood estimator of Chapman and Robson (1960). As *L. capensis* is not directly targeted by the hook and line fishery at Lake Gariep (Ellender *et al.*, 2010b), *Z* was assumed to be equal to natural mortality (*M*).

A non-parametric bootstrap procedure (Efron & Tibshirani, 1986) was used to estimate the standard error (SE), the coefficient of variance (CV) and confidence intervals (CI) for *Z*. For this purpose, random data sets were generated by resampling length-at-age data with replacement based on a dynamic age-length-key. The Ricker (1975) and the Chapman and Robson (1960) model were executed 1000 times and the percentile method (Buckland, 1984) was used to estimate the 95% confidence intervals from the resulting bootstrap vectors.

USING PER-RECRUIT APPROACHES TO EXPLAIN LIFE HISTORY

Per-recruit analysis is commonly used to assess the population response to changes in the fishing mortality *F* and is based on the assumption that recruitment is constant and independent of spawner biomass or population fecundity. In other words, per-recruit analysis basically models the changes in relative biomass (or spawner biomass) over a cohort's life span as a function of growth in weight and survival. In this chapter, this approach was explicitly applied to further investigate the effects of the estimated life history parameters on the unexploited *L. capensis* population (assuming $Z = M$). Biomass-per-recruit (BR) and spawner biomass-per-recruit (SBR) were determined as a function of age (t) for each sex (s) given as:

$$BR_t^s = \begin{cases} w_t^{\,s} \exp(-tZ^s) & 0 > t > \max \\ w_t^{\,s} \exp(-tZ^s)/(1-\exp(Z^s)) & t = \max \end{cases}$$

and

$$SBR_t^s = \begin{cases} w_t^s \psi_t^s \exp(-tZ^s) & 0 > t > \max \\ w_t^s \psi_t^s \exp(-tZ^s)/(1-\exp(Z^s)) & t = \max \end{cases},$$

where $w_t^s = \alpha L_t^{s\,b}$ is the mass of an animal at age (t), L_t^s is length-at-age for each sex (s), α and β are the parameters of the length-weight relationship, ψ_t^s is the proportion of mature females and males at age (t) and Z^s is the sex-specific instantaneous rate of total mortality.

5.3 RESULTS

AGE AND GROWTH

Of the 512 otolith pairs used for age determination, 34 (6.2%) were rejected as unreadable. The APE index was 4.94% and the mean CV was 6.95%. The maximum number of accepted opaque zone counts (age) was nine for males and twelve for females. Length-at-age was described adequately using both growth models and no violation of the assumed homoscedasticity of residuals was apparent. As no significant difference was found between models using a Likelihood Ratio Test ($\chi^2 = 0.03$, df = 1, $p = 0.86$), the three-parameter von Bertalanffy function was chosen to describe the growth of *L. capensis* because it has fewer parameters, and it is therefore statistically more robust. A Likelihood Ratio Test showed that growth differed significantly between males and females ($\chi^2 = 17.2$, df = 3, $p < 0.05$), with females attaining a larger maximum size than males. The data from unsexed juveniles were then pooled with male, female and combined data from both sexes. The fitted parameters for the von Bertalanffy growth curve are summarised in Table 5.1.

Table 5.1. Parameter estimates [95% C.I.] of length-at-age data using the von Bertalanffy growth function with a normal error distribution for *Labeo capensis*, sampled at Lake Gariep, South Africa.

Parameter	Juv. + Males (n = 310)		Juv. + Females (n = 345)		Combined (n = 566)	
L_∞ (mm F_L)	387.7	[358.8, 435.7]	433.8	[402.9, 477.9]	417.1	[394.4, 450.6]
K (yr^{-1})	0.25	[0.18, 0.32]	0.20	[0.15, 0.26]	0.21	[0.17, 0.26]
t_0 (yrs)	-0.54	[-1.21, -0.05]	-0.64	[-1.21, -0.20]	-0.70	[-1.24, -0.27]

The observed and predicted length-at-age and 95% confidence intervals for male and female *L. capensis* are illustrated in Fig. 5.1. The linear regressions of the natural logarithm-transformed length-weight relationships showed no significant differences between males and females (intercepts: $p = 0.24$, slopes: $p = 0.27$). The data were

therefore pooled and the length-weight described as w(g) = 0.0000024 x F_L (mm) $^{3.132}$ (n = 743, r^2 = 0.97).

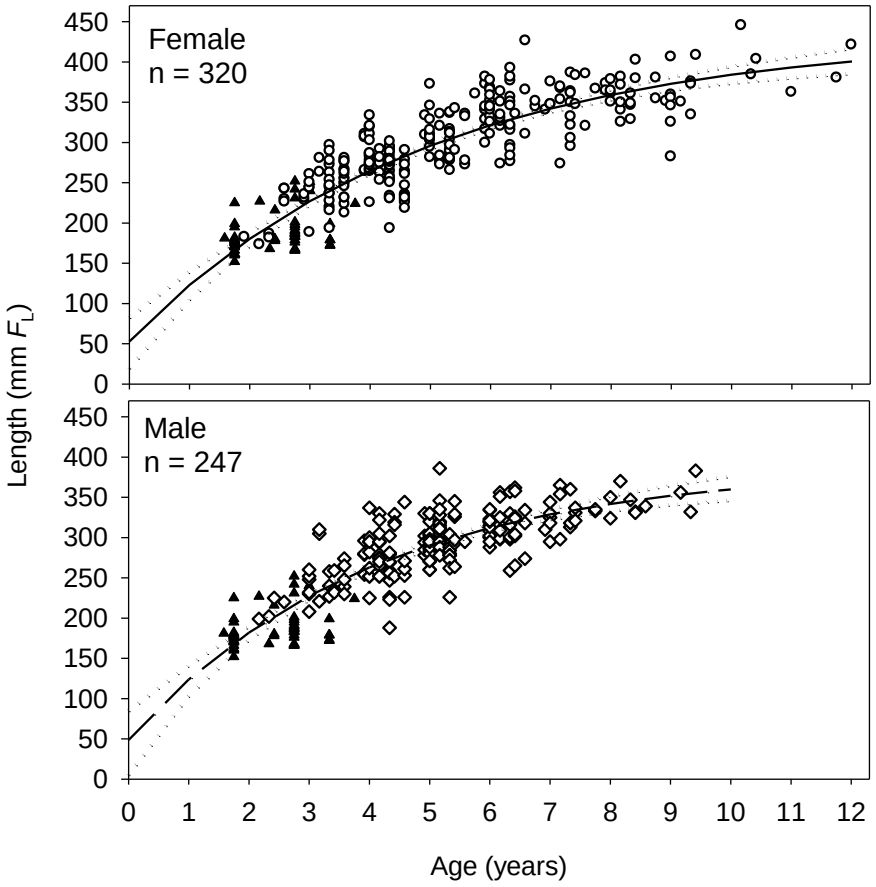

Fig. 5.1. Length-at-age data for *Labeo capensis* sampled at Lake Gariep, South Africa, using whole otoliths (n = 525). Growth was described by the von Bertalanffy growth model assuming a normal error distribution. The growth curve fit for females (○; n =263) and juveniles (▲; n = 72) is indicated by a solid line and that for males (◊; n = 190) and juveniles (▲; n = 72) by a dashed line. Thin dotted lines represent the upper and lower 95% confidence intervals of each estimated growth curve.

REPRODUCTIVE BIOLOGY

The length-at-(50%) maturity was calculated at 298 mm F_L (δ_L = 12 mm^{-1} F_L) for males and at 323 mm F_L (δ_L = 19 mm^{-1} F_L) for females (Fig. 5.2). The estimated asymptotic maturity (m_∞) was 0.65 for males and 1.00 for females (Fig. 5.2).

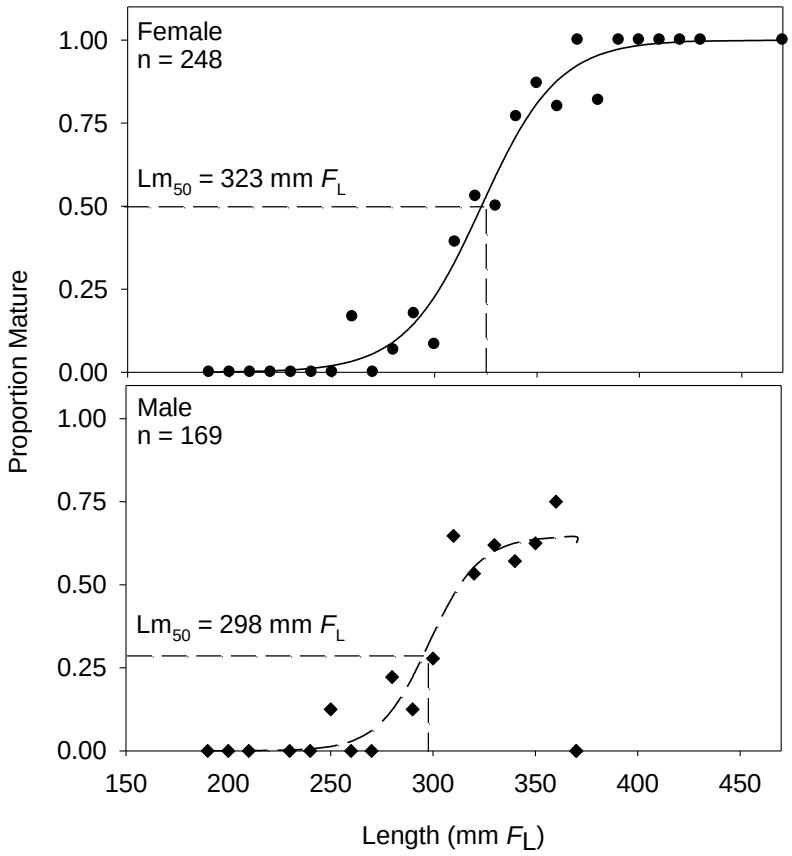

Fig. 5.2. Logistic ogives fitted to the proportion of reproductively active female and male *Labeo capensis* from Lake Gariep, South Africa. Lm_{50} = length-at-(50%)-maturity.

Maturation of the males proceeded faster (δ_t = 0.68 yr^{-1}) than maturation of the females (δ_t = 0.93 yr^{-1}) and age-at-(50%)-maturity was estimated at 5.3 and 6.2 years for males and females, respectively. The proportions of mature fish per age group and sex are summarised in Table 5.2.

Table 5.2. Predicted proportion of mature *Labeo capensis* per age class.

Age (years)	1	2	3	4	5	6	7	8	9	10	11	12
Female	0.00	0.03	0.06	0.13	0.27	0.46	0.67	0.83	0.92	0.96	0.98	0.99
Male	0.00	0.00	0.01	0.07	0.39	0.86	0.98	1.00	1.00			

The proportion of reproductively active stages in adult (> 320 mm F_L) *L. capensis* indicated that reproductive activity extended from spring until late summer (October - March) (Fig. 5.3). However, the pattern of gonadal recrudescence revealed considerable

variability within and between spawning seasons, and no consistent correlation was apparent when gonadal development was assessed against changes in the lake's water level (Fig. 5.3).

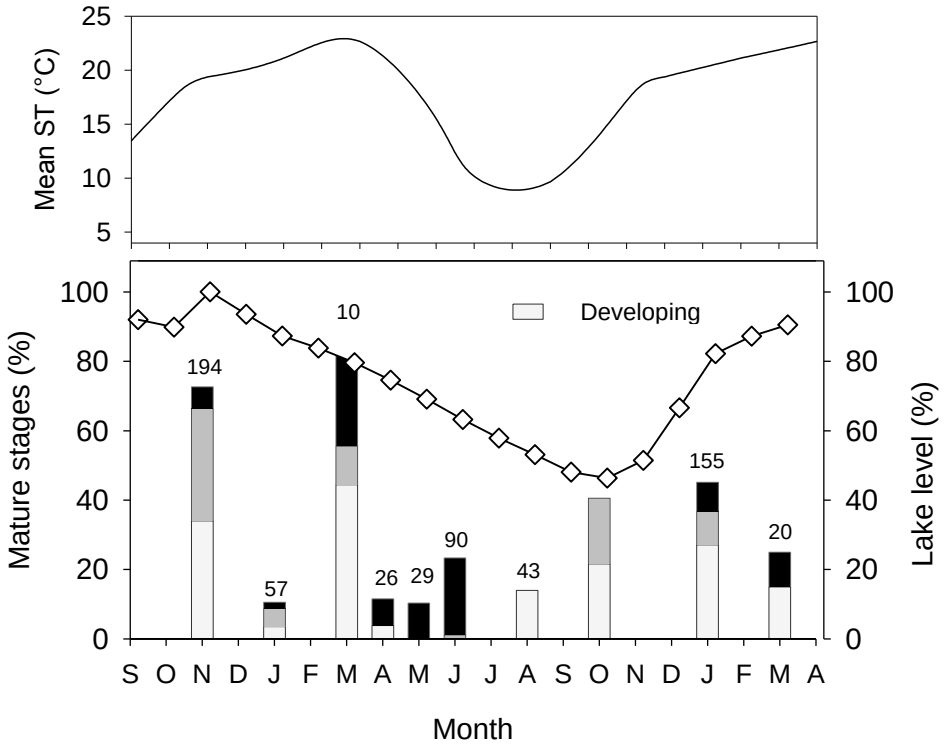

Fig. 5.3. Proportion of reproductively active adult (> female Lm50) *Labeo capensis* (combined bar height) from Lake Gariep and lake levels expressed as percent of the full capacity (◊, solid line) for the period from September 2006 to March 2008. The proportion of adult reproductive stages is illustrated within each bar. Numbers above bars denote the sample size. The upper graph illustrates general trends in mean surface water temperature in °C (ST) based on measurements taken during bi-monthly gillnet surveys (May 2007 – March 2008), which were then interpolated across the study period.

This variability was exemplified by the large decrease in the proportion of reproductively active gonads by January 2007 (10.5%) and a subsequent increase to a maximum (89%) by March 2007, while water levels constantly receded over the same period. During the subsequent months (April – August 2007), reproductive activity was consistently low, with more than 72% of gonads categorised as resting. Between April and June 2007, the few reproductively active *L. capensis* were dominated by spent individuals, whereas by August 2007, all reproductively active gonads (14%) were

categorised as developing (Fig. 5.3). By October 2007, spawning activity had increased again, and of the 40.5% reproductively active gonads, 18.9% and 21.6% were categorised as ripe and developing, respectively. The proportion of reproductively mature specimens was further increased by January 2008 (45.2%), and the first spent individuals became apparent (8.4%). In contrast to the previous year, however, spawning activity had decreased again by March 2008 (25%).

GILLNET SELECTIVITY

Labeo capensis was the most abundant species in the multifilament gillnet catches and accounted for 2324 (75 %) of the 3805 measured fish. Most *L. capensis* were caught in the 77m m (n = 892) and 65 mm (n = 813) mesh sizes (Table 5.3). The 153-mm mesh size caught less than 0.001% of the total sample (n = 9), and was therefore excluded from the SELECT model. It should be noted that the excluded individuals caught in the 153-mm mesh size also increased the robustness of the SELECT model, as it reduced the degrees of freedom from 133 to 99 without significantly influencing the model fit ($\chi^2 = 0.02$, df = 34, $p = 1.00$).

Table 5.3. Size frequency 3085 *Labeo capensis* caught by five experimental gillnet mesh sizes.

	Mesh Size				
L_i (mm F_L)	46 mm	65 mm	76 mm	105 mm	152 mm
120	1	0	0	0	0
130	0	0	0	0	0
140	0	0	0	0	0
150	1	0	0	0	0
160	16	0	0	0	0
170	54	0	0	0	0
180	72	2	0	0	0
190	56	4	1	0	0
200	34	0	0	0	0
210	14	5	0	0	0
220	3	43	3	0	0
230	2	122	3	0	0
240	2	150	6	1	0
250	1	131	31	0	0
260	0	118	73	1	0
270	1	96	161	0	0
280	2	70	180	1	0
290	2	39	136	3	0
300	0	15	87	2	0
310	0	7	84	2	1
320	0	5	61	13	0
330	0	0	35	34	1
340	0	3	12	56	0
350	1	2	7	77	0
360	1	0	3	57	0
370	0	1	6	45	1
380	0	0	0	28	0
390	0	0	2	16	0
400	0	0	1	9	2
410	0	0	0	1	1
420	0	0	0	0	1
430	0	0	0	0	1
440	0	0	0	0	0
450	0	0	0	1	1
Total	263	813	892	347	9

Estimated model parameters and goodness-of-fit statistics are summarised in Table 5.4. The scaling parameters, k_1 and k_2, that are used to determine the maximum length at capture and the standard deviation for each selectivity curve were estimated at 3.81 and 0.16, respectively.

Table 5.4. Summary of the parameters and scaling parameters k_1 and k_2 estimated using the log-linear SELECT model (Millar & Holst, 1997) based on a normally distributed selection curve with a proportional spread. *LL*: maximised log-likelihood value.

Paramater	k_1	k_2	*LL*	Residual deviance	Null deviance	*df*	r^2
Estimates	3.81	0.16	-7457	365	6802	99	0.95

The SELECT model explained 95% of the variation in the data (Table 5.4), indicating that the model fitted the data well (Fig. 5.4). The highly selective properties of each mesh size were evident by the clearly defined unimodal distributions (Fig. 5.4).

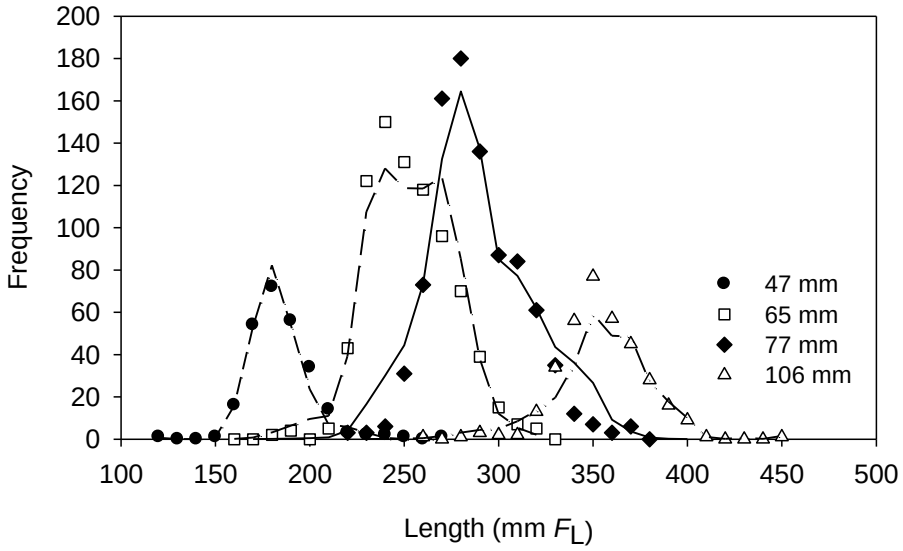

Fig. 5.4. Observed (symbols) and model predicted (lines) gillnet catches of *Labeo capensis* using the SELECT method (Millar & Holst, 1997).

Point estimates and standard deviations for fork lengths with the highest probability of being captured for each of the different mesh sizes employed are summarised Table 5.5.

Table 5.5. Predicted lengths (FL mm) at maximum selectivity (μ) and standard deviations (σ) for five gillnet selectivity curves estimated for *Labeo capensis*.

	Mesh Size				
Parameter	46 mm	65 mm	76 mm	105 mm	152 mm
μ	177.7	247.5	294.4	403.4	581.8
σ	18.6	26.0	30.9	42.3	61.0

The estimated selectivity curves indicated that the observed upper size range in the *L. capensis* population (L_{max} = 470 mm F_L) was well-covered by the 106 mm mesh size (Fig. 5.5). The relatively wide gaps between the modes of the 77 mm and 106 mm mesh sizes and the 106 mm and 152 mm mesh sizes were also clearly noticeable.

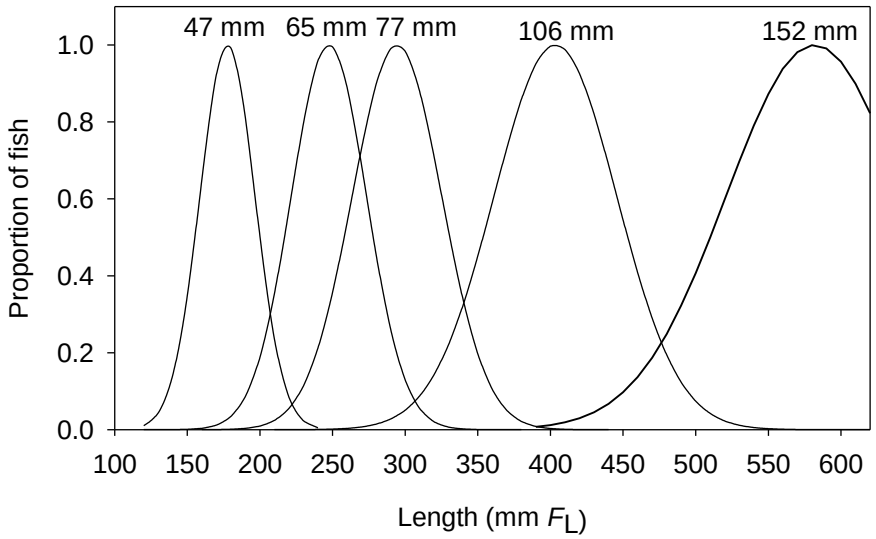

Fig. 5.5. Relative gillnet selectivity curves estimated for *Labeo capensis* using the SELECT method (Millar & Holst, 1997).

POPULATION STRUCTURE

The observed proportion of females and males in each 10-mm F_L size class is illustrated in Fig. 5.6. The adult population (> 320 mm F_L) was female-dominated with an adult sex ratio of 2.5 females : 1 male and differing significantly from unity (χ^2 = 106.8, df = 4, $p < 0.05$). The sex ratio in smaller size classes (≤ 320 mm F_L) was 1 female : 1 male and was not significantly different from unity (χ^2 = 16.0, df = 14, p = 0.31). The proportion of males and females in the smaller size classes was therefore assumed to be equal (Fig. 5.6).

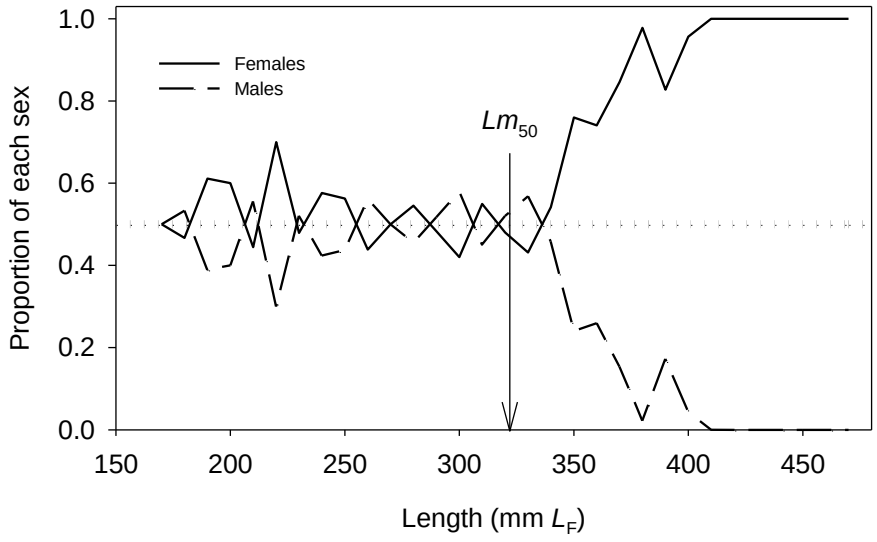

Fig. 5.6. Observed proportion of male (dashed line) and female (solid line) *Labeo capensis* in each 10 mm F_L size class. The arrow denotes the length-at-(50%)-maturity (Lm_{50}) estimated for females and the horizontal line a 1:1 sex ratio.

The observed and predicted size structures showed that the uncorrected gillnet length frequency data largely overestimated the abundance of fish in the size range from 240 to 300 mm F_L and underestimated, in particular, the female dominated size classes from 340 to 370 mm F_L (Fig. 5.7).

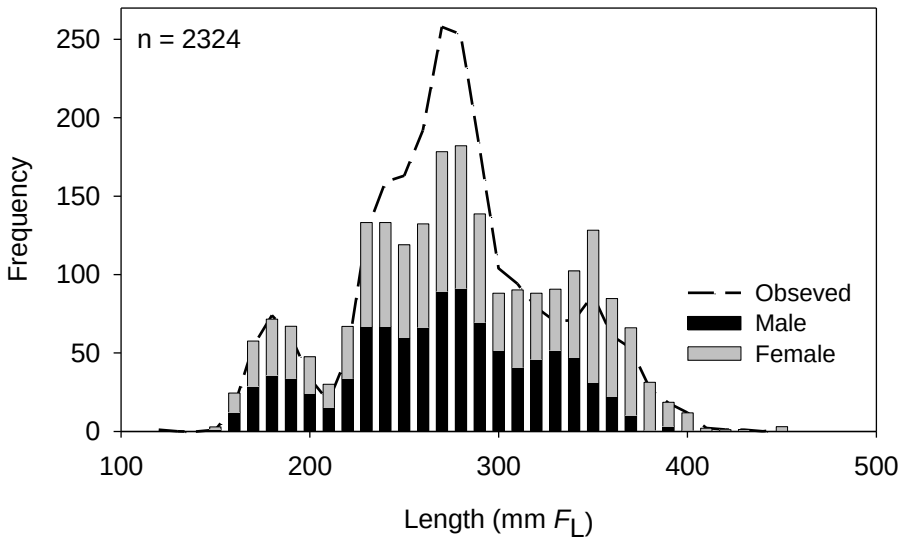

Fig. 5.7. Observed (dashed line) and gillnet selectivity corrected (bars) length-frequencies for *Labeo capensis* sampled during bi-monthly gillnet surveys (2007-08) at Lake Gariep.

Age frequencies derived from selectivity-corrected sex-specific length-frequency data (Fig. 5.7) are illustrated in Fig. 5.8. Catch curves were fitted over the same range of age classes for males and females (4 - 9 years), and a multiple linear regression analysis revealed that the slopes, representing the total mortality (*Z*), differed significantly between sexes ($p < 0.05$). Female age classes from age-10 to age-12 were also excluded from the catch curve analysis because the sample size in these age groups comprised fewer than three aged specimens (Fig. 5.8).

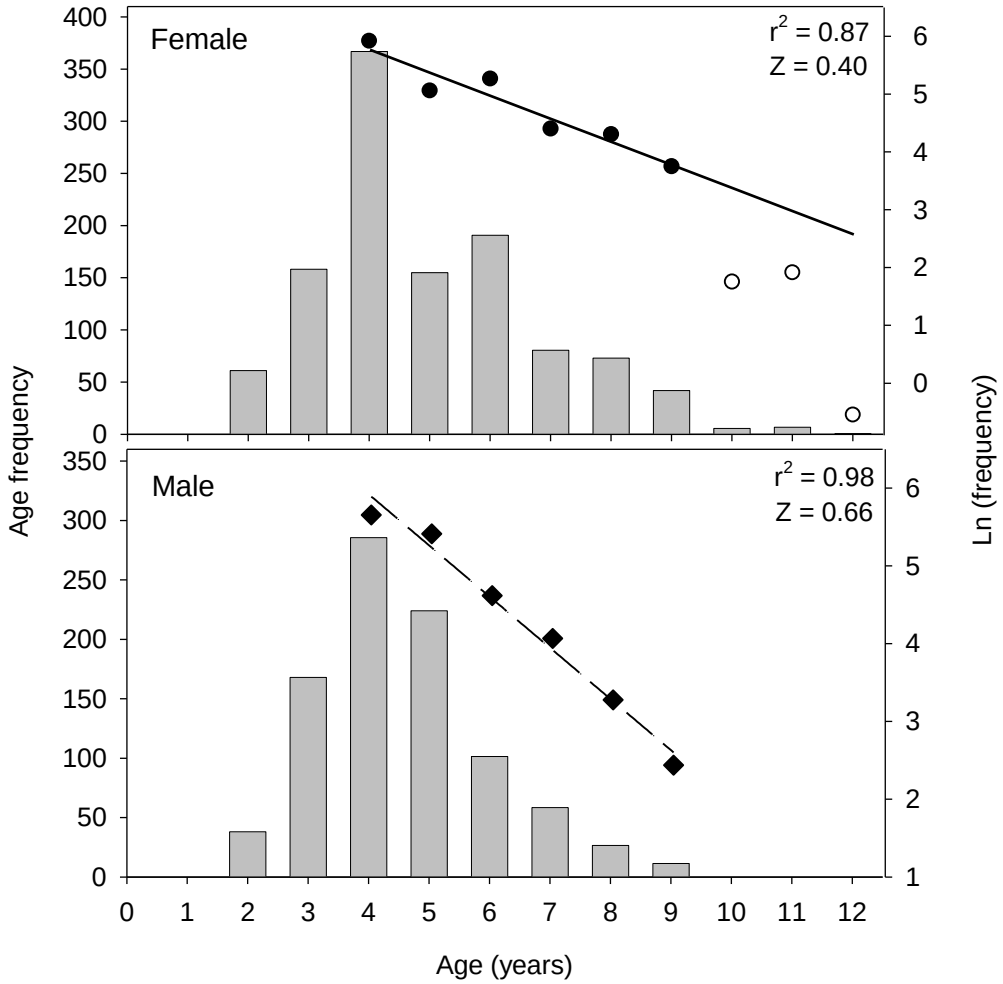

Fig. 5.8. *Labeo capensis* age-frequency histogram and resultant catch curves generated from age-length keys for females (n = 262) and males (n = 190), which were normalised by gillnet selectivity corrected, sex-specific length-frequency data (n = 2324) from Lake Gariep, South Africa.

Total mortality estimates ($Z = M$) derived from catch curve analyses and using the maximum likelihood estimator by Chapman and Robson (1960) are summarized in Table 5.6. The estimated CVs and 95% confidence intervals obtained from the non-parametric bootstrap procedure showed that total mortality estimates from the Chapman and Robson (1960) method were more robust than the results from the catch curve analyses (Table 5.6). Due to the similarity in the total mortality estimates for males, the statistically more robust Chapman and Robson (1960) estimate of $Z = 0.65$ [95% CI = 0.58 - 0.72] yr^{-1} for males was accepted for further analyses. In contrast, catch curve analyses resulted in a smaller mortality estimate for the females ($Z = 0.40$ yr^{-1}) than the Chapman and Robson (1960) estimator ($Z = 0.52$ yr^{-1}), and in order to account for this increased uncertainty, the mean of both methods, $Z = 0.46$ yr^{-1} [95% CI = 0.40 - 0.54 yr^{-1}] was considered to be more appropriate for female *L. capensis*.

Table 5.6. Estimates of the instantaneous rates of total mortality ($Z = M$) for the *Labeo capensis* population at Lake Gariep, South Africa.

Method	Sex	Estimate	CV (%)	95% CI
Chapman and Robson (1960)	F	0.52	3.9	[0.48, 0.56]
	M	0.65	5.3	[0.58, 0.72]
Catch Curve Analysis	F	0.40	12.7	[0.32, 0.52]
	M	0.66	13.9	[0.52, 0.90]
Mean	F	0.46	7.2	[0.40, 0.54]
	M	0.66	8.7	[0.56, 0.79]

Under steady-state assumptions, the predicted male and female BR and SBR for the unexploited *L. capensis* population are illustrated in Fig. 5.9. Total mortality estimates for age groups age-0 to age-4 were unavailable (Fig. 5.9). However, as male to female ratio was 1:1 in size classes smaller than 320 mm F_L, and as the estimated mean lengths-at-age of age-4 males of 264 [259 - 268] mm F_L and females of 261 [257 - 265]

mm F_L were below 320 mm F_L, it could be assumed that mortality rates were also equal for both sexes in these age groups. Consequently, total mortality for age-1 to age-4 fish was conventionally set to the lower estimate obtained for the females (Z = 0.46 yr^{-1}). The maximum BR was predicted for age-4 fish of both sexes, which was younger than the estimated age-at-(50%) maturity (Fig. 5.9). Subsequently, BR declined faster in males than in females from age-4 onwards, resulting in a rapidly increasing dominance of female BR in older age classes (Fig. 5.9). As a consequence, total female SBR was predicted to be double that of males (Fig. 5.9), with males attaining a maximum SBR one year earlier (age-5) than females (age-6).

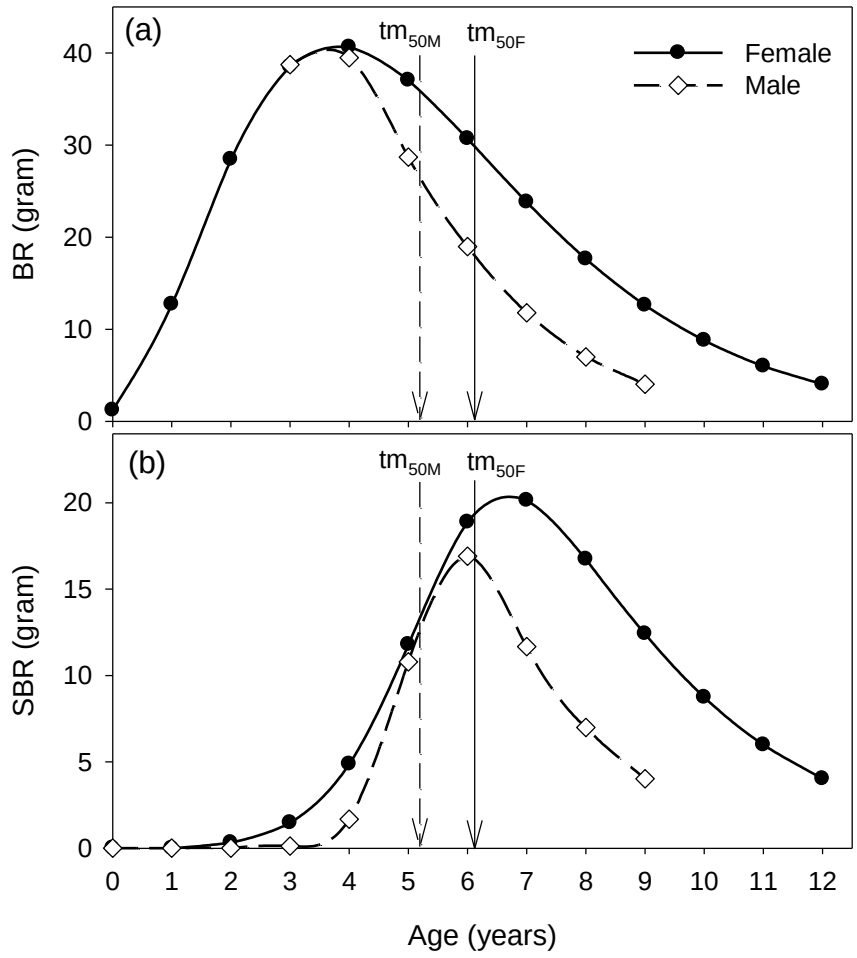

Fig. 5.9. Predicted biomass-per-recruit (a) and spawner biomass-per-recruit (b) as a function of age in males and females of the unexploited *Labeo capensis* population in Lake Gariep, South Africa. The arrows denote the age-at-(50%)-maturity for males (tm_{50M}) and females (tm_{50F})

5.4 DISCUSSION

This chapter is the first to provide validated otolith-derived, age-based life history parameters for *L. capensis* using robust maximum likelihood estimation procedures. A study on age validation using chemical marking and edge analysis has previously provided evidence for an annual growth zone deposition in astericus otoliths of *L. capensis* in Lake Gariep (Winker *et al.*, 2010; Appendix I), which allowed for relative reliably estimation of lengths-at-age upon which estimates of growth, age-at-maturity and mortality rates were based. Lack of estimates on ageing precision in previous studies on *L. capensis* precluded a within-species comparison. The estimated precision of growth zone counts (APE = 4.94%; CV = 6.95%) was, however, similar to the within-reader precision found for astericus otoliths of common carp in Lake Gariep (Chapter 3). Campana (2001) found that the median APE of 131 reviewed ageing studies was 5.5%, which suggests that precision from this study was well within the expected range.

The results from the SELECT method highlighted the importance of correcting for the highly selective properties of gillnet fleets to make accurate predictions of size- and age-structure and total mortality rates. By comparing various selectivity models, Booth and Potts (2006) demonstrated that the SELECT method can provide accurate and statistically robust selectivity estimates for the morphometrically similar cyprinid *Labeo umbratus*. Although not trivial from a mathematical perspective, the SELECT model is relatively easy to implement. The good model fits obtained for gillnet catches of *L. capensis* (r^2 = 0.95) provide further evidence for the good predictive properties that have been attributed to this method (Millar & Holst, 1997; Millar & Fryer, 1999; Booth & Potts, 2006).

Labeo capensis' life history parameters revealed that this species is a relatively slow-growing and long-lived species, with females attaining maximum ages (t_{max}) of up to 12 years. Maturation proceeded faster in males than in females, but was, in general, considerably delayed (male tm_{50} = 5.3 years; female tm_{50} = 6.1 years) with female length-at-(50%)-maturity (323 mm F_L) attained at approximately 75% of the maximum theoretical size.

A comparison of growth and maturity estimates derived from previous studies on *L. capensis* indicated that slow growth and delayed maturity are typical traits for this species (Table 9). Growth performance was compared based on the index Φ' = log K + 2 log L_∞ (cm), which was suggested by Pauly and Munro (1984) to allow for direct comparison of the von Berlanffy growth parameters K and L_∞. On closer inspection of the computed Φ' values, the low values for the 1978/79 year class in Vanderkloof Dam (Φ' = 2.30, 2.34) appeared to be outliers that differed significantly from the rest of the data set (t-value = 6.39, $p < 0.05$) and were therefore excluded from further analyses. The remaining Φ'-values showed a relatively narrow range (Φ' = 2.56 - 2.77) for both impoundment and riverine populations of the Orange River system, suggesting a similar growth performance throughout the native range of *L. capensis*. The relatively slow growth of this species becomes particularly pertinent when *L. capensis* Φ' -values are compared to the significantly faster growth performance (Φ' = 3.18 - 3.20) reported for the non-native common carp *C. carpio* population in Lake Gariep (t-value = 10.25, $p < 0.05$) (Chapter 4).

Growth performance estimates obtained in this study appeared to be slightly lower when compared to studies where growth was derived from back-calculated length-at-age data based on scale interpretations (Table 5.7). Although it is possible that because

L. capensis is a riverine species and growth conditions may therefore be more favourable under lotic conditions and during the filling phase of reservoirs (Bodaly & Lesack, 1984; Tómasson *et al.*, 1985), in this case, such interpretation on a relatively fine scale should be treated cautiously. Previous studies that used scales recorded maximum ages of 7 - 10 years (Table 5.7), whereas the interpretation of otoliths suggested that a maximum life span of 12-16 years can be expected (Tómasson, 1983). Little or no growth in scales of older fish often causes age to be underestimated, which seems to be a common trend in studies using scales (Barnes & Power, 1984; Francis *et al.*, 1992; Booth & Buxton, 1997; Vilizzi & Walker, 1999; Phelps *et al.*, 2007). Underestimation of the age of older fish inevitably results in faster growth rates, larger mean length-at-age and larger theoretical asymptotic length estimates (Booth & Buxton, 1997), which would therefore alternatively explain the slightly higher Φ'-values computed for the riverine populations and for Lake Gariep's early impoundment population (Table 5.7). When considering the overall similarity of Φ'-values and taking into account that scale-based growth estimates might be slightly overestimated, there was no indication in the data that *L. capensis* drastically changed its growth performance to adapt to the more lacustrine conditions of Lake Gariep. Similarly, delayed maturity appeared to be a relatively conservative trait of this species with female age-at-(50%)-maturity frequently attained at an age older than half of the observed maximum life span (Table 5.7).

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Table 5.7 Ageing methods, von Bertalanffy growth parameters, growth performance Φ' = 2log(L_∞/10)+log(K) (Pauly & Munro, 1984), length-at-(50%)-maturity (Lm_{50}), age-at-(50%)-maturity, maximum observed age (t_{max}) of *Labeo capensis* from different localities of the Orange system.

Locality	Sex	Method	L_∞	K	t_0	Φ'	Lm_{50}	tm_{50}	t_{max}	tm_{50} / t_{max}	Period	Source
Lake Gariep	Male	otoliths	388	0.25	-0.54	2.58	298	5.3	9	0.59	2007-08	This Study
	Female	otoliths	434	0.20	-0.64	2.58	322	6.1	12	0.51	2007-08	
Lake Gariep	Male	scales	562	0.15	0.35	2.68	280	4.9	8	0.62	1972-77	Hamann (1981)
	Female	scales	647	0.12	0.01	2.70	360	6.8	10	0.68	1972-77	
Vanderkloof Dam	Male	otoliths	506	0.19	0.48	2.69	330	6.0	13	0.46	1977/78	Tomasson (1984)
	Female	otoliths	609	0.16	0.03	2.77	380	6.1	16	0.38	1977/78	
	Male	otoliths	533	0.07	0.10	2.30	330	13.9	13	-	1978/79	
	Female	otoliths	742	0.04	0.20	2.34	380	18.1	16	-	1978/79	
	Male	otoliths	593	0.11	0.20	2.59	330	7.6	13	0.58	1979/80	
	Female	otoliths	688	0.09	0.39	2.63	380	9.3	16	0.58	1979/80	
	Male	otoliths	490	0.15	0.38	2.56	330	7.8	13	0.60	1980/81	
	Female	otoliths	557	0.13	0.43	2.61	380	9.2	16	0.58	1980/81	
Orange River	Male	scales	363	0.39	-0.10	2.71	-	-	8	-	1976	Mulder (1976)
	Female	scales	510	0.19	-0.57	2.70	-	-	10	-	1976	
Caledon River	Male	scales	-	-	-	-	200	3.4	8	0.43	1970-71	Baird (1976)
Caledon River	Female	scales	-	-	-	-	230	4.1	8	0.51	1970-71	
Vaal River	Male	scales	-	-	-	-	260	3.7	8	0.46	1969-71	Mulder (1973)
Vaal River	Female	scales		-	-	-	310	4.7	9	0.52	1969-71	
Vaal River	Combined	scales	491	0.23	0.38	2.74	310	-	9		1969-71	
Hardap Dam	Male	scales	-	-	-	-	253	4	7	0.57	1988-92	Van Zyl et al. (1995)
Hardap Dam	Female	scales	-	-	-	-	260	4	7	0.57	1988-92	

The observed similarity in growth performance and maturation also supports the general conclusion of Skelton (1991) that fishes of the genus *Labeo* typically show little adjustment to artificially created impoundments. An exception seems to be *Labeo umbratus*, which is sympatric with *L. capensis* in the Orange River system, but which is also native to larger systems further south (Skelton, 1986). In contrast to *L. capensis*, *L. umbratus* reveals that large variations in the growth and maturity that indicate a high degree of plasticity as a response to system-specific environmental conditions (Potts *et al.*, 2006b), which may also explain why this species can tolerate a wide range of different environmental conditions in small reservoirs (Potts *et al.*, 2006b; Potts *et al.*, 2006a)

Both sexes grew at a similar rate until the onset of maturation, after which males showed a relative decline in growth rate and significantly higher mortality rates, explaining the larger maximum length and age attained by females. The lower adult mortality in female *L. capensis* was also reflected in the highly skewed female-dominated sex ratio of adult fish, a trend that has also been found in other populations of *L. capensis* (Mulder, 1973; Baird, 1976; Gaigher *et al.*, 1980; Tómasson *et al.*, 1984). As female body mass and fecundity increase exponentially with size (Gaigher *et al.*, 1980; Tómasson *et al.*, 1984), the competitive advantage of this strategy has been suggested to increase the total egg production capacity in the population (Gaigher *et al.*, 1980; Potts *et al.*, 2006a), while simultaneously reducing intra-specific resource competition in the adult population (Nikolskii, 1969; Gaigher *et al.*, 1980). This was effectively demonstrated by the applied SBR model, which showed that the sex-specific trade-offs among growth, maturity and mortality resulted in a female SBR that was double the weight of the male SBR (Fig. 9).

While the higher mortality rates predicted for male *L. capensis* might be partly explained by their earlier maturation (Charnov *et al.*, 2001; Shuter *et al.*, 2005), there are also indications that sex-specific differences in mortality rates are directly related to the spawning behaviour of this species. Tweddle and Davies (1997) suggested that ripe-running males remain congregated at the spawning ground to breed with individual females, which move up from deeper water, release their eggs and return to the open water again. Thus spawning males are likely to exhibit the more exhausting spawning behaviour and are exposed longer to predation and injuries at the, usually, shallow spawning sites.

The choice of spawning sites may depend on the availability of suitable habitat. Spawning seems to occur preferably between newly inundated vegetation in flooded riparian areas as well as in impoundments (Mulder, 1973; Gaigher *et al.*, 1980; Tómasson *et al.*, 1984), but spawning behaviour has also been observed over shallow riffles in the highly regulated lower Orange River (Cambray, 1985). Synchronised longitudinal mass spawning migrations, as has been described for many other *Labeo* species (Skelton *et al.*, 1991; Weyl & Booth, 1999; Rutaisire & Booth, 2005), have never been reported for *L. capensis* (Mulder, 1973; Baird, 1976; Gaigher *et al.*, 1980; Tómasson *et al.*, 1984; van Zyl *et al.*, 1995). Instead, the observed asynchrony in the maturation of adult fish over a prolonged breeding season indicates that *L. capensis* forms a non-homogeneous breeding population throughout the impoundment, which also agrees with the results from previous studies (Gaigher *et al.*, 1980; Tómasson *et al.*, 1984).

Individual females have been reported to spawn all their eggs simultaneously when local conditions for spawning are favourable (Gaigher *et al.*, 1980; Tómasson *et al.*,

1984; Tweddle & Davies, 1997), which was evident by a complete absence of eggs in most of the spent specimens that were examined. Oocyte development for individual females can therefore be considered to be synchronous (Booth & Weyl, 2000). This spawning behaviour can be seen as an adaptation for maximising individual batch fecundity during flood periods that normally last for only a few days. Other notable traits, which are favourable for such a reproductive strategy, are the species' high fecundity (Baird, 1976; Gaigher *et al.*, 1980; Tómasson *et al.*, 1984), as well as the short incubation time of the eggs, which lasts only between one and three days (Mulder, 1973; Tómasson *et al.*, 1984; Skelton, 1986). Males, in contrast, seem to form larger aggregations at the spawning site (Tweddle & Davies, 1997), which may result in increased competition for individual females that come to the spawning site, and release all their eggs at once. This would imply that males follow a batch spawning strategy within a single spawning event. The competitive advantage of this strategy would be that males are able to maximise their reproductive output by fertilising more than one female.

Delayed maturation in association with an extended life span and high individual batch fecundity are commonly observed traits in fish that inhabit systems with strong seasonal fluctuations in environmental conditions (Gaigher *et al.*, 1980; Winemiller & Rose, 1992; Olden *et al.*, 2006; Tedesco *et al.*, 2008). This life history adaptation allows such populations to persist during extended periods of unsuitable spawning conditions, and take advantage of conditions during favourable years, while simultaneously maximising individual fitness (Winemiller & Rose, 1992; Tedesco *et al.*, 2008).

Classical *r*- and *K*-selection theory was originally developed for terrestrial animals (MacArthur & Wilson, 1967; Pianka, 1970), but has also been used to predict that fish in stable aquatic environments tend towards am artricial (*K*-strategists) life history style, while fish in unstable habitats follow a precocial life history strategy (*r*-strategists) (Adams, 1980; Laurenson & Hocutt, 1985; Weyl & Booth, 1999). Typically, *K*-strategists are characterised as long-lived species that attain larger sizes and that mature late, whereas *r*-strategists are short-lived, grow to a small size and mature early. Interestingly, neither the *r*-selected nor *K*-selected life history style seems to sufficiently account for the observed life history characteristics of *L. capensis*. Several quantitative life history studies identified similar shortcomings of the two-dimensional *r*-*K* continuum and generally referred to the lack of at least a third axis required to describe the variations of life history styles in fishes (Winemiller, 1989; Winemiller & Rose, 1992; Winemiller, 1992; Reznick *et al.*, 2002; King & McFarlane, 2003; Olden *et al.*, 2006; Tedesco *et al.*, 2008).

Based on patterns of life history variations in tropical freshwater fishes and North American freshwater and marine fishes, Winemiller (1989) and Winemiller and Rose (1992) predicted three primary life history strategies resulting from adaptive responses to environmental predictability and variability, which are represented by the endpoints of a triangular continuum model. The authors provided the following descriptions of biological characteristics and habitat attributes for each strategy: (i) opportunistic strategists are small-bodied, rapidly maturing, short-lived fishes that typically inhabit harsh and unpredictable environments; (ii) equilibrium strategists are small- to medium-bodied fishes with intermediate ages-at-maturity, low fecundity per spawning event but high juvenile survivorship due to greater parental care that typically inhabit stable environments, and (iii) periodic strategists are relatively long-lived, larger-

bodied fishes with delayed maturation and high batch fecundity per spawning event associated with reduced juvenile survivorship, and that typically inhabit highly seasonal environments.

The results from the present study suggest that *L. capensis* is likely located in the proximity to the endpoint of the periodic strategists, and although some aspects such as fecundity and spawning behaviour were not investigated here, there seems to be sufficient evidence from the literature to support this characterisation (Mulder, 1973; Gaigher *et al.*, 1980; Tómasson *et al.*, 1984; Skelton, 1986). Periodic strategists are considered to be the least adapted to habitats that have become temporally stable and that are subject to low resource availability due to decreased inundation of floodplains from damming (Olden *et al.*, 2006). The availability of periodic floodplains, in conjunction with inundated vegetation mediated by the unregulated inflow of the Orange River and local erratic rains, may therefore have played a vital role for the successful establishment of *L. capensis* in Lake Gariep.

CHAPTER 6

Estimating confidence intervals for the expected CPUE from delta-models: A model application to the analysis of gillnet and angler catch rates from Lake Gariep

6.1 INTRODUCTION

Fisheries-independent data collected using a randomly stratified sampling design are considered the most suitable information available to construct indices of abundance (Steffanson, 1996; Harley *et al.*, 2001; Maunder & Langley, 2004). These data are costly, often difficult to collect, and are therefore rarely or only insufficiently available for economically less important fisheries (e.g. many inland and coastal fisheries). As a result, estimates of relative abundance often rely solely on fisheries-dependent catch and effort data (Punt *et al.*, 2000; Maunder & Punt, 2004). These data introduce additional challenges to the reliable estimation of relative abundance because additional factors such as changes in effort allocation, gear or fishing behaviour also need to be accounted for (Hilborn & Walters, 1992; Quinn & Deriso, 1999; Harley *et al.*, 2001; Campbell, 2004; Maunder & Punt, 2004).

Catch-per-unit-effort (CPUE) data are probably the most common source of fisheries information, where CPUE is usually assumed to be linearly proportional to abundance (Quinn & Deriso, 1999; Campbell, 2004; Maunder & Punt, 2004). Mean CPUE is usually estimated for each area and sampling event and then integrated together to calculate a mean index of abundance for the population. This approach conventionally falls into the category of design-based methods and only allows drawing inference based on the randomness induced by the underlying sampling design (Smith, 1990;

Chen *et al.*, 2004). As a consequence, factors that potentially have effects on the distribution of fish (e.g. depth, habitat, temperature) can only be analysed individually by averaging over all possible samples, but not as an entity. Underlying environmental processes that may also influence abundance are often unexplored (Smith, 1990; Steffanson, 1996).

By contrast, in a model-based approach, expected CPUE is related to a set of explanatory variables and then standardised according to standard conditions (e.g. standardised to a given strata during a given year). Model-based approaches therefore aim to adjust for factors that influence catch rates other than abundance and are an attempt to standardise CPUE with the objective to make it comparable between seasons, areas or years (e.g. Punt *et al.*, 2000; Campbell, 2004; Maunder & Punt, 2004). The application of Generalized Linear Models (GLMs) (Nelder & Wedderburn, 1972) is the most frequently employed modelling approach used to standardise CPUE (Maunder & Punt, 2004; Venables & Dichmont, 2004). These models are based on the assumption that the response variable (CPUE) originates from an underlying stochastic process that can be described by a known statistical distribution. The determination of the least-biased statistical distribution is, however, not arbitrary and forms a major component of ongoing research (Pennington, 1983; Myers & Pepin, 1990; Lo *et al.*, 1992; Steffanson, 1996; Punt *et al.*, 2000; Syrjala, 2000; Dick, 2004; Ortiz & Arocha, 2004; Minami *et al.*, 2007; Shono, 2008; MacNeil *et al.*, 2009).

In most cases, the response variable is directly modelled as CPUE, with the choice of statistical distribution restricted to those that are suitable for continuous data (e.g. normal, log-normal or gamma). Alternatively, if catches were to be expressed in numbers, distributions that are appropriate for discrete count data (e.g. Poisson or

negative binomial) may be selected (O'Neill & Faddy, 2003; Ortiz & Arocha, 2004; Minami *et al.*, 2007). For discrete count data, effort can then be modelled as an offset and assumed to be known without error (Ortiz & Arocha, 2004; Penston *et al.*, 2008). From a variety of error models that could be used to model catch rates, the most frequently selected distribution remains the log-normal (Quinn & Deriso, 1999; Campbell, 2004; Maunder & Punt, 2004). As CPUE data are typically positively skewed, the choice of this distribution is based on the assumption that the data can be normalised using a natural logarithm-transformation. An undesirable consequence of taking the logarithm is that adjustments are necessary in order to analyse data sets that include zero catches. The most commonly applied adjustment is to add a constant to all catches. Such 'zero-adjusted' log-normal models have, however, been criticised, because the often arbitrary choice of this constant (usually 1 or some fraction, say 10%, of mean CPUE) may result in inadequate model fits and therefore introduce bias into parameter estimates and their associated measures of uncertainty (Ortiz *et al.*, 2000; Punt *et al.*, 2000; Maunder & Punt, 2004; Ortiz & Arocha, 2004; Fletcher *et al.*, 2005).

In recent years, delta models, also known as hurdle, conditional or zero-altered models, have gained popularity and have been suggested as being advantageous when too many zeros are present in the data (Lo *et al.*, 1992; Steffanson, 1996; Ortiz *et al.*, 2000; Punt *et al.*, 2000; Rodriguez-Marin *et al.*, 2003; Ortiz & Arocha, 2004). In most of these studies, while the analyses were rigorous to determine the best feasible model for predicting standardised CPUE indices, they often did not provide estimates about the actual precision of the model predicted CPUE in form of 95% confidence intervals. Estimating precision is important, since fisheries research is usually associated with risk assessments and management recommendations, where confidence limits for

CPUE estimates are usually required and certainly preferable in addition to analytical expressions.

While delta-models are commonly used to analyse CPUE data from marine fisheries and by-catch species, this approach has rarely been applied to data from freshwater systems. The objective of this Chapter was therefore to evaluate the application of delta-lognormal and delta-gamma GLMs for analysing fisheries-independent experimental gillnet catches and fisheries-dependent angler catches, which were collected at Lake Gariep between 2007 and 2008. This aims to determine suitable error distributions to analyse such CPUE data and to identify factors that might explain temporal and spatial differences in catch rates. The species of interest were the two endemic cyprinids, *Labeo capensis* and *Labeobarbus aeneus*, and non-native common carp *Cyprinus carpio*. The distributional assumptions of the two models were assessed by generating random data sets from Monte-Carlo simulations of the fitted models and comparing them to the observed data. Further model diagnostics applied included randomised quantile residual plots (Dunn & Smyth, 1996), deviance tables and Akaike's Information Criterion (AIC) (Akaike, 1972). Finally, a general parametric bootstrapping procedure is described to allow for the estimation of 95% confidence intervals for standardised CPUE.

6.2 MATERIALS AND METHODS

SAMPLING AND DATASETS

Most of the approximately 400 km shoreline of Lake Gariep is surrounded by nature reserves and angling is restricted to two principal areas (Ellender *et al.*, 2010a). Each of these fishing areas covers a shoreline of approximately 35 km. One is in the vicinity of

the small towns Oviston and Venterstad and the other area is near Gariep Dam close to the dam wall. The fishing areas are about 40 km apart from each other (Fig. 6.1).

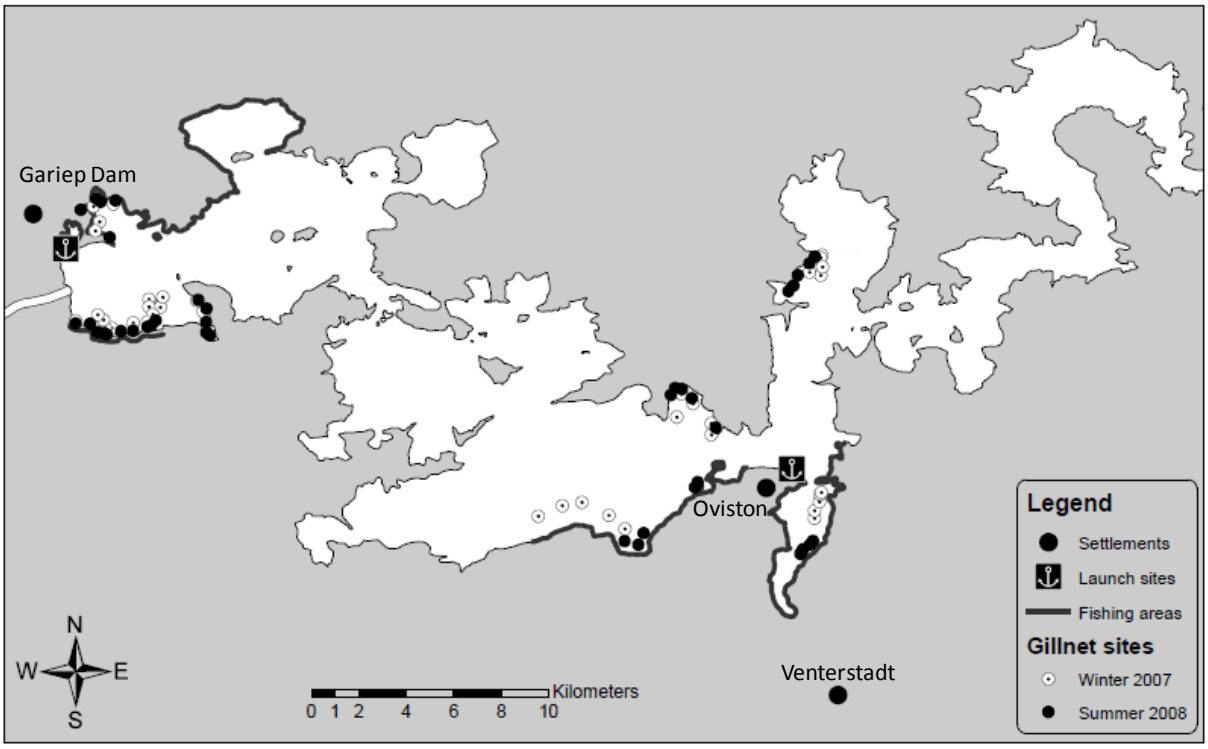

Fig. 6.1. Map of Lake Gariep showing the gillnet sites sampled in winter 2007 and summer 2008 and the strata of the two principle areas, where angler roving creel surveys were conducted between March 2007 and January 2008.

The fisheries-independent gillnet data used in this Chapter were collected during the two seasonal experimental gillnet surveys conducted in winter (June 2007) and summer (January 2008) described in (Chapter 2). Sampling was logistically confined to a 10 km radius from the two permanently accessible launching sites at Oviston (middle dam) and Gariep Dam (close to the dam wall) (Fig. 6.1). The sampling design was equally stratified across seasons in that an equal proportion of nets were employed along fished and unfished strata in both sampling areas, respectively. As a proxy for the likely bottom-type at each gillnet site, the composition of the next adjacent shoreline was recorded as percentage silt, gravel, stones and boulders. In the morning, dissolved oxygen concentration and water temperature were recorded using an OxyGuard oxygen probe and total dissolved solids, conductivity, and pH were measured using a Hanna

HI98129 Combo pH and Electrical Conductivity Meter at the each sampling site. Gillnet catches were separated by species, weighed to the nearest 0.1 kg and expressed as CPUE in units of $kg.net^{-1}.night^{-1}$. This is the metric for catch rates that has been used in most comparable studies on Southern African inland waters (Booth & Weyl, 2004; Weyl *et al.*, 2007; Booth & Khumalo, 2009; Richardson *et al.*, 2009).

Fisheries-dependent data were collected as part of a bi-monthly angler roving creel survey that was conducted between March 2007 and January 2008 (Ellender, 2008; Ellender *et al.*, 2010b). Angler interviews were conducted for five days (three weekdays and two weekend days) during each sampling period in each of the two principle fishing areas at Oviston/Venterstad and at Gariep Dam (Fig. 6.1). Starting points and direction of the survey were randomly drawn for each sampling day. Angler catches were separated by species and weighed to the nearest 0.1 kg. During the interview, the time fished and the gear used (number of rods and hand lines) were recorded. If anglers fished in a group, the catch and numbers of rods and hand lines were divided by the number of group members and the group was treated as a single observation. Individual CPUE for each interview was expressed as $kg.angler^{-1}.h^{-1}$ (Ellender *et al.*, 2010b). More detailed information regarding the roving creel survey sampling protocol, user group characterisation, participation, effort allocation and estimated total annual harvest is available in Ellender (2008) and Ellender *et al.* (2009; 2010a; 2010b).

DELTA-MODELS

Delta-models are basically a modification of the Δ–distribution, which is a log-normal distribution that is adjusted to include zeros (Aitchison, 1955; Pennington, 1983). This distribution has a probability *p* that a zero observation occurs and, hence, a probability

(1-*p*) for a positive observation. If a positive observation occurs, it is assumed to originate from a log-normal distribution. The expected mean of the Δ–distribution can be expressed as:

$$\mathrm{E}(y) = (1-p)\exp(\mu + \frac{\sigma^2}{2}),$$

where μ and σ are the mean and standard deviation of the natural logarithm-transformed positive observations, respectively (Smith, 1990). A GLM framework allows choosing from several distributions for the positive observations, while the probability of a zero observation p is usually modelled with covariates using a logistic regression model. Delta-models are therefore the product of a logistic regression and a second model that is selected to describe the positive observations. In other words, the "hurdle" of a value being non-zero has to be overcome before modelling the positive observations conditional on at least one non-zero observation. The general form of the delta model is:

$$\Pr(Y \mid x, y) = \begin{cases} p(x) & y = 0 \\ (1-p(x))\dfrac{f(y)}{1-f(0)} & y > 0 \end{cases},$$

where x_i denotes a random binary variable with 1 and 0 assigned to the zero and positive observations, respectively, and $f(y)$ denoting the distribution chosen to describe the positive observations.

The probability p_i for any binary observation x_i being zero can be modelled with covariates using a logit link function:

$$\text{logit}(\, p(x_i)) = \ln\left(\frac{p(x_i)}{1-p(x_i)}\right) = \mathbf{W}_i^T \boldsymbol{\alpha}\,,$$

where $\mathbf{W}_i$ is the vector that specifies the explanatory variables for the i^{th} value of the response variable x and $\boldsymbol{\alpha}$ denotes the vector of coefficients. The expected probability $\hat{p}$ of catching at least one fish can be calculated as a function of explanatory variables that are fixed to a set of standard conditions, $\mathbf{W}_0^T$, and the estimated coefficient vector $\hat{\boldsymbol{\alpha}}$, such that:

$$\hat{p} = \frac{\exp(\mathbf{W}_0^T \hat{\boldsymbol{\alpha}})}{1+\exp(\mathbf{W}_0^T \hat{\boldsymbol{\alpha}})}\,.$$

In this study, the log-normal and the gamma distribution will be considered for analysing the continuous positive CPUE data ($CPUE_{pos}$), as they represent the most frequently assumed distributions for positive catch rates (Myers & Pepin, 1990; Smith, 1990; Lo *et al.*, 1992; Steffanson, 1996; Punt, 2000; Ye *et al.*, 2001; Brynjarsdóttir & Stefánsson, 2004; Ortiz & Arocha, 2004). Both distributions have a probability mass only for positive values and can describe data sets for which the majority of the probability mass is at low values but there is a heavy right tail (Brynjarsdóttir & Stefánsson, 2004).

Normalising positive CPUE observations ($CPUE_{pos}$) by the natural logarithm transformation remains the standard procedure used to analyse CPUE data (Quinn & Deriso, 1999; Maunder & Starr, 2003; Battaile & Quinn, 2004; Campbell, 2004). In this case, the difference between the log-transformed observed and predicted CPUE values can be described by the normal probability density function (PDF) as:

$$f(y \mid \mu, \sigma) = \frac{1}{\sqrt{2\pi\sigma}} \exp\left(- \frac{(\ln(y) - \mu)^2}{2\sigma^2} \right) \quad \text{for } y > 0 \ ,$$

where y denotes $CPUE_{pos}$ and μ and σ describe the mean and the standard deviation of natural logarithm-transformed $CPUE_{pos}$ data.

The response $\ln(CPUE_{pos})$ for each observation $\ln(y_i)$ can be modelled with a set of covariates using the GLM framework with an identify link function, such that

$$\ln(\text{CPUE}_{\text{pos}}) = \mu_i = \mathbf{X}_i^T \boldsymbol{\beta} \ ,$$

where $\mathbf{X}_i$ is the vector of the explanatory variables for the positive data and $\boldsymbol{\beta}$ is the corresponding vector of coefficients. From a lognormal distribution, the expected quantity of $CPUE_{pos}$ for the standardised covariates is given by:

$$\mathrm{E}\left[\text{CPUE}_{\text{pos}}(\mathbf{X}_0^T \hat{\boldsymbol{\beta}})\right] = \exp(\hat{\mu} + \frac{\hat{\sigma}^2}{2}) \ ,$$

where $\hat{\sigma}$ is the maximum likelihood estimate of the model standard deviation (residual standard error) of the form:

$$\hat{\sigma} = \sqrt{\frac{\sum_i (\ln(y_i) - \mu_i)^2}{m}}$$

with *m* denoting the number of positive observations. A bias-corrected natural estimate for the expected CPUE for the delta-lognormal model is given by (Fletcher *et al.*, 2005) as:

$$\mathrm{E}\left[\mathrm{CPUE}(\mathbf{W}_0^T\hat{\boldsymbol{\alpha}}, \mathbf{X}_0^T\hat{\boldsymbol{\beta}})\right] = (1-\hat{p})\exp(\hat{\mu} + \frac{\hat{\sigma}^2}{2}). \qquad \text{(Equation 1)}$$

Maximum likelihood estimates of $\hat{\boldsymbol{\alpha}}$ and $\hat{\boldsymbol{\beta}}$, and therefore derived maximum likelihood estimates of $\hat{p}_i$, $\hat{\mu}_i$ and $\hat{\sigma}$ can then be obtained via non-linear maximization of the combined binomial and normal log-likelihood function of the form:

$$LL = (n-m)\sum_{y_i=0}\ln(1-p_i) + m\sum_{y_i>0}\ln(p_i) - m\ln(2\pi) - m\ln(\sigma) - \sum_{y_i>0}\frac{(\ln(y_i)-\mu_i)^2}{2\sigma^2}.$$

Note that as both log-likelihood components have no term in common (the first two terms and the last three terms, respectively), each log-likelihood component can be modelled separately (Welsh *et al.*, 1996).

The gamma distribution has been suggested as an alternative to the log-normal distribution (Myers & Pepin, 1990; Steffanson, 1996). The PDF of the gamma distribution is conventionally expressed as:

$$f(y \mid \theta, k) = \frac{y^{\theta-1} \exp(-y/k)}{\Gamma(\theta) k^{\theta}} \qquad \text{for } y > 0 \ ,$$

where $\Gamma(\cdot)$ is the gamma function, θ is the scale parameter and k is the shape parameter. In a GLM framework, it is, however, more convenient to express the gamma PDF in terms of the mean $\mu = \theta k$ (Steffanson, 1996), such that:

$$f(y \mid \mu, \theta) = \frac{y^{\theta-1} \exp(-y\theta/\mu)}{\Gamma(\theta)\left(\frac{\mu}{\theta}\right)^{\theta}} \quad \text{for } y > 0 \ .$$

When applying the gamma error model to the positive observations, the response variable CPUE_{pos} can be modelled in its untransformed state and related to explanatory variables using the logarithmic link function, so that:

$$\text{CPUE}_{\text{pos},i} = \mu_i = \exp(\mathbf{X}_i^T \boldsymbol{\beta}) \, .$$

Correspondingly, the expected value for a standardised set of covariates is given by

$$\text{E}\left[\text{CPUE}_{\text{pos}}(\mathbf{X}_0^T \hat{\boldsymbol{\beta}})\right] = \hat{\mu}$$

and the expected CPUE using the delta-gamma model is calculated as (Steffanson, 1996)

$$\text{E}\left[\text{CPUE}(\mathbf{W}_0^T \hat{\boldsymbol{\alpha}}, \mathbf{X}_0^T \hat{\boldsymbol{\beta}})\right] = \hat{p}\,\hat{\mu} \, . \qquad \text{(Equation 2)}$$

Maximum likelihood estimates of $\hat{\boldsymbol{\alpha}}$ and $\hat{\boldsymbol{\beta}}$, and therefore $\hat{p}_i$, $\hat{\mu}_i$ and $\hat{\theta}$, for the delta-gamma model are then obtained by maximising the corresponding log-likelihood function of the form:

$$LL = (n-m)\sum_{y_i=0}\ln(1-p_i) + m\sum_{y_i>0}\ln(p_i) + (1-\theta)\sum_{y_i>0}\ln(y_i) - m\ln(\Gamma(\theta)) - m\theta\sum_{y_i>0}\left[\ln\left(\frac{\mu_i}{\theta}\right) - \frac{\theta}{\mu_i}y_i\right].$$

Note that the gamma log-likelihood component of the above function was rewritten to reflect the common estimation procedure applied in a GLM framework in that the scale parameter *k* was replaced by μ_i / θ.

MODEL SELECTION AND DIAGNOSTICS

The optimal combination of explanatory variables for each model component was selected using a stepwise forward-backward selection procedure based on the AIC as the primary criterion. The AIC determines the weight of evidence for each combination of variables as:

$$AIC = 2k - 2LL,$$

where k is the number of parameters in the GLM and LL denotes the maximised log-likelihood function of the fitted model. Therefore, the decrease in the negated log-likelihood function is penalised for every added degree of freedom, so that the smallest possible AIC can be used as a criterion to identify the most parsimonious set of explanatory variables for each error model. For all delta-models, binomial, log-normal and gamma components were examined separately, which resulted in a total of 18 model components (given the two datasets for each of the three species).

Based on a preliminary analysis, a total of five explanatory variables were selected from the gillnet dataset, while seven explanatory variables were considered for standardising angler CPUE (Table 6.1). According to the AIC, the environmental parameters temperature, pH, conductivity and total dissolved solids did not increase the predictive power of the gillnet CPUE models for any of the three species and were therefore excluded. To avoid too many substrate categories, percentage silt, as opposed to gravel, stones and boulder, was used as a proxy for the bottom-type characterisation at each gillnet site. For the angler CPUE data, the factors 'time fished' and 'fishers' were only tested for predicting the probability of capture. They were not, however, considered as covariates for the second component of the angler CPUE delta-models as their product, by definition, already determines the unit effort of the $CPUE_{pos}$ response.

Non-linear relationships between the response and the predictor variables can be included in GLMs through the link function, interaction terms and by transforming the explanatory variables (Maunder & Punt, 2004). To determine the optimal relationship between explanatory variables and the response CPUE, all continuous variables were evaluated in their untransformed and natural logarithm-transformed state. Additionally, the quadratic term of each continuous predictor was considered for the model fitting procedure. Adding the quadratic term of a predictor variable can potentially improve the predictive capability of the model as it induces extra curvature to the response surface (Battaile & Quinn, 2004; Maunder & Punt, 2004; Venables & Dichmont, 2004; Sousa *et al.*, 2007). The weight of evidence for the second degree interaction between the categorical factors period and area was examined for all models. Analyses (not shown here) revealed that other interaction terms were insubstantial or, in some instances, compromised the models in that the log-likelihood optimisation algorithm failed to converge.

Table 6.1. Summary of selected candidate explanatory variables used to standardise fisheries-independent gillnet CPUE data and fisheries-dependent angler CPUE data.

Predictor	Type	Description
Fisheries-independent CPUE		
period	Categorical	Seasonal sampling periods: Winter 2007 and Summer 2008
area	Categorical	Principle sampling areas Oviston and Gariep Dam
fished	Categorical	Determines whether nets were set along fished or unfished strata
silt %	Continuous	Percentage of silt composition along the shore line parallel to the gillnet; used as a proxy for bottom-type at the gillnet site
DO %	Continuous	Surface water dissolved oxygen percent saturation ; a common environmental predictor for fish assemblages
Fisheries-dependent CPUE		
period	Categorical	Bi-monthly sampling periods (Feb/Mar, Apr/May, Jun/Jul, etc.)
area	Categorical	Principle sampling areas Oviston and Gariep Dam
time fished	Continuous	Time fished (h) from the start of the fishing day until the interview
fishers	Continuous	Number of anglers in a group
rod	Continuous	Number of rods per angler
hand line	Continuous	Number of hand lines per angler

The significance of each model parameter was tested using log-likelihood ratio tests. Deviance tables were constructed for each error distribution, species and dataset. These tables were used in a stepwise manner to assess how much of the deviance could be explained by each additional factor. The change in deviance with every added explanatory variable is approximately χ^2-distributed, so that the χ^2-statistic can be applied to evaluate the significance of including a factor based on the degrees of freedom added to the model. The total deviance explained by the best fitting model compared to the null model is then equivalent to the pseudo-coefficient of variation (R^2) (Swartzman *et al.*, 1992), such that:

$$R^2 = 1 - \frac{\text{Residual deviance}}{\text{Null deviance}},$$

where the residual deviance refers to the total deviance of the best fitting model and the null deviance is the sum of deviance of the null model, which is fitted without any explanatory variables. In other words, the null deviance represents the deviance explained by the overall mean of the response.

PARAMETRIC BOOTSTRAP

In this section, a parametric bootstrapping procedure is described, which is applied to estimate 95% confidence intervals for the standardised CPUE values. The following steps were used for the parametric bootstrap method:

(1) For a given dataset (y_i, $\mathbf{W}_i^T$, $\mathbf{X}_i^T$) derive the maximum likelihood estimates of $\hat{\boldsymbol{\alpha}}$ and $\hat{\boldsymbol{\beta}}$ for both delta-models. For each observation *i* compute the expected probability of a zero response $\hat{p}_i$ and the expected value for the positive response $\hat{\mu}_i$ corresponding to each observation y_i.

(2) Execute the following two steps (a) and (b) at least 1000 times:

(a) First, generate a pseudo-dataset based on the underlying distributional assumptions. For each observation *i* in bootstrap replicate *j*, generate a random uniform between 0 and 1. If the random uniform is less than $\hat{p}_i$ then let the randomly generated response $y_{i,j}^*$ be equal to 0, otherwise generate $y_{i,j}^*$ from a log-normal distribution as a function of $\hat{\mu}_i$ and $\hat{\sigma}^2$, and from a gamma distribution as a function of θ and $\theta/\hat{\mu}_i$.

(b) For each bootstrap pseudo-sample ($y_{i,j}^*$, $\mathbf{W}_i^T$, $\mathbf{X}_i^T$) derive and save the maximum likelihood estimates of $\hat{\boldsymbol{\alpha}}_j^*$ and $\hat{\boldsymbol{\beta}}_j^*$, and compute the expected standardised CPUE as a function of $\text{CPUE}_j^*(\mathbf{W}_0^T\hat{\boldsymbol{\alpha}}_j^*, \mathbf{X}_0^T\hat{\boldsymbol{\beta}}_j^*)$ for each of the two delta-models (see equations 1 and 2).

3) Summarise the bootstrap data by applying the percentile method (Buckland, 1984) to estimate 95% confidence intervals for the standardised CPUE quantities from the resulting bootstrap vectors $\mathbf{CPUE}^{*}$.

COMPARING ALTERNATIVE ERROR MODELS

For each dataset for each given species, Monte-Carlo simulations were used to evaluate the distributional assumptions of parametrically-generated pseudorandom datasets against the frequency distribution of the observed CPUE data. For this purpose, 1000 pseudorandom datasets were generated for each delta-model as described in the previous section (step 2a) and the mean frequency of each bin was plotted against the observed frequency distribution. The corresponding 95% confidence intervals were plotted by applying the percentile method (Buckland, 1984) to the sorted vectors of randomly generated frequencies of each class.

The goodness-of-the-fit of each delta-model component was additionally assessed using randomized quantile residuals in form of quantile-quantile (Q-Q) plots (Dunn & Smyth, 1996). Quantile residuals were suggested to be suited to residual analysis for GLMs in general, because, apart from sampling variability, quantile residuals are expected to be exactly normally distributed provided the 'correct' error model is chosen (Dunn & Smyth, 1996).

Model fitting, model diagnostically analyses and parametric bootstrapping were conducted in R version 2.9.2 (R Development Core Team, 2009). Algorithms that allow for the generation of random variables from a gamma distribution are available in the *MASS* package (Venables & Ripley, 2002) and the function for computing randomised quantile residuals is included in the *statmod* package (Smyth, 2008).

6.3 RESULTS

A total of eight species were sampled during the two seasonal fisheries-independent gillnet surveys including one rainbow trout *Oncoryncus mykiss* and one rock catfish *Austroglanis sclateri* (Table 6.2). Of these, five species were also observed in the shore angler catches (Table 6.2). Numerically and by weight, *L. capensis* and *L. aeneus* dominated the gillnet catches, whereas *C. carpio* was the most dominant species in the angler catches (Table 6.2).

Table 6.2. Species composition expressed as percent of total number (n = 2376) and total weight (n = 1172 kg) of fish caught at Lake Gariep during gillnet surveys in winter 2007 and summer 2008; and total number (n = 2340 fish) and total weight (n = 2139 kg) of fish caught by anglers interviewed on Lake Gariep between February 2007 and January 2008.

Species name	Gillnet catch composition		Angler catch composition	
	No. (%)	Mass (%)	No. (%)	Mass (%)
Labeo capensis	54.2	36.6	11.5	7.0
Labeobarbus aeneus	39.6	46.2	8.8	7.5
Cyprinus carpio	2.3	4.3	72.1	78.5
Labeobarbus kimberleyensis	1.9	6.9	0.3	0.3
Clarias gariepinus	1.0	5.2	7.7	6.8
Labeo umbratus	0.9	0.7	-	-
Oncorhynchus mykiss	< 0.1	< 0.1	-	-
Austroglanis sclateri	< 0.1	< 0.1	-	-

OBSERVED CATCH RATES

The frequency distributions of the observed gillnet CPUE for the three investigated species are presented in Fig. 6.2. The proportions of zero catches in the gillnet data were 1.3% for *L. capensis*, 13.8% for *L. aeneus* and 70.0% for *C. carpio* (n = 80 net nights). Although *L. capensis* had the highest probability of being caught by gillnets, the nominal mean CPUE was higher for *L. aeneus* with 6.71 $kg.net^{-1}.night^{-1}$ compared to 5.36 $kg.net^{-1}.night^{-1}$ for *L. capensis*. For both species, maximum observed CPUE values were relatively high with 57.40 $kg.net^{-1}.night^{-1}$ for *L. capensis* and 48.10 $kg.net^{-1}.night^{-1}$ for *L. aeneus*, but catch rates of at least 25 $kg.net^{-1}.night^{-1}$ were more

frequently observed for *L. aeneus* (Fig. 6.2). As a result, positive catch rates of both species were highly right-skewed. In comparison to the two endemic cyprinids, the mean nominal gillnet CPUE for *C. carpio* was low at 0.63 $kg.net^{-1}.night^{-1}$ and a maximum observed CPUE of 7.30 $kg.net^{-1}.night^{-1}$.

Angler CPUE data were obtained from a total of 512 angler interviews conducted by Ellender (2008). The angler catches generally comprised of a large amount of zero catches (Fig. 7.3). In contrast to the gillnet data, *C. carpio* represented the species with the highest probability of being caught by hook and line and was present in more than 60% of the angler catches, whereas CPUE data for *L. capensis* and *L. aeneus* contained more than 85% zeros. As with the gillnet CPUE, positive catch rate frequencies were considerably skewed and therefore far from being normally distributed (Fig. 7.3). The nominal mean CPUE for *L. capensis* (0.05 $kg.angler^{-1}.hour^{-1}$) and *L. aeneus* (0.06 $kg.angler^{-1}.hour^{-1}$) were extremely low with maximum CPUE observations not exceeding 2.5 $kg.angler^{-1}.hour^{-1}$ (Fig. 6.3). The nominal mean CPUE of *C. carpio* was much higher (0.47 $kg.angler^{-1}.hour^{-1}$) with a maximum observed CPUE of 5.12 $kg.angler^{-1}.hour^{-1}$, which implied that *C. carpio* is the main target species in this fishery.

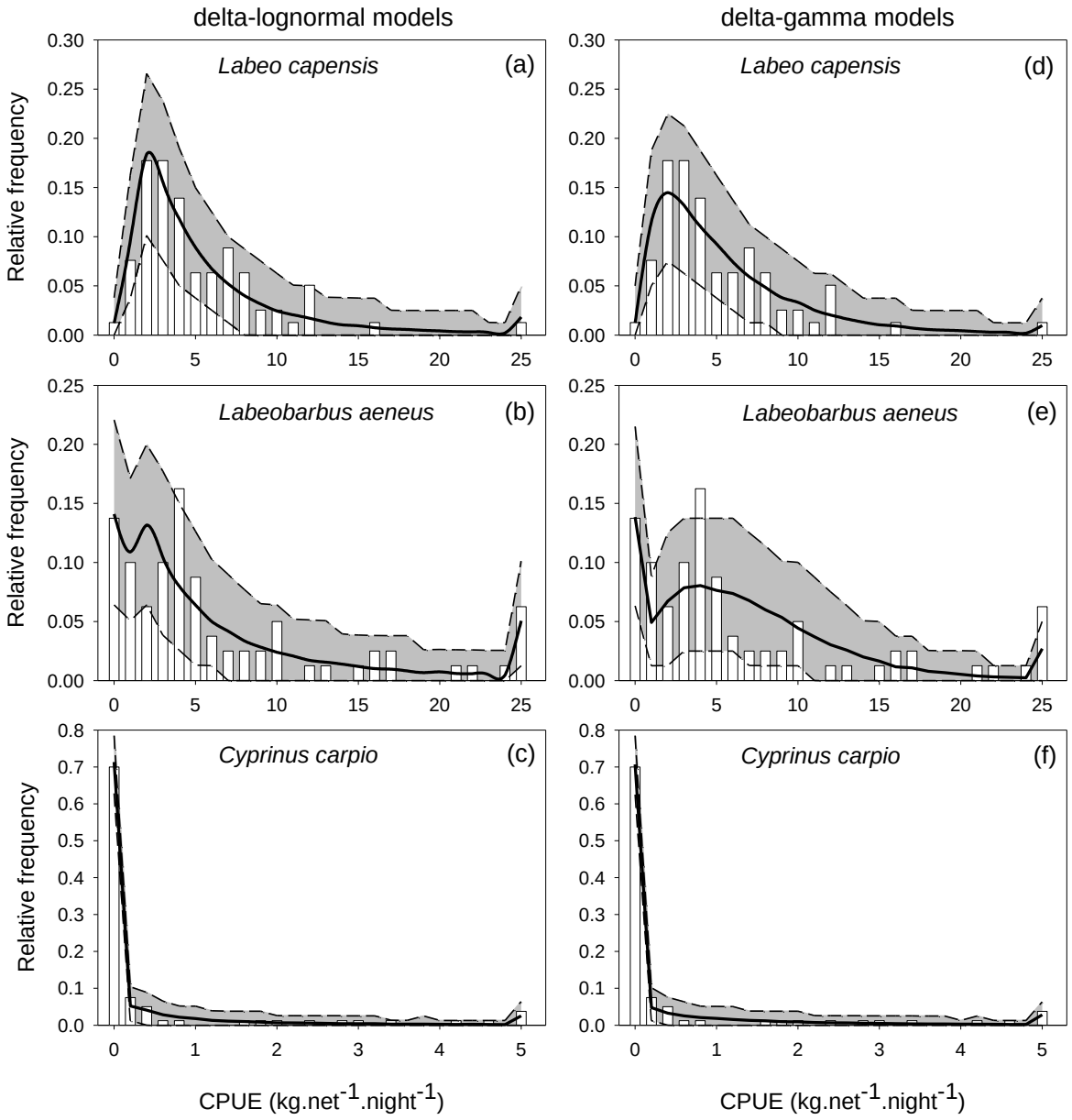

Fig. 6.2. Observed gillnet CPUE (kg.net^{-1}.night^{-1}) frequency distributions (bars) compared to the mean (solid lines) of parametrically-generated frequency distributions derived from the fitted delta-lognormal (a) - (c) models and the fitted delta-gamma models (d) - (f) using Monte-Carlo simulations (n = 80 net nights). Grey areas within dashed borders demarcate upper and lower 95% confidence intervals for the generated frequency distributions.

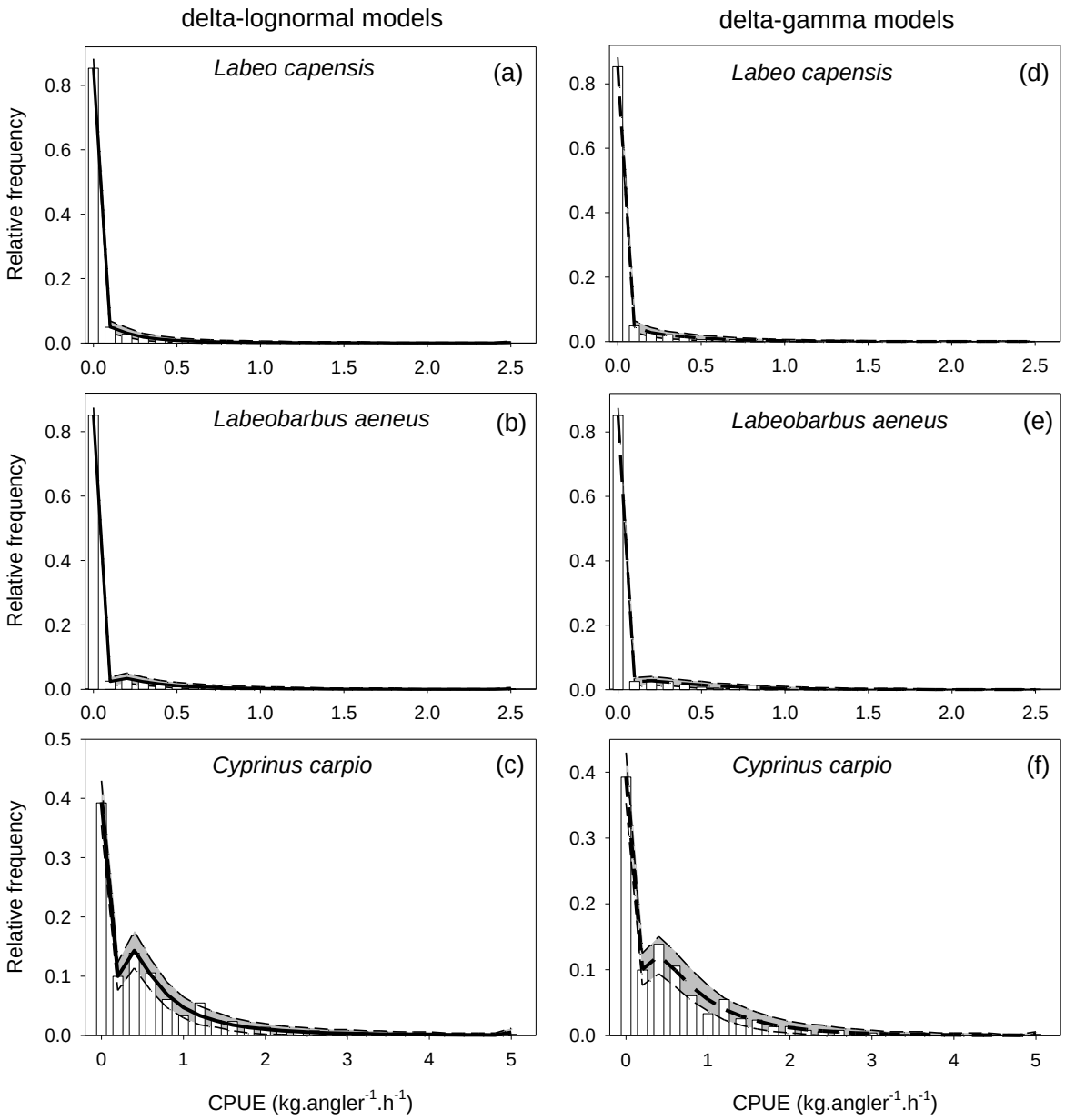

Fig. 6.3. Observed angler CPUE (kg.angler^{-1}.h^{-1}) frequency distributions (bars) compared to the mean (solid lines) of parametrically-generated frequency distributions derived from the fitted delta-lognormal (a) - (c) models and the fitted delta-gamma models (d) - (f) using Monte-Carlo simulations (n = 512 angler interviews). Grey areas within dashed borders demarcate upper and lower 95% confidence intervals for the generated frequency distributions.

ERROR MODELS

The observed frequencies and the mean of the frequency distributions from 1000 generated pseudo-datasets are shown in Fig. 6.2 and Fig. 6.3. By design, delta-models simulated the frequency of zero catches accurately and also captured the highly skewed nature of the data well, although some differences were noted. Both delta-models

differed most for the gillnet CPUE of *L. capensis* and *L. aeneus* (Fig. 6.2 a, b), which might be explained by the relatively large variation of positive values in these two datasets. The largest discrepancy between the two models was evident for the *L. aeneus* gillnet CPUE (Fig. 6.2 b). In this case, the delta-gamma model expected the highest frequency probability at around 4 $kg.net^{-1}.night^{-1}$, which also concurred with the observed data. The delta-lognormal, in contrast, performed better in predicting the frequency of the 1 $kg.net^{-1}.night^{-1}$ class, but largely overestimated the frequency of the 2 $kg.net^{-1}.night^{-1}$ class. For the three angler datasets, observed and simulated frequency distributions were generally similar (Fig. 6.3). Only the *C. carpio* angler CPUE showed some evidence that the delta-lognormal distribution performed slightly better in simulating the observed frequency of the 2 $kg.net^{-1}.night^{-1}$ class (Fig. 6.3 c).

Analysis of randomised quantile residuals for the binomial, log-normal and gamma GLMs of the most parsimonious delta-models is summarised in Fig. 6.4 and Fig. 6.5 in the form of Q-Q plots. The goodness-of-fit of each component can be graphically evaluated by assessing the deviation of the Q-Q points along a 1:1 relationship between the sorted randomised quantile residuals and their corresponding standard normal quantiles (Fig. 6.4; Fig. 6.5). In general, Q-Q plots showed moderate deviations from the expected standard normal distribution of quantile residuals and therefore provided no evidence for violation of the distributional assumptions by any of the models investigated (Fig. 6.4; Fig. 6.5). In particular, the Q-Q plots for the binomial GLMs showed little departure from the expected 1:1 relationship, which indicated that the probability of zero catches was well-described by the logistic regression models. Although the graphical differentiation between the log-normal and gamma GLMs was to some degree limited because of their relative close proximity to each other, there seemed to be a consistent pattern in that the quantile residuals of the gamma model

marginally better approximated the expected standard normality for the positive gillnet CPUE (Fig. 6.4 d - f), while the fitted log-normal models performed slightly better for the positive angler CPUE (Fig. 6.5 d - f).

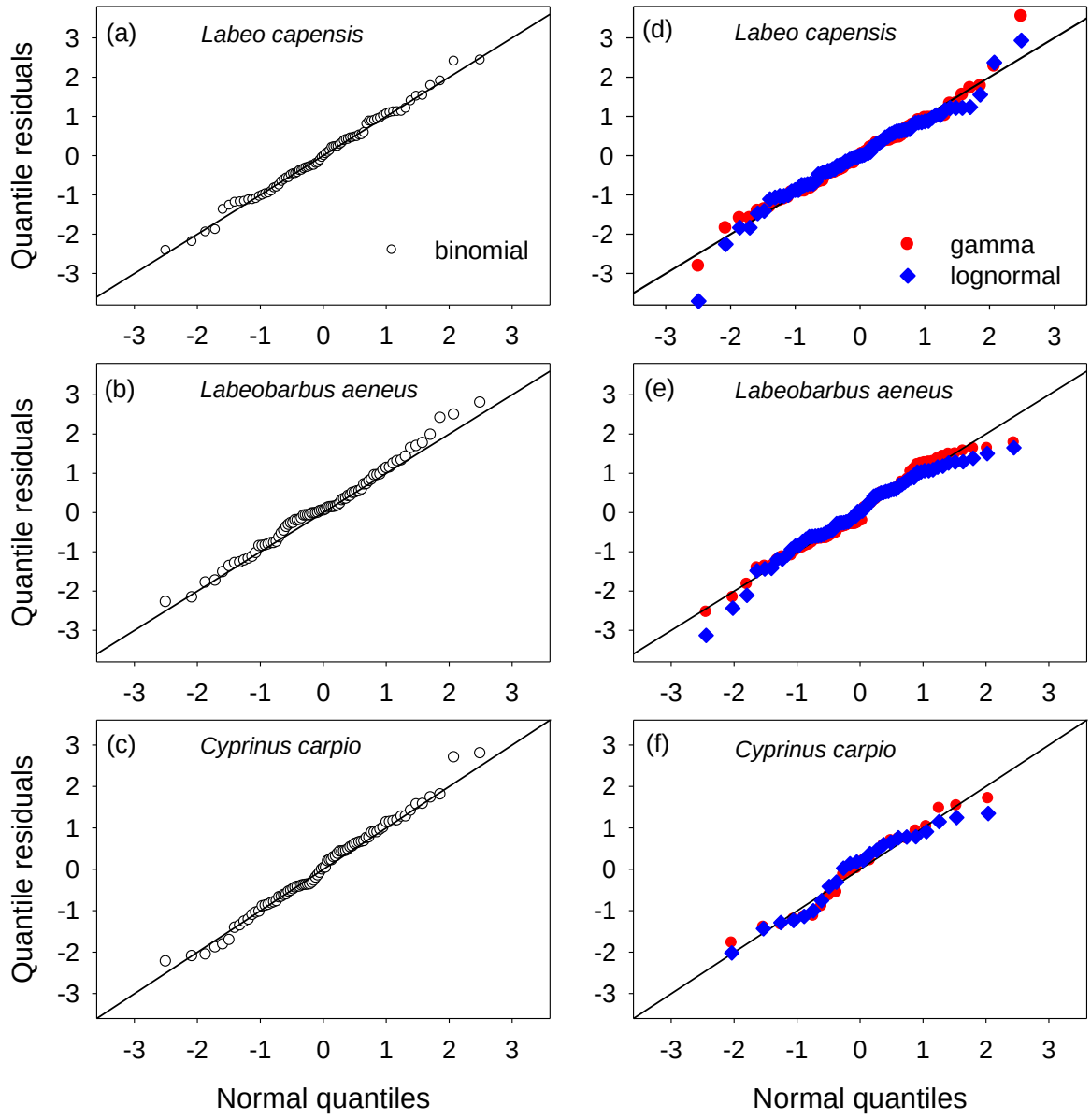

Fig. 6.4. Quantile-quantile plots from the analysis of gillnet CPUE data showing randomised quantile residuals and their corresponding standard normal quantiles for the best-fitting binomial models (a) - (c) and the best-fitting log-normal and gamma model (d) – (f). The straight lines represent a 1:1 relationship.

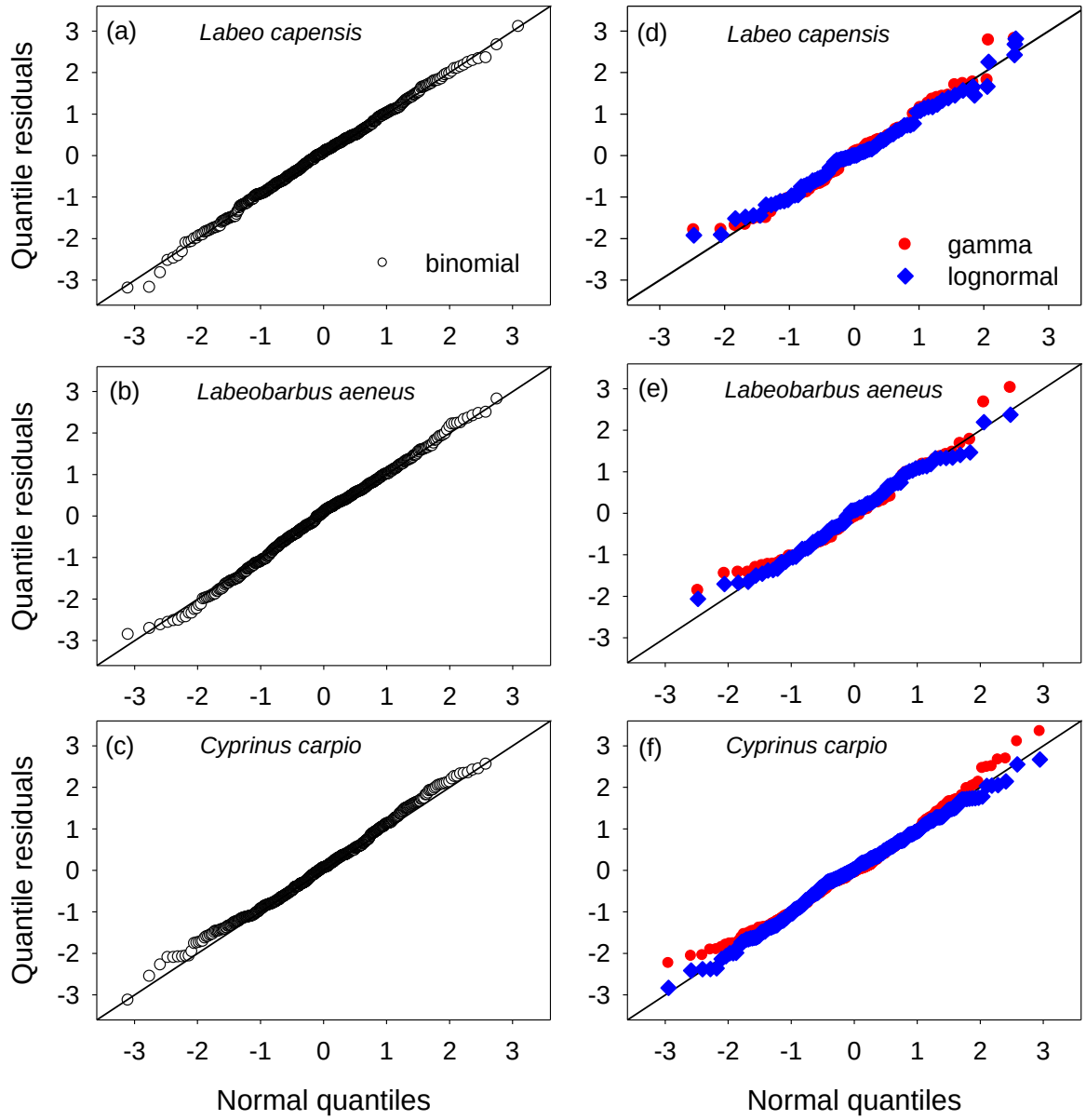

Fig. 6.5. Quantile-quantile plots from the analysis of angler CPUE data showing randomised quantile residuals and their corresponding standard normal quantiles for the best-fitting binomial models (a) - (c) and the best-fitting lognormal and gamma model (d) – (f). The straight lines represent a 1:1 relationship.

MODEL FITTING

Estimated coefficients, and their associated variability, for each of the 18 fitted model components are summarised in Table 6.3 and Table 6.4. Note that the estimated coefficients derived for the binomial GLMs are expressed such that they represent the probability of capture (1-*p*). Second degree interactions between 'period' and 'area'

were included in the selected log-normal and gamma GLMs for the gillnet $CPUE_{pos}$ of *L. aeneus* and the angler $CPUE_{pos}$ of *L. capensis* and *C. carpio* (not shown in Table 6.4 a, c). None of the considered predictors were informative enough to be included in the binomial regression models for *L. capensis* (Table 6.3 a) and *L. aeneus* (Table 6.3 b), which resulted in the selection of the null model (intercept only). The predicted mean probability of capture was therefore expected to be constant and predicted to be 0.99 [95% CI = 0.96 – 1.00] and 0.86 [95% CI = 0.78 – 0.94], for *L. capensis* and *L. aeneus*, respectively.

Table 6.3. Estimated coefficients and their standard errors (in parentheses) of the most parsimonious delta-model components for gillnet CPUE of (a) *Labeo capensis,* (b) *Labeobarbus aeneus* and (c) *Cyprinus carpio*.

(a)	*Labeo capensis*		
Model	Binomial	Log-normal	Gamma
Intercept	4.369 (1.006)***	1.244(0.108)***	1.473 (0.222)***
Oviston	-	-	-0.405 (0.258)
% silt	-	-	0.026(0.012)*
% silt^2	-	-	-0.0002(0.0001)
(b)	*Labeobarbus aeneus*		
Model	Binomial	Log-normal	Gamma
Intercept	1.836 (0.325)***	-5.155(2.044)*	-4.020 (1.617)*
summer08	-	-0.454(0.602)	-0.622 (0.477)
Oviston	-	1.196(0.366)**	0.912 (0.289)**
% oxygen	-	0.067(0.022)**	0.062 (0.017)***
summer08:Oviston	-	-1.631(0.519)**	-1.388(0.410)**
(c)	*Cyprinus carpio*		
Model	Binomial	Log-normal	Gamma
Intercept	-4.116 (0.950)***	-1.863(0.924)	-1.467 (0.648)*
Summer 08	1.205 (0.650)	1.316(0.654)	1.316(0.654)**
% silt	0.029 (0.009)***	0.014(0.009)	0.017(0.006)*
fished	1.132 (0.639)**	-	-

Significance levels based on log-likelihood ratio tests are marked as '*', $p < 0.05$; '**', $p < 0.01$ and '***', $p < 0.001$.

Table 6.4. Estimated coefficients and their standard errors (in parentheses) of the most parsimonious delta-model components for angler CPUE of (a) *Labeo capensis,* (b) *Labeobarbus aeneus* and (c) *Cyprinus carpio*.

(a)	*Labeo capensis*		
Model	Binomial	Log-normal	Gamma
Intercept	-2.433(0.396)***	-2.161(0.387)***	-1.796(0.363)***
ln(time fished)	0.722(0.235)**	-	-
ln(fishers)	0.521(0.253)*	-	-
Apr/May	-	0.591(0.509)	0.917(0.477)
Jun/Jul	-	1.283(0.671)	1.147(0.628)
Aug/Sep	-	1.079(0.742)	0.717(0.695)
Oct/Nov	-	0.541(0.500)	0.468(0.468)
Dec/Jan	-	0.286(0.509)	0.898(0.477)
Oviston	1.012(0.227)***	0.346(0.671)	0.494(0.832)
(b)	*Labeobarbus aeneus*		
Model	Binomial	Log-normal	Gamma
Intercept	-6.716 (1.323)***	-2.001(0.271)***	-1.517(0.287)**
ln(time fished)	0.576(0.230)*	-	-
rod	1.266(0.438)**	0.298(0.146)**	0.242(0.106)*
rod^2	-0.133(0.081)	-	
hand line	1.321(0.419)**	0.252(0.112)*	0.232(0.119)
hand line^2	-0.185(0.076)*	-	-
Apr/May	3.844 (1.088)***	-	-
Jun/Jul	2.004 (1.177)	-	-
Aug/Sep	2.261 (1.113)*	-	-
Oct/Nov	3.236 (1.078)**	-	-
Dec/Jan	3.122 (1.099)**	-	-
Oviston	-0.499(0.171)	-0.796(0.368)*	-0.535(0.390)
(c)	*Cyprinus carpio*		
Model	Binomial	Log-normal	Gamma
Intercept	-2.494 (0.545)***	-0.941(0.283)**	-0.791(0.288)**
ln(time fished)	1.128(0.177)***	-	-
ln(fishers)	0.371(0.247)	-	-
rod	0.797(0.257)***	0.500(0.146)***	0.635(0.148)***
rod^2	-	-0.044(0.025)	-0.071(0.026)**
hand line	0.797(0.717)**	0.349(0.116)**	0.416(0.118)***
hand line^2	-0.056(0.036)	-0.027(0.015)	-0.038(0.015)**
Apr/May	-0.045 (0.351)	-0.849(0.246)***	-0.728(0.251)**
Jun/Jul	-0.401 (0.382)	-0.913(0.312)**	-0.861(0.317)**
Aug/Sep	-1.052 (0.391)*	-0.347(0.282)	-0.348(0.287)
Oct/Nov	0.073 (0.393)	-0.514(0.240)*	-0.429(0.244)
Dec/Jan	0.385 (0.385)	-0.506(0.253)*	-0.566(0.257)*
Oviston	-0.499(0.171)	-1.314(0.287)***	-1.344(0.292)***

Significance levels based on log-likelihood ratio tests are marked as '*', $p < 0.05$; '**', $p < 0.01$ and '***', $p < 0.001$.

In all but one instance, the selected combinations of explanatory variables did not differ between the log-normal and gamma GLMs (Table 6.3; Table 6.4). The only exception was the *L. capensis* gillnet $CPUE_{pos}$, for which the AIC selected the null model when assuming a lognormal distribution, but suggested that the predictors '%silt', '%silt^2' and 'area' had sufficient explanatory power to be included when a gamma distribution was assumed (Table 6.3 a). Log-likelihood ratio tests conducted for the selected gillnet model parameters of the log-normal and gamma GLMs generally revealed higher significance levels for the estimated coefficients of the gamma models (Table 6.3), while the estimated coefficients for the angler GLMs showed similar significance levels for both error models (Table 6.4).

Table 6.5 summarises the model statistics including the pseudo-R^2, the AIC and the maximised log-likelihood values (*LL*) for the binomial, log-normal and gamma GLM components. The derived pseudo-R^2 values showed that the gamma GLMs could explain more variation in the gillnet data than the log-normal GLMs (Table 6.5 a) and that the log-normal distribution performed better or equally well for modelling the angler $CPUE_{pos}$ (Table 6.5 b). A comparison among model components for the same datasets emphasised that the AIC values were closely related to the magnitude of the maximised log-likelihood value. This is not surprising when considering the formula of the AIC. Interestingly, the AIC suggested the opposite to the pseudo-R^2 in that the AIC values calculated for the gillnet $CPUE_{pos}$ were consistently lower for log-normal GLMs, while the gamma GLMs resulted in lower AIC values for the angler $CPUE_{pos}$. Although sometimes understood differently, it should be emphasised that maximised log-likelihood values, and therefore by definition also the AIC, cannot be used to directly compare the performance of different error models. This is particularly obvious when attempting to compare gamma and the log-normal models, because in contrast to

the gamma model, the log-normal log-likelihood function is calculated from the natural logarithm transformed response and is therefore expected to differ largely in magnitude from the log-likelihood derived from a comparable gamma GLM (Table 6.5).

Table 6.5. Diagnostic statistics for the model components of the best-fitting delta-lognormal and delta-gamma GLMs for (a) gillnet and (b) angler CPUE data. The summary includes residual degrees of freedom (Res. df), the pseudo-coeffitient of variation (R^2), the AIC, the maximised log-likelihood value (*LL*) and the estimated parameters σ and θ of the lognormal and gamma models, respectively.

Parameter	Model	Res. df	R^2	AIC	*LL*	*s; q*
Gillnet CPUE						
Labeo capensis	Binomial	79	0.00	12.75	-5.38	-
	Log-normal	78	0.00	220.26	-108.13	0.96
	Gamma	75	0.13	421.08	-194.11	1.43
Labeobarbus aeneus	Binomial	79	0.00	66.06	-5.38	-
	Lognormal	64	0.31	205.01	-107.34	1.02
	Gamma	64	0.36	400.22	-194.11	1.45
Cyprinus carpio	Binomial	79	0.28	12.75	-5.38	-
	Log-normal	23	0.18	224.69	-107.34	1.42
	Gamma	23	0.24	421.08	-194.11	0.90
Angler CPUE						
Labeo capensis	Binomial	508	0.08	401.97	-196.99	-
	Log-normal	74	0.29	239.45	-106.72	1.096
	Gamma	74	0.25	-25.51	25.75	1.221
Labeobarbus aeneus	Binomial	511	0.29	330.76	-153.38	-
	Log-normal	75	0.14	211.62	-100.81	0.94
	Gamma	75	0.08	16.58	-3.29	1.39
Cyprinus carpio	Binomial	503	0.18	588.83	-282.42	-
	Log-normal	298	0.18	812.45	-389.22	0.868
	Gamma	298	0.18	413.83	-189.92	1.643

To select the most suitable error model for each dataset, it was assumed that the choice between the delta-lognormal and the delta-gamma GLM can be made based on (1) the Monte-Carlo simulation results (Fig. 6.2; Fig. 6.3), (2) the Q-Q plots (Fig. 6.4; Fig. 6.5)

and (3) the pseudo-R^2 (Fig. 6.5), whereas the consideration of the latter was based on the assumption that distributional assumptions of both delta-models could generally be justified by (1) and (2). Although there was no clear evidence for selecting either delta-model for a given dataset, the overall corroborative evidence from the analyses presented in the previous sections of this Chapter indicated that the delta-gamma model should be assumed when analysing the gillnet CPUE, whereas the delta-lognormal seemed to be marginally more appropriate for analysing the angler CPUE.

CPUE INDICES FOR FISHERIES-INDEPENDENT GILLNET CATCHES

The fitted delta-gamma GLMs were chosen to make predictions of the expected gillnet CPUE and to examine abundance patterns based on the selected covariates after first controlling for the effects. Fig. 6.6 illustrates that the gillnet CPUE for *L. capensis* was predicted highest at sites with bottom-types comprising approximately 60% silt and lowest where no silt was present. The Gariep site, close to the dam wall, was predicted to produce higher CPUE than the middle dam at Oviston (Fig. 6.6). The gamma GLM explained 13.15% total variation in the data with the factor 'area' contributing a significant 6.08% (Fig. 6.6). However, in contrast to the factor '%silt', the estimated coefficient for 'area' was not significant in the gamma GLM (Table 6.3 a), which was also shown by the large overlap of the estimated 95% confidence intervals when comparing the two areas (Fig. 6.6).

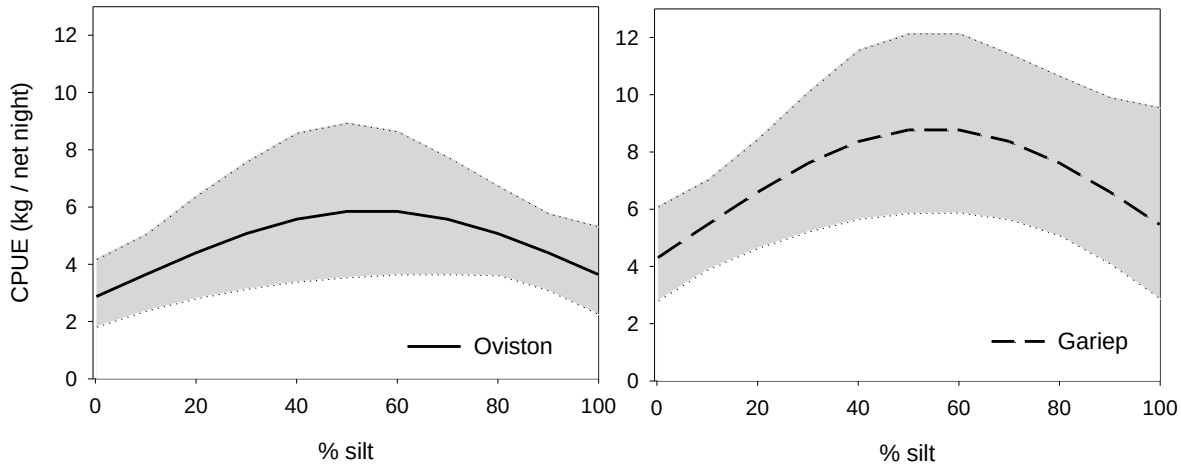

Fig. 6.6. Estimates of the expected CPUE of *Labeo capensis* for the areas Oviston and Gariep and plotted against the approximated percentage of silt of the bottom composition. Grey areas within the dashed borders show the estimated upper and lower 95% confidence intervals.

Table 6.6. Analysis of deviance table for the two components of the delta-gamma GLM fitted to the gillnet CPUE of *Labeo capensis*. The table summarises the residual degrees of freedom (Res. df), degrees of freedom (df), residual deviance (Res. Dev.), changes in the residual deviance (Δ Dev), the percentage of the total deviance explained by each sequentially added factor (% explained), and corresponding *p*-values when a χ^2-test was to test for significance.

Species			*Labeo capensis*			
Binomial						
Model structure	Res. d.f.	d.f.	Res. Dev.	Δ Dev	% explained	*p*
NULL	78		10.75			
% deviance explained					0.00	
Gamma						
Model structure	Res. df	df	Res. Dev.	Δ Dev.	% explained	*p*
NULL	79		70.832			
+ Area	78	1	66.524	4.308	6.08	*
+ % silt	77	1	64.961	1.563	2.21	
+ % silt^2	76	1	61.516	3.444	4.86	
% deviance explained					13.15	

In order to compare the expected CPUE of *L. aeneus* between areas and seasonal sampling periods, CPUE was first standardised to the observed mean '%oxygen' values for each period and site, which are summarised in Table 6.7. The resulting standardised CPUE trends showed strong seasonal variations between areas and periods (Fig. 6.8),

with significantly higher CPUE expected at the Gariep site during the summer of 2008. Based on the results from the analysis of deviance (Table 6.8), most of these variations were attributed to spatial and temporal differences in mean '%oxygen', as this factor alone contributed 25.08% ($p < 0.001$) to the total deviance of 35.73% explained by the gamma GLM (Table 6.7). The predicted exponential relationship between the factor '%oxygen' and CPUE is presented in Fig. 6.8.

Table 6.7. Mean and standard deviation (in parentheses) and the range of percent oxygen saturation (%oxygen) measurements recorded in the surface water at each gillnet site (n = 80). The means were used to model standardised CPUE of *Labeobarbus aeneus* for the areas Oviston and Gariep during winter 2007 and summer 2008.

Season	Parameter	Oviston	Gariep
Winter 07'	Mean (SD)	86.3 (1.7)	91.9 (3.7)
	Min	83.8	89.2
	Max	84.8	96.7
Summer 08'	Mean (SD)	99.4 (7.7)	115.6 (9.5)
	Min	78.2	106.8
	Max	103.8	137.9

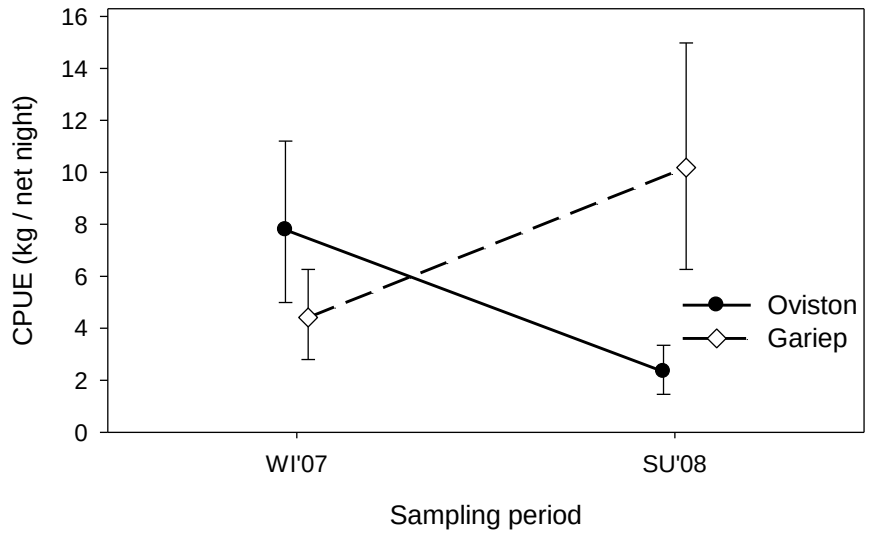

Fig. 6.7. Standardised CPUE of *Labeobarbus aeneus* for the areas Oviston and Gariep during winter 2007 and summer 2008. Error bars show the estimated upper and lower 95% confidence intervals.

Table 6.8. Analysis of deviance table for the two components of the delta-gamma GLM fitted to the gillnet CPUE of *Labeobarbus aeneus*. The table summarise the residual degrees of freedom (Res. df), degrees of freedom (df), residual deviance (Res. Dev.), changes in the residual deviance (Δ Dev), the percentage of the total deviance explained by each sequentially added factor (% explained), and corresponding *p*-values when a χ^2-test was to test for significance.

Species			*Labeobarbus aeneus*			
Binomial						
Model structure	Res. Df	df	Res. Dev.	Δ Dev	% explained	*p*
NULL	78		64.06			
% deviance explained					0.00	
Gamma						
Model structure	Res. df	df	Res. Dev.	Δ Dev.	% explained	*p*
NULL	68		82.00			
+ period	67	1	81.79	0.205	0.25	
+ area	66	1	79.88	1.915	2.34	
+ period:area	65	1	73.25	6.624	8.08	**
+ % oxygen	64	1	52.70	20.557	25.07	***
% deviance explained					35.73	

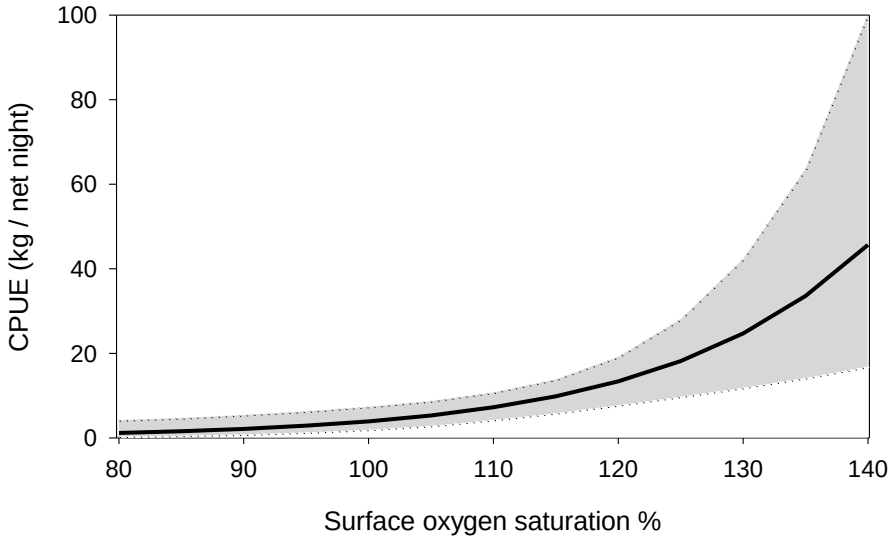

Fig. 6.8. Predicted relationship between CPUE the percent oxygen saturation in the surface water ('%oxygen') for *Labeobarbus aeneus*. The remaining predictors were fixed to: site = Gariep and period = summer08. Grey areas within the dashed borders show the estimated upper and lower 95% confidence intervals.

Figure 6.9 illustrates the predicted effects of the factors 'fished' and '%silt' on the probability of capture and on the expected CPUE of *C. carpio* . The seasonal effect on

the CPUE of *C. carpio* is illustrated in Fig. 6.10, indicating that significantly higher gillnet catch rates can be expected during summer. The binomial GLM explained 28.7% of the variation in the data, of which a highly significant fraction of 15.0% ($p < 0.001$) was explained by the factor '%silt'. The predicted probability of capturing *C. carpio* increased significantly as proportion of silt became larger (Fig. 6.9; Table 6.3 c). Unexpected was the much higher probability of encountering *C. carpio* in gillnets that were set along strata, where this species was frequently targeted by shore anglers (Fig. 6.9; Table 6.3 c).

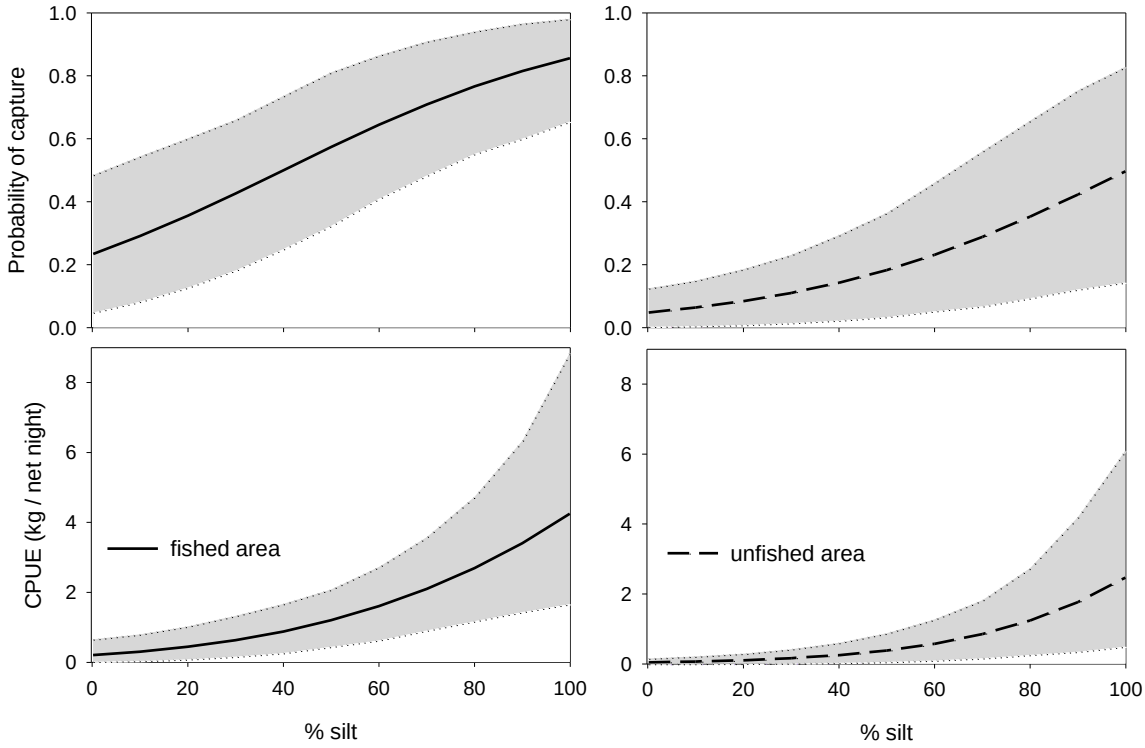

Fig. 6.9. Predicted relationships between the responses probability of capture (upper panel) and combined gillnet CPUE of *Cyprinus carpio* (lower panel), and the effects of fished and unfished areas and the approximated percentage of silt at bottom. The effects were predicted for the factor period = summer08. Grey areas within the dashed borders show the estimated upper and lower 95% confidence intervals.

The factor 'fished' accounted for 8.9% ($p < 0.01$) of the variation in the data and the results from the log-likelihood ratio test suggested that this factor was significant for predicting the probability of capture ($p < 0.01$) (Table 6.3 c). The most parsimonious

gamma GLM only included the factors '%silt' and 'period', which explained 14.3% ($p < 0.05$) and 9.5% ($p < 0.05$) of the variation in the data, respectively.

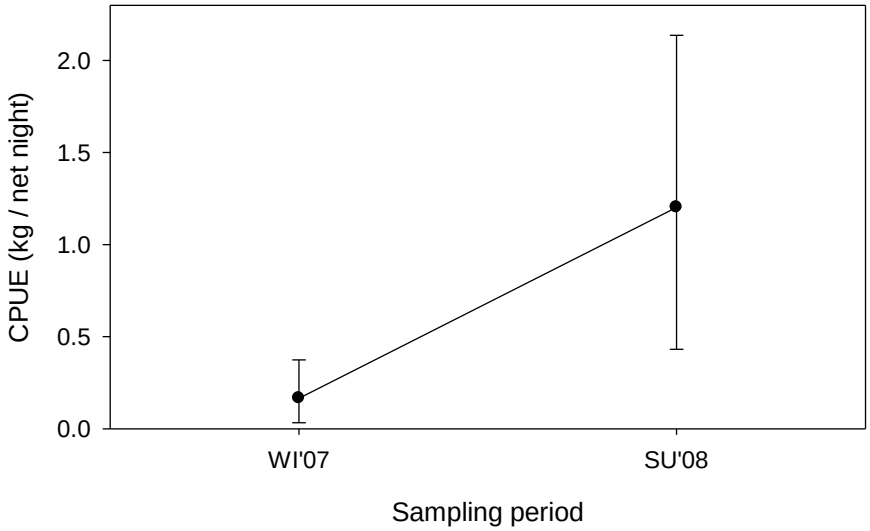

Fig. 6.10. Standardised CPUE of *Cyprinus carpio* for the winter survey in 2007 and the summer survey in 2008. The effect was predicted for a fished area that comprises 50% silt at the bottom.

Table 6.9. Analysis of deviance table for the two components of the delta-gamma GLM fitted to the gillnet CPUE of *Cyprinus carpio*. The table summarise the residual degrees of freedom (Res. df), degrees of freedom (df), residual deviance (Res. Dev.), changes in the residual deviance (Δ Dev), the percentage of the total deviance explained by each sequentially added factor (% explained), and corresponding *p*-values when a χ^2-test was used to test for significance.

Species	*Cyprinus carpio*					
Binomial						
Model structure	Res. df	df	Res. Dev.	Δ Dev	% explained	*p*
NULL	78		97.74			
+ period	77	1	94.34	3.40	3.48	
+ % silt	76	1	79.37	14.97	15.39	***
+ fished	75	1	70.50	8.87	9.50	**
% deviance explained					28.37	
Gamma						
Model structure	Res. df	df	Res. Dev.	Δ Dev	% explained	*p*
NULL	23		40.855			
+ period	22	1	36.983	3.873	9.48	*
+ % silt	21	1	31.134	5.849	14.32	*
% deviance explained					23.79	

CPUE INDICES FOR FISHERIES-DEPENDENT ANGLER CATCHES

Delta-lognormal GLMs were used to analyse the angler CPUE. The predicted bimonthly trends in CPUE for *L. capensis*, *L. aeneus* and *C. carpio* are illustrated in Fig. 6.11. In order to first control the fisheries-dependent factors, the expected bi-monthly CPUE was standardised to an angler who fished with two rods and no hand line for six hours.

The results, presented in Fig. 6.11, illustrate that the predicted CPUE of the endemic species *L. capensis* and *L. aeneus* were strongly dependent on the factor 'area', which for both species explained a significant fraction of the total deviance in the binomial and log-normal GLMs. As a result, higher CPUE was generally expected at the Gariep site close to the dam wall (Fig. 6.11). The bootstrap-based confidence intervals suggested, however, that predicted CPUE trends for *L. capensis* were associated with a high degree of uncertainty. With the exception of the February/March sampling period at Oviston, the angler CPUE of *C. carpio* showed similar trends between the two areas. The estimated confidence intervals indicated that the seeming decline in CPUE of *C. carpio* during the winter months could not be determined with significance given the variation in the data (Fig. 6.11).

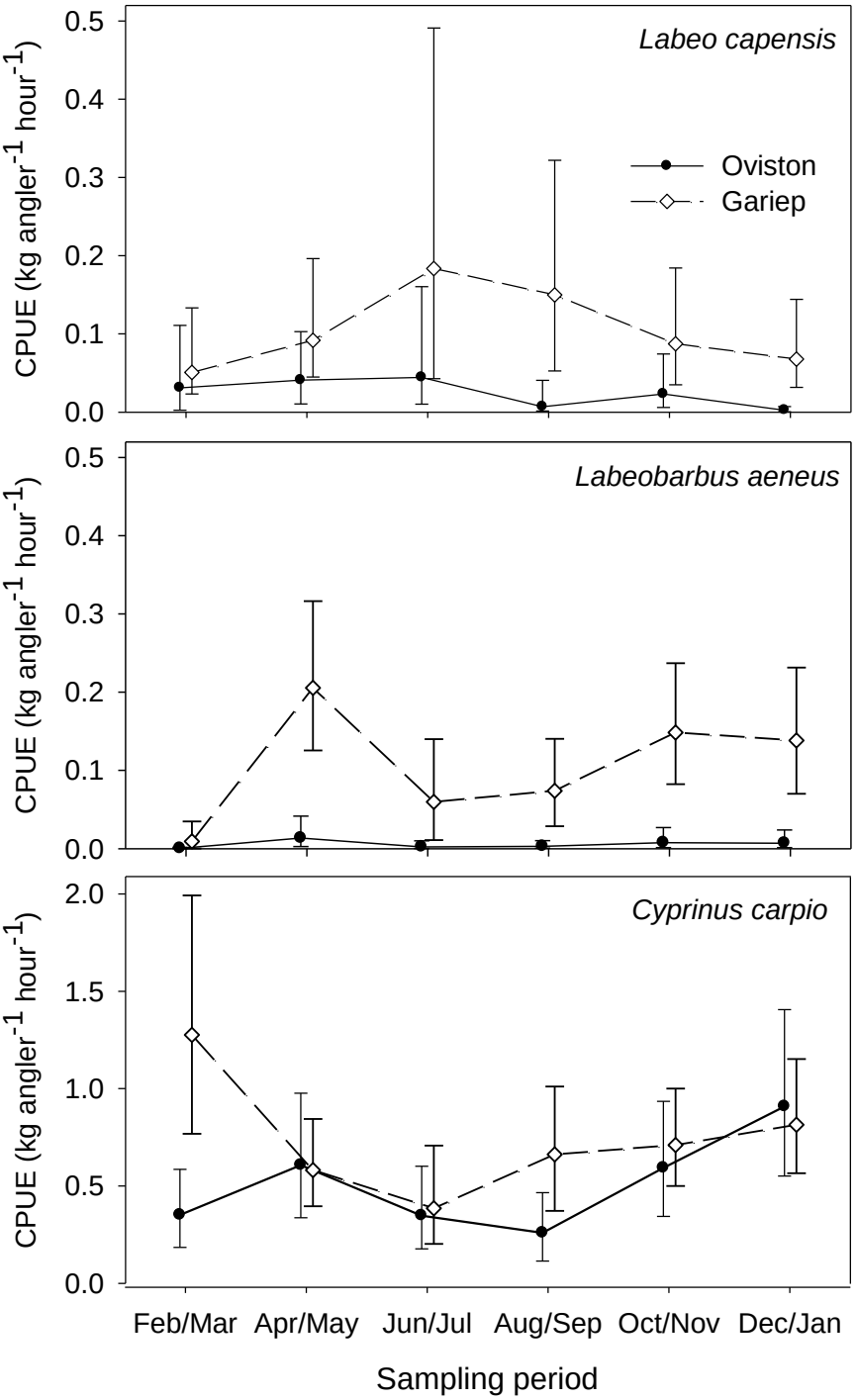

Fig. 6.11. Predicted angler CPUE trends of *Labeo capensis, Labeobarbus aeneus* and *Cyprinus carpio* for bi-monthly sampling periods between February 2007 and January 2009. In order to control for effects, the expected CPUE was standardised to an angler that fished with two rods for six hours.

Although the percentages of total deviance explained by the binomial and log-normal GLMs were different among the three species (Table 6.10 - Table 6.12), the results suggested that catch rates were generally dependent on the fisheries-dependent covariates 'time fished', 'rods' and 'hand lines' (see Table 6.4).

Table 6.10. Analysis of deviance table for the two components of the delta-lognormal GLM fitted to the angler CPUE of *Labeo capensis*. The table summarise the residual degrees of freedom (Res. d.f), degrees of freedom (d.f.), residual deviance (Res. Dev.), changes in the residual deviance (Δ Dev), the percentage of the total deviance explained by each sequentially added factor (% explained), and corresponding *p*-values when a χ^2-test was used to test for significance.

Species	*Labeo capensis*					
Binomial						
Model structure	Res. df.	df	Res. Dev.	Δ Dev	% explained	*p*
NULL	511		426.56			
+ ln(time fished)	510	1	415.47	11.09	2.60	***
+ ln(fishers)	509	1	409.03	6.44	1.51	*
+ area	508	1	393.97	15.06	3.53	***
% deviance explained					7.64	
Log-normal						
Model structure	Res. df	df	Res.Dev.	Δ Dev	% explained	*p*
NULL	74		106.08			
+ period	69	5	95.73	10.35	9.76	
+ area	68	1	89.86	5.87	5.53	*
+ period : area	63	5	75.61	14.25	13.43	*
% deviance explained					28.72	

Table 6.11. Analysis of deviance table for the two components of the delta-lognormal GLM fitted to the angler CPUE of *Labeobarbus aeneus*. The table summarise the residual degrees of freedom (Res. df), degrees of freedom (df), residual deviance (Res. Dev.), changes in the residual deviance (Δ Dev), the percentage of the total deviance explained by each sequentially added factor (% explained), and corresponding *p*-values when a χ^2-test was used to test for significance.

Species	*Labeobarbus aeneus*					
Binomial						
Model structure	Res. df	df	Res. Dev.	Δ Dev	% explained	*p*
NULL	511		430.07			
+ ln(time fished)	510	1	424.71	5.36	1.25	*
+ rod	509	1	419.41	5.30	1.23	*
+ rod2	508	1	418.96	0.45	0.10	
+ hand line	507	1	415.86	3.10	0.72	
+ hand line2	506	1	407.88	7.98	1.86	**
+ period	501	5	375.51	32.37	7.53	***
+ area	500	1	306.76	68.75	15.99	***
% deviance explained					28.67	
Log-normal						
Model structure	Res. df	df	Res. Dev.	Δ Dev	% explained	*p*
NULL	75		73.72			
rod	74	1	68.73	4.988	6.77	*
hl	73	1	67.26	1.476	2.00	
area	72	1	63.16	4.093	5.55	*
% deviance explained					14.32	

The predicted effect of these factors on the probability of capture and the expected CPUE of *C. carpio* are illustrated in Fig. 6.12. In general, the factor 'time fished' had positive effects on the probability of capture of all three species (Table 7.4) and generally explained significant fractions of the deviance in the binary data (Table 7.9-7.11). In the *C. carpio* example (Fig. 6.12), the addition of the quadratic term 'rod^2' in the log-normal GLM and 'hand line^2' in the binomial and log-normal GLM (Table 6.3 c) resulted in a strong non-linear relationship between the predicted CPUE and the number of rods and hand lines (Fig. 6.12). Interestingly, the peaks in the probability of capture and CPUE were independently predicted for six hand lines in the binomial GLM and six rods and six hand lines in the gamma GLM, respectively (Fig. 6.12). In

general, higher CPUE was predicted for anglers that used rods instead of hand lines (Fig. 6.12).

Table 6.12. Analysis of deviance table for the two components of the delta-lognormal GLM fitted to the angler CPUE of *Cyprinus carpio*. The table summarise the residual degrees of freedom (Res. df), degrees of freedom (df), residual deviance (Res. Dev.), changes in the residual deviance (Δ Dev), the percentage of the total deviance explained by each sequentially added factor (% explained), and corresponding *p*-values when a χ^2-test was to test for significance.

Species	*Cyprinus carpio*					
Binomial						
Model structure	Res. d.f.	d.f.	Res.Dev.	D Dev	% explained	*p*
NULL	511		685.96			
+ ln(time fished)	510	1	616.79	69.17	10.08	***
+ ln(fishers)	509	1	616.78	0.01	0.00	
+ rod	508	1	608.23	8.55	1.25	**
+ hand line	507	1	586.33	21.9	3.19	***
+ hand line^2	506	1	583.99	2.34	0.34	
+ period	501	5	565.74	18.25	2.66	**
+ area	500	1	564.83	0.91	0.13	
% deviance explained					17.66	
Lognormal						
Model structure	Res. d.f.	d.f.	Res.Dev.	D Dev	% explained	*p*
NULL	310		270.82			
+ rod	309	1	264.63	6.188	2.28	***
+ rod^2	308	1	264.46	0.176	0.06	
+ hand line	307	1	255.02	9.441	3.49	**
+ hand line^2	306	1	251.24	3.772	1.39	
+ period	305	1	242.28	8.963	3.31	***
+ area	300	5	239.94	2.339	0.86	***
+ period : area	295	5	222.51	17.433	6.44	***
% deviance explained					17.84	

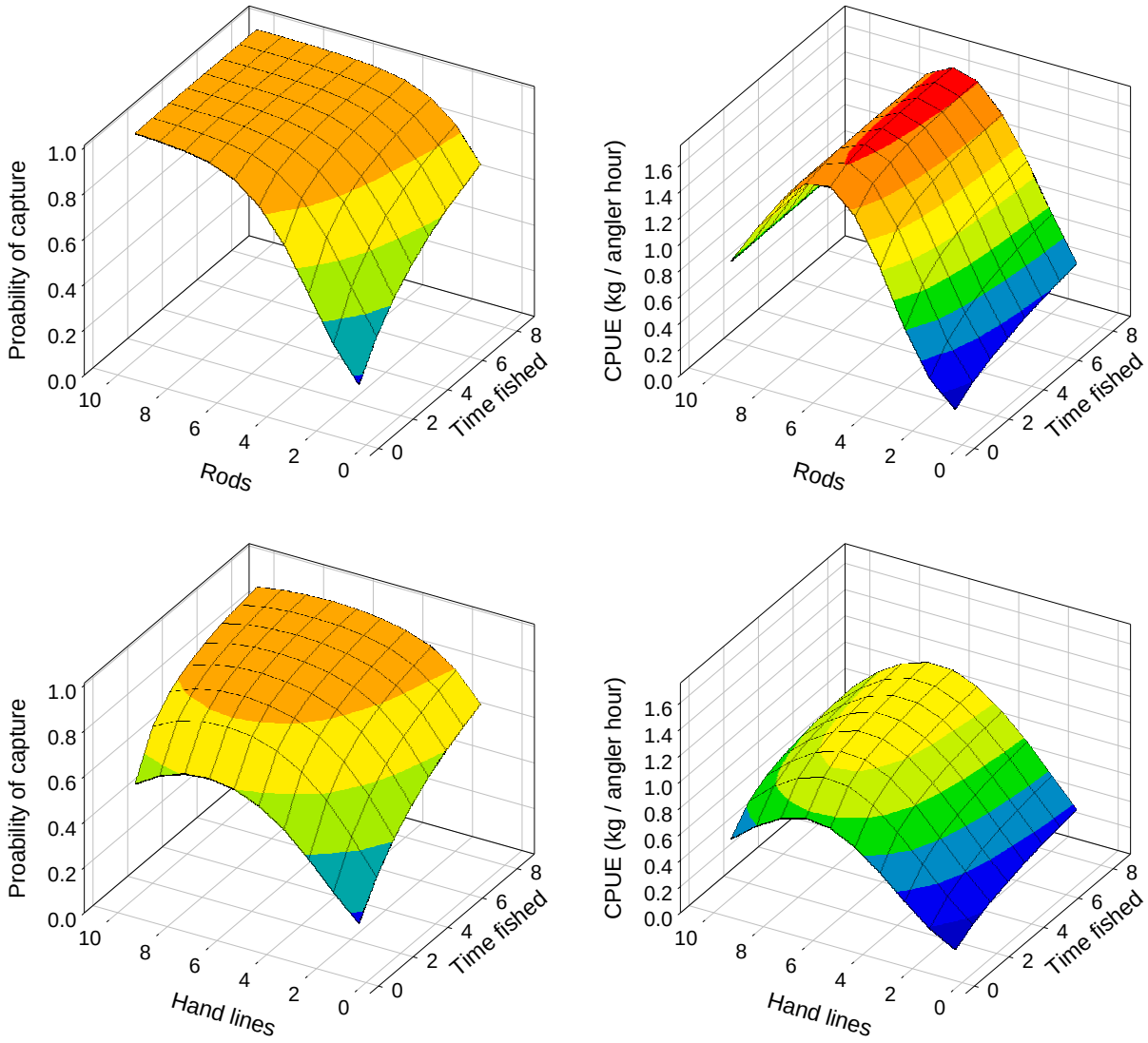

Fig. 6.12. Response surfaces of the probability of capture (left panel) and combined angler CPUE for *Cyprinus carpio* (right panel) as a function of rods or handlines and time fished. In order to assess the effect of the quantity of fishing gear used the expected probability of capture and CPUE was standardised to an angler that fished with either a changing number of rods but zero handlines (upper panel) or with a changing number of handlines but zero rods (lower panel).

6.4 DISCUSSION

In this Chapter, delta-lognormal and delta-gamma models were evaluated for their suitability to standardise fisheries-independent experimental gillnet data and fisheries-dependent angler data for the abundant cyprinids *L. capensis*, *L. aeneus* and non-native *C. carpio* in Lake Gariep. The results suggest that both models were appropriate to handle both the varying proportion of zero catches (1.3 – 85.3%) and the highly right

skewed data. In particular, the results from the Monte-Carlo simulations indicated that both fitted delta-models performed well, simulating the observed CPUE frequency distributions and the variation within the data. This Chapter therefore supports the results from similar studies, which suggested that delta-lognormal and delta-gamma models provide a flexible option to analyse a variety of different CPUE data sources including catch and effort data of shark fisheries (Punt *et al.*, 2000; MacNeil *et al.*, 2009; Megalofonou *et al.*, 2009), billfishes (Ye *et al.*, 2001; Rodriguez-Marin *et al.*, 2003; Ortiz & Arocha, 2004; Su *et al.*, 2008), or catch rates from stratified scientific trawl surveys of commercially important finfish resources (Steffanson, 1996; Sousa *et al.*, 2007; Rooper & Martin, 2009). This flexibility was also demonstrated by the good performance of the delta-models for the *L. capensis* gillnet data, which only comprised a single zero observation. In cases when the proportion of zero catches is small, the application of a delta-model framework is usually considered unnecessary (Rooper & Martin, 2009). Nevertheless, even the smallest proportions of zeros in data, requires some sort of manipulation of the observed response when assuming a log-normal or gamma distribution. By contrast, the general form of the delta-model allows modelling the response more directly and has the property that it reduces to a simple log-normal or gamma model if the probability of capture is one.

A crucial component of any model selection procedure is to statistically examine the underlying assumptions pertaining to the distribution of errors, as it has been shown that even small departures from the assumed error model can result in considerable bias when estimating abundance indices (Myers & Pepin, 1990; Syrjala, 2000; Dick, 2004; Ortiz & Arocha, 2004). Discriminating between statistical distributions is neither straightforward nor trivial because it is impossible to make direct comparisons based on model-specific statistics such as the log-likelihood or the closely related AIC (Ortiz &

Arocha, 2004; Su *et al.*, 2008; MacNeil *et al.*, 2009; but see Dick, 2004). In this study, the choice between the delta-lognormal GLM and the delta-gamma GLM was therefore based on more than one criterion. The graphical evaluations using Monte-Carlo simulations and randomised Q-Q plots provided useful tools to inspect how well the considered error models could support the observed data. Only if both of these criteria were sufficiently satisfied, was the amount of variation explained by each model (pseudo-R^2) considered as the third criterion.

Although the log-normal distribution can be suitable in the presence of heavily right-tailed positive observations, estimating the mean and variance from the gamma distribution was suggested to be less sensitive in the presence of small violations of distributional assumptions (Myers & Pepin, 1990; Syrjala, 2000). Syrjala (2000) linked the lack of robustness of the log-normal distribution, and hence the delta-lognormal distribution, to data sets that contained both very small and very large observations. He demonstrated that, as the difference between smallest and largest values in the sample increases, the log-normal estimator of the mean becomes more biased. In particular, the presence of very small observations was shown to cause a disproportional increase in the variance σ^2 and therefore result in a considerable bias due to the functional form of the bias-adjusted log-normal estimator (i.e. $E(y) = \exp(\mu+\sigma^2/2)$). The relatively large departures between the smallest and the largest CPUE observations, particularly in gillnet catches of *L. capensis* (CPUE: 0.1 – 57.4 kg.net^{-1}.night^{-1}) and *L. aeneus* (CPUE: 0.2 – 41.8 kg.net^{-1}.night^{-1}), therefore, support the choice of the more robust delta-gamma GLM for modelling the gillnet CPUE (Myers & Pepin, 1990; Syrjala, 2000). Conversely, the angler datasets provided strong support that angler CPUE closely resembled a delta-lognormal distribution, in which case the delta-lognormal estimator of the mean is usually considered the least biased option to obtain reliable CPUE

estimates (Aitchison, 1955; Pennington, 1983; Smith, 1990; Syrjala, 2000; Brynjarsdóttir & Stefánsson, 2004). While a comprehensive investigation into the properties and specific behaviours of the log-normal and the gamma distribution was beyond the objectives of this Chapter, detailed analyses on this topic can, for example, be found in Pennington (1983), Myers and Pepin (1990) and Syrjala, (2000).

Determining the precision of estimated abundance indices has been identified as one of the major challenges of CPUE standardisation (Smith, 1997; Maunder & Punt, 2004). An analytical approximation of confidence limits is already complicated by the often complex spatial and temporal structure of CPUE datasets. However, it is even more difficult to compute the precision when CPUE indices are estimated from delta-models, because this requires deriving confidence intervals from a mixture of two distributions. Although there has been some recent progress in the development of analytical methods for approximating confidence intervals from simple delta-models (Welsh *et al.*, 2000; Fletcher & Faddy, 2007; Fletcher, 2008), bootstrapping is considered to be the more appropriate, and general, approach when dealing with relatively complex data and modelling frameworks (Hilborn & Walters, 1992; Smith, 1997; Maunder & Punt, 2004; Fletcher *et al.*, 2005; Potts & Elith, 2006). The choice of bootstrapping over analytical confidence intervals is obvious in those cases where confidence intervals are constructed from approximated standard errors assuming the normal distribution on the basis of the central limit theorem for a finite population (Cochrane, 1977; Thompson, 1992; Smith, 1997; Fletcher *et al.*, 2005). The resultant confidence intervals are always symmetric and therefore likely to be uninformative when dealing with heavily skewed data. This is further exemplified by the possibility of obtaining negative CPUE values for a lower confidence limit as it is not possible to catch less than zero fish. In contrast, a parametric bootstrap approach can estimate confidence intervals that are asymmetric

relative to predicted CPUE, suggesting that the upper and lower bounds reflect the skewness inherent in the CPUE datasets more appropriately (Smith, 1997; Fletcher *et al.*, 2005; Fletcher, 2008).

Although this study has focused on the estimation of confidence intervals for delta-lognormal and delta-gamma models, the described parametric bootstrap procedure provides a generalised framework for any type of delta- and zero-inflated mixture models and can, in principle, be applied to several estimation frameworks including GLMs, Generalized Linear Mixed Models (GLMMs) or Generalized Additive Models (GAMs) (Hastie *et al.*, 2001). This generalisation is possible because the random response vectors are directly generated from the chosen distribution (here: as a function of $\hat{p}_i$, $\hat{\mu}_i$ and $\hat{\sigma}^2$ or θ, respectively) (Efron, 1985), to which any specified model can be refitted according to the required number of bootstrap iterations, while the original data structure is maintained. Statistical applications, which allow generating random response vectors from delta- and zero-inflated count models (e.g. delta-Poisson/negative binomial or zero-inflated Poisson/negative binomial), are available in the *pscl* package (Jackman, 2008) or *VGAM* package (Yee, 2010) in R version 2.9.2 (R Development Core Team, 2009), and an example of parametric bootstrapping applied to zero-inflated models was outlined by Jung *et al.*, (2003). In general, once set up, the parametric bootstrap algorithm was easily implemented for any of the six analysed datasets. It is therefore expected that parametric bootstraps have the potential to be more frequently applied to estimate informative confidence intervals around estimated abundance indices.

The predicted trends of gillnet CPUE from the most parsimonious delta-gamma models allowed for some broader characterisations of the abundance patterns of *L. capensis*, *L.*

aeneus and *C. carpio* in Lake Gariep. The high encounter probability (98%) by gillnets indicated that *L. capensis* was consistently abundant over all the different bottom-types sampled in this study, which were, however, confined to water depths of 3 m. Although there was some evidence that mixed-bottoms (~ 60% silt) represented a preferred habitat-type, the effect '%silt' and its second order polynomial '%silt^2' could only explain 4.8% and 2.2% of the total variation in the data, respectively, so that bottom-type is expected to be a relatively weak predictor of abundance for this species. Experimental deepwater gillnet surveys conducted in Lake Vanderkloof, a large turbid impoundment situated 65 km downstream from Lake Gariep, revealed that *L. capensis* was the only species that also occurred in high densities in water depths below 10 m, with catches of this species occasionally recorded in up 48 m water depth (Jackson *et al.*, 1983). Being described as a specialised substratum feeder that ingests large quantities of detritus from the bottom and scrapes algae from rocks (Eccles, 1986; Skelton, 1986), such broad utilisation of the benthic habitat niche is probably closely related to the species' ability to utilise low trophic food sources, which are potentially available across all benthic habitat types, irrespective of depth.

While riverine populations of *L. aeneus* are known to have an omnivorous diet that includes algae, vegetation, aquatic and terrestrial invertebrates, impoundment population were found to depend primarily on zooplankton (Bruton, 1985; Tómasson *et al.*, 1985; Eccles, 1986). Although *L. aeneus* had the highest nominal gillnet CPUE (6.71 kg.net^{-1}.night^{-1}) as well as the highest frequency of very large catches (> 25 kg.net^{-1}.night^{-1}), the probability of encountering this species in gillnet catches (86%) was low compared to *L. capensis* (98%). This combination can possibly be linked to patchiness in the horizontal distribution of lake zooplankton, which is commonly caused by wind-induced currents in larger water bodies (Thackeray *et al.*, 2004). The

most parsimonious delta-gamma model for *L. aeneus* predicted that the relationship between CPUE and '%oxygen' sharply increased at oxygen saturation levels in the surface water of more than 110%. This suggests that large aggregations of *L. aeneus* can be most likely expected in areas where the surface layer of the water column is supersaturated with oxygen, which is typically an indication of high phytoplankton production (Benejam *et al.*, 2008). Phytoplankton production is the primary energy source of most pelagic food webs, and, as a result, positive correlations between phytoplankton biomass and the abundance of zooplanktivoures cyprinids in reservoirs have been commonly reported (Tómasson *et al.*, 1985; Swierzowskia *et al.*, 2000; Prchalová *et al.*, 2008; Prchalová *et al.*, 2009).

Several studies on reservoirs found decreasing trophic gradients along the longitudinal axes from the tributary to the dam area, which were associated with decreases in plankton production and the biomass of cyprinids (Swierzowskia *et al.*, 2000; Olin *et al.*, 2002; Seda *et al.*, 2007; Prchalová *et al.*, 2008; Prchalová *et al.*, 2009). Furthermore, originally riverine fishes often seem to avoid the lentic conditions in the downstream environment of impoundments, and, therefore, tend to concentrate in the tributary areas (Dorgeloh, 1995; Lionberger & Hubert, 2007; Prchalová *et al.*, 2008; Prchalová *et al.*, 2009). The model predictions of the present study, however, revealed a reverse trend, with standardised gillnet and angler CPUE indicating overall higher abundances of *L. capensis* and *L. aeneus* at sampling sites close to the dam wall. In general, these results agree with the findings by Tómasson *et al.* (1985) who suggested that sharp increases inorganic suspensoid loads in Vanderkloof Dam caused *L. capensis* and *L. aeneus* to disperse from the tributary area and move to the more lacustrine environment close to the dam wall. High inorganic suspensoid loads have a suppressing effect on the phytoplankton production due decreased light penetration into the water

column (Bruton, 1985). As a result of the gradual settlement of silt and clay suspensoids with increasing distance to the river inflow, the lentic areas of highly turbid impoundments were considered to be more productive (Bruton, 1985; Tómasson *et al.*, 1985). In particular, the significant correlation between large catches of *L. aeneus* and increased dissolved oxygen saturation in the surface water close to the dam wall in summer 2008 (> 106%) compared to the middle dam (< 97%), suggested a similar dynamic in Lake Gariep. It is therefore likely that detailed turbidity measurements from each gillnet sampling site would have increased the predictive power of the delta-gamma models for *L. aeneus* and possibly *L. capensis* by explaining additional variation in the data.

In contrast to the two endemic cyprinids, gillnet CPUE of *C. carpio* showed no differences between sampling sites close to the dam wall and in the middle dam, indicating that the species' spatial distribution was more influenced by other factors. The binomial GLM could explain more variation in the data (28%) than the gamma GLM (24%), which was probably related to the large proportion of zero catches (60%) and hence the small number of positive observations (n = 32) that were available to draw inference based on the gamma GLM. Both the binomial and the gamma GLM suggested that bottom-type was the strongest predictor for the abundance of *C. carpio*. The strong exponential relationship between gillnet CPUE and increasing silt substrate is generally in agreement with the species' preference to benthic foraging on soft-bottom habitats (Lammens & Hoogenboezem, 1991; Zambrano & Hinojosa, 1999; Zambrano *et al.*, 2001; Barthelmes & Braemick, 2003; Khan, 2003), which also can be related to the ability of *C. carpio* to effectively separate food items such as benthic invertebrates and seeds from soiled mixtures (Sibbing & Uribe, 1984; Sibbing, 1988). The significantly lower gillnet CPUE in winter 2007 indicated that *C. carpio* was

perhaps less active, possibly due to the colder water temperatures (mean = 10.2 °C; range: 8.7 °C - 11.3 °C) (Cooke *et al.*, 2003). The significantly higher probability of capturing *C. carpio* at gillnetting sites located along fished areas seemed at first to be contradicted. However, the removal of *C. carpio* in the fished areas might possibly be counter-balanced by the effect of groundbaiting (Arlinghaus & Mehner, 2003; Lewin *et al.*, 2006), a commonly observed practice among both recreational and subsistence anglers that is inteded to attract *C. carpio* into the fished areas. Moderate groundbaiting can effectively increase the carrying capacity of *C. carpio* due to increased nutrient input (Arlinghaus & Mehner, 2003), which could increase *C. carpio* movement into the only two areas accessible for angling.

From an ecological perspective, fisheries-independent gillnet data were generally more informative than the angler data. The standardised angler CPUE for *L. capensis* and *L. aeneus* was low, but associated with relative wide confidence limits, which emphasised the uncertainty about the predicted trends for these two species. This indirectly supports the impression by Ellender *et al.*, (2010b), who considered the two endemic species as an occasional by-catch rather than being directly targeted in the mainly *C. carpio* directed fishery of Lake Gariep. The analysis of *C. carpio* angler CPUE identified some important factors that affected the catch of subsistence and recreational anglers. Most of the variance in the data was explained by the fisheries-dependent effects ‘time fished’ (binomial GLM only) and ‘number of rods and handlines used’. The binomial GLM illustrated that the probability of capturing at least one *C. carpio* increased quickly during the first hours of fishing, and started to approach an asymptote after approximately six hours of fishing. A delta-modelling approach provides the option to account for this non-linear effect by standardising the probability of capture to a fixed time fished. As it is often logistically impossible to interview all anglers by the end of

their fishing day (O'Neill & Faddy, 2003; Ellender *et al.*, 2010b), this seems to be particularly appealing for applications to angler roving creel survey data, as such standardisation procedure is likely to reduce bias caused by zero catches due to very short times fished by the time of the interview. The strong curvature in the response surface of the *C. carpio* angler CPUE predicted that CPUE attained a relative maximum for either six rods or six handlines, whereas rods were predicted to be generally the more efficient gear. The predicted negative effect for angling with more than six lines on the *C. carpio* CPUE could be explained by increased noise and disturbance at the shoreline due to higher frequencies of casting, re-baiting and reeling-in and hence an increased movement of the angler at the shore. In general, this result suggests that expressing effort as hours fished per angler is preferable over the unit lines fished per hour, when attempting to standardise angler CPUE, as the predicted convex relationship between lines and CPUE provided strong evidence that CPUE and the quantity of gear used per angler are likely to be linearly disproportional.

The differences in species composition between fisheries-independent gillnet data and fisheries-dependent angler data generally highlighted the importance of considering more than one data source (or sampling gear) before drawing inference about relative abundances. The angler dataset alone, for example, would have indicated that non-native *C. carpio* was the most dominant species in the system, as it contributed close to 80% of the weight in the angler catches, whereas the CPUE from the gillnet catches suggested that *C. carpio* only forms a minor component of the ichthyomass (< 5%). Unfortunately, there is limited information to determine the relative efficiency of sampling gears for *C. carpio*, as well as, for the two endemic species, *L. capensis* and *L. aeneus*. A reliable estimation of the likely species composition was not possible. There is, however, some evidence in the literature that *C. carpio* has the ability to avoid

gillnets better than many other fishes (Hunter & Wisby, 1964; Barthelmes & Doering, 1996). By contrast, studies on the gillnet selectivity of *L. capensis*, its congener *Labeo umbratus*, and *L. aeneus* suggested that these species are effectively selected by gillnets (Booth & Potts, 2006; Ellender, 2008; Chapter 5). Thus, *C. carpio* is probably more abundant than implied by its low CPUE in the gillnet catches.

CHAPTER 7

Differential colonisation patterns in non-native common carp *Cyprinus carpio* and two native cyprinids in Lake Gariep

7.1 INTRODUCTION

Theoretical and quantitative studies have shown that factors determining the invasion success of non-native fishes are associated with life history traits, environmental tolerance levels, ecological opportunities, species diversity and the level of human induced disturbance on the ecosystem (Baltz & Moyle, 1993; Moyle & Light, 1996; Kolar & Lodge, 2002; Bøhn *et al.*, 2004; Koehn, 2004; Marchetti *et al.*, 2004; Olden *et al.*, 2006; Johnson *et al.*, 2008). These factors are not mutually exclusive, and therefore the mechanisms leading to invasion processes are expected to be complex and multivariate in nature (Moyle & Light, 1996; Kolar & Lodge, 2002; Marchetti *et al.*, 2004; Olden *et al.*, 2006). A notable example of this complexity is the interaction between the construction of reservoirs and aquatic invasions (Kolar & Lodge, 2002; Havel *et al.*, 2005; Johnson *et al.*, 2008). By flooding large areas of terrestrial habitat, impoundments rapidly convert an extensive and often heterogeneous stream habitat into a large standing water body. As a result, it might be expected that the newly created impoundment facilitates invasions by providing an increased number of niche opportunities, which are initially unoccupied (Johnson *et al.*, 2008). Additionally, the construction of reservoirs can often lead to considerable changes in flow, flooding and temperature regimes, which in turn may favour species with wider environmental tolerances (Kolar & Lodge, 2002; Havel *et al.*, 2005; Okada *et al.*, 2005). It has also been found that the alteration of environmental conditions, both biotic and abiotic, often result in the displacement of native riverine strategists with widespread invasive

generalists that commonly exhibit more favourable life history characteristics to successfully colonise severely altered freshwater systems (Pringle *et al.*, 2000; Rahel, 2002; Olden *et al.*, 2006). As with the initial invasion, the colonisation of impoundments often exhibits multiple successions (Kolar & Lodge, 2002; Bøhn *et al.*, 2004; Havel *et al.*, 2005; Gjelland *et al.*, 2007) such that the factors facilitating initial colonisation of young reservoirs may not necessarily reflect the long-term patterns of population dynamics of non-native and native species after the system has "matured".

Fish surveys conducted before the construction of Lake Gariep, suggested that the riverine fish fauna was mainly dominated by the two large endemic riverine cyprinids, Orange River mudfish *Labeo capensis* and smallmouth yellowfish *Labeobarbus aeneus*, while non-native common carp *Cyprinus carpio* was relatively scarce in catches (Jubb & Farquharson, 1965; Jubb, 1972; Skelton, 1986). However monitoring of the post-impoundment fish populations reported a rapid increase in the biomass of *C. carpio* shortly after the closure of Lake Gariep (Hamman, 1980).

The aim of this Chapter was to investigate the ecological role of *C. carpio* and its potential impact on the population dynamics of two native cyprinids. To achieve this aim, underlying processes of the long-term population demographics of *L. capensis*, *L. aeneus* and *C. carpio* were examined using stable isotope analysis and historical and present gillnet catch data in conjunction with stochastic age-structured population model simulations.

7.2 MATERIALS AND METHODS

STABLE ISOTOPE STUDY

Stable nitrogen and carbon isotope analysis was used to investigate the current food web dynamics in Lake Gariep, almost four decades post-impoundment. Fish were sampled between April 2007 and March 2008 by means of gillnetting, seine netting and angling. The ichthyofauna of Lake Gariep is depauperate, comprising eight indigenous and four non-native species (Table 1.1, Chapter 1). Of the four non-native species, brown trout *Salmo trutta*, rainbow trout *Oncorhyncus mykiss* and largemouth bass *Micropterus salmoides* are extremely rare in this region (Skelton, 1986). As *S. trutta* was entirely absent from the samples and only one individual of each of the latter two species were caught during the entire study period (October 2006 – May 2008), samples of these species were not available for the stable isotope analysis. Only a single endemic rock-catfish *Austroglanis sclateri* was caught in the gillnets and no sample was taken. No banded tilapia *Tilapia spermanii* were captured in Lake Gariep. Of the remaining seven fish species, a total of 72 individuals were collected (Fig. 7.1). After each specimen was measured, a small tissue sample was removed from the dorsal musculature, stored in a clean Eppendorf tube and immediately placed on ice until further processing on the same day.

Zooplankton samples were collected by towing a modified WP2 plankton net (570 mm mouth diameter and 0.2 nm mesh aperture size) diagonally from depths between 8 m and 20 m to the surface. All zooplankton tows were conducted just after sunset during March 2008 at different offshore sites. Zooplankton samples were identified based on species keys available in Hart *et al.*, (1983) and Allanson *et al.*, (1990). Samples were individually sorted and > 150 individuals per species per sample were placed in clean Eppendorf tubes. The zooplankton of Lake Gariep consisted of copepods and

cladocerans. The two dominant copepods, *Lovenula excellence* and *Metadiaptomus merindianus*, were separated by species (Fig. 7.1). Small cyclopoid copepods were occasionally observed, but not in sufficient enough numbers to be included in the analysis. The three observed cladoceran species *Daphnia gibba*, *D. barbata* and *D. longispina* were combined and grouped under *Daphnia* spp. (Fig. 7.1). The large copepod *L. excellence* is the only species known to be predatory, while the remainder of the zooplankton are grazers (Hart, 1986).

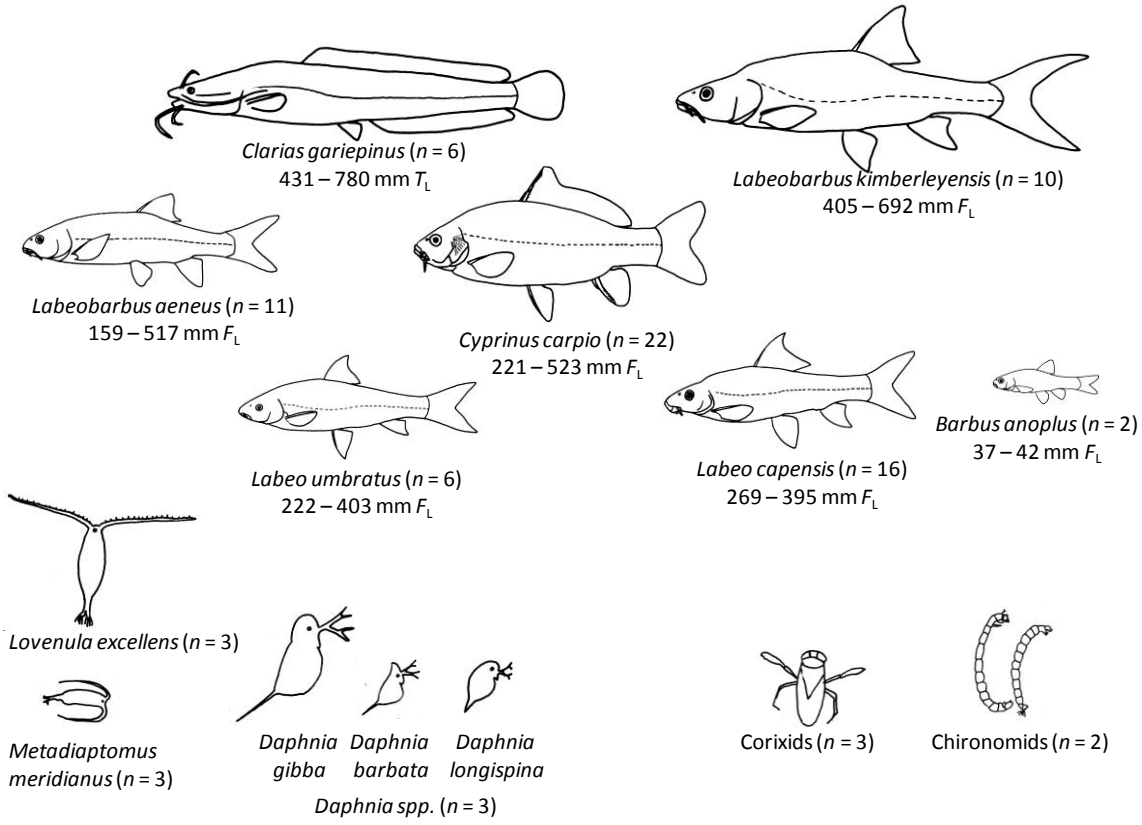

Fig. 7.1. Fishes and invertebrates collected for stable isotope analysis from Lake Gariep. Size ranges for fish samples is shown below the species names. *n*: number of samples analysed; F_L: fork length; T_L: total length.

In the absence of specialised zoobenthos sampling gear (e.g. an Eckman grab), sampling effort for zoobenthic invertebrates was confined to the shallow littoral margins. The sampling of zoobenthos was conducted in March 2008 when water levels were high (91% lake level) and large shallow areas had been recently inundated. During this period the zoobenthos of the shallow littoral zone seemed to be

quantitatively dominated by chironomid larvae and corixids, which is generally in accordance with observations from other turbid South African reservoirs (Allanson & Jackson, 1983; Hart, 1999). Chironomid larvae were individually picked from collected debris and detritus with > 100 specimens collected per sample (Fig. 7.1). The more mobile corixids were caught using hand-held insect nets and 10-20 specimens were collected per sample (Fig. 7.1). All zoobenthos samples were placed in clean Eppendorf tubes, which were kept on ice until further processing on the same day.

In order to obtain samples of particulate organic matter (POM) from the water column, 5 l surface water samples where taken from offshore areas (n = 3). Filamentous cyanobacteria colonies were skimmed from the surface using a small net (500 μm mesh size), rinsed off the net with Milli-Q water and stored in clean zip-lock bags (n = 4). The processing of the 'mixed' POM, and concentrated cyanobacteria samples involved filtering onto pre-combusted GFF filters, followed by manual removal of all visible zooplankton and other contaminants under a dissection microscope.

Processing

All samples were dried for at least 24 hours at 50 °C on the same day they were sampled. Dried samples were ground to fine powder, weighed and placed in tin capsules. Stable isotope signatures for $\delta^{13}C$ and $\delta^{15}N$ were determined using a continuous flow Isotope Ratio Mass Spectrometer. ANU sucrose and air were used as internal standards and calibrated against International Atomic Energy reference materials. Results are expressed in standard delta notation, $\delta X = [(R_{sample} / R_{standard}) - 1] \times 1000$, where X is the element of interest and R denotes the ratios $^{13}C/^{12}C$ and $^{15}N/^{14}N$, respectively.

Stable isotope analysis

Relatively high carbon to nitrogen ratios (C:N) in tissue samples of *Labeobarbus kimberleyensis* (mean = 4.11 ± 1.71) indicated increased levels of ^{13}C-depleted lipids when compared to the average C:N of 3.17 ± 0.23 for the six other fish species (Kiljunen *et al.*, 2006). The δ^{13}C data for *L. kimberleyensis* were subsequently lipid-normalised using the empirical model suggested by Kiljunen *et al.* (2006). To investigate the food web structure, niche space diagrams were constructed based on biplots of the mean δ^{15}N and δ^{13}C (± SD) per species or group. Defining the niche space of species by a convex hull area that encompasses the δ^{13}C - δ^{15}N biplots has been advocated as a useful tool to represent the trophic diversity of a system (Layman *et al.*, 2007), and it was suggested that the convex hull area encompassed by species-specific individual δ^{13}C - δ^{15}N biplots can be used as a measure of the corresponding niche space occupied (Zambrano *et al.*, 2010). In accordance with Zambrano *et al.* (2010), this approach was adapted to specifically evaluate the trophic niche partitioning among the three species *L. capensis*, *L. aeneus* and *C. carpio*. Integration of both the total convex hull area for each species and any overlapping portions with the other two species was conducted in *R version 2.9.2* using the *spatstat* package (Baddeley & Turner, 2005). A two-dimensional Kolmogorov-Smirnov (2DKS) test (Peacock, 1983; Fasano & Franceschini, 1987; Press *et al.*, 1992; Garvey *et al.*, 1998) was conducted to test the null-hypothesis that the niche spaces occupied by the three species were not significantly different when pair-wise compared against each other. The 2DKS test compares two observed bivariate distributions non-parametrically. Fasano and Franceschini's (1987) generalised version of the 2DKS was implemented in *R*, using the algorithms from Press *et al.*, (1992).

POST-IMPOUNDMENT CATCH RATE TRENDS

It was assumed that gillnet catch-per-unit-effort (CPUE) expressed in units of mass of fish per standardised net night could be used as an index for changes in the relative biomass of a fish species over time (Chapter 6).

Current experimental gillnet data (2007-2008)

Current catch data for *L. capensis*, *L. aeneus* and *C. carpio* were collected during gillnet surveys conducted in winter 2007 and summer 2007/08 (Chapter 2). The multifilament gillnets employed were 45 m long and consisted of five 9-m panels with varying mesh sizes that were approximately 3 m deep (Table 7.1). During each survey, a total of 40 nets were set parallel to the shore along the 2.5 – 3 m depth contour (mean = 2.8 m). All nets were set overnight with soak times ranging from 8 to 12 hours.

Table 7.1. Mean stretched mesh sizes of the different series of multifilament gillnets used during the period 1971-1979 (Hamman 1980; 1981) and during the present study. *n*: number of net nights sampled during summer surveys for the period 1971-1976 and winter and summer surveys in 2007-2008.

Sampling period	Mesh sizes (mm)								*n*	Fleet (m)
2007/08	-	47	65	77	-	105	-	152	40	45
1976/77	40	50	64	-	85	110	-	146	15	200
1977/78, 1979/80	35	45	57	73	93	-	118	150	20-26	200
1971-1976	-	44	64	76	89	102	114	146	34-48	350

Historical experimental gillnet data (1971-1979)

The historical experimental gillnet data for *L. capensis*, *L. aeneus* and *C. carpio* used in this Chapter were sourced from results presented in Hamman (1981) for the period 1971-1980. Sampling during that period was conducted using three different series of multifilament gillnets (Table 7.1) that were set overnight (Hamman, 1981). Initial gillnet surveys between 1971 and 1976 were conducted quarterly (spring, summer, autumn and winter), but in the years 1977/78 and 1979/80, sampling was only

conducted during summer. The catch data were available in the form of seasonal mean CPUE in units of kg.species^{-1}.net night^{-1} that had been adjusted to a standard of a 350 m long and 2.8 m deep gillnet (Hamman, 1980; 1981).

Data selection and evaluation

For the analysis, only the historical CPUE averages from summer samples were considered as reference points for changes in relative biomass, because these were the only records that were consistently available for all years. However, as the present dataset only comprises a single summer survey (2007/08) to estimate current levels of relative biomass, the results from the winter 2007 survey were also included as an additional reference value.

Non-parametric confidence intervals for these two CPUE means were estimated using the non-parametric bootstrap procedure described by Efron & Tibshirani (1986). For this purpose, the summer and winter CPUE data were resampled with replacement 1000 times and the mean CPUE was calculated for each of the randomly generated data sets (B_U: U = 1, 2,…,1000). The percentile method (Buckland, 1984) was then applied to estimate confidence intervals from the resulting bootstrap vectors, where the 2.5% and the 97.5% percentiles were chosen to obtain lower and upper 95% confidence intervals, respectively.

The principle gillnet areas surveyed during the periods 1971-77 and 1977-1979 (Hamman, 1980; 1981) are illustrated together with individual gillnet sites sampled in winter 2007 and summer 2007/08 in Fig. 7.2. Generally, historical gillnet surveys covered a larger area, whereas the sampling during the present study was logistically confined to a 10 km radius from the launching sites located in the vicinity of the

settlements of Oviston and Gariep Dam (Fig. 7.2). However, as historical and present gillnet surveys were both based on stratified sampling and comprised a relatively large number of net nights (Table 7.1), with most of the sampling sites located in similar proximities to the shore (Fig. 7.2), it was assumed that the randomness induced by the historical and present sampling designs was sufficient to proceed with the standardisation and analysis of the long-term CPUE trends.

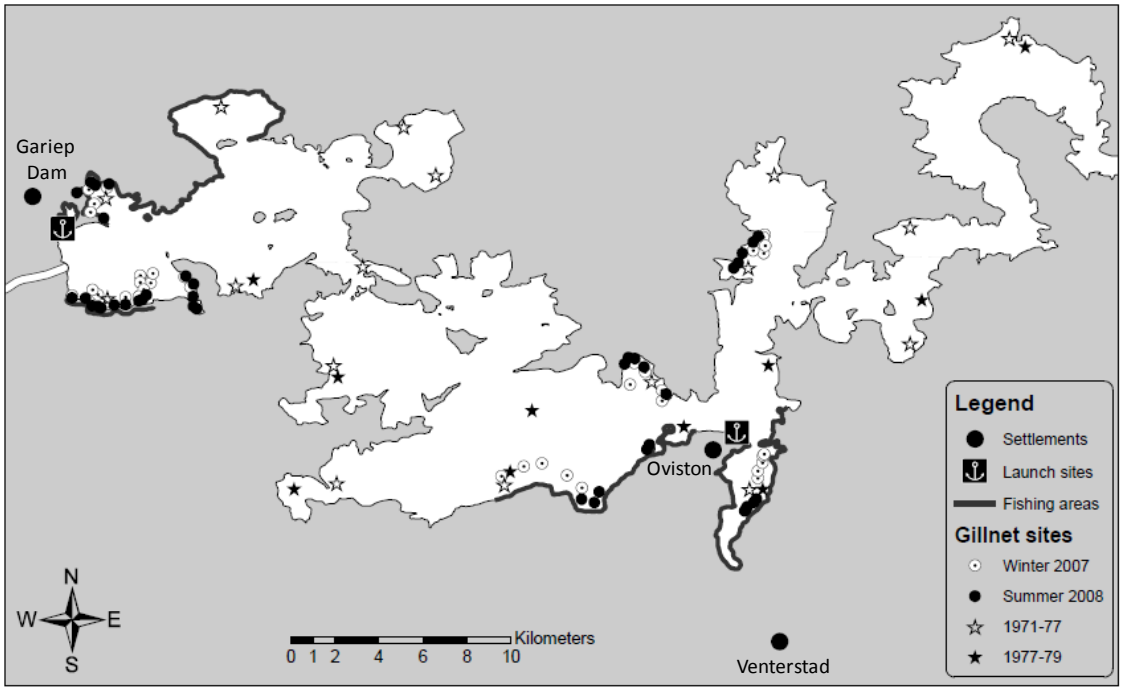

Fig. 7.2. Map of Lake Gariep showing the gillnetting areas sampled in the periods 1971-77 and 1977-1979 and individual sampling sites survey in Winter 2007 and in summer 2007/08

Standardisation of current and historical gillnet catches

To compare historical and current CPUE data, mean nominal CPUE was standardised to units of kg.100 m net^{-1}.night^{-1} and then adjusted to account for potential biases induced by the selective properties of the four types of multifilament gillnets used during the different survey periods (Table 7.1). The steps applied to adjust for the effect of gillnet selectivity are illustrated in Fig. 7.3, using data for *L. capensis* as an example.

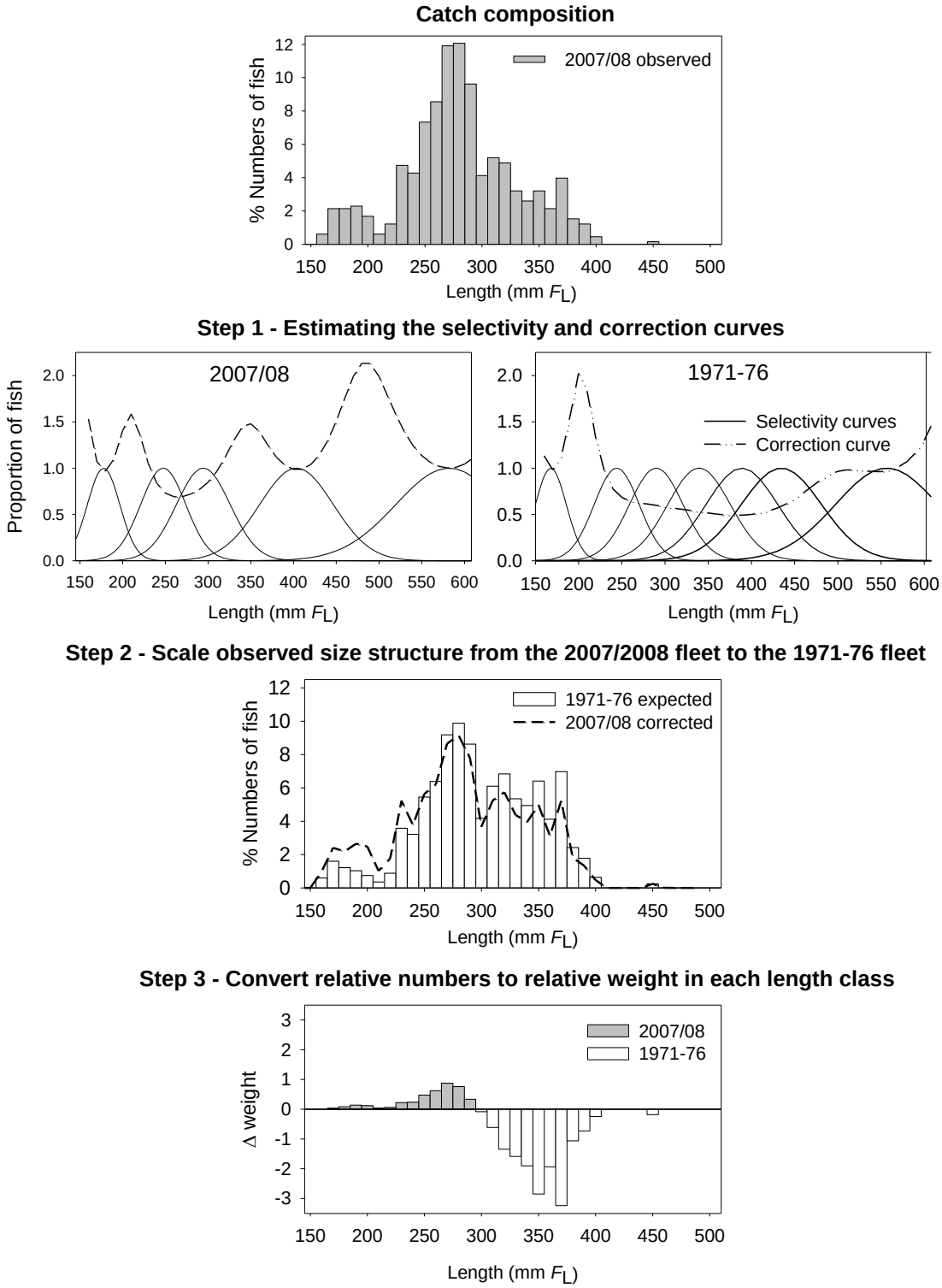

Fig. 7.3. A schematic that illustrates the three steps taken to adjust for the selectivity of the different gillnet types, using the example of scaling the current CPUE (2007/2008) of *Labeo capensis* to the CPUE expected if the gillnet fleet from 1971-1976 would have been used to sample the current population. In this example, the calculated ratio of relative weights (step 3) suggested a 25% higher CPUE, if the fleet from 1971-1976 would have been used instead of the current fleet.

These steps involved: (1) calculating gillnet correction curves for the current gillnet fleet (2007-08) and the selectivity curves for the three types of gillnet fleets employed during 1971-1979, (2) scaling the observed length frequency distribution from the current catches to the length frequency distribution expected if any of the three historical gillnet types would have been used instead, by sequentially multiplying the correction curves of the current fleet and the selectivity curves from the historical gillnet fleets with the observed length frequencies from the current catches, and (3) converting length frequencies into relative weight in each length class to determine the ratio of the relative weight expected if the current population would have been sampled with any of the historical gillnet fleets to the relative weight calculated for the current gillnet catches (Fig. 7.3).

In the first step, gillnet selectivity was estimated for the current fleet using the SELECT method advocated by Millar and Holst (1997). This method is based on a generalised linear modelling approach and has been suggested to be an accurate approach for estimating selectivity parameters for multi-meshed gillnets (Millar & Holst, 1997; Millar & Fryer, 1999; Booth & Potts, 2006; Carol & García-Berthou, 2007, Chapter 5). The required length-frequency data were obtained from the gillnet catches of the present study, which also included samples from eight additional smaller bi-monthly surveys (5 - 10 net nights) that were all carried out between May 2007 and March 2008. All fish caught by the same gillnet fleet, were separated by species, measured to the nearest mm F_L and the mesh size was recorded. The SELECT model parameters and corresponding selectivity curves for *L. capensis* and *L. aeneus* are presented in Chapter 5 and in Ellender (2008) for the two respective species.

If it is assumed that the probability of a fish in length class L being retained in any mesh size m_i follows a normal distribution of the form

$$S_i(L) = \exp\left(-\frac{(L-\mu_i)^2}{\sigma_i^2}\right),$$

then the mean and the standard deviation for mesh size m_i can be calculated as $\mu_i = m_i k_1$ and $\sigma_i = m_i \sqrt{k_2}$, respectively, where k_1 and k_2 are scaling parameters estimated by the SELECT model (Fig. 7.3). As each gillnet type consisted of an equal proportion of mesh size coverage (Hamman, 1980), the same fishing effort was assumed for each mesh size. Based on this assumption, the relative selectivity $S_j(L)$ for a fish of length L being caught by a multi-mesh gillnet j that consists of I panels of varying mesh sizes i was calculated as (Millar & Fryer, 1999)

$$S_j(L) = \frac{1}{I}\sum_{i=1}^{I} S_{i,j}\,.$$

The index j = 1 will be used to refer to the selectivity of the gillnet fleet employed during the present study and j = 2 - 4 refers to the three gillnet types used by Hamman (1980; 1981), with $S_{2-4}(L)$ representing the corresponding gillnet selectivity required for step 2 (Fig. 7.3). The pseudo-coefficient of determination (R^2) was calculated to evaluate the goodness-of-the-fit for each of the fitted SELECT models and was determined by

$$R^2 = 1 - \frac{\text{Residual deviance}}{\text{Null deviance}}.$$

The second step in the standardisation procedure was to estimate the expected frequency of fish in length class *L* that would have been caught if the gillnets that had been used in the present study (*j* = 1) were non-selective and then calculate the frequency of the fish in *L* that would have been expected for each type of the historical gillnets (*j* = 2 - 4) (Fig. 7.3). The corresponding equation used to calculate this expected frequency is given by

$$\hat{f}_L = f_L \frac{S_{2-4}(L)}{S_1(L)},$$

where f_L is the observed length frequency in the present gillnet catches and $\hat{f}_L$ is the frequency to be calculated for any of the historical gillnet fleets. The ratios of the relative weight expected if the current population would have been sampled with each of the historical gillnet fleets to the relative weight in the current gillnet catches (Fig. 7.3) were calculated as:

$$q_{2-4} = \frac{\sum_{\mathrm{L}} \hat{f}_L a L^b}{\sum_{\mathrm{L}} f_L a L^b},$$

where *a* and *b* are the coefficients of the length-weight relationship for each species (Table 7.3). As the current population structure was directly estimated (Fig. 7.3), it was assumed that an adjustment of the current CPUE to the selectivity of historical gillnet fleets would result in the least bias. However, as only the CPUE of one type of gillnet could be used as baseline, all CPUE values were standardised to the selective properties of the gillnet fleet used for the period 1971-1976 because this was the longest

consistent time series available. The calculation of the corresponding correction factors for each gillnet type *j* are summarised in Table 7.2. Note that the possibility of a slight bias was admitted for the corrected CPUE from summer surveys in 1976/77, 1977/78 and 1979/80, due to uncertainties about the population size structures at that time.

Table 7.2. Calculations of correction factors used to adjust CPUE for the selective properties of the gillnet-types (*j* = 1-4) employed during post impoundment surveys (1971-1979; 2007-2008). The CPUE from gillnets used during surveys 1971-1976 (*j* =2) were used as the baseline data.

Survey period	2007/08	1971-76	1976/77	1977/78, 1979/80
Gillnet-type	*j* = 1	*j* =2	*j* =3	*j* =4
Correction Factor	$c_1 = q_2$	$c_2 = 1$	$c_3 = \frac{q_2}{q_3}$	$c_4 = \frac{q_2}{q_4}$

TRENDS IN POPULATION SIZE STRUCTURES

Length-frequency samples from summer catches of the season 2007/2008 were corrected for the effect of gillnet selectivity, such that $\tilde{f}_L = f_L / S_1(L)$, where $\tilde{f}_L$ is the expected frequency of a fish in size class *L*, if gillnets were non-selective, and f_L is frequency observed in the gillnet catches. Due to a paucity of length data for *C. carpio*, the length frequency samples collected by the same gillnets during the period May 2007 - March 2008 were pooled to obtain a better representation of the population size structure. Historical relative length frequency data from summer gillnet catches, starting in summer 1972/73, were reconstructed from scanned figures presented in Hamann (1980; 1981), using the software *GIMP 2.6*. According to Hamman (1980), these relative length frequencies had been corrected for gillnet selectivity using the Beverton-Holt model, as described by Regier & Robson (1966), and were therefore assumed to be representative for the population size-structure at that time.

MODELLING POPULATION DEMOGRAPHICS

An age-structured production modelling approach (e.g. Clark, 1991; Quinn & Deriso, 1999; Booth, 2004; Brown & Walker, 2004; Quinn & Collie, 2005; Hilborn, 2010) was adapted to evaluate the consequences of different life history traits on the predictions of colonisation time trajectories for *L. capensis*, *L. aeneus* and *C. carpio*. These trajectories were modelled as changes in relative biomass and then assessed against the observed long-term trends of standardised CPUE.

General modelling framework

In an age-structured production model (ASPM), the number males and females of each age in year *y* is typically governed by

$$N^s_{t,y+1} = \begin{cases} \phi^s R_{y+1} & \text{if } t = 1 \\ N^s_{t-1,y} \exp(-Z^s_{t-1,y}) & \text{if } 1 < t < t_{\max} \\ N^s_{t-1,y} \exp(-Z^s_{t-1,y}) + N^s_{t,y-1} \exp(-Z^s_{t,y}) & \text{if } t = t^s_{\max} \end{cases},$$

where $N^s_{t,y}$ is the number of individuals of sex *s* and age *t*, in year *y*, R_y is the number of 1-year old recruits at the start of year *y*, ϕ^s is the sex ratio, $t^s_{\max}$ is the maximum observed age of sex *s*, and $Z^s_{t,y}$ is the sex-specific instantaneous rate of total mortality of a fish at age *t* in year *y*, with

$$Z^s_{t,y} = M^s + S^s_{t,y} F ,$$

where *M* denotes the instantaneous rate of natural mortality for males and females, $S_{t,y}^{s}$ is the fisheries selectivity at age *t* for sex *s* and *F* is the fishing mortality rate. The 1-year old sex ratio, ϕ^{s}, was assumed to be 1:1.

In order to predict the biomass trajectories for the period 1970-2010, the biomass in year *y* was calculated as:

$$B_y = \sum_s N_{t,y}^{s} w_t^{s}$$

where w_t^{s} is the weight of an individual of sex *s* at age *t* calculated as function of length-at-age *t* of a fish of sex *s*, $L_t{}^{s}$, such that $w_t^{s} = aL_t{}^{sb}$, where a and b are the sex-specific length-weight relationship coefficients. Length-at-age was described by using the von Bertalanffy equation for *L. capensis* and *L. aeneus* (Chapter 5; Ellender, 2008)

$$L_t = L_\infty (1 - e^{-K(t-t_0)}),$$

and Schnute model for *C. carpio* (Chapter 4)

$$L_t = \left[L_1{}^{b'} + (L_2{}^{b'} - L_1{}^{b'}) \frac{1 - e^{-a'(t-t_1)}}{1 - e^{-a'(t_2-t_1)}} \right]^{\frac{1}{b'}},$$

where L_∞ is the predicted asymptotic length, *K* is the Brody growth coefficient and t_0 is the theoretical age of a zero-length fish; t_1 is the smallest age in the sample; t_2 is the oldest fish in the sample; L_1 the estimated mean length at t_1 old fish; L_2 the estimated

mean length at t_2 and *a'* and *b'* are the Schnute model growth parameters (Ricker, 1975; Schnute, 1981).

Egg production of the fish population in year *y* was calculated as

$$E_y = N^s_{t,y} \psi_t f_t ,$$

where ψ_t is the fraction of the population which are mature females at age *t*, and f_t is the number of eggs of a female at age *t*. For *L. capensis* and *L. aeneus*, ψ_t was determined by

$$\psi_t = \frac{1}{1+\exp(-(t-tm_{50})/\delta)} ,$$

where tm_{50} is the age-at-50% maturity and δ is the steepness parameter of the logistic ogive. For *C. carpio*, observed proportions of mature females at age *t* were directly obtained from results presented in Chapter 4. The numbers of eggs produced by a female of age *t* was determined by $f_t = \omega L_t^{\kappa}$, where the coefficients ω and κ describe the power relationship between the length of a female and the average number of eggs she can produce.

If a Ricker spawner-recruitment (S-R) model is assumed to account for early life history density-dependence, the number of recruits R_y for year *y* is calculated as

$$R_t = \alpha E_{y-1} \exp(-\beta E_{y-1}) \exp\left(\varepsilon - \frac{\sigma^2}{2}\right),$$

where the relationship between the number of recruits at age-1 and the population's egg production in the previous year is described by the parameters α and β of the Ricker S-R curve. The last component of the equation represents a stochastic extension to simulate the effect of log-normal recruitment variability on the biomass time trajectories of the populations, where ε denotes the normally distributed random variable with mean zero and the standard deviation σ.

The base case scenario

Due to the 27 year gap between the early impoundment CPUE data (1971-80) and the present study (2007-2008), the relative biomass index was considered to be insufficiently long to be directly incorporated in the ASPM. Instead, the model assumption was made that the current fish population would have stabilised at a steady-state, close to 40 years after impoundment. The current population dynamics were modelled in terms of two deterministic dynamic pool models, biomass per recruit and egg production per recruit (Fig. 7.4), which were calculated as

$$BR = \sum_{t=1}^{t_{max}} N_t^s w_t^s \qquad \text{and} \qquad ER = \sum_{t=1}^{t_{max}} N_t^s \psi_t f_t \ .$$

The number of fish at age 1, N_0, was set at unity with males and females assumed in equal numbers ($N_t^s = 0.5$) as $\phi^s = 0.5$. For older fish, the numbers per recruit for sex *s* are then governed by the exponential decay model $N_t^s = N_{t-1}^s \exp(-(M^s + FS_{t-1}^s))$. The

predicted biomass trajectories were expressed as the percentage of *BR* based on the current *F*.

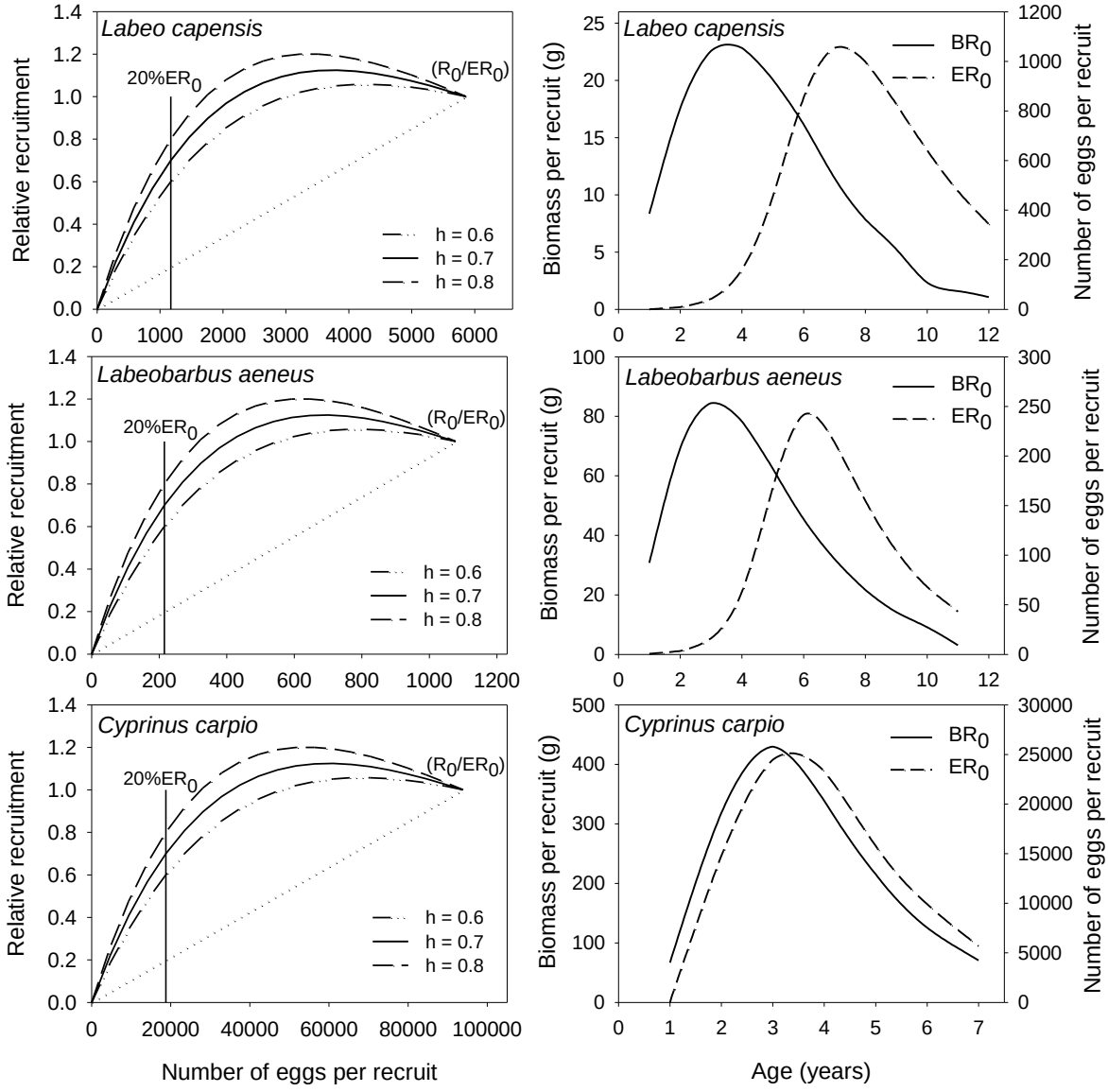

Fig. 7.4. The left panels illustrate the relationship between relative recruitment and the egg production per recruit (*ER*) to the replacement line (dotted line) that joins the points (0, 0) and (R_0, ER_0) for *Labeo capensis*, *Labeobarbus aeneus* and *Cyprinus carpio*. The 'steepness' parameter *h* is defined as the relative recruitment that is expected when *ER* is reduced to 20% of ER_0. The right panels illustrate biomass-per-recruit with $F = 0$ (BR_0) and ER_0 as a function of age for all species.

In the absence of fishing mortality, it was assumed that the resulting deterministic quantity ER_0 represents the average egg production per recruit at the population's carrying capacity (Myers *et al.*, 1999; Myers *et al.*, 2001). Booth (2004) and Booth and

Weyl (2004) demonstrated that, in the absence of S-R data, the Ricker S-R curve parameters α and β can be determined from a per-recruit perspective. In accordance to their approach, α and β were estimated in terms of two parameters, the egg production per recruit at equilibrium, ER_0 , and the 'steepness' parameter *h*, such that

$$\alpha = \exp\left(\ln\left(\frac{R_0 h ER_0^{\,0.2}}{R_0^{\,0,2}\, 0.2 ER_0} \right) /(1-0.2) \right) \qquad \text{and} \qquad \beta = \frac{\ln(h/0.2)}{ER_0(1-0.2)},$$

where R_0 was set to unity (R_0 = 1) to describe the recruitment that is expected when egg production equals ER_0 (Fig. 7.4).

In general, the 'steepness' of the S-R curve determines the average intensity of compensation in the recruitment process and therefore describes the sensitivity of recruitment to changes in the yearly egg production or spawning stock biomass (e.g. Hilborn & Walters, 1992; Hilborn, 2010). The steepness parameter *h* is therefore defined from a per-recruit perspective, as the fraction of pristine recruitment when egg production is reduced to 20% of pristine levels (Booth, 2004; Booth & Weyl, 2004). For example, if *h* = 0.7, one would expect 70% of the recruitment when the egg production of a population is reduced to 20%, relative to the expected average recruitment from a population's egg production at carrying capacity.

In order to initiate the model, population biomasses in 1970 were set to 3% of the current biomass per recruit at assumed equilibrium BR_0 , or

$$BR_{1970} = \sum_{t=1}^{t\max} 0.03 N_t^s w_t^s ,$$

where $N_t^s = N_{t-1}^s \exp(-M^s)$. The calculation of the value of 3% was based on an initial, and crude, assumption that if the populations are able to fully utilise the newly created impoundment, the ratio of the roughly estimated surface area encompassing the original stretch of the Orange River (before 1970) to the surface area of Lake Gariep should be approximately proportional to the change in the carrying capacity, such that

$$\frac{\text{Orange River before 1970 (km}^2\text{)}}{\text{Lake Gariep (km}^2\text{)}} \approx \frac{\text{55 km long x 0.25 km wide}}{\text{364 km}^2} \approx 0.03 .$$

Note that other factors such as interspecific competition or possible changes in life history traits were not considered for the *base case* scenario of the model.

Model parameters

The life history parameters used as input parameters for the model are summarised in Table 7.3. Unless stated otherwise, the parameters for *L. aeneus* were obtained from Ellender (2008), while the parameters for *C. carpio* and *L. capensis* were presented in Chapter 4 and Chapter 5, respectively. Power relationships of the length of a mature female and the average number of eggs produced were available in Hamman (1981). All age-dependent parameters (L_t, w_t, F, M, $\psi_{t,}$ and f_t) used are based on astericus otolith-aged fish (Chapter 4; Chapter 5; Ellender, 2008). Astericus otoliths were validated as the most suitable ageing structure for all three species (Winker *et al.*, 2010; Chapter 3). It is admitted that the *base-case* model scenarios rely on the initial and crude assumption that life history parameters such growth rate, survival or fecundity

are temporarily invariant, which explicitly ignores the possible influence of temporal changes in hydrology, turbidity or food resources on these key population variables. This assumption will therefore be re-examined later in this chapter.

Table 7.3. Input parameter values for the age-structured production models. Parameter estimates are from Chapter 5 for *Labeo capensis*, Ellender (2008) for *Labeobarbus aeneus* and Chapter 4 for *Cyprinus carpio*. The fecundity parameters ω and κ for the three species were obtained from Hamman (1981). W-L, weight-length relationship

Species		*Labeo capensis*		*Labeobarbus aeneus*		*Cyprinus carpio*	
Description	Parameter	Females	Males	Females	Males	Female	Male
Age/Growth	L_∞ (mm)	433.8	387.7	491.7	398.3	-	-
	K (yr^{-1})	0.20	0.25	0.23	0.33	-	-
	t_0 (yr)	-0.64	-0.54	-0.29	-0.34	-	-
	L_1 (mm)	-	-	-	-	39.3	39.9
	L_2 (mm)	-	-	-	-	555.8	473.3
	a' (yr^{-1})	-	-	-	-	0.83	1.12
	b '	-	-	-	-	-0.03	-0.32
	t_1 (yr)	-	-	-	-	0.17	0.17
	t_2 (yr)	-	-	-	-	6.17	6.17
	t_{max} (yr)	12	9	11	10	7	7
W-L	a	$2.4x10^{-6}$	$2.4x10^{-6}$	$7.3x10^{-6}$	$9.1x10^{-6}$	$5.3x10^{-5}$	$5.3x10^{-5}$
	b	3.132	3.132	3.119	3.081	2.829	2.829
Maturity	Lm_{50} (mm)	322.9	298.0	354.0	231.4	344.8	295.9
	δ_L (yr^{-1})	18.7	12.4	20.0	40.8	45.6	37.7
	tm_{50} (yr)	6.21	5.32	5.24	2.30	2.15	1.95
	δ (yr^{-1})	0.93	0.68	0.64	0.76	-	-
Fecundity	f	122.33	-	318.35	-	14300.85	-
	k	0.017	-	0.009	-	0.006	-
Mortality	M (yr^{-1})	0.46	0.65	0.54	0.47	0.60	0.60
	F (yr^{-1})	0.00	0.00	0.00	0.00	0.12	0.12

As the estimated annual harvest rates of *L. capensis* and *L. aeneus* were low with less than 0.2 $kg.species^{-1}.ha^{-1}$ (Ellender *et al.*, 2010b), the effect of the fishing mortality *F* on these two populations was assumed to be zero (see Chapter 5). The instantaneous

rates of natural mortality M^s were therefore set equal to Z^s, which was based on direct estimates from catch curve analyses (Ellender, 2008; Chapter 5). *Cyprinus carpio* was considered as lightly-exploited with M and F estimated at 0.60 yr^{-1} and 0.12 yr^{-1}, respectively, for both sexes (Chapter 4). The fishing selectivity of shore anglers was assumed to be knife-edge at age-2, which corresponded to the age that was fully-recruited in the catches from angling competitions held at Lake Gariep (Chapter 4). As fishing effort had not been considered as a factor that may have potentially influenced the early post-impoundment trends in population demographics of *C. carpio* (Hamman, 1980), the estimated F was only included in the ASPM from 1981 onwards.

In contrast to the population-specific S-R parameters α and β, the estimate of the steepness parameter h of the S-R relationship has the advantage that it is directly transferable from population to population (Hilborn & Liermann, 1998). As no S-R data for the three species were available, three S-R curves were estimated per species corresponding to the steepness values of h = 0.6, h = 0.7 and h = 0.8 (Fig. 7.4). These values were based on the analysis of S-R relationships from a total of 249 populations of fish from 57 species (Myers *et al.*, 1999) and, according to the results from an analysis by Rose *et al.* (2001), correspond to the typical range expected for the broader spectrum of periodic strategists. Periodic strategists, as opposed to equilibrium or opportunistic strategists, can be characterised as relatively fecund fishes with medium to large body sizes and no parental care that typically inhabit periodic environments (Winemiller & Rose, 1992). With regard to the results on the life history of *L. capensis* (Chapter 5), *L. aeneus* (Ellender, 2008) and *C. carpio* (Chapter 4), it was assumed that all three species can be broadly described by this characterisation. By the same token, σ = 0.6 represented the average variation in Ricker S-R curves of periodic strategists

analysed by Rose *et al.* (2001) and was used to describe the amount of variation expected in the recruitment process.

For each scenario, 200 replicates of the stochastic model were generated using Monte-Carlo simulation. The corresponding 95% confidence intervals were plotted by applying the percentile method (Buckland, 1984) to the sorted vectors of simulated population biomass trajectories.

7.3 RESULTS

FOOD WEB ANALYSIS

The biplot of isotopic mean values revealed two distinct groups of invertebrates, with zooplankton being relatively depleted in $\delta^{13}C$ (mean $\delta^{13}C$: -26.4 – -25.3‰) compared to the more $\delta^{13}C$-enriched corixids and chironomids (mean $\delta^{13}C$: -22.6 – -21.8‰) (Fig. 7.5). Invertebrate mean $\delta^{14}N$ values generally ranged from 8.1‰ for chironomids to 10.5 ‰ for *L. meridianus*, which probably represents the $\delta^{14}N$ range that can be expected for the trophic position of primary consumers in Lake Gariep. The only exception was the predatory copepod *L. excellence*, which had a mean $\delta^{14}N$ of 13.0‰, and was slightly more $\delta^{13}C$-enriched relative to the grazing zooplankton, indicating that *L. excellence* primarily preys on the latter. Compared to the grazing zooplankton (*L. meridianus* and *Daphnia* spp.), bulk POM and cyanobacteria were considerably enriched in $\delta^{13}C$ with a mean isotopic difference of 4.4‰ between the two groups (Fig. 7.5), indicating that zooplankton were ^{13}C-depleted relative to its alleged food source. This differnece seems to be a common phenomenon in freshwater systems as similar patterns have also been reported from 21 out of 24 lakes throughout the United Kingdom (Grey *et al.*, 2000). The piscivore *L. kimberleyensis* had the most enriched $\delta^{14}N$ values of the food web plot and was also enriched in $\delta^{13}C$ values relative to all

other fishes except *Barbus anoplus* (Fig. 7.5). The lowest $\delta^{14}N$ and $\delta^{13}C$ values among fishes were found in samples of *Labeo umbratus* (Fig. 7.5).

The relatively low $\delta^{13}C$ and high $\delta^{14}N$ signature of *L. aeneus* indicated that zooplankton are primary food resource for this species (Fig. 7.5). In comparison to *L. aeneus*, *L. capensis* and *C. carpio* mean $\delta^{13}C$ values that were relatively ^{13}C enriched, suggesting a greater assimilation of carbon from benthic production sources (Fig. 7.5). Compared to *C. carpio*, *L. capensis* samples were relatively depleted in ^{14}N, which implies that this species generally feeds on lower trophic levels of the benthic food web than *C. carpio* (Fig. 7.5).

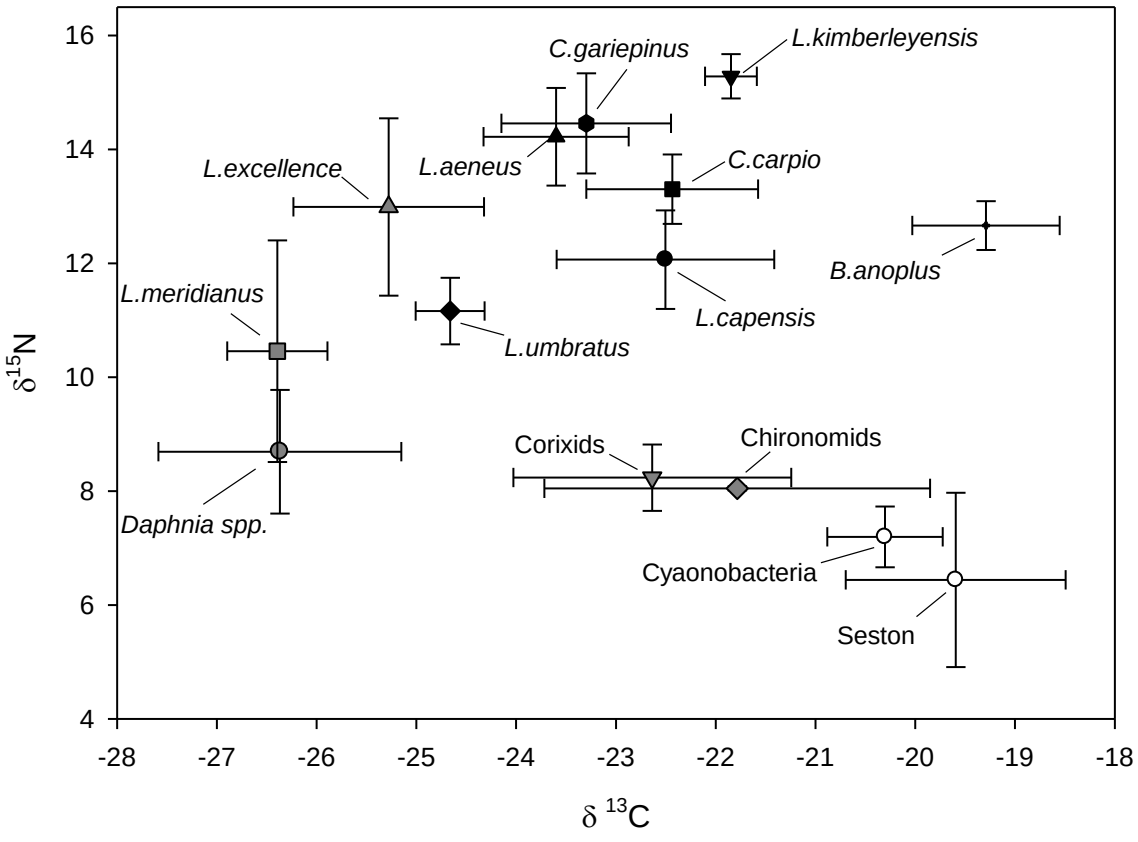

Fig. 7.5. Biplot showing the mean and standard deviation (error bars) of $\delta^{13}C$ and $\delta^{15}N$ values for fishes (solid symbols), aquatic invertebrates (grey symbols) and base resources (open symbols) from Lake Gariep.

The comparison of the convex hull areas encompassed by species-specific individual $\delta^{13}C$-$\delta^{15}N$ biplots showed that the overlapping spaces of the two endemic species *L. capensis* and *L. aeneus* was less than 1% (Fig. 7.6). The largest overlapping portion in niche space was 15.8% between *C. carpio* and *L. capensis*, whereas the convex hull areas of *C. carpio* and *L. aeneus* overlapped by only 7.0% (Fig. 7.6).

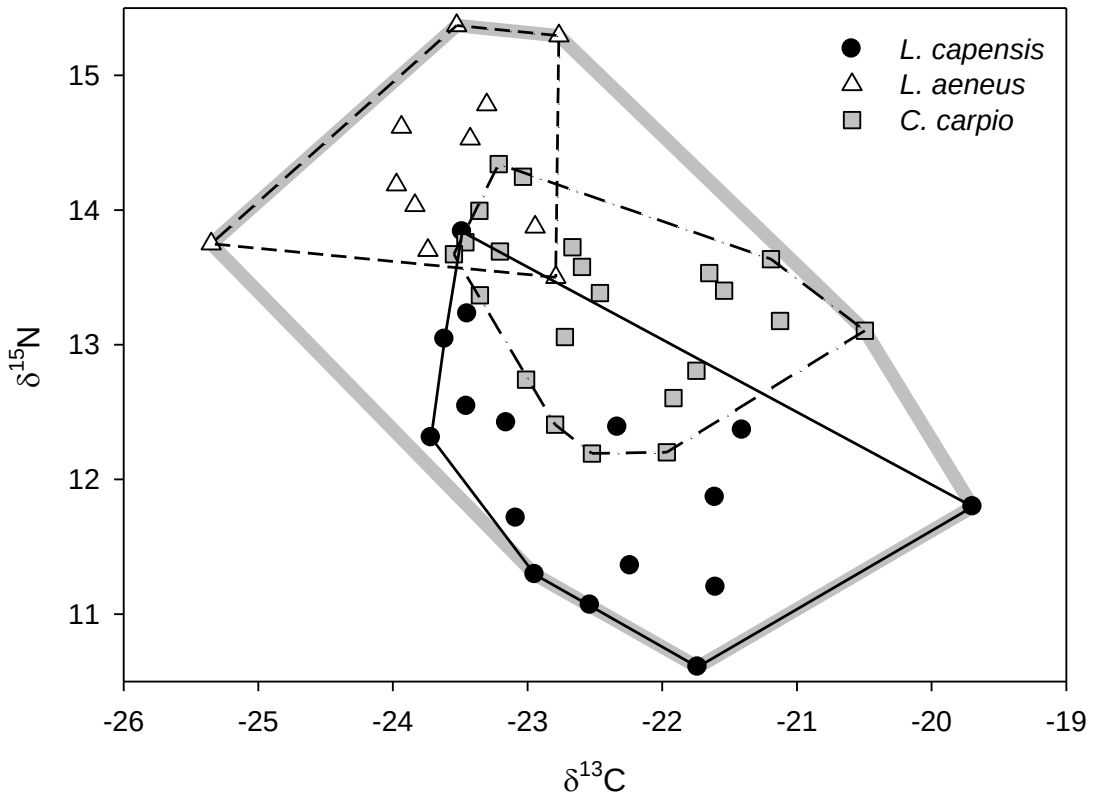

Fig. 7.6. Trophic niche space of *Labeo capensis, Labeobarbus aeneus and Cyprinus carpio* (Zambrano *et al.*, 2010). Each symbol represents the $\delta^{13}C$-$\delta^{15}N$ bi-plot for an individual fish. The polygons encompass the convex hull area for each species. The thick grey shaded line represents the convex hull area for the niche space of all three species combined.

The convex hull area of *L. capensis* accounted for the largest proportion (45.1%) of the total niche space encompassed by the $\delta^{13}C$ - $\delta^{15}N$ biplots of all three species. By contrast, the niche space of *C. carpio* and *L. aeneus* occupied a much smaller area of the total niche space, with 26% and 21%, respectively (Fig. 7.6). The null hypothesis that there was no significant difference between the species-specific distributions of $\delta^{13}C$ - $\delta^{15}N$ biplots was rejected by the 2DKS tests for all three pair-wise comparisons

(*C. carpio* vs. *L. capensis*: $D = 0.61$, $p < 0.05$; *C. carpio* vs. *L. aeneus*: $D = 0.70$, $p < 0.05$; *L. capensis* vs. *L. aeneus*: $D = 0.80$, $p < 0.05$).

GILLNET SELECTIVITY

A total of 2324 *L. capensis*, 1213 *L. aeneus* and 105 *C. carpio* were caught during the gillnet surveys conducted between May 2007 and March 2008. Because the numbers of *L. capensis* ($n = 9$) and *L. aeneus* ($n = 4$) caught in the 153 mm mesh size accounted for less than 0.01% of the samples, this mesh size was excluded from the SELECT models for these two species (see Chapter 5). The estimated scaling parameters, k_1 and k_2, used to calculate the mean size at capture and standard deviation for any of the given mesh sizes are summarised together with model statistics in Table 7.4.

Table 7.4. Summary statistics of parameters estimated using the log-linear SELECT model (Millar & Holst, 1997) based on a normally distributed selection curve with a proportional spread, together with the scaling parameters k_1 and k_2.

Parameter	k_1	k_2	*LL*	Residual deviance	Null deviance	df	R^2
Labeo capensis	3.81	0.16	-7457.0	364.7	6801.9	99	0.95
Labeobarbus aeneus	3.92	0.30	-2705.3	221.3	2905	106	0.92
Cyprinus carpio	2.66	0.20	-28.8	60.2	348.9	114	0.83

Observed and model-predicted proportions of fish per length class are illustrated in Fig. 7.7. Despite moderate departures between observed and model-predicted length frequencies of *C. carpio* for the 65 mm and 77 mm mesh sizes, the SELECT model generally performed well in predicting the observed proportions of fish in each length class for all three species (Fig. 7.7).

The observed proportion in numbers and weight of fish caught per mesh size varied substantially between the three species (Fig. 7.7). In terms of weight, the 77 mm mesh size was most efficient to retain *L. capensis* (38.5%), followed by the 105 mm mesh

size (33.2%), while the 105 mm mesh size accounted for the majority of the *L. aeneus* catch (60%). Only the largest mesh size of 153 mm contributed effectively to the CPUE of *C. carpio*, as this mesh size alone accounted for close 80% of the catch in weight (Fig. 7.7).

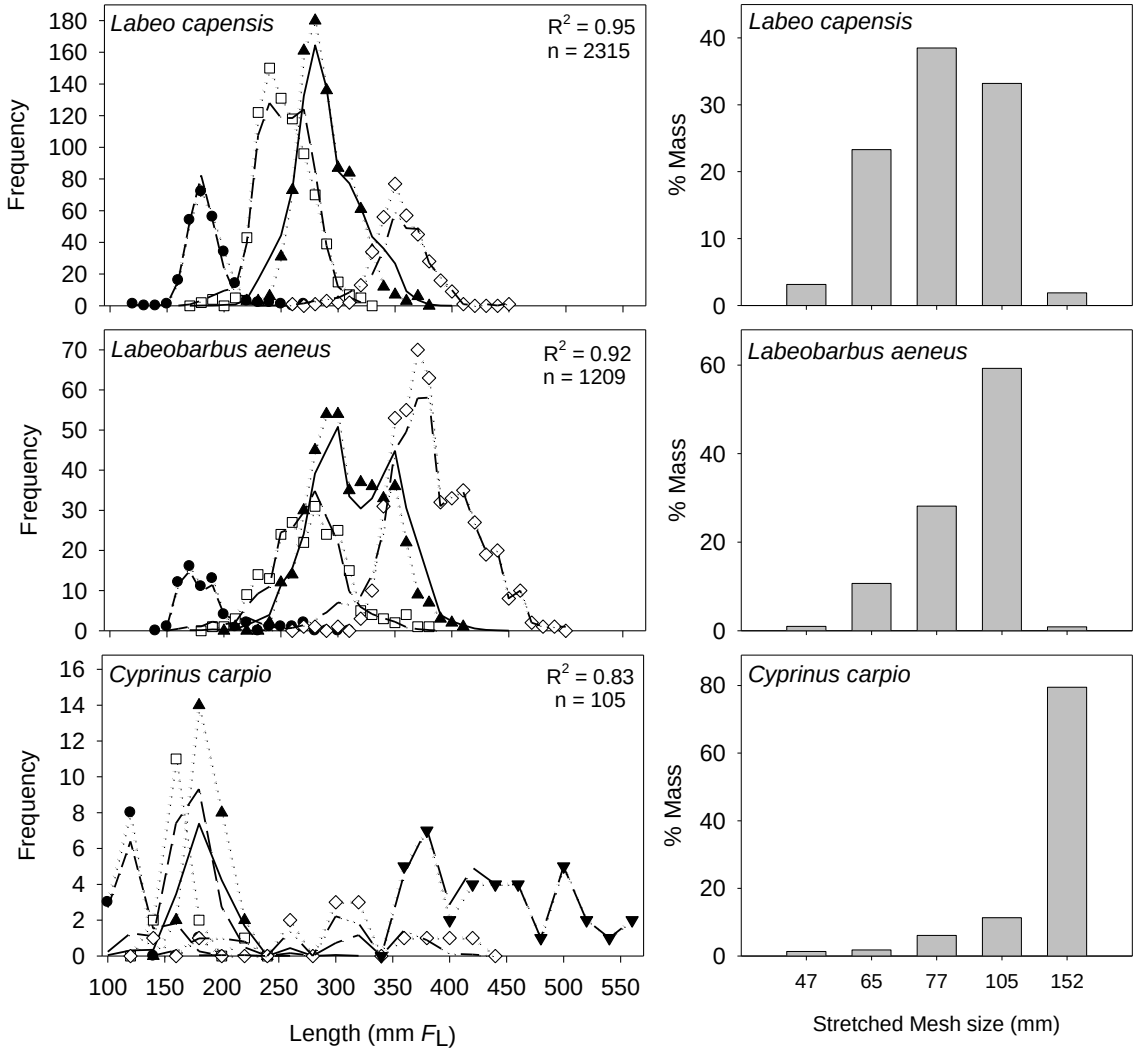

Fig. 7.7. The left panels illustrate the observed (symbols) and model predicted (lines) length frequencies in gillnet catches (2007-2008) of *Labeo capensis*, *Labeobarbus aeneus* and *Cyprinus carpio* using the SELECT method (Millar & Holst, 1997). The right panels illustrate the observed percentages of weight per species caught by each mesh size.

STANDARDISED CPUE TRENDS

The observed nominal CPUE (scaled to a kg.100 m net^{-1}.night^{-1}) and correction factors used to standardise these values with regard to the selective properties of the different gillnet fleets (Table 7.2) are provided in Table 7.5.

Table 7.5. Nominal CPUE in kg.100.m.net.night^{-1} by species and survey period and correction factors used to adjust the nominal CPUE for the selective properties of the four different gillnet-types (j =1 -4). Note that the mean CPUE from the gillnet type (j = 2) was used as the baseline data. The original nominal CPUE for the period 1971-1980 had been scaled to a 350 m net night (Hamann 1980; 1981).

Species	*Labeo capensis*		*Labeobarbus aeneus*		*Cyprinus carpio*		
Seasons	nominal CPUE	correction factor	nominal CPUE	correction factor	nominal CPUE	correction factor	Gillnet type j
S 71/72	0.61	1.00	0.17	1.00	3.05	1.00	2
S 72/73	0.73	1.00	0.40	1.00	4.61	1.00	2
S 73/74	2.28	1.00	2.62	1.00	5.48	1.00	2
S 74/75	4.22	1.00	3.65	1.00	4.74	1.00	2
S 75/76	2.61	1.00	1.19	1.00	9.83	1.00	2
S 76/77	2.56	1.51	3.84	1.32	2.28	0.98	3
S 77/78	2.17	1.51	4.02	1.32	2.74	0.98	4
S 79/80	2.29	1.59	1.57	1.55	1.53	0.91	4
W 07	11.05	1.44	14.80	1.25	0.65	0.68	1
S 07/08	12.70	1.44	16.03	1.25	2.12	0.68	1

Compared to the current gillnet fleet, it was predicted that had sampling of the current populations been done with the gillnet fleet from 1971-1976, CPUE for *L. capensis* and *L. aeneus* would have been 44% and 25% higher, respectively, while *C. carpio* CPUE would have accounted for only 68% of the CPUE observed in current fleet (Table 7.5). The lower CPUE of *L. capensis* and *L. aeneus* in the current fleet can be attributed to the higher proportion of effort allocated to the relatively inefficient mesh sizes of 47 mm and 153 mm (40% of effort, 5 panels), relative to the 1971-1976 fleet where the two comparable mesh sizes 46 mm and 146 mm accounted for an overall smaller fraction of the fleet's total effort (28.6%, 7 panels). Conversely, the high proportion of

effort by the 153 mm mesh size (20% of effort, 5 panels) was mainly responsible for the higher *C. carpio* catch rates observed for the current fleet than predicted for the fleet from 1971-1976 (Table 7.5). The gillnet fleets that were used in summer 1976/77 and during 1977/78 and 1979/80 both included two panels with relatively small mesh sizes (< 60 mm; Table 7.1), which contributed 33.3% (6 panels) and 28.6% (7 panels) of the fleet's total effort. This relatively high proportion of effort in combination with the low CPUE expected for such small mesh sizes explains the lesser efficiency of these gillnet fleets that was predicted for all three species when compared to the current fleet (Table 7.5).

The standardised gillnet CPUE of *L. capensis* indicated a slow population increase from 0.61 kg.100 m net^{-1}.night^{-1} in summer 1971/72 to 3.55 kg.100 m net^{-1}.night^{-1} in summer 1979/80, the last year of the early impoundment survey period (Fig. 7.8). The initial standardised CPUE of *L. aeneus* increased from 0.17 kg.100 m net^{-1}.night^{-1} in summer 1971/72 to 3.65 kg.100 m net^{-1}.night^{-1} in 1974/75, but showed a decrease in summer 1975/76 (Fig. 7.8). Over the next two summer seasons *L. aeneus* CPUE increased again to a relative maximum of 6.55 kg.100 m net^{-1}.night^{-1} in summer 1977/78. Two years later, in summer 1979/80, the population's standardised CPUE had decreased again to 2.49 kg.100 m net^{-1}.night^{-1} (Fig. 7.8). Compared to the two endemic species, *C. carpio* exhibited the fastest initial increase in CPUE from 3.05 kg.100 m net^{-1}.night^{-1} in 1971/72 to 9.83 kg.100 m net^{-1}.night^{-1}in summer 1976/1977. The standardised CPUE from the next three summer surveys showed, however, a rapid decrease in CPUE, which then reached a relative minimum of 1.39 kg.100 m net^{-1}.night^{-1} by the end of the initial survey period in 1979/80 (Fig. 7.8).

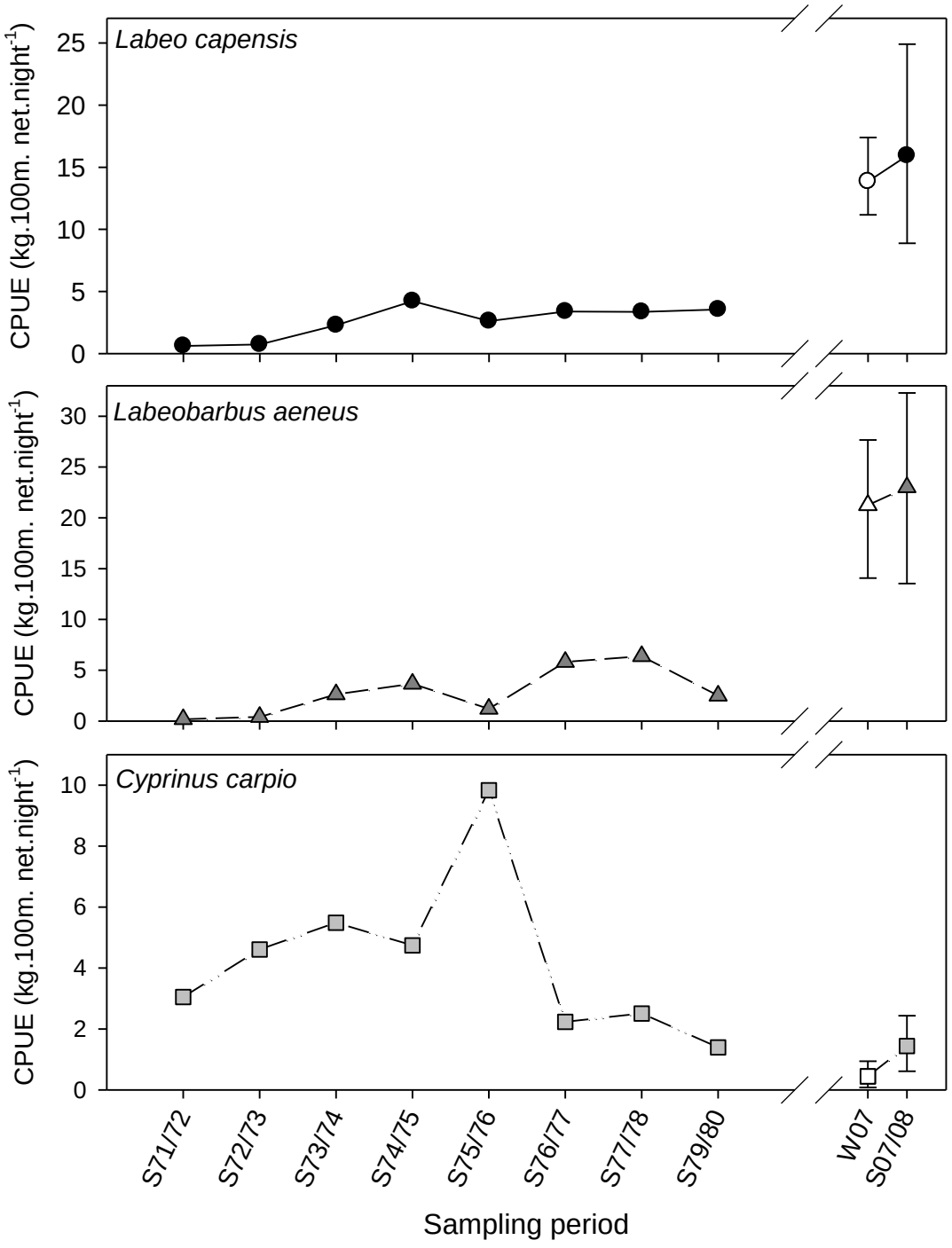

Fig. 7.8. Post-impoundment trends of standardised gillnet CPUE from summer surveys 1971-1979 (Hamann 1981), and winter (open symbols) and summer surveys 2007-2008 (present study) illustrated for *Labeo capensis, Labeobarbus aeneus* and *Cyprinus carpio*

Almost four decades after impoundment, the standardised CPUE from summer 2007/08 indicated a substantial increase in the biomasses of both *L. capensis* and *L. aeneus*, with standardised CPUE values of 15.93 [95% CI = 8.88 – 24.91] kg.100 m net^{-1}.night^{-1} and

23.00 [95% CI = 13.53 – 32.29] kg.100 m net night^{-1}, respectively. The standardised CPUE from the winter gillnet survey in 2007 strongly supported this trend, and although the mean winter CPUE of the two species was slightly lower, the CPUE from this period exhibited less variation as indicated by the narrower upper and lower 95% confidence limits (Fig. 7.8). By contrast, the biomass of *C. carpio* seemed to have remained at a low level, with standardised summer CPUE estimated at 1.44 [95% CI = 0.61 – 2.44] kg.100 m net^{-1}.night^{-1} and therefore similar to CPUE from summer 1979/80. As expected from the results in Chapter 6, the *C. carpio* CPUE from winter 2007 was even lower at 0.44 [95% CI = 0.08 – 0.94] kg.100 m net^{-1}.night^{-1} (Fig. 7.8).

TRENDS IN POPULATION SIZE STRUCTURES

Changes in the population size structures from the summers 1972/73 to 1979/80 (Hamman, 1980; 1981) and the estimated size structures for summer 2007/08 are illustrated for *L. capensis*, *L. aeneus* and *C. carpio* in Fig. 7.9. The initial length frequency distributions of *L. capensis* and *L. aeneus* from 1972/73 were dominated by size classes of juvenile fish < 200 mm F_L. The length-frequency distribution of *L. capensis* showed two prominent modes in summer 1972/73, with maxima in the 160 mm F_L and 200 mm F_L size classes. According to the estimated von Bertalanffy growth parameters for *L. capensis* (Table 7.3), the expected mean length for age-2 *L. capensis* would correspond to approximately 180 mm F_L. Although it is unclear whether the two modes comprised two year classes of age-1 and age-2 fish or a single year class of two year olds, it is likely that these relatively strong size classes mainly represented juveniles that were born after Lake Gariep was impounded in 1970.

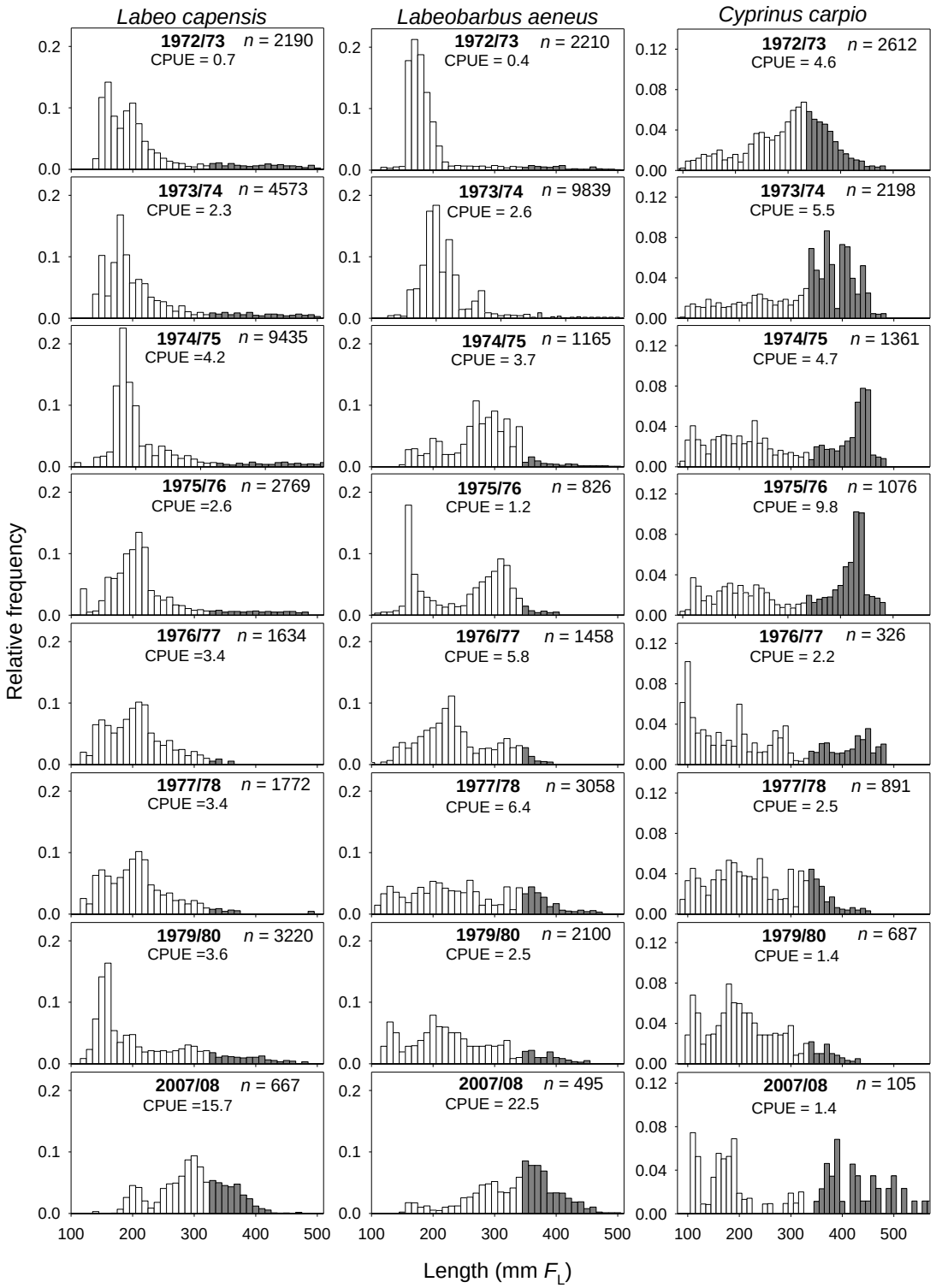

Fig. 7.9. Trends in selectivity corrected relative length frequency distributions of summer gillnet catches from 1971-1979 and 2007/08 for *Labeo capensis*, *Labeobarbus aeneus* and *Cyprinus carpio.* Grey bars denote size classes larger than the female length-at-50%-maturity obtained from Chapter 4, Chapter 5 and Ellender (2008); CPUE, standardised summer CPUE (kg.100 m net^{-1}.night^{-1})

Based on the *L. aeneus* growth parameters estimated by Ellender (2008) (Table 7.3), the mean lengths of age-2, age-3 and age-4 *L. aeneus* would be expected at around 200 mm F_L and 260 mm F_L and 310 mm F_L, respectively. As the distinct mode of small fish in the 1972/73 sample had a maximum at 170 mm F_L and peaked sequentially at 200 mm F_L in 1973/74, at 270 mm F_L in 1974/75 and at 310 mm F_L in 1975/1976, it could be assumed that this mode signified a relatively strong year class of one or two year old post-impoundment recruits. The *L. aeneus* population size structure from 1975/1976 then indicated a second strong year class of post-impoundment recruits evident by a prominent mode with a maximum in 160 mm F_L size class.

The small proportion of mature *L. capensis* and *L. aeneus* in summer 1972/73 most likely comprised the individuals from the pre-impoundment riverine population (Fig. 7.9). The length frequency trends of the *L. capensis* population indicated that these fish disappeared entirely from the gillnet catches in 1976/77, at a time, where a small fraction of the post-impoundment recruits appeared to have started recruiting into the mature segment of the population. Similarly, larger *L. aeneus* specimens (> 400 mm F_L) were not represented in the gillnet catches during summers 1975/76 and 1976/77. These two years therefore seemed to represent a transition period as a result of a gradual disappearance of large *L. aeneus* from the original river population and a lag of the incoming post-impoundment recruits, with the latter only having attained larger size classes > 400 mm F_L by summer 1977/78 (Fig. 7.9).

The prominent mode in *C. carpio* size structure from summer 1972/73 had a maximum in the 330 mm F_L size class, which subsequently progressed into size classes > 400 mm F_L during 1974/75 and 1975/76 (Fig. 7.9). According to the life history parameters in Table 7.3, the size class of 330 mm F_L was similar to the estimated mean length-at-age

for males and females of ~ 310 mm F_L, and could therefore potentially correspond to the expected mean length-at-age of a two year fish within the current population. This would indicate that the prominent mode in the 1972/73 population size structure represented a relatively strong year class of age-2 *C. carpio*, possibly as a result of the first post-impoundment spawning season in 1970/71. The decrease in the proportion of large mature *C. carpio* between 1975/76 and 1976/77 was associated with the observed decrease in CPUE from 9.83 kg.100 m net^{-1}.night^{-1} to 2.24 kg.100 m net^{-1}.night^{-1} (Fig. 7.8; Fig. 7.9). The proportion of mature *C. carpio* then reached a minimum by the end of the initial survey period in summer 1979/80.

The estimated size structure of the *L. capensis* and *L. aeneus* populations from summer 2007/2008 in combination with high CPUE indicated that a relatively large spawner biomass had established in comparison to the first ten years after impoundment (Fig. 7.9). While *C. carpio* CPUE in 2007/2008 was at a similar low level in 1979/80, the proportion of mature individuals in the *C. carpio* was relatively large compared to the length distributions from 1976/77 to 1979/80.

MODELLING POPULATION DEMOGRAPHICS

When parameterised according to the life history parameters in Table 7.3, the population trajectories from the deterministic ASPM predicted that, depending on the steepness *h* of S-R relationship, it would take between 16 and 23 years for the *L. capensis* population, and between 13 and 18 years for the *L. aeneus* population, to increase from an initial 3% biomass in 1970 to 80% of the populations' theoretical equilibrium biomass (BR_0) (Fig. 7.10). By contrast, the population trajectories for *C. carpio* predicted that an increase of biomass from 3% to 80% of BR_0 would occur 8 to 12 years after impoundment. The deterministic *C. carpio* biomass trajectories were

generally less sensitive to changes in *h* (Fig. 7.10). Further, the relatively low *F* of 0.12 yr^{-1} had little effect on the predicted population biomass of *C. carpio* given that it only resulted in reductions by 2% (*h* = 0.8) to 6% (*h* = 0.6) of the population biomass relative to BR_0.

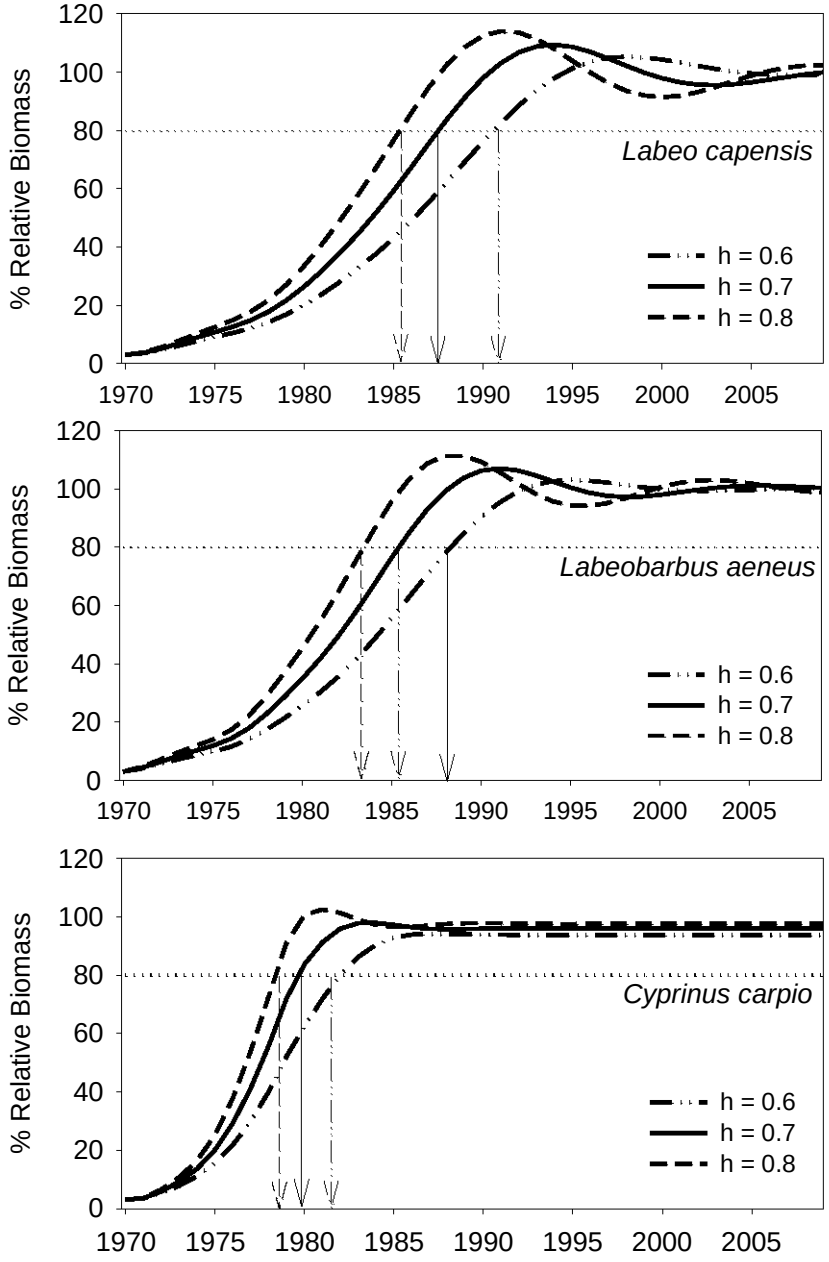

Fig. 7.10. Population colonisation biomass trajectories expressed as percentage of biomass per recruit, *BR,* for *Labeo capensis, Labeobarbus aeneus* and *Cyprinus carpio* assuming a Ricker spawner-recruitment relationship with the steepness parameters *h* = 0.6 - 0.8. The initial population biomass in 1970 was set to 3% of BR_0.

The predicted faster population growth of *C. carpio* is explained by its relatively fast growth, early maturation (~ age-2), short maximum life span (t_{max} = 7 years), and high fecundity, in comparison to the two endemic species in this impoundment (Table 7.3; Fig. 7.4). At equilibrium, the egg production of *C. carpio* was estimated at ~ 100,000 eggs per recruit, with 3-year-olds contributing the most eggs. In comparison, the egg production for *L. capensis* and *L. aeneus* was estimated at ~ 6000 and ~1000 eggs per recruit, respectively, with 8-years-old *L. capensis* and 7-years-old *L. aeneus* representing the ages that contribute to most of the egg production (Fig. 7.4). As a result, post-impoundment recruits of *C. carpio* could theoretically contribute to the population's egg production within two to three years following the impoundment of Lake Gariep, which explains the relatively early acceleration in the predicted population growth rate (Fig. 7.10). By contrast, it is estimated that more than six years would have to pass in order for the recruits of the two endemic species to contribute to the populations' reproduction potential. This is also illustrated by the biomass trajectories for the two species, which predicted that the relatively slow initial increase in population biomass quickened after 1976 (Fig. 7.10).

The relationships between standardised gillnet CPUE, as an index of relative biomass, and the model-predicted population biomass trajectories are illustrated in Fig. 7.11. For this purpose, the gillnet CPUE from summer 2007/2008 was set equal to the corresponding percentage biomass that was predicted by the deterministic ASPM, while the historical CPUE values (1971 – 1980) expressed as percentages relative to this value.

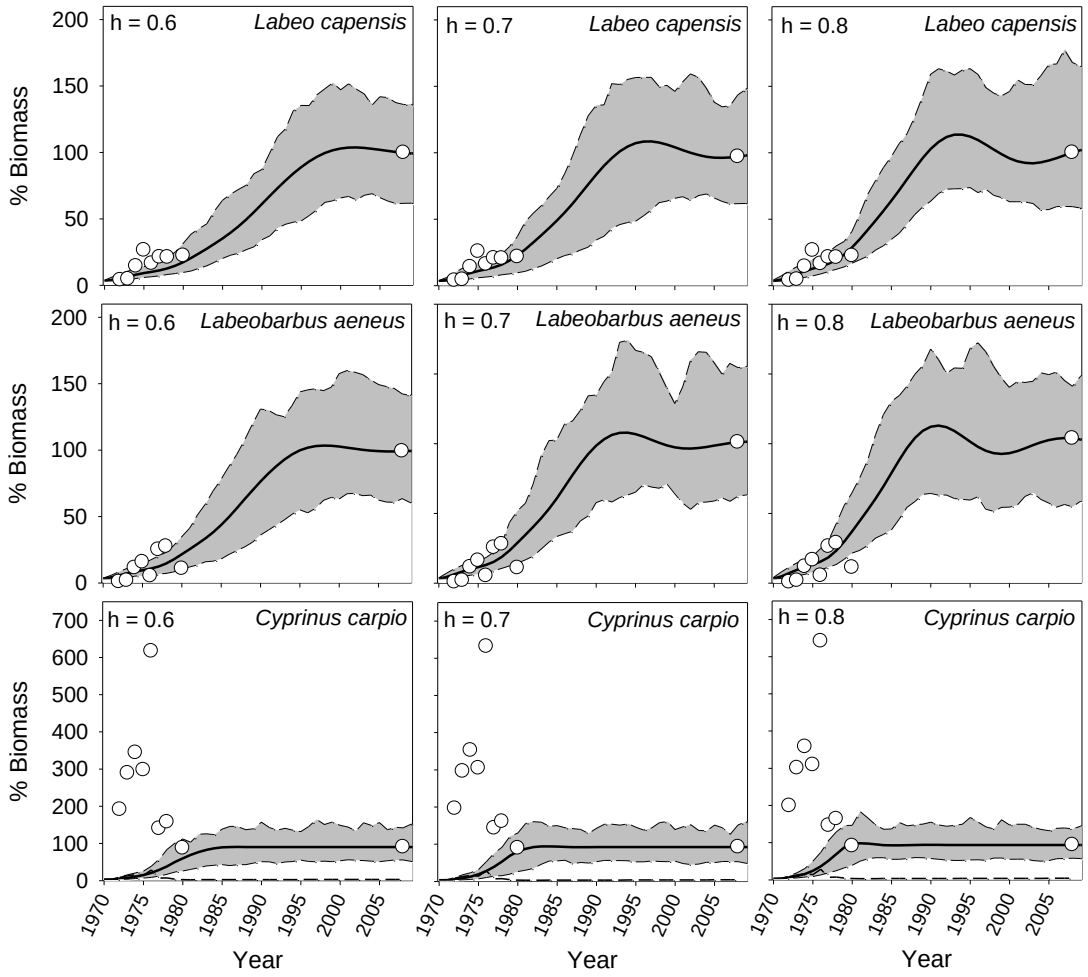

Fig. 7.11. Comparison of observed CPUE (open dots) and predicted biomass time trajectories as percentage of biomass per recruit *BR* for *Labeo capensis, Labeobarbus aeneus* and *Cyprinus carpio* assuming the Ricker spawner-recruitment relationship with the steepness parameters h = 0.6 - 0.8. The initial population size in 1970 was set to 3% of BR_0. Grey areas with dashed borders show the simulated stochastic effect of recruitment variability assuming a log-normal error with a CV = 0.6.

The relatively slow increases in standardised gillnet CPUE of *L. capensis* and *L. aeneus* during the first ten years post-impoundment were generally in accordance with the predicted population biomass trajectories from the ASPMs (Fig. 7.11). The earliest standardised CPUE data from summer 1971/72 corresponded to approximately 4% and 1% of BR_0 for *L. capensis* and *L. aeneus*, respectively, indicating that, from a deterministic point of view, the crude approximation of 3% initial population biomass in 1970 was rather conservative for *L. aeneus*. The 95% confidence limits derived from the stochastic model simulations showed that the incorporation of recruitment

variability resulted in relatively little variation when both populations were at low abundances, but that larger fluctuations in biomass could be expected as the populations approached BR_0. Notable was that the ratios of the historical CPUE of *L. capensis* and *L. aeneus* to the CPUE from the current populations were relatively insensitive to the expected variations around BR_0. For example, if the current CPUE of *L. capensis* would have been set equal to 60% or 160% of BR_0, which roughly corresponded to the 95% confidence intervals for the stochastic biomass trajectories (Fig. 7.11), then this would have resulted in proportions of biomasses that would correspond to approximately 2% and 6% of BR_0 in 1971/72 instead of the estimated deterministic 4% of BR_0 (Fig. 7.11). Given that most of the standardised CPUE values fell within the 95% confidence limits of the relative biomass trajectories, the *base-case* models for *L. capensis* and *L. aeneus* were assumed to provide a range of adequate scenarios to explain the post-impoundment population biomass developments of the two species.

In contrast to the two endemic species, all three *base-case* S-R scenarios for *C. carpio* failed to explain the 'boom and bust' pattern that emerged from the standardised CPUE data during the early post-impoundment colonisation phase (1971-1980) (Fig. 7.11). The standardised CPUE from 1971/72 and 1975/76, for example, corresponded to approximately 200% and to more than 600% of the assumed BR_0, which was in sharp contrast to the deterministic ASPM predictions that were expected at around 10% and less than 25% of BR_0, respectively. Only the ratio of the CPUE from 1979/80 to the current CPUE fell within the 95% confidence intervals that were explained by the stochastic ASPM (Fig. 7.11). As a result, the three *base-case* scenarios were considered as insufficient to model the post-impoundment biomass development of *C. carpio* in Lake Gariep.

Simulating alternative colonisation scenarios for Cyprinus carpio

In an attempt to explore potential mechanisms that may possibly better explain the apparent discrepancy between the standardised CPUE data and the model-predicted biomass trajectories for *C. carpio*, the ASPM was used to explore two alternative but non-conflicting scenarios.

The first scenario was based on the consideration that food source availability was less limited during the first post-impoundment years, such that density-dependent processes may have had less depressing effects on the growth and survival of the *C. carpio* population. To explore the potential consequences of this scenario on the population demographics of *C. carpio*, it was assumed that these favourable conditions lasted five years and terminated with the rapid decrease in *C. carpio* CPUE by summer 1976/77 (Fig. 7.8). To simulate this scenario, the expected length-at-age of *C. carpio* was increased stepwise by 10% and 20% and natural mortality was decreased stepwise to 75% and 50% of the current $M = 0.60\ yr^{-1}$ between 1970 and 1976 (Fig. 7.12).

The second scenario explored the possibility that the *C. carpio* population was not capable of fully utilising the newly created impoundment, such that the increase in Lake Gariep's carrying capacity was essentially smaller in proportion to the increase in lake surface area. This scenario was simulated by increasing the initial population biomass in 1970 from 3% to 6%, 9% and 12%, which would effectively result in a decrease of the theoretical carrying capacity to 50%, 33% and 25% of the lake surface area (Fig. 7.12).

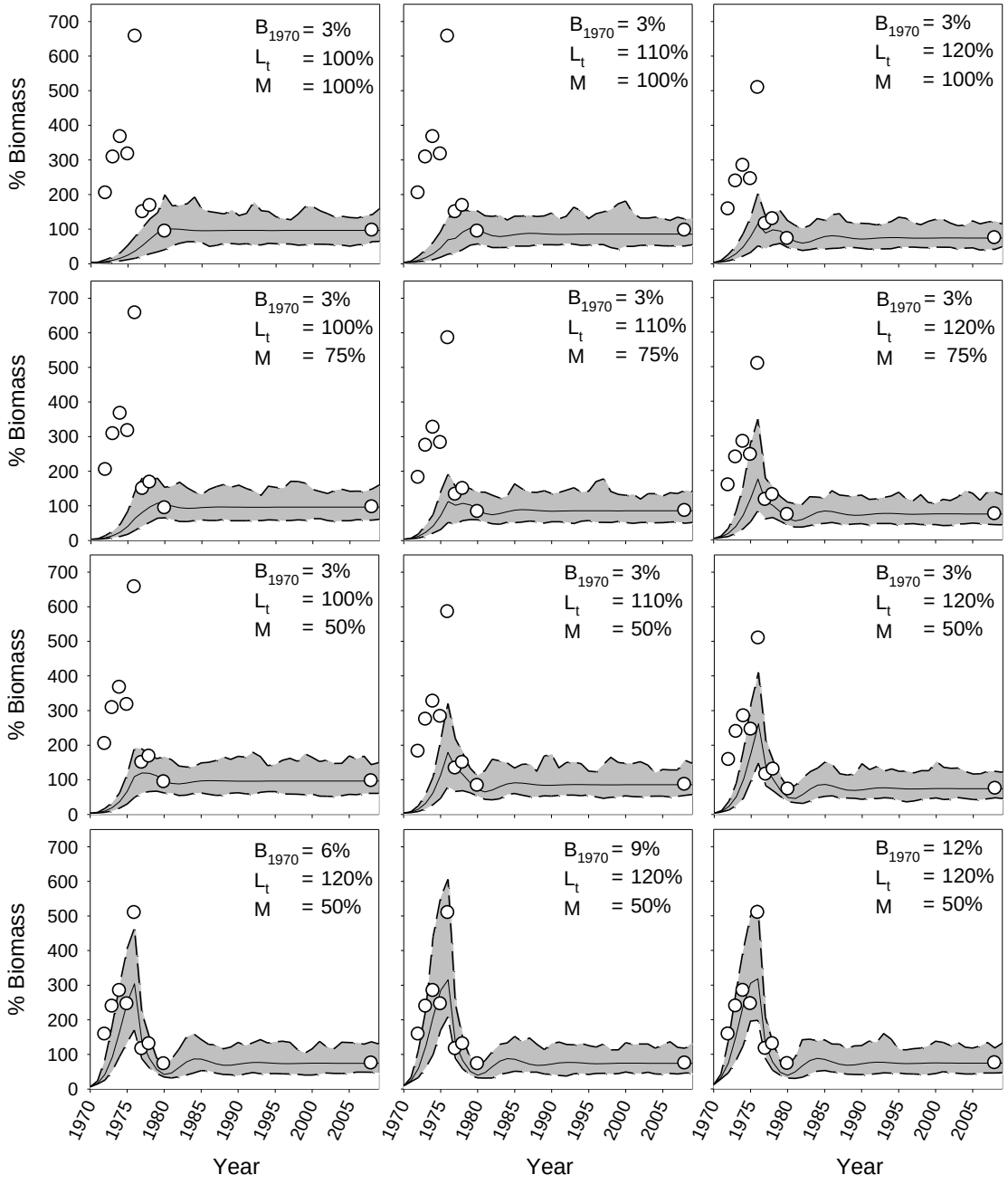

Fig. 7.12. Alternative model scenarios for the *Cyprinus carpio* biomass time trajectories expressed as percentage of biomass per recruit *BR*. The simulations illustrate effects of increased length-at-age (L_t) by 10% and 20% and reduced natural mortality (M) by 75% and 50% during the first six years after impoundment (1970-1976), as well as the effect of increasing the assumed initial biomass in 1970 (B_{1970}) from 3% to 6%, 9% and 12% of BR_0. Grey areas with dashed borders show the simulated stochastic effect of recruitment variability assuming a lognormal distribution with a CV = 0.6. The steepness parameter of the spawner-recruitment relationship was set to h = 0.8 for the model-scenarios.

The simulation results for the first scenario indicated that only the combined effects of both an increase of length-at-age by 20% and a decrease of M to 50% during the first

five years after impoundment could, to some extent, explain the pattern that emerged from the ratio of historical to present CPUE data (Fig. 7.12), whereas if both factors were changed independently, a notable difference between standardised CPUE and model-predicted biomass trajectories remained (Fig. 7.12). Similarly, an increase in the initial biomass from 1970 alone (not shown here) only influenced the ratio of historical to current CPUE, but had no effect on the shape of predicted biomass trajectories compared to the *base-case* scenario. The best simulation results were obtained when an increase of length-at-age by 20% and a decrease of *M* to 50% were combined with a simultaneously increase to 9% or 12% of the initial biomass from 1970 (Fig. 7.12).

7.4 DISCUSSION

For each the three species investigated, the lag period between colonisation and maximum biomass differed and appeared to have been inherently linked to their population-specific life histories. The *C. carpio* population exhibited a pulse-like colonisation during the initial post-impoundment phase (1971-1980), which was evident by a clear 'boom and bust' pattern in the standardised gillnet CPUE data combined with relatively low abundance at its current population level. By contrast, *L. capensis* and *L. aeneus* both showed slower population growth, but overall seemed to attain substantially higher biomass levels almost some four decades post-impoundment. This suggests a slow but successful colonisation of the lacustrine environment created by the impoundment of Lake Gariep.

Investigating changes in population demographics generally relies on the fundamental assumption that CPUE is proportional to abundance (e.g. Quinn & Deriso, 1999), and, as such, fisheries-independent data are considered the most suitable information

available (Harley *et al.*, 2001; Maunder & Punt, 2004). It was therefore assumed that the experimental gillnet CPUE data used in this Chapter provided a relatively reliable measure for detecting temporal changes in population biomass, considering that gillnet selectivity was standardised. This, however, must not detract from evidence suggesting that the standardised gillnet CPUE data cannot be used to quantify the populations' biomass composition (Chapter 6).

An important aspect regarding the interpretation of the *base-case* model results is that the modelling framework ignored the possible influence of temporal variations in key environmental variables, such as turbidity, hydrology or food resources, on growth, survival or fecundity of the three populations. Furthermore, the analysis of the post-impoundment population dynamics was constrained by the absence CPUE data between the early post-impoundment surveys (1971-1980) and the gillnet surveys conducted during the present study (2007-2008), which resulted in uncertainty about population demographics during the period between 1980 and 2007. In order to explore these model limitations and uncertainties, and also to provide reasonable biological explanations for the abundance patterns that emerged from the historical and present gillnet CPUE data, it was necessary to first examine several aspects that could have influenced the long-term population demographics of the three species. These aspects include life history patterns, interspecific competition, the possible effects of fishing and change in environmental conditions.

Life history

Based on life history theory, it can be assumed that post-impoundment population demographics should have developed within biological limits that are governed by

growth, survival, age at first reproduction, maximum age, age-specific fecundity, and recruitment success (e.g. Stearns, 1976; Roff, 1984; Stearns, 1992; Winemiller, 1992). Although recent investigations into the life history of the three species provided reliable population-specific life history parameters (Chapter 4; Chapter 5; Ellender 2008), no data were available on the relationship between recruitment and either biomass or egg production. To overcome this limitation, it was assumed that all three species can be broadly characterised as periodic strategists, thereby justifying the S-R variability and the range of steepness parameters used for the ASPM, as these were found to represent typical values for fishes with comparable life history patterns (Rose *et al.*, 2001).

The periodic life history strategy is seen as an adaptation to maximise fitness in systems that are exposed to large environmental variability and strong seasonality (Winemiller & Rose, 1992; Olden *et al.*, 2006; Tedesco *et al.*, 2008), similar to the conditions prevailing in Lake Gariep (Chapters 4 & 5). Population demographics of periodic strategists are typically governed by large fluctuations in year-class strengths, with occasionally exceptional recruitment that can compensate for unfavourable environmental conditions (Winemiller, 1992; Rose *et al.*, 2001; Winemiller, 2005). At low abundance, the S-R relationship should show a relatively strong compensatory effect to ensure that typically low juvenile survival can be offset by longevity and delayed maturity (Winemiller & Rose, 1992; Rose *et al.*, 2001; King & McFarlane, 2003). Furthermore, interrelated traits such as growth, maturity and survival are generally less influenced by environmental variations than the growth and survival rates during the early life stages. This ensures that some individuals live long enough to reproduce successfully despite longer periods during which environmental conditions are unfavourable for the survival of their offspring (King & McFarlane, 2003; Winemiller, 2005).

According to the triangular continuum model suggested by Winemiller and Rose (1992), the life history traits of *L. capensis* probably best agree with the typical characteristics of a periodic strategist (Chapter 5). These characteristics include a relatively long generation time (t_{max} = 12 years), delayed maturation (female tm_{50} = 6.2 years), high batch fecundity, a short period of spawning activity, and no parental care (Chapter 5). As the life history parameters of *L. capensis* and *L. aeneus* were remarkably similar (Table 7.3), it was not unexpected that their post-impoundment population demographics appeared to follow comparable patterns to those predicted for riverine fishes that most closely resembled the periodic life history strategy (Winemiller, 1989; Winemiller & Rose, 1992; Olden *et al.*, 2006; Tedesco *et al.*, 2008).

Several life history traits of the *C. carpio* population, such as large body size, high fecundity and presumably low juvenile survival due to spawning in temporarily unstable environments (Chapter 4), indicated that this species can be generally positioned within the broader spectrum of the periodic strategy (Winemiller & Rose, 1992). There were, however, some marked differences compared to the two endemic species. In particular, the substantially faster somatic growth, earlier age-at-maturity (female tm_{50} = 2.2 years) and shorter generation times (t_{max} = 7 years) of the *C. carpio* population represent traits that maximise the population growth potential, rather than decrease the risk of low adult survival during periods of unfavourable environmental conditions (Winemiller & Rose, 1992; King & McFarlane, 2003; Winemiller, 2005). As such, the biomass of C. *carpio* has the potential to increase faster during productive environmental regimes than the biomass of either of the two endemic species, which, on other hand, implies that strong density-dependent responses mediated by food source depletion are more likely to cause substantial biomass losses in the *C. carpio*

population (Rose *et al.*, 2001; King & McFarlane, 2003; Bøhn *et al.*, 2004; Winemiller, 2005; Fox *et al.*, 2007; Bøhn *et al.*, 2008).

Fast growth, earlier maturity, short generation times, and thus a high intrinsic rate of population increase are considered typical traits that maximise the colonising capability of fishes in general (e.g. Winemiller & Rose, 1992), and of *C. carpio* in particular (Koehn, 2004; Weber & Brown, 2009). This also indicates that the *C. carpio* population of Lake Gariep exhibited a mix of periodic and opportunistic (*r*-selected) life history attributes (Winemiller, 1992; Chapter 4). However, as Fox *et al.* (2007) emphasised, it is often difficult to generalise life history strategies for fishes like *C. carpio* (or in their example pumpkinseed *Lepomis gibbosus*) that have colonised a wide range of freshwater systems (Casal, 2006; Zambrano *et al.*, 2006) and show high levels of phenotypic plasticity in their life history traits (Balon, 1995; Reznick *et al.*, 2002; Balon, 2004; Bøhn *et al.*, 2004; Koehn, 2004; Matsuzak *et al.*, 2009; Weber & Brown, 2009; Chapter 4). In this regard, it has been argued that phenotypic plasticity can be considered adaptive in that it directly acts on life history traits in response to resource availability (Reznick *et al.*, 2002; Bøhn *et al.*, 2004; Fox *et al.*, 2007). These results seem to be supported by the observation that growth rates and longevity of *C. carpio* revealed large intraspecific variations (Chapter 4), even within the same system (Vilizzi & Walker, 1999; Brown & Walker, 2004; Brown *et al.*, 2005). By comparison, no significant differences were found between the growth performances of riverine and impoundment *L. capensis* populations (Chapter 5). Notable is that age-at-maturity seems to be a rather conservative trait in all three species (Ellender, 2008; Weyl *et al.*, 2009; Chapter 4; Chapter 5).

In general, the ASPM provided an effective means to model the effects of large fluctuations in year-class strengths on the age- and sex-structure of the populations dynamically, incorporate density-dependent survival in the early juvenile phase, and simulate high levels of environmental stochasticity. Overall, there was no evidence for any severe violation of the model assumptions pertaining to the base-case scenarios for the two endemic species. According to the ASPM simulation results for *C. carpio*, however, it appears possible that its growth and survival rates may have exhibited high levels of phenotypic plasticity in response to changes in food availability, as may have been caused by increased interspecific competition or shifts in the environmental regime. This would have evidently resulted in the violation of base-*case* scenario for *C. carpio* regarding the assumed temporal invariance in its life history parameters.

Interspecific competition

Interspecific competition usually refers to the competition for food sources and habitat space between species. Empirical and theoretical evidence suggests that intraspecific competition can result in decreased survival and reduced individual growth (Fox, 1994; Bøhn *et al.*, 2004; Magnan *et al.*, 2005; Bøhn *et al.*, 2008), and may therefore cause a substantial reduction in a population's growth rate. As a portion of the available niche space could be occupied by a competing species, interspecific competition may also result in a decrease of the species-specific carrying capacity. In this regard, stable isotope analysis has become an important, albeit indirect, assessment tool for investigating the level of interspecific competition within foodwebs (Mercado-Silva *et al.*, 2009; Zambrano *et al.*, 2010) as it can provide important insights into trophic niche relationships among species (Vander Zanden *et al.*, 1999).

The results from the stable isotope analysis suggested trophic niche segregation between the two abundant endemic species *L. capensis* and *L. aeneus*, with less than 1% of overlap between their estimated trophic niche spaces. Although riverine populations of *L. aeneus* are known to have an omnivorous diet, which includes algae, macrophytes, aquatic and terrestrial invertebrates, there is strong empirical evidence that populations of this species occurring in impoundments have adapted to forage primarily on zooplankton (Bruton, 1985; Tómasson *et al.*, 1985; Eccles, 1986; Chapter 6). More specifically, Eccles (1986) observed that the species' diet in Lake Vander Kloof comprised a large proportion of the large predatory copepod *L. excellence*, which generally agrees with the observed isotope signatures of *L. aeneus* relative to its presumed zooplankton prey in Lake Gariep. In contrast to *L. aeneus*, the isotope signatures of *L. capensis* indicated that this species predominantly feeds on benthic resources lower in the food web. This is not surprising, as this species has been described as a specialised substratum feeder that uses its ventral mouth to ingest large quantities of detritus from the bottom and scrapes algae from rocks (Schoonbee, 1969; Eccles, 1986; Skelton, 1986). The ability of *L. capensis* to efficiently utilise detritus as a food resource has been linked to its large gut length to fork length ratio (mean = 14.9), which is usually seen as a specialisation to detrital feeding (Kruger & Mulder, 1973; Skelton, 1986). By comparison, the mean gut length to fork length ratio in *L. aeneus* is only 1.7 (Kruger & Mulder, 1973). Similar to *L. capensis*, adult *C. carpio* primarily forages on benthic food items (Sibbing, 1988; Britton *et al.*, 2007; Weber & Brown, 2009), which may explain why the highest proportion of overlap in trophic niche spaces (15.8%) was observed between these two species. However, in comparison to *L. capensis*, *C. carpio* seemed to prey predominantly on benthic food resources that are of higher trophic origin. This finding also agrees with results from the comprehensive investigation into the intra-oral food processing abilities of *C.*

carpio by Sibbing (1988), who suggested that *C. carpio* is highly efficient in utilising benthic invertebrates, even when these are mixed with large quantities of non-food particles, but that low trophic food items such as detritus (< 250 µm), algae and macrophytes can usually not be efficiently processed.

The results from the 2DKS test suggest that these relatively distinct patterns of species-specific $\delta^{13}C$-$\delta^{15}N$ biplots were non-random and therefore unlikely to be coincidental, which is commonly seen as an indication that factors other than interspecific competition are more important in influencing demographics in the species assemblage (Baltz & Moyle, 1993; Moyle & Light, 1996; Zambrano *et al.*, 2006; Mercado-Silva *et al.*, 2009). This result, however, may not apply to small juveniles of the three species that share the marginal zones of Lake Gariep (Cambray *et al.*, 1978). As interspecific competition among juveniles may cause strong interannual variation in recruitment depending on the reproductive success of other species, it cannot be ruled out that a sequence of recruitment failures could have caused the rapid decline in gillnet CPUE of *C. carpio* after summer 1975/76. In general, however, this scenario appears unlikely because (1) the gillnet CPUE of the two endemic species at that time was still relatively low compared to current levels, (2) there was no evidence for sequential recruitment failures in the historical length frequency distributions, and (3) the higher reproductive capacity (i.e. ER_0) of *C. carpio* in combination with its substantially faster somatic growth rate compared to the two endemic species (Table 8.3; Chapter 4) would rather favour *C. carpio* recruitment.

Changes in environmental conditions

The standardised gillnet CPUE provided evidence that the biomass of the *C. carpio* population increased rapidly during the first five years after the inundation of Lake

Gariep, which was followed by a substantial population decline by more than 85% over the next three years. Similar anomalies in population demographics during initial post-impoundment phases have been reported for reservoirs across a wide range of different freshwater systems (Vanderpuye, 1981; Bodaly & Lesack, 1984; Kapasa & Cowx, 1991; Poddubny & Galat, 1995; Araya *et al.*, 2005; de Mérona *et al.*, 2005; Hoeinghaus *et al.*, 2005; Okada *et al.*, 2005; Albrecht *et al.*, 2009). These were explained by the well-documented phenomenon known as 'trophic upsurge' or 'heterotrophic phase', which typically occurs during the initial stage of reservoir formation due to the release of large amounts of nutrients from inundated biota and terrestrial soil. The increased productivity during this phase generally results in population explosions of rapidly colonising benthic invertebrates, and in particular chironomid larvae (McLachlan, 1970; Lowe-McConnell, 1987; Popp & Hoagland, 1995; Holz *et al.*, 1997; Hall *et al.*, 1999). These, in turn, may provide an abundant food source for benthivores such as *C. carpio* (Sibbing, 1988; García-Berthou, 2001; Britton *et al.*, 2007). The trophic upsurge phase may end abruptly with general decrease in productivity, essentially signifying a regime shift from allochthonous to predominantly autochthonous productivity (McLachlan, 1970; Lowe-McConnell, 1987; Hall *et al.*, 1999; Okada *et al.*, 2005).

In systems that are inhabited by relatively diverse fish faunas, population-specific responses to these processes are regarded as difficult to predict because of the complexity in trophic interactions and often chaotic patterns in population successions (Okada *et al.*, 2005). Furthermore, several studies were confronted with the problem to distinguish between the influence of changes in environmental conditions and differential impacts of selective fishing pressure on the fish community (Vanderpuye, 1981; Cowx & Kapasa, 1995; Petrere, 1996; Hoeinghaus *et al.*, 2005; Okada *et al.*, 2005). Unlike many other impoundments, the situation in Lake Gariep appears to be

notably less complex mainly due to three reasons. Firstly, the fish fauna is depauperate and dominated by the two indigenous species, *L. capensis* and *L. aeneus*, with *C. carpio* being the only alien to the system that occurs in notable abundance. Secondly, the trophic foodweb interactions in Lake Gariep appear to be relatively simple and indicated low levels of interspecific competition between post-recruits of the three abundant cyprinids. Thirdly, the impact of the existent recreational and subsistence hook and line bank anglers on *L. capensis* and *L. aeneus* is considered negligible (F = 0) (Ellender, 2008; Ellender *et al.*, 2010b; Chapter 5), while *C. carpio* is only lightly exploited (Ellender *et al.*, 2010b; Chapter 4), which, according to the results from the ASPM, had little impact on its population dynamics. Considering these results, a trophic upsurge scenario appears overall the most plausible explanation for the large amplitude in the pulse-like colonisation pattern of the *C. carpio* population during the initial post-impoundment phase, rather than the impact of fishing and intraspecific competition; although it can not be excluded that the latter may have influenced the populations to some extent.

It might have been anticipated that the more lentic conditions of Lake Gariep would have lead to an increase in density of *C. carpio*. However, contrary to this prediction, the ASPM simulations showed improved empirical model fits for scenarios where initial biomass levels of *C. carpio* were set disproportionally higher to the increase in surface area by impoundment. This would therefore suggest that current *C. carpio* densities are lower than compared to the pre-impoundment environment of the Orange River. One possible explanation is that environmental resistance could have been responsible for limiting the long-term colonisation success of non-native *C. carpio* (Baltz & Moyle, 1993; Moyle & Light, 1996). The *C. carpio* population appears to predominantly rely on zoobenthic food sources and was found to only occur in higher

abundance in areas that comprise soft-bottom habitats (Chapter 6). Because of high inorganic turbidity and the relatively deep bathymetry (mean depths = 16.3 m; maximum depth > 50 m) of Lake Gariep (Chapter 2), the system's production potential of zoobenthos is likely to be limited (Allanson & Jackson, 1983; Bruton, 1985; Hart, 1999), and benthic species, such as chironomids, may be considerably less abundant in deeper areas of the impoundment (McLachlan, 1970). One could therefore expect that the present-day environmental conditions in Lake Gariep are suboptimal for supporting high *C. carpio* densities.

In conclusion, the establishment of the *C. carpio* population did not prevent the slow but successful long-term establishment of the two large endemic cyprinids, which developed within the biological limits of their life history characteristics and showed surprisingly specialised trophic niches within the impoundment.

CHAPTER 8

Synthesis and Conclusions

The invasion and spread of introduced fishes have been identified as one of the major contributors to the current biodiversity crisis threatening freshwater ecosystems globally (Dudgeon *et al.*, 2006). Consequently, understanding the processes and not necessarily documenting the patterns by which non-native species invade and colonise new aquatic environments and those that lead to successful establishments with potential consequences for the native fauna is a pressing ecological research issue (Baltz & Moyle, 1993; Moyle & Light, 1996; Kolar & Lodge, 2001; Marchetti *et al.*, 2004; Olden *et al.*, 2006; Vander Zanden & Olden, 2008; Leprieur *et al.*, 2009).

This thesis contributes to understanding these processes with regard to *C. carpio* in southern Africa. The principle research approaches used to achieve this are outlined in the flow chart illustrated in Fig. 8.1. As is summarised in this figure, life history theory and ecological niche theory provided a fundamental basis for developing the conceptual framework of this thesis.

While the life history of *L. aeneus* in Lake Gariep was investigated by Ellender (2008), it remained a priority to estimate reliable life history parameters for *C. carpio* and *L. capensis* using robust maximum likelihood-based estimation procedures. These parameters were not only crucial for the understanding of their biology in Lake Gariep (Chapters 4 & 5), but were also required as input parameters for developing the age-structured production model (ASPM) to simulate their long-term post-impoundment population demographics in Chapter 7.

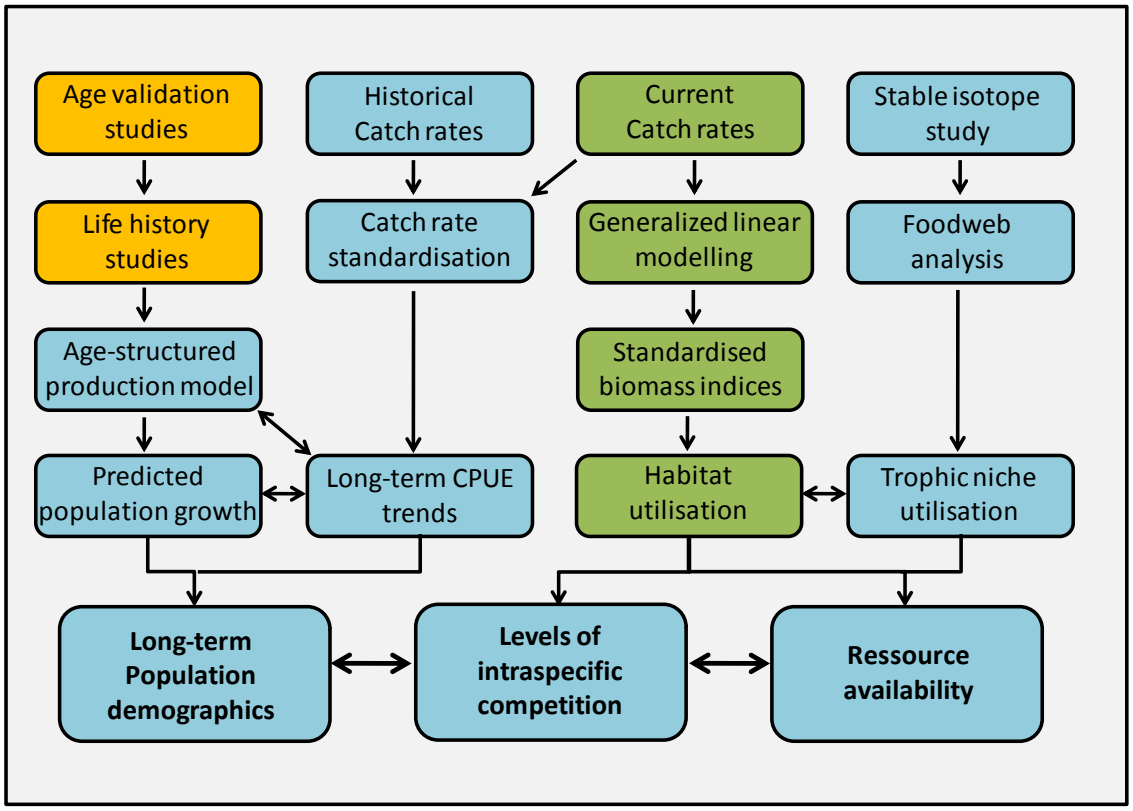

Fig. 8.1. Flow chart illustrating the principle research approaches used to assess the status and ecological role of *Cyprinus carpio* in comparison to two endemic cyprinids, *Labeo capensis* and *Labeobarbus aeneus*. : Chapters 3, 4 & 5; : Chapter 6; : Chapter 7.

Since a prerequisite for any life history study is to determine the age of fishes accurately (Campana & Thorrold, 2000), growth zone deposition rates in otoliths were validated for *C. carpio* in Chapter 3 and for *L. capensis* in Winker *et al.* (2010; Appendix I). The findings of Chapter 3 represent the first direct validation of two growth increments in otoliths of *C. carpio*, and have therefore the potential to significantly contribute to the knowledge on accurate ageing of this species. The investigation into the life history of *C. carpio* (Chapter 4) is the first to provide otolith-derived age-based life history parameters for any *C. carpio* population in Africa. The growth rate of this species appeared to follow a distinct biphasic pattern and showed a pronounced change with the onset of maturation at age-2. On intraspecific comparison of growth performances, the Lake Gariep population exhibited faster growth than has

been reported for any population in Europe, Australia or America. This fast growth rate is possibly a trade-off with reduced adult survival and a short lifespan (t_{max} = 7 years).

The life history comparisons in Chapter 4 revealed conspicuous differences between feral *C. carpio* and its wild form found in the Danube basin (Balon, 1995). In contrast to feral populations, maturation in females of the wild form was notably delayed, which is probably an adaptation to riverine environments that are influenced by large environmental fluctuations and strong seasonal changes (Winemiller, 1992; Olden *et al.*, 2006; Tedesco *et al.*, 2008). Fitness maximisation in such environments is thought to be achieved by a trade-off between delayed maturation and increased longevity, thereby increasing the probably that some individuals live long enough to reproduce successfully despite the high probability of consecutive years with low survival conditions for their offspring. Conversely, maturation at a younger age, which is a consistent trait in feral *C. carpio*, implies a faster population growth potential (Chapter 7) and therefore a shift towards a colonising strategy when compared to the wild form (Chapter 4). These considerations, however, also aroused the suspicion that the capability of *C. carpio* to rapidly invade new environments may well be the result of centuries of human domestication (Chapter 4).

In Lake Gariep, *C. carpio* shares its habitat with the large benthivorous cyprinid *L. capensis* (Chapters 6 & 7). The life history of this species evolved under the influence of the harsh, unpredictable and seasonal environmental conditions of the Orange River system and revealed some interesting characteristics (Chapter 5). Both sexes grew at a similar rate until the onset of maturation, after which males showed a relative decline in growth rate and significantly higher mortality rates. Based on per-recruit models, it could be demonstrated that these sex-specific differences resulted in a female spawner

biomass that was double the weight of the male spawner biomass. Given that intraspecific competition for resources ultimately will limit the biomass of a fish population, this strategy can essentially be seen as a trade-off between increased population fecundity (egg production) and a decrease in the number of spawning males (sperm production). This finding therefore highlights the importance of incorporating a sex-structured component into the ASPM framework in Chapter 7. In comparison to *C. carpio*, *L. capensis* exhibited significantly slower growth and delayed maturation, but it was also found that female survival and maximum age were notably higher. In general, *L. capensis*' life history closely resembled the typical characteristics predicted for riverine periodic strategists (Winemiller, 1992; Olden *et al.*, 2006; Tedesco *et al.*, 2008), as it also exhibits high batch fecundity, erratic periods of spawning activity, and lack of parental care (Chapter 5). Although riverine periodic strategists were often found to experience the greatest declines as a result of reservoir construction, this study provides evidence that *L. capensis* was able successfully establish in Lake Gariep (Chapters 5 - 7). In this regard, it is considered to be an important aspect that *L. capensis*, unlike many congeners, appears to be able to use temporarily available floodplains as in-lake spawning grounds (Chapter 5).

The principal aim of Chapter 6 was to identify predictor variables that explain temporal and spatial differences in catch rates of *L. capensis*, *L. aeneus* and *C. carpio*, as these could provide implications for potential habitat segregation among the three species (Fig. 8.1). Large proportions of zeros and strong skewness in the catch-per-unit-effort (CPUE) data did not permit the use conventional analysis techniques, such as standard Generalized Linear Models (GLMs) or ANOVA, without risking the introduction of bias into parameter estimates, their significance levels and other associated measures of uncertainty (Ortiz *et al.*, 2000; Punt *et al.*, 2000; Maunder & Punt, 2004; Ortiz &

Arocha, 2004; Fletcher *et al.*, 2005). This is a common problem with CPUE data and in such cases the use delta-lognormal and delta-gamma GLMs has been suggested as being advantageous (Lo *et al.*, 1992; Steffanson, 1996; Ortiz *et al.*, 2000; Punt *et al.*, 2000; Rodriguez-Marin *et al.*, 2003; Ortiz & Arocha, 2004). These GLMs were therefore evaluated for their suitability to standardise fisheries-independent experimental gillnet data and fisheries-dependent angler data for *L. capensis*, *L. aeneus* and *C. carpio* in Lake Gariep. Confidence intervals around predicted abundance indices were obtained through the development of a parametric bootstrap procedure. The parametric bootstrap algorithm is relatively easy to implement, irrespective of the complexity in the data structure, and provides a generalised approach for estimating informative measures of uncertainty from delta- and zero-inflated mixture models.

Based on Monte-Carlo simulations and standard model diagnostics, it could be demonstrated that both models performed-well in accounting for both the varying proportion of zero catches and the skewness in the CPUE datasets of three species. The resulting standardised abundance indices allowed for some broader characterisations of the habitat utilisation of the three species. Non-native *C. carpio* is predominantly confined to benthic soft-bottom habitats. The benthivorous *L. capensis*, by contrast, is able to utilise a broader range of benthic habitat types and is consistently abundant throughout the impoundment. The *L. aeneus* population is highly mobile within the impoundment and showed significant differences in its spatial abundance pattern between seasons. The strongest predictor for large aggregations of this species was the occurrence of oxygen supersaturation in the surface water, which typically indicates increased phytoplankton production. This, in turn, attracts zooplankton assemblages, resulting in optimal foraging conditions for this zooplanktivorous cyprinid (Chapter 7).

These findings also provided valuable additional information regarding the interpretation of the results from the stable isotope analysis in Chapter 7, which was used to determine the major trophic linkages within Lake Gariep's foodweb (Fig. 8.2). Both approaches combined suggest relatively distinct trophic niche segregation among these three dominant cyprinids (Fig. 8.2), which provides evidence that competition for niche opportunities had minor influences on their post-impoundment population dynamics (Chapter 7).

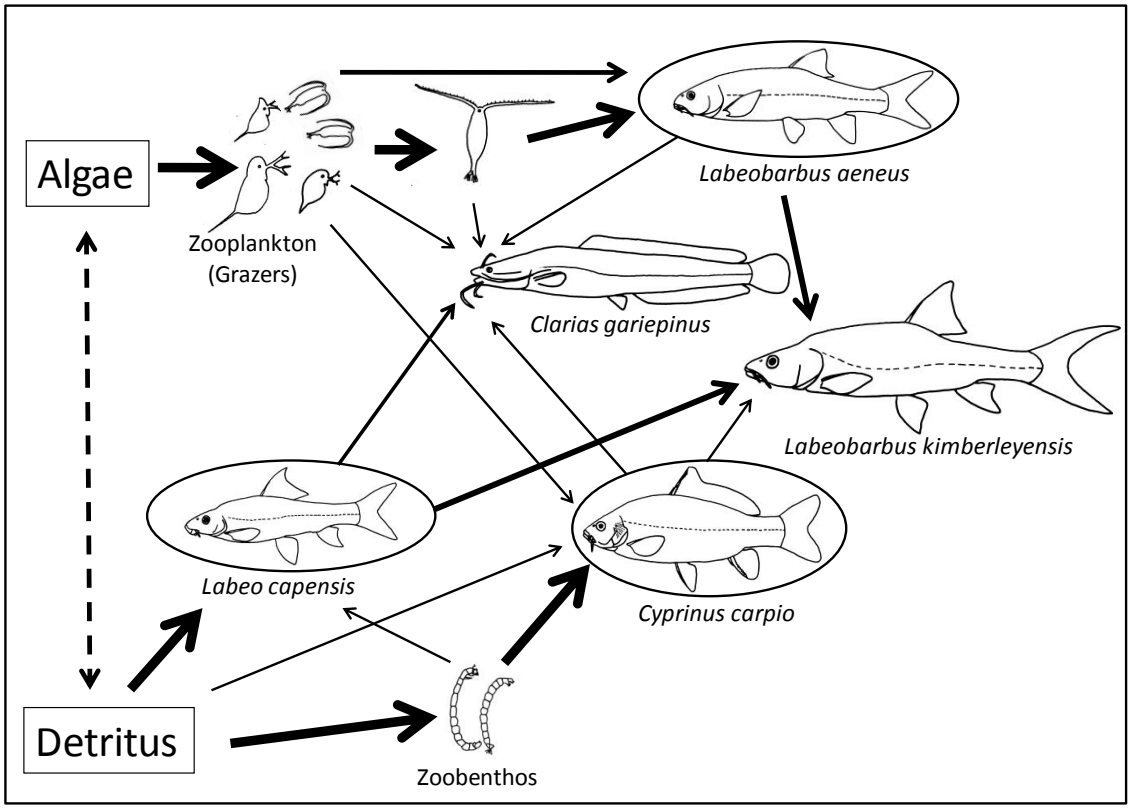

Fig. 8.2. Simplified foodweb of Lake Gariep illustrating relative distinct trophic niche segregation among *Labeo capensis*, *Labeobarbus aeneus* and *Cyprinus carpio.* The relative importance of foodweb links is highlighted by relative thickness of the arrows.

Once life history parameters had been estimated for *C. carpio* (Chapter 4), *L. capensis* (Chapter 5) and *L. aeneus* (Ellender, 2008), a stochastic ASPM framework was developed in an attempt to simulate their post-impoundment population demographics in Lake Gariep (Fig. 8.1). This framework allows not only for the dynamic modelling of the age- and sex-structure of the population but also can formally incorporate

density-dependent and stochastic processes into the population models (Quinn & Collie, 2005). Standardised historical and present gillnet CPUE data indicated a slow population growth of *L. capensis* and *L. aeneus* during the first ten post-impoundment years, but showed surprisingly high biomass levels some four decades after impoundment. These long lag periods between colonisation and maximum biomass in the two endemic populations could be in both cases corroborated by the stochastic ASPM simulation results, suggesting that life history was the major determinant for the long-term trends in the colonisation and successful establishment of *L. capensis* and *L. aeneus* in Lake Gariep.

The differential and more complex colonisation pattern in the long-term population demographics of *C. carpio*, exemplifies the difficulties in predicting invasion processes for species that exhibit high levels of phenotypic plasticity in their life history traits, which appears to be a pervasive trait in many highly invasive fishes (Bøhn *et al.*, 2004; Hoffmeister *et al.*, 2005; Chapter 4; Fox *et al.*, 2007). In retrospect, a rapid adaptive response to increased food available during the first five years after the closure of Lake Gariep, which was mediated by increased somatic growth and adult survival, provides the most plausible explanation for the 'boom and bust' pattern that emerged from standardised CPUE data of *C. carpio*. The multifaceted research approach used in this thesis was therefore necessary to generate sufficient data to support the conclusion made in Chapter 7 that "*the establishment of the C. carpio population did not prevent the slow but successful long-term establishment of the two large endemic cyprinids, which developed within the biological limits of their life history characteristics and showed a surprisingly specialised trophic niche utilisation within the impoundment*."

Uncertainties and Future Research

Whereas the analyses in Chapters 3 to 5 and Appendix I provide a robust foundation for the comprehensive description of the biology and life history strategies of adult *C. carpio* and *L. capensis*, there are still considerable gaps of knowledge pertaining to the biology and population dynamics of their juveniles. Future research should in particular focus on filling the gap of information on growth and aspects of intra- and interspecific competition for food resources and habitat during the crucial larval and juvenile life stages, as competition during these life stages is potentially most intense.

The results in Chapter 6 demonstrate that delta-lognormal and delta-gamma models represent suitable error distributions for handling the varying proportions of zeros in the experimental gillnet and fisheries-dependent angler catch and effort datasets from Lake Gariep. This was an important prerequisite for indentify statistically significant factors that could explain some of the temporal and spatial differences in catch rates. Although the experimental gillnet survey data were considered more valuable in terms of detecting these factors, there is considerable scope for improvement of sampling protocol. In retrospect, it was, for example, expected that the inclusion of detailed turbidity measurements into the delta-GLMs could have enabled improved predictions with regard to the distribution of the two native species. The lack of accurate and consistent turbidity measurements is therefore recognised as short-coming of this thesis. A more general limitation of the samling design was that it did not permit to examine changes in relative abundance and species composition with increasing depth and distance offshore. Such additional data could, however, provide valuable information to provide stronger and more direct evidence for the habitat utilisation of *L. capensis*, *L. aeneus* and *C. carpio* with important implications for the species-specific

carrying capacity of Lake Gariep. Future research projects should therefore consider extending the sampling design with the aim generate more detailed data in this regard.

The investigation into the food web dynamics of Lake Gariep using stable isotope analysis was the first of its kind conducted on any South African impoundment with the potential to be applied over a wide range of different freshwater systems within the region. In particular, comparisons of food web functioning among systems as well as aspects such as the effect of downstream succession within river systems are expected to have the potential to become key future research areas. It should, however, be recognised that the analysis of stable isotope signatures represents a rather indirect assessment approach in terms of specific food resource utilisation and the potential of competition. A dedicated feeding study based on classical gut content analysis would provide in-depth understanding of the breath of food items consumed and could potentially corroborate the results from the stable isotope analysis. There is virtually no literature on the abundance, species composition and spatial and temporal distribution of zoobenthos within South African impoundments. A detailed quantitative study of the zoobenthos resource in Lake Gariep was beyond the scope this study. Thus, considerable uncertainty remains regarding the ecological importance and functioning of zoobenthos within the food web. This aspect needs to be addressed in future studies, as it can be expected to be a crucial factor that may determine a system's fish production potential in general and risks as consequences of *C. carpio* introductions in particular.

REFERENCES

Adams, P. B. (1980). Life history patterns in marine fishes and their consequences for fisheries management. *Fishery Bulletin* **78**, 1-12.

Ahmet, A. L. P. & Sűleyman, B. (2000). Growth conditions and stock analysis of the carp (*Cyprinus carpio*, Linnaeus 1758) population in Gőlhisar Lake. *Turkish Journal of Zoology* **24**, 291-304.

Aitchison, J. (1955). On the distribution of a positive random variable having a discrete probabilty mass at the origin. *Journal of the American Statistical Association* **50**, 901-908.

Akaike, H. (1972). Information theory as an extension of the maximum likelihood principle. In *Second International Symposium on Information Theory* (Petrov, B. N. & Csaki, F., eds.), pp. 267–281. Budapest: Akademiai Kiado.

Albrecht, M., Caramaschi, É. & Horn, M. (2009). Population responses of two omnivorous fish species to impoundment of a Brazilian tropical river. *Hydrobiologia* **627**, 181-193.

Allanson, B. R., Hart, R. C., O'Keeffe, J. H. & Robart, R. D. (1990). *Inland waters of southern Africa*. Dordrecht: Kluwer Academic Publisher.

Allanson, B. R. & Jackson, B. C. (1983). Limnology and fisheries potential of Lake le Roux. p. 182. Pretoria: South African Nation Scientific Programmes Report, CSIR.

Anon (1959). Importation of carp. *Piscator* **46**, 47.

Araya, P. R., Agostinho, A. A. & Bechara, J. A. (2005). The influence of dam construction on a population of *Leporinus obtusidens* (Valenciennes, 1847) (Pisces, Anostomidae) in the Yacyretá Reservoir (Argentina). *Fisheries Research* **74**, 198-209.

Arlinghaus, R. & Mehner, T. (2003). Socio-economic characterisation of specialised common carp (*Cyprinus carpio* L.) anglers in Germany, and implications for inland fisheries management and eutrophication control. *Fisheries Research* **61**, 19-33.

Baddeley, A. & Turner, R. (2005). Spatstat: an R package for analyzing spatial point patterns. *Journal of Statistical Software* **12**, 1-42.

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

Balon, E. K. (1995). Origin and domestication of the wild carp, *Cyprinus carpio*: from Roman gourmets to the swimming flowers. *Aquaculture* **129**, 3-48.

Balon, E. K. (2004). About the oldest domesticates among fishes. *Journal of Fish Biology* **65**, 1–27.

Baltz, D. M. & Moyle, P. B. (1993). Invasion resistance to introduced species by a native assemblage of California stream fishes. *Ecological Applications* **3**, 246-255.

Barnes, M. A. & Power, G. (1984). A comparison of otolith and scale ages for western Labrador lake whitefish, *Coregonus clupeaformis*. *Environmental Biology of Fishes* **10**, 297-299.

Barthelmes, D. & Braemick, U. (2003). Variability of a cyprinid lake ecosystem with special emphasis on the native fish fauna under intensive fisheries management including common carp (*Cyprinus carpio*) and silver carp (*Hypophthalmichthys molitrix*). *Limnologica* **33**, 10-28.

Barthelmes, D. & Doering, P. (1996). Sampling efficiency of different fishing gear used for fish faunistic surveys in stagnant water bodies. *Limnologica* **26**, 191–198.

Battaile, B. C. & Quinn, T. J. (2004). Catch per unit effort standardization of the eastern Bering Sea walleye pollock (*Theragra chalcogramma*) fleet. *Fisheries Research* **70**, 161-177.

Beamish, C. A., Booth, A. J. & Deacon, N. (2005). Age, growth and reproduction of largemouth bass, *Micropterus salmoides*, in Lake Manyame, Zimbabwe. *African Zoology* **40**, 63-69.

Beamish, R. J. & Fournier, D. A. (1981). A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Sciences* **38**, 982-983.

Benejam, L., Benito, J., Ordóñez, J., Armengol, J. & García-Berthou, E. (2008). Short-term effects of a partial drawdown on fish condition in a eutrophic reservoir. *Water, Air and Soil Pollution* **190**, 3-11.

Bodaly, R. A. & Lesack, L. F. W. (1984). Response of a boreal northern pike (*Esox lucius*) population to lake impoundment: Wapaw Bay, Southern Indian lake, Manitoba. *Canadian Journal of Fisheries and Aquatic Sciences* **41**, 706-715.

Bøhn, T., Amundsen, P.-A. & Sparrow, A. (2008). Competitive exclusion after invasion? *Biological Invasions* **10**, 359-368.

Bøhn, T., Sandlund, O. T., Amundsen, P.-A. & Primicerio, R. (2004). Rapidly changing life history during invasion. *Oikos* **106**, 138-150.

Booth, A. J. (2004). Determination of cichlid-specific biological reference points. *Fisheries Research* **67**, 307-316.

Booth, A. J. & Buxton, C. D. (1997). The biology of the panga, *Pterogymnus laniarius* (Teleostei: Sparidae), on the Agulhas Bank, South Africa. *Environmental Biology of Fishes* **49**, 207-226.

Booth, A. J. & Khumalo, N. (2009). Age, growth and reproduction of *Marcusenius pongolensis*, *Oreochromis mossambicus* and *Schilbe intermedius* in an oligotrophic impoundment in Swaziland. *African Journal of Ecology* **48**, 481–489.

Booth, A. J. & Potts, W. M. (2006). Estimating gill-net selectivity for *Labeo umbratus* (Pisces: Cyprinidae), and an evaluation of using fyke-nets as a non-destructive sampling gear in small reservoirs. *Fisheries Research* **79**, 202–209.

Booth, A. J. & Weyl, O. L. F. (2000). Histological validation of gonadal macroscopic staging criteria for *Labeo cylindricus* (Pisces: Cyprinidae). *African Zoology* **35**, 223-231.

Booth, A. J. & Weyl, O. L. F. (2004). Investigations into a potential directed fishery for *Labeo cylindricus* on Lake Chicamba, Mozambique. *African Zoology* **39**, 77-90.

Bremner, J. M., Rogers, J. & Willis, J. P. (1990). Sedimentological aspects of the 1988 Orange River floods. *Transactions of the Royal Society of South Africa geoscience review* **47**, 247-294.

Britton, J., Davies, G. & Harrod, C. (2010). Trophic interactions and consequent impacts of the invasive fish *Pseudorasbora parva* in a native aquatic foodweb: a field investigation in the UK. *Biological Invasions* **12**, 1533-1542.

Britton, J. R., Boar, R. R., Grey, J., Foster, J., Lugonzo, J. & Harper, D. M. (2007). From introduction to fishery dominance: the initial impacts of the invasive carp Cyprinus carpio in Lake Naivasha, Kenya, 1999 to 2006. *Journal of Fish Biology* **71**, 239-257.

Brown, P., Green, C., Sivakumaran, K. P., Stoessel, D. & Giles, A. (2004). Validating otolith annuli for annual age determination of common carp. *Transactions of the American Fisheries Society* **133**, 133-196.

Brown, P., Sivakumaran, K. P., Stoessel, D. & Gilles, A. (2005). Population biology of carp (*Cyprinus carpio* L.) in the mid-Murray River and Barmah Forest Wetlands, Australia. *Marine and Freshwater Research* **56**, 1151-1164.

Brown, P. & Walker, T. I. (2004). CARPSIM: stochastic simulation modelling of wild carp (*Cyprinus carpio* L.) population dynamics, with applications to pest control. *Ecological Modelling* **176**, 83-97.

Bruton, M. N. (1985). The effects of suspensoids on fish. *Hydrobiologia* **125**, 221-241.

Brynjarsdóttir, J. & Stefánsson, G. (2004). Analysis of cod catch data from Icelandic groundfish surveys using generalized linear models. *Fisheries Research* **70**, 195-208.

Buckland, S. T. (1984). Monte-Carlo confidence intervals. *Biometrics* **40**, 811-817.

Bwanika, G., Murie, D. & Chapman, L. (2007). Comparative age and growth of Nile tilapia (*Oreochromis niloticus* L.) in lakes Nabugabo and Wamala, Uganda. *Hydrobiologia* **589**, 287-301.

Cambray, J. A. (1985). Observations on the spawning of *Labeo capensis* and *Clarias gariepinus* in the regulated lower Orange River, South Africa. *South African Journal of Science* **81**, 318-321.

Cambray, J. A. (2003). The need for research and monitoring on the impacts of translocated sharptooth catfish, *Clarias gariepinus*, in South Africa. *African Journal of Aquatic Science* **28**, 191–195.

Cambray, J. A., Handiek, S. & Handiek, Q. (1978). The juvenile fish population in the marginal areas of the Hendrik Verwoerd Dam. *Journal of the Limnological Society of Southern Africa* **4**, 21-30.

Campana, S. E. (1999). Chemistry and composition of fish otoliths: pathways, mechanisms and applications. *Marine Ecology Progress Series* **188**, 263-297.

Campana, S. E. (2001). Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology* **59**, 197-242.

Campana, S. E., Annand, M. C. & McMillan, J. I. (1995). Graphical and statistical methods for determining the consistency of age determinations. *Transactions of the American Fisheries Society* **24**, 131-138.

Campana, S. E. & Thorrold, S. R. (2000). Otoliths, increments, and elements: keys to a comprehensive understanding of fish populations? *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 30-38.

Campbell, R. A. (2004). CPUE standardisation and the construction of indices of stock abundance in a spatially varying fishery using general linear models. *Fisheries Research* **70**, 209-227.

Carol, J. & García-Berthou, E. (2007). Gillnet selectivity and its relationship with body shape for eight freshwater fish species. *Journal of Applied Ichthyology* **23** 654–660.

Casal, C. M. V. (2006). Global documentation of fish introductions: the growing crisis and recommendations for action. *Biological Invasions* **3**, 3-11.

Chang, W. Y. B. (1982). A statistical method for evaluating the reproducibility of age determination. *Canadian Journal of Fisheries and Aquatic Sciences* **39**, 1208-1210.

Chapman, D. G. & Robson, D. S. (1960). The analysis of a catch curve. *Biometrics* **16**, 354-368.

Charnov, E. L., Turner, T. F. & Winemillar, K. (2001). Reproductive constraints and the evolution of life histories with indeterminate growth. *Proceedings of the National Academy of Sciences* **98**, 9460-9464.

Chen, J., Thompson, M. E. & Wu, C. (2004). Estimation of fish abundance indices based on scientific research trawl surveys. *Biometrics* **60**, 116-123.

Chumchal, M. M., Nowlin, W. H. & Drenner, R. W. (2005). Biomass-dependent effects of common carp on water quality in shallow ponds. *Hydrobiologia* **545**, 271-277.

Clark, W. G. (1991). Groundfish exploitation rates based on life history parameters. *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 734-750.

Cochrane, K. L. (1985). The population dynamics and sustainable yield of the major fish species in Hartbeespoort Dam. PhD Thesis, University of the Witwatersrand, Johannesburg, South Africa.

Cochrane, K. L. (1987). The biomass and yield of the dominant fish species in Hartbeespoort Dam, South Africa *Hydrobiologia* **146**, 89-96.

Cochrane, W. G. (1977). *Sampling techniques.* New York: John Wiley & Sons, Inc.

Compton, J. S. & Maake, L. (2007). Source of the suspended load of the upper Orange River, South Africa. *South African Journal of Geology* **110**, 339-348.

Cooke, S. J., Grant, E. C., Schreer, J. F., Philipp, D. P. & Devries, A. L. (2003). Low temperature cardiac response to exhaustive exercise in fish with different levels of winter quiescence. *Comparative Biochemistry and Physiology, Part A: Molecular & Integrative Physiology* **134** 157–165.

Cowx, I. G. & Kapasa, C. K. (1995). Species changes in reservoir fisheries following impoundment: the case of Lake Itezhi-tezhi, Zambia. In *The impact of species*

changes in African Lakes (Pitcher, T. J. & Hart, P. J. B., eds.), pp. 321-332. London: Chapman & Hall.

Crivelli, A. J. (1981). The biology of common carp, *Cyprinus carpio* L., in the Camargue, southern France. *Journal of Fish Biology* **18**, 271-290.

de Mérona, B., Vigouroux, R. & Tejerina-Garro, F. (2005). Alteration of fish diversity downstream from Petit-Saut Dam in French Guiana. Implication of ecological strategies of fish species. *Hydrobiologia* **551**, 33-47.

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

de Moor, I. J. & Bruton, M. N. (1988). Atlas of the alien and translocated indigenous aquatic animals in southern Africa. In *South African National Scientific Programmes Report*, p. 310 pp.

Dick, E. J. (2004). Beyond `lognormal versus gamma': discrimination among error distributions for generalized linear models. *Fisheries Research* **70**, 351-366.

Dorgeloh, W. G. (1995). Fish distribution in relation to turbidity gradients in a man-made lake, Sterkfontein Dam (South Africa). *Water S.A.* **21**, 95-99.

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z.-I., Knowler, D. J., Lévêque, C., Naiman, R. J., Prieur-Richard, A.-H., Soto, D., Stiassny, M. L. J. & Sullivan, C. A. (2006). Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews* **81**, 163-182.

Dunn, P. K. & Smyth, G. K. (1996). Randomized quantile residuals. *Journal of Computational and Graphical Statistics* **5**, 236–244.

Dwyer, K. S., Walsh, S. J. & Campana, S. E. (2003). Age determination, validation and growth of Grand Bank yellowtail flounder (*Limanda ferruginea*). *ICES Journal of Marine Science* **60**, 1123-1138.

Eccles, D. H. (1986). Diet of the cyprinid fish *Barbus aeneus* (Burchell) in the P.K. Le Roux Dam, South Africa, with special reference to the effect of turbidity on zooplanktivory. *South African Journal of Zoology* **21**, 257-263.

Efron, B. (1982). Nonparametric estimates of standard error: the jack-knife, the bootstrap and other methods. *Biometrika* **68**, 589-599.

Efron, B. (1985). Bootstrap confidence intervals for a class of parametric problems. *Biometrika* **72**, 45-58.

Efron, B. & Tibshirani, R. (1986). Bootstrap methods for standard errors, confidence intervals, and other measures of statistical accuracy. *Statistical Science* **1**, 54–77.

Egertson, C. J. & Downing, J. A. (2004). Relationship of fish catch and composition to water quality in a suite of agriculturally eutrophic lakes. **61**, 1784–1796

Egger, B., Meekan, M., Salzburger, W., Mwape, L., Makasa, L., Shapola, R. & Sturmbauer, C. (2004). Validation of the periodicity of increment formation in the otoliths of a cichlid fish from Lake Tanganyika, East Africa. *Journal of Fish Biology* **64**, 1272-1284.

Ellender, B. R. (2008). The impact of angling on smallmouth and largemouth yellowfish, *Labeobarbus aeneus* and *Labeobarbus kimberleyensis*, in Lake Gariep, South Africa. MSc Thesis, Rhodes University, Grahamstown, South Africa.

Ellender, B. R., Traas, G. R. L., Winker, H. & Weyl, O. L. F. (2010a). The application of a mark-recapture model to estimate subsistence angler participation in rural fisheries. *Fisheries Management and Ecology* **17**, 19-27.

Ellender, B. R., Weyl, O. L. F. & Winker, H. (2009). Who uses the fishery resources in South Africa's largest impoundment? Characterising subsistence and recreational fishing sectors on Lake Gariep. *Water SA* **35**, 679-684.

Ellender, B. R., Weyl, O. L. F., Winker, H. & Booth, A. J. (2010b). Quantifying annual harvests from South Africa's largest impoundment. *Water SA* **36**, 45-51.

Fairall, N. & Hamann, K. C. D. (1977). Population structure of two *Labeo* species in the Hendrik Verwoerd Dam as determined by gill net sampling. *Journal of the Limnological Society of Southern Africa* **3**, 9-12.

Fasano, G. & Franceschini, A. (1987). A multidimensional version of the Kolmogorov–Smirnov test. *Monthly Notices of the Royal Astronomical Society* **225**, 155-170.

Fernàndez-Delgado, C. (1990). Life history patterns of the common carp, *Cyprinus carpio*, in the estuary of the Guadalquivir River in south-west Spain. *Hydrobiologia* **206**, 19-28.

Fletcher, D. (2008). Confidence intervals for the mean of the delta-lognormal distribution. *Environmental and Ecological Statistics* **15**, 175-189.

Fletcher, D. & Faddy, M. (2007). Confidence intervals for expected abundance of rare species. *Journal of Agricultural, Biological, and Environmental Statistics* **12**, 315-324.

Fletcher, D., MacKenzie, D. & Villoutas, E. (2005). Modelling skewed data with many zeros: A simple approach combining ordinary and logistic regression. *Environmental and Ecological Statistics* **12**, 45-54.

Flury, B. D. & Levri, E. P. (1999). Periodic logistic regression. *Ecology* **80**, 2254-2260.

Fournier, D. A., Sibert, J. R., Majkowski, J. & Hampton, J. (1990). MULTIFAN a likelihood-based method for estimating growth parameters and age composition for multiple length frequency data sets illustrated using data for southern bluefin tuna. *Canadian Journal of Fisheries and Aquatic Sciences* **47**, 301–317.

Fox, M. G. (1994). Growth, density, and interspecific influences on pumpkinseed sunfish life histories. *Ecology* **75**, 1157-1171.

Fox, M. G., Vila-Gispert, A. & Copp, G. H. (2007). Life-history traits of introduced Iberian pumpkinseed *Lepomis gibbosus* relative to native populations. Can differences explain colonization success? *Journal of Fish Biology* **71**, 56-69.

Francis, R. I. C. C., Paul, L. J. & Mulligan, K. P. (1992). Ageing of adult snapper (*Pagrus auratus*) from otolith annual ring counts: Validation by tagging and

oxytetracycline injection. *Australian journal of marine and freshwater research. Melbourne* **43**, 1069–1089.

Gaigher, I. G., Hamman, K. C. D. & Thorne, S. C. (1980). Possible adaptive signifiance of sex ratio and sexual differences in size at maturity in the Orange River Labeo, *Labeo capensis. Journal of the Limnological Society of Southern Africa* **35-38**.

García-Berthou, E. (2001). Size- and depth-dependent variation in habitat and diet of the common carp (*Cyprinus carpio*). *Aquatic Sciences* **63**, 466-476.

Garvey, J. E., Marschall, E. A. & Wright, R. A. (1998). From star charts to stoneflies: Detecting relationships in continuous bivariate data. *Ecology* **79**, 442–447.

Gehrke, P. C., Brown, P., Schiller, C. B., Moffatt, D. B. & Bruce, A. M. (1995). River regulation and fish communities in the Murray-Darling river system, Australia. *Regulated Rivers: Research & Management* **11**, 363-375.

Gido, K. B. (2000). Long-term changes in reservoir species assemblage: stability in an unpredictable environment. *Ecological Applications* **10**, 1517-1529.

Gido, K. B., Schaefer, J. F. & Pigg, J. (2004). Patterns of fish invasions in the Great Plains of North America. *Biological Conservation* **118**, 121-131.

Gjelland, K. Ø., Bøhn, T. & Amundsen, P. A. (2007). Is coexistence mediated by microhabitat segregation? An in-depth exploration of a fish invasion. *Journal of Fish Biology* **71**, 196-209.

Gozlan, R. E., Britton, J. R., Cowx, I. G. & Copp, G. H. (2010). Current knowledge on non-native freshwater fish introductions. *Journal of Fish Biology* **76**, 751-786.

Grey, J., Jones, R. I. & Sleep, D. (2000). Stable isotope analysis of the origins of zooplankton carbon in lakes of differing trophic state. *Oecologia* **123**, 232-240.

Hall, R. I., Leavitt, P. R., Dixit, A. S., Quinlan, R. & Smol, J. P. (1999). Limnological succession in reservoirs: a paleolimnological comparison of two methods of reservoir formation. *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 1109–1121.

Hamman, K. C. D. (1980). Post-impoundment trends in the fish populations of the Hendrik Verwoerd dam, South Africa. *Journal of the Limnological Society of Southern Africa* **6**, 101-108.

Hamman, K. C. D. (1981). Aspekte van die bevolkingsdinamika van die Hendrik Verwoerddam met verwysing na die ontwikkeling van ‘n visserybestuursplan. PhD Thesis, Rand Afrikaans University, Johannesburg, South Africa.

Harley, S. J., Myers, R. A. & Dunn, A. (2001). Is catch-per-unit-effort proportional to abundance? *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 1760-1772.

Hart, R. C. (1986). Aspects of the feeding ecology of turbid water zooplankton. In situ studies of community filtration rates in silt-laden Lake le Roux, Orange River, South Africa. *Journal of Plankton Research* **8**, 401-426.

Hart, R. C. (1999). On the limnology of Spioenkop, a turbid reservoir on the upper Thukela River, with particular reference to the structure and dynamics of its plankton community. *Water SA* **25**, 519-527.

Hart, R. C., Allanson, B. R. & Selkirk, W. T. (1983). The biological basis of fish production. In *Limnology and Fisheries potential of Lake Le Roux* (Allanson, B. R. & Jackson, B. C., eds.), pp. 26-64. Pretoria: South African Nation Scientific Programmes Report.

Hastie, T., Tibshirani, R. & Friedman, J. (2001). *The elements of statistical learning: data mining, inference, and prediction.* New York: Springer-Verlag.

Havel, J. E., Lee, C. E. & Vander Zanden, M. J. (2005). Do reservoirs facilitate invasions into landscapes? *Bioscience* **55**, 518–525

Hecht, T. (1980). A comparison between otolith and scale methods of ageing, and the growth of *Sarotherodon mossambicus* (Pisces: Cichlidae) in a Venda impoundment (Southern Africa). *South African Journal of Zoology* **15**, 222-228.

Hilborn, R. (2010). Pretty good yield and exploited fishes. *Marine Policy* **34**, 193-196.

Hilborn, R. & Liermann, M. (1998). Standing on the shoulders of giants: learning from experience in fisheries. *Reviews in Fish Biology and Fisheries* **8**, 273-283.

Hilborn, R. & Walters, C. J. (1992). *Quantitative fisheries stock assessment: choice, dynamics and uncertainty*. New York: Chapman and Hall.

Hinojosa-Garro, D. & Zambrano, L. (2004). Interactions of common carp (*Cyprinus carpio*) with benthic crayfish decapods in shallow ponds. *Hydrobiologia* **515**, 115-122.

Hoeinghaus, D. J., Agostinho, A. A., Gomes, L. C., Pelicice, F. M., Okada, E. K., Latini, J. D., Kashiwaqui, E. A. L. & Winemiller, K. O. (2005). Effects of river impoundment on ecosystem services of large tropical rivers: Embodied energy and market value of artisanal fisheries. *Conservation Biology* **23**, 1222–1231.

Hoenig, J. M. (1983). Empirical use of longevity data to estimate mortality rates. *Fishery Bulletin* **82**, 898-903.

Hoffmeister, T., Vet, L., Biere, A., Holsinger, K. & Filser, J. (2005). Ecological and evolutionary consequences of biological invasion and habitat fragmentation. *Ecosystems* **8**, 657-667.

Holz, J. C., Hoagland, K. D., Spawn, R. L., Popp, A. & Andersen, J. L. (1997). Phytoplankton community response to reservoir aging, 1968–92. *Hydrobiologia* **346**, 183-192.

Hunter, J. R. & Wisby, W. J. (1964). Net avoidance behavior of carp and other species of fish. *Journal of the Fisheries Research Board of Canada* **21**, 613-633.

Jackman, S. (2008). *pscl*: classes and methods for *R* developed in the political science computational laboratory. Stanford: Department of Political Science, Stanford University.

Jackson, B. C., Cambray, J. A., Eccles, D. H., Hamman, K. C. D., Tomasson, T. & White, P. N. (1983). Distribution, structure and relative abundance of fish populations. In *Limnology and fisheries potential of Lake le Roux* (Allanson, B. R. & Jackson, B. C., eds.), pp. 77-107. Pretoria: South African National Scientific Programmes report No. 77.

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

Jackson, Z. J. & Quist, M. C. (2007). Precision of scales and dorsal spines for estimating the age of common carp. *Journal of Freshwater Ecology* **22**, 231-240.

Jensen, A. C. (1970). Validation of ages determined from otoliths of Gulf of Maine cod. *Transactions of the American Fisheries Society* **99**, 359-362.

Johnson, P. T. J., Olden, J. D. & Vander Zanden, M. J. (2008). Dam invaders: impoundments facilitate biological invasions into freshwaters. *Frontiers in Ecology and the Environment* **6**, 357-363.

Jubb, R. A. (1972). The Hendrik Verwoerd Dam and Orange River fishes. *Piscator* **84**, 22-26.

Jubb, R. A. & Farquharson, F. L. (1965). The fresh water fishes of the Orange River drainage basin. *South African Journal of Science* **61**, 118-126.

Jung, B. C., Jhun, M. & Lee, J. W. (2003). Bootstrap tests for overdispersion in a zero-inflated Poisson regression model. *Biometrics* **61**, 626-629.

Kapasa, C. K. & Cowx, I. G. (1991). Post-impoundment changes in the fish fauna of Lake Itezhi-tezhi, Zambia. *Journal of Fish Biology* **39**, 783-793.

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

Khan, T. A. (2003). Dietary studies on exotic carp (*Cyprinus carpio* L.) from two lakes of western Victoria, Australia. *Aquatic Sciences - Research Across Boundaries* **65**, 272-286.

Khan, T. A., Wilson, M. E. & Khan, M. T. (2003). Evidence for invasive carp mediated trophic cascade in shallow lakes of western Victoria, Australia. *Hydrobiologia* **506-509**, 465-472.

Kiljunen, M., Grey, J., Sinisalo, T., Harrod, C., Immonen, H. & Jones, R. I. (2006). A revised model for lipid-normalizing $\delta^{13}C$ values from aquatic organisms, with implications for isotope mixing models. *Journal of Applied Ecology* **43**, 1213–1222.

King, J. R. & McFarlane, G. A. (2003). Marine fish life history strategies: applications to fishery management. *Fisheries Management and Ecology* **10**, 249-264.

Koehn, J. D. (2004). Carp (*Cyprinus carpio*) as a powerful invader in Australian waterways. *Freshwater Biology* **49**, 882-894.

Kolar, C. S. & Lodge, D. M. (2001). Progress in invasion biology: predicting invaders. *Trends in Ecology & Evolution* **16**, 199-204.

Kolar, C. S. & Lodge, D. M. (2002). Ecological predictions and risk assessment for alien fishes in North America. *Science* **298**, 1233–1236.

Kruger, E. J. & Mulder, P. F. S. (1973). Gut length and food habitats of fish - a note. *Newsletter of the Limnological Society of southern Africa* **20**, 1-7.

Kulhanek, S. A., Ricciardi, A. & Leung, B. (in press). Is invasion history a useful tool for predicting the impacts of the world's worst aquatic invasive species? *Ecological Applications*.

Lammens, E. & Hoogenboezem, W. (1991). Diets and feeding behavior. In *Cyprinid fishes* (Winfield, I. J. & Nelson, J. S., eds.), pp. 353-376. London: Chapman and Hall.

Laurenson, L. B. J. & Hocutt, C. H. (1985). Colonisation theory and invasive biota: The Great Fish River, a case history. *Environmental Monitoring and Assessment* **6**, 71-90.

, C. G. & Post, D. M. (2007). Can stable isotope ratios provide for community-wide measures of trophic structure. *Ecology* **88**, 42-48.

Leprieur, F., Brosse, S., García-Berthou, E., T.Oberdorff., Olden, J. D. & Townsend, C. R. (2009). Scientific uncertainty and the assessment of risks posed by non-native freshwater fishes. *Fish and Fisheries Research* **10**, 88–97.

Lester, N. P., Shuter, B. J. & Abrams, P. A. (2004). Interpreting the von Bertalanffy model of somatic growth in fish: the cost of reproduction. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **271**, 1625–1631.

Lewin, W.-C., Arlinghaus, R. & Mehner, T. (2006). Documented and potential biological impacts of recreational fishing: Insights for management and conservation. *Reviews in Fisheries Science* **14**, 305–367.

Lionberger, P. & Hubert, W. H. (2007). Introduced species and abiotic factors affect longitudinal variation in small fish assemblages in the Wind River Watershed, Wyoming. *Journal of Freshwater Ecology* **22**, 287-295.

Lo, N. C., Jacobson, L. D. & Squire, J. L. (1992). Indices of relative abundance for fish spotter data based on delta-lognormal models. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 2515-2526.

Lougheed, V. L., Crosbie, B. a. & Chow-Fraser, P. (1998). Predictions on the effect of common carp (*Cyprinus carpio*) exclusion on water quality, zooplankton, and submergent macrophytes in a great lakes wetland. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 1189–1197.

Lowe-McConnell, R. H. (1987). *Ecological studies in tropical fish communities.* Cambridge: Cambridge University Press (Cambridge Tropical Biology Series).

Lowe, S., Browne, M., Boudjelas, S. & De Poorter, M. (2000). 100 of the world's worst invasive alien species: A selection from the Global Invasive Species Database., p. 12. Gland, Switzerland: The Invasive Species Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN).

MacArthur, R. H. & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton: Princeton University Press.

MacDonald, P. D. M. & Pitcher, T. J. (1979). Age-groups from size-frequency data: a versatile and efficient method of analyzing distribution mixtures. *Journal of the Fisheries Research Board Canada* **36**, 987-1001.

MacNeil, M. A., Carlson, J. K. & Beerkircher, L. R. (2009). Shark depredation rates in pelagic longline fisheries: a case study from the Northwest Atlantic. *ICES Journal of Marine Science* **66**, 1-12.

Magnan, P., Proulx, R. & Plante, M. (2005). Integrating the effects of fish exploitation and interspecific competition into current life history theories: an example with lacustrine brook trout (*Salvelinus fontinalis*) populations. *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 747–757.

Marchetti, M. P., Moyle, P. B. & Levine, R. (2004). Alien fishes in California watersheds: characteristics of successful and failed invaders. *Ecological Applications* **14**, 587-596.

Matsuzak, S. S., Mabuchi, K., Takamura, N., Nishida, M. & Washitani, I. (2009). Behavioural and morphological differences between feral and domesticated strains of common carp *Cyprinus carpio*. *Journal of Fish Biology* **75**, 1206–1220.

Maunder, M. N. & Langley, A. D. (2004). Integrating the standardization of catch-per-unit-of-effort into stock assessment models: testing a population dynamics model and using multiple data types. *Fisheries Research* **70**, 389-395.

Maunder, M. N. & Punt, A. (2004). Standardizing catch and effort data: a review of recent approaches. *Fisheries Research* **70**, 171-195.

Maunder, M. N. & Starr, P. J. (2003). Fitting fisheries models to standardised CPUE abundance indices. *Fisheries Research* **63**, 43-50.

McLachlan, A. J. (1970). Some effects of annual fluctuations in water level on the larval chironomid communities of Lake Kariba. *Journal of Animal Ecology* **39**, 79-90.

Megalofonou, P., Damalas, D., Deflorio, M. & Metrio, G. D. (2009). Modeling environmental, spatial, temporal, and operational effects on blue shark by-catches in the Mediterranean long-line fishery. *Journal of Applied Ichthyology* **25**, 47-55.

Mercado-Silva, N., Helmus, M. R. & Vander Zanden, M. J. (2009). The effects of impoundment and non-native species on a river food web in Mexico's central plateau. *River Research and Applications* **25**, 1090–1108.

Millar, R. B. & Fryer, R. J. (1999). Estimating the size-selection curves of towed gears, traps, nets and hooks. *Reviews in Fish Biology and Fisheries* **9**, 89-116.

Millar, R. B. & Holst, R. (1997). Estimation of gillnet and hook selectivity using log-linear models. *ICES Journal of Marine Science* **54**, 471-477.

Minami, M., Lennert-Cody, C. E., Gao, W. & Román-Verdesoto, M. (2007). Modeling shark bycatch: the zero-inflated negative binomial regression model with smoothing. *Fisheries Research* **84**, 210-221.

Moyle, P. B. & Light, T. (1996). Fish invasions in California: do abiotic factors determine success? *Ecology* **77**, 1666-1670.

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

Myers, R. A., Bowen, K. G. & Barrowman, N. J. (1999). Maximum reproductive rate of fish at low population sizes. *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 2404-2419.

Myers, R. A., MacKenzie, D., Bowen, K. G. & Barrowman, N. (2001). What is the carrying capacity for fish in the ocean? A meta-analysis of population dynamics of North Atlantic cod. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 1464–1476.

Myers, R. A. & Pepin, P. (1990). The robustness of lognormally-based estimators of abundance. *Biometrics* **46**, 1185-1192.

Nelder, J. A. & Wedderburn, R. W. M. (1972). Generalised linear models. *Journal of the Royal Statistical Society: Series A* **132**, 107-120.

Nikolskii, G. V. (1969). *The theory of fish population dynamics as the biological background for rational exploitation and management of fishery resources.* Edinburgh: Oliver & Boyd

O'Neill, M. F. & Faddy, M. J. (2003). Use of binary and truncated negative binomial modelling in the analysis of recreational catch data. *Fisheries Research* **60**, 471-477.

Ojuok, J., Njiru, M., Mugo, J., Morara, G., Wakwabi, E. & Ngugi, C. (2008). Increase dominance of common carp, *Cyprinus carpio* L: the boon or the bane of Lake Naivasha fisheries? *African Journal of Ecology* **46**, 445-448.

Okada, E. K., Agostinho, A. A. & Gomes, L. C. (2005). Spatial and temporal gradients in artisanal fisheries of a large neotropical reservoir, the Itaipu Reservoir, Brazil. *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 714-724.

Olden, J. D., Poff, N. L. & Bestgen, K. R. (2006). Life-history strategies predict fish invasions and extirpations in the Colorado River basin. *Ecological Monographs* **76**, 25-40.

Olin, M., Rask, M., Ruuhljärvi, J., Kurkilahti, M., Ala-Opas, P. & Ylönen, O. (2002). Fish community structure in mesotrophic and eutrophic lakes of southern Finland: the relative abundances of percids and cyprinids along a trophic gradient. *Journal of Fish Biology* **60**, 593-612.

Olsen, E. M., Knutsen, H., Gjøsæter, J., Jorde, P. E., Knutsen, J. A. & Stenseth, N. C. (2004). Life history variation among local populations of Atlantic cod from the Norwegian Skagerrak coast. *Journal of Fish Biology* **64**, 1725-1730.

Ormseth, O. A. & Norcross, B. L. (2009). Causes and consequences of life-history variation in North American stocks of Pacific cod. *ICES Journal of Marine Science* **66**, 349-357.

Ortiz, M. & Arocha, F. (2004). Alternative error distribution models for standardization of catch rates of non-target species from a pelagic longline fishery: billfish species in the Venezuelan tuna longline fishery. *Fisheries Research* **70**, 275-297.

Ortiz, M., Legault, C. M. & Ehrhardt, N. M. (2000). An alternative method for estimating bycatch from the U.S. shrimp trawl fishery in the Gulf of Mexico, 1972–1995. *Fishery Bulletin* **98**.

Parkos, J. J., Santucci Jr, V. J. & Wahl, D. H. (2003). Effects of adult common carp (*Cyprinus carpio*) on multiple trophic levels in shallow mesocosms. *Canadian Journal of Fisheries & Aquatic Sciences* **60**, 182.

Partridge, L. & Sibly, R. (1991). Constraints in the evolution of life histories. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* **332**, 3-13.

Pauly, D. (1980). On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. *Journal of Conservation CIEM* **39**, 175–192.

Pauly, D. & Munro, J. L. (1984). Once more on the comparison of growth in fish and invertebrates. *ICLARM Fishbyte* **2**, 21.

Peacock, J. A. (1983). Two-dimensional goodness-of-fit testing in astronomy. *Monthly Notes of the Royal Astronomical Society* **202**, 615-627.

Penne, C. R. & Pierce, C. L. (2008). Seasonal distribution, aggregation, and habitat selection of common carp in Clear Lake, Iowa. *Transactions of the American Fisheries Society* **137**, 1050-1062.

Pennington, M. (1983). Efficient estimators of abundance, for fish and plankton surveys. *Biometrics*, **39**, 281-286.

Penston, M. J., Millar, C. P., Zuur, A. & Davies, I. M. (2008). Spatial and temporal distribution of *Lepeophtheirus salmonis* (Krøyer) larvae in a sea loch containing Atlantic salmon, *Salmo salar* L., farms on the north-west coast of Scotland. *Journal of Fish Diseases* **31**, 361-371.

Petersen, C. G. J. (1891). Eine Methode zur Bestimmung des Alters und Wuchses der Fische. *Mitteilungen der Deutschen Seefischerei-Vereins* **11**, 226-235.

Petrere, M. (1996). Fisheries in large tropical reservoirs in South America. *Lakes and Reservoirs: Research and Management* **2**, 111-133.

Phelps, Q. E., Edwards, K. R. & Willis, D. W. (2007). Precision of five structures for estimating age of common carp. *North American Journal of Fisheries Management* **27**, 103-105.

Pianka, E. R. (1970). On ‘‘r’’ and ‘‘K’’ selection. *American Naturalist* **104**, 592-597.

Pimentel, D., Lach, L., Zuniga, R. & Morrison., D. (2000). Environmental and economic costs associated with non-indigenous species in the United States. *Bioscience* **50**, 53–65.

Poddubny, A. G. & Galat, D. L. (1995). Habitat associations of upper Volga river fishes: Effects of reservoirs. *Regulated Rivers: Research and Management* **11**, 67-84.

Popp, A. & Hoagland, K. (1995). Changes in benthic community composition in response to reservoir aging. *Hydrobiologia* **306**, 159-171.

Potts, J. M. & Elith, J. (2006). Comparing species abundance models. *Ecological Modelling* **199**, 153-163.

Potts, W. M., Booth, A. J., Hecht, T. & Andrew, T. G. (2006a). The life history and fishery potential of *Labeo umbratus* (Teleostei: Cyprinidae) in five small South African reservoirs. *African Journal of Aquatic Science* **31**, 285-295.

Potts, W. M., Booth, A. J., Hecht, T. & Andrew, T. G. (2006b). Predictor variables for moggel (*Labeo umbratus*) biomass and production in small South African reservoirs. *African Journal of Aquatic Science* **31**, 107-118.

Prchalová, M., Kubečka, J., Čech, M., Frouzová, J., Draštík, V., Hohausová, E., Jůza, T., Kratochvíl, M., Matěna, J., Peterka, J., Říha, M., Tušer, M. & Vašek, M. (2009). The effect of depth, distance from dam and habitat on spatial distribution of fish in an artificial reservoir. *Ecology of Freshwater Fish* **18**, 247-260.

Prchalová, M., Kubečka, J., Vašek, M., Peterka, J., Seda, J., Jůza, T., Říha, M., Jarolím, O., Tušer, M., Kratochvíl, M., Čech, M., Draštík, V., Frouzová, J. & Hohausová, E. (2008). Distribution patterns of fishes in a canyon-shaped reservoir. *Journal of Fish Biology* **73**, 54-78.

Press, W. H., Flannery, B. P., Teukolsky, S. A. & Vetterling, W. T. (1992). *Numerical recipes in C: the art of scientific computing.* Cambridge,: Cambridge University Press.

Pringle, C. M., Freeman, M. C. & Freeman, B. J. (2000). Regional effects of hydrologic alterations on riverine macrobiota in the New World: tropical-temperate comparisons. *Bioscience* **50**, 807.

Punt, A., Walker, T. I., Taylor, B. L. & Pribac, F. (2000). Standardization of catch and effort data in a spatially-structured shark fishery. *Fisheries Research* **45**, 129-145.

Punt, A. E. (2000). Extinction of marine renewable resources: a demographic analysis. *Population Ecology* **42**, 19-27.

Quinn, T. J. & Collie, J. S. (2005). Sustainability in single-species population models. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* **360**, 147-162.

Quinn, T. J. & Deriso, R. B. (1999). *Quantitative fish dynamics*. New York: Oxford University Press.

R Development Core Team (2009). *R*: A language and environment forstatistical computing. . Vienna: R Foundation for Statistical Computing.

Rahel, F. J. (2002). Homogenization of freshwater faunas. *Annual Review of Ecology and Systematics* **33**, 291-315.

Rapp, T., Cooke, S. J. & Arlinghaus, R. (2008). Exploitation of specialised fisheries resources: The importance of hook size in recreational angling for large common carp (*Cyprinus carpio* L.). *Fisheries Research* **94**, 79-83.

Regier, H. A. & Robson, D. S. (1966). Selectivity of gillnets, especially to lake white fish. *Journal of the Fisheries Research Board Canada* **23**, 423-454.

Reznick, D., Bryant, M. J. & Bashey, F. (2002). r- and K-Selection Revisited: The Role of Population Regulation in Life-History Evolution. *Ecology* **83**, 1509-1520.

Richardson, T. J., Booth, A. J. & Weyl, O. L. F. (2009). Rapid biological assessment of the fishery potential of Xonxa Dam, near Queenstown, South Africa. *African Journal of Aquatic Science* **34**, 87-96.

Ricker, W. E. (1975). Computation and interpretation of biological statistics of fish populations. *Fisheries Research Board of Canada Bulletin* **191**, 1-382.

Rodriguez-Marin, E., Arrizabalaga, H., Ortiz, M., Rodriguez-Cabello, C., Moreno, G. & Kell, L. T. (2003). Standardization of bluefin tuna, *Thunnus thynnus*, catch per unit effort in the baitboat fishery of the Bay of Biscay (Eastern Atlantic). *ICES Journal of Marine Science* **60**, 1216-1231.

Roff, D. A. (1984). The evolution of life history parameters in teleosts. *Canadian Journal of Fisheries and Aquatic Sciences* **41**, 989–1000.

Rooper, C. N. & Martin, M. H. (2009). Predicting presence and abundance of demersal fishes: a model application to shortspine thornyhead *Sebastolobus alascanus*. *Marine Ecology Progress Series* **379**, 253–266.

Rose, K. A., Cowan Jr, J. H., Winemiller, K. O., Myers, R. A. & Hilborn, R. (2001). Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. *Fish and Fisheries* **2**, 293-327.

Rosenberg, D. M., McCully, P. & Pringle, C. M. (2000). Global-scale environmental effects of hydrological alterations: Introduction. *Bioscience* **50**, 746-751.

Rutaisire, J. & Booth, A. J. (2005). Reproductive biology of ningu, *Labeo victorianus* (Pisces : Cyprinidae), in the Kagera and Sio Rivers, Uganda. *Environmental Biology of Fishes* **73**, 153-162.

Schnute, J. (1981). A versatile growth model with statistically stable parameters. *Canadian Journal of Fisheries and Aquatic Sciences* **38**, 1128-1140.

Schoonbee, H. J. (1969). Notes on the food habits of fish in Lake Barberspan, Western Transvaal, South Africa. *Verhandlungen der Internationalen Vereinigung fur theoretische und angewandte Limnologie* **17**, 689-701.

Scott, L. E. P., Skelton, P. H., Booth, A. J., Verheust, L., Harris, R. & Dooley, J. (2006). Atlas of southern African freshwater fishes. *Smithiana* **2**, 303 pp.

Seda, J., Petrusek, A., Machacek, J. & Smilauer, P. (2007). Spatial distribution of the *Daphnia longispina* species complex and other planktonic crustaceans in the heterogeneous environment of canyon-shaped reservoirs. *Journal of Plankton Research* **29**, 619-628.

Shono, H. (2008). Application of the Tweedie distribution to zero-catch data in CPUE analysis. *Fisheries Research* **93**, 154-162.

Shuter, B. J., Lester, N. P., LaRose, J., Purchase, C. F., Vascotto, K., Morgan, G., Collins, N. C. & Abrams, P. A. (2005). Optimal life histories and food web position: linkages among somatic growth, reproductive investment, and mortality. *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 738-746.

Sibbing, F. (1988). Specializations and limitations in the utilization of food resources by the carp, (*Cyprinus carpio*): a study of oral food processing. *Environmental Biology of Fishes* **22**, 161-178.

Sibbing, F. A. & Uribe, R. (1984). Regional specializations in the oro-pharyngeal wall and food processing in the carp (*Cyprinus carpio* L.). *Netherlands Journal of Zoology* **35**, 377-422.

Simon, C. A. & Booth, A. J. (2007). Population structure and growth of polydorid polychaetes that infest cultured abalone *Haliotis midae*. *African Journal of Marine Science* **29**, 499-509.

Sivakumaran, K. P., Brown, P., Stoessel, D. & Giles, A. (2003). Maturation and reproductive biology of female wild carp, *Cyprinus carpio*, in Victoria, Australia. *Environmental Biology of Fishes* **68**, 321-332.

Skelton, P. (1986). Fish of the Orange-Vaal system. In *The ecology of river systems* (Davies, B. R. & Walker, K. F., eds.), pp. 143-159. Dordrecht: Dr W. Junk Publishers.

Skelton, P. (2001). *A Complete Guide to the Freshwater Fishes of Southern Africa.* Cape Town, South Africa: Struik Publisher.

Skelton, P. H., Tweddle, D. & Jackson, P. B. N. (1991). Cyprinids of Africa. In *Cyprinid Fishes. Systematics, Biology and Exploitation.* (Winfield, I. J. & Nelson, J. S., eds.), pp. 211-239. London: Chapman & Hall.

Smith, B. B. & Walker, K. F. (2004). Spawning dynamics of common carp in the River Murray, South Australia, shown by macroscopic and histological staging of gonads. *Journal of Fish Biology* **64**, 336-354.

Smith, K. A. & Deguara, K. (2003). Formation and annual periodicity of opaque zones in sagittal otoliths of *Mugil caphalus* (Pisces: Mugilidae). *Marine and Freshwater Research* **54**, 57-67.

Smith, S. J. (1990). Use of statistical models for the estimation of abundance from groundfish trawl surveys. *Canadian Journal of Fisheries and Aquatic Sciences* **47**, 894-903.

Smith, S. J. (1997). Bootstrap confidence limits for groundfish trawl survey estimates of mean abundance. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 606-630.

Smyth, G. K. (2008). *statmod*: statistical modelling. R Package Version 1.3.6.

Sousa, P., Lemos, R. T., Gomes, M. C. & Azevedo, M. (2007). Analysis of horse mackerel, blue whiting, and hake catch data from Portuguese surveys (1989–1999) using an integrated GLM approach. *Aquatic Living Resources* **20**, 105-116.

Stearns, S. C. (1976). Life-history tactics: A review of the ideas. *The Quarterly Review of Biology* **51**, 3-47.

Stearns, S. C. (1992). *The evolution of life histories*. Oxford: Oxford University Press.

Steffanson, G. (1996). Analysis of groundfish survey abundance data: combining the GLM and delta approaches. *ICES Journal of Marine Science* **53**, 577-588.

Su, N.-J., Yeh, S.-Z., Sun, C.-L., Punt, A. E., Chen, Y. & Wang, S.-P. (2008). Standardizing catch and effort data of the Taiwanese distant-water longline fishery in the western and central Pacific Ocean for bigeye tuna, *Thunnus obesus*. *Fisheries Research* **90**, 235-246.

Swartzman, G., Huang, C. & Kaluzny, S. (1992). Spatial analysis of Bering Sea groundfish survey data using generalized additive models. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 1366-1378.

Swierzowskia, A., Godlewskab, M. & Półtorakb, T. (2000). The relationship between the spatial distribution of fish, zooplankton and other environmental

parameters in the Solina reservoir, Poland. *Aquatic Living Resources* **13**, 373–377.

Syrjala, S. E. (2000). Critique on the use of the delta distribution for the analysis of trawl survey data. *ICES Journal of Marine Science* **57**, 831-842.

Tedesco, P., Hugueny, B., Oberdorff, T., Dürr, H., Mérigoux, S. & de Mérona, B. (2008). River hydrological seasonality influences life history strategies of tropical riverine fishes. *Oecologia* **156**, 691-702.

Tempero, G. W., Ling, N., Hicks, B. J. & Osborne, M. W. (2006). Age composition, growth, and reproduction of koi carp (*Cyprinus carpio*) in the lower Waikato region, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **40**, 571-583.

Thackeray, S. J., Glen George, D., Jones, R. I. & Winfield, I. J. (2004). Quantitative analysis of the importance of wind-induced circulation for the spatial structuring of planktonic populations. *Freshwater Biology* **49**, 1091-1102.

Thompson, S. K. (1992). *Sampling.* New York: Wiley & Sons, Inc.

Tómasson, T. (1983). The biology and management considerations of abundant large cyprinids in Lake Le Roux, Orange River, South Africa. PhD Thesis, Rhodes University, Grahamstown, South Africa.

Tómasson, T., Bruton, M. N. & Hamman, K. C. D. (1985). The demography and management of large cyprinids in a reservoir on the orange river, South Africa. *Fisheries Research (Amsterdam)* **3**, 279-308.

Tómasson, T., Cambray, J. A. & Jackson, P. B. N. (1984). Reproductive biology of four large riverine fishes (Cyprinidae) in a man- made lake, Orange River, South Africa. *Hydrobiologia* **112**, 179-195.

Treer, T., Varga, B., Safner, R., Anicic, I., Piria, M. & Odak, T. (2003). Growth of the common carp (*Cyprinus carpio*) introduced into the Mediterranean Vransko Lake. *Journal of Applied Ichthyology* **19**, 383-386.

Tweddle, D. & Davies, M. T. T. (1997). Preliminary observations on the fish populations of the recently-impounded Katse reservoir, Lesotho. *Southern African Journal of Aquatic Sciences* **23**, 7-20.

van Rensburg, B. J., Weyl, O. L. F., Davies, S. J., van Wilgen, L. J., Peacock, D. S., Spear, D. & Chimimba, C. T. (in press). Invasive vertebrates of South Africa. In *Biological invasions: economic and environmental costs of alien plant, animal, and microbe species.* (Pimentel, D., ed.). Boca Raton, Florida: CRC Press.

van Zyl, C. J., Hay, C. J. & Steyn, g. J. (1995). Some aspects of the reproduction biology of *Labeo capensis* (Smith, 1941) (Pisces, Cyprinidae) in relation to exploitation and extreme environmental conditions in Hardap Dam, Nambia. *Southern African Journal of Aquatic Sciences* **21**, 88-98.

Vander Zanden, J. & Olden, J. D. (2008). A management framework for preventing the secondary spread of aquatic invasive species. *Canadian Journal of Fisheries and Aquatic Sciences* **65**, 1512–1522.

Vander Zanden, M. J., Casselman, J. M. & Rasmussen, J. B. (1999). Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature* **401**, 464-467.

Vanderpuye, C. J. (1981). Further observation of the distribution and abundance of fish stocks in Volta Lake, Ghana. *Fisheries Research* **1**, 319-343.

Venables, W. N. & Dichmont, C. M. (2004). GLMs, GAMs and GLMMs: an overview of theory for applications in fisheries research. *Fisheries Research* **70**, 319-337.

Venables, W. N. & Ripley, B. D. (2002). *Modern Applied Statistics with S.* New York: Springer.

Vila-Gispert, A. & Moreno-Amich, R. (2002). Life-history patterns of 25 species from European freshwater fish communities. *Environmental Biology of Fishes* **65**, 387-400.

Vilizzi, L. & Walker, K. F. (1999). Age and growth of common carp, *Cyprinus carpio*, in the River Murray, Australia: validation, consistency of age interpretation, and growth models. *Environmental Biology of Fishes* **54**, 77-106.

Vilizzi, L., Walker, K. F., Jain, T., McGlennon, D. & Tsymbal, V. (1998). Interpretability and precision of annulus counts for calcified structures in carp, *Cyprinus carpio* L. *Archiv fuer Hydrobiologie* **143**, 121-127.

Weber, M. J. & Brown, M. L. (2009). Effects of common carp on aquatic ecosystems 80 years after "carp as a dominant": ecological insights for fisheries management. *Reviews in Fisheries Science* **17**, 524–537.

Welsh, A. H., Cunningham, R. B. & Chambers, R. (2000). Methodology for estimating the abundance of rare animals: seabird nesting on north-east Herald Cay. *Biometrics* **56**, 22-30.

Welsh, A. H., Cunningham, R. B., Donnelly, C. F. & Lindenmayer, D. B. (1996). Modelling the abundance of rare species: statistical models for counts with extra zeros. *Ecological Modelling* **88**, 297-308.

Weyl, O. L. F. & Booth, A. J. (1999). On the life history of a cyprinid fish, *Labeo cylindricus*. *Environmental Biology of Fishes* **55**, 215–225.

Weyl, O. L. F., Potts, W., Rouhani, Q. & Britz, P. (2007). The need for inland fisheries policy in South Africa: A case study of the North West Province. *Water SA* **33**, 497-504.

Weyl, O. L. F., Stadtlander, T. & Booth, A. J. (2009). Establishment of translocated populations of smallmouth yellowfish, *Labeobarbus aeneus* (Pisces: Cyprinidae), in lentic and lotic habitats in the Great Fish River system, South Africa. *African Zoology* **44**, 93-105.

Winemiller, K. (2005). Life history strategies, population regulation, and implications for fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 872-885.

Winemiller, K. & Rose, K. A. (1992). Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 2196-2218.

Winemiller, K. O. (1989). Patterns of variation in life history among South American fishes in seasonal environments. *Oecologia* **81**, 225-241.

Winemiller, K. O. (1992). Life history and the effectiveness of sexual selection. *Oikos* **63**, 318-327.

Winker, H., Ellender, B. R., Weyl, O. L. F. & Booth, A. J. (2010). Validation of growth zone deposition in otoliths of two large endemic cyprinids in Lake Gariep, South Africa. *African Zoology* **45**, 133-138.

Ye, Y., Al-Husaini, M. & Al-Baz, A. (2001). Use of generalized linear models to analyze catch rates having zero values: the Kuwait driftnet fishery. *Fisheries Research* **53**, 151-168.

Yee, T. W. (2010). VGLMs and VGAMs: An overview for applications in fisheries research. *Fisheries Research* **101**, 116-126.

Zambrano, L. & Hinojosa, D. (1999). Direct and indirect effects of carp (*Cyprinus carpio* L.) on macrophyte and benthic communities in experimental shallow ponds in central Mexico. *Hydrobiologia* **408-409**, 131-138.

Zambrano, L., Martinez-Meyer, E., Menezes, N. & Townsend Peterson, A. (2006). Invasive potential of common carp (*Cyprinus carpio*) and Nile tilapia (*Oreochromis niloticus*) in American freshwater systems. *Canadian Journal of Fisheries and Aquatic Sciences* **63**, 1903-1910.

Zambrano, L., Scheffer, M. & Martinez-Ramos, M. (2001). Catastrophic response of lakes to benthivorous fish introduction. *Oikos* **94**, 344-350.

Zambrano, L., Valiente, E. & Vander Zanden, M. (2010). Food web overlap among native axolotl (*Ambystoma mexicanum*) and two exotic fishes: carp (*Cyprinus carpio*) and tilapia (*Oreochromis niloticus*) in Xochimilco, Mexico City. *Biological Invasions* **12**, 3061-3069.

APPENDIX I

Winker, H., Ellender, B.R., Weyl, O.L.F. & Booth, A.J. (2010). Validation of growth zone deposition in otoliths of large endemic cyprinids in Lake Gariep, South Africa. ***African Zoology*** **45, 133-138.**

Validation of growth zone deposition in otoliths of two large endemic cyprinids in Lake Gariep, South Africa

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We tested the hypothesis that growth zones in the astericus otoliths of smallmouth yellowfish (*Labeobarbus aeneus*) and Orange River mudfish (*Labeo capensis*) were deposited annually. Two methods, fluorochrome marking and edge analysis of otoliths were used. For fluorochrome marking, specimens of both species were injected with 60 mg/kg fish mass oxytetracycline hydrochloride (OTC) and released into large earthen ponds under ambient conditions adjacent to Lake Gariep. Twenty-three *L. aeneus* and one *L. capensis* were recaptured 10–14 months later. Edge analysis was based on the optical interpretation of *L. aeneus* (n = 342) and *L. capensis* (n = 512) otolith margins collected between November 2006 and May 2008 from Lake Gariep. The frequency distribution of opaque margins over time was fitted using a binomial periodic regression. The estimated cycle length was not significantly different from a hypothesized 12 months for both species. The number of growth zones distal to the OTC mark was consistent with findings from the edge analysis, providing evidence that growth zones in astericus otoliths of both species can be interpreted as annuli.

Key words: oxytetracycline hydrochloride, validation, chemical tagging, edge analysis, otolith, Cyprinidae, Orange River, binomial periodic regression.

Determining fish age is an important component of any biological study because it allows for the estimation of rates of maturity, mortality and growth (Campana & Thorrold 2000). Fish are usually aged by counting growth zones on calcified structures such as otoliths. These growth zones, visible as alternating opaque and translucent bands, are deposited as a consequence of variations in calcium metabolism, which, in fishes, is often controlled by seasonal factors such as temperature, reproductive investment and feeding (Campana 1999). Consequently, species-specific and locality-specific variations in the frequency of growth zone deposition have been reported (Fowler 1990; Lou 1992; Weyl & Hecht 1998). The determination of the rate at which growth zones are deposited is therefore considered a fundamental requirement for the accurate interpretation of age (Campana 2001). Two commonly applied methods of validation are chemical marking and edge analysis (Campana 2001; Campana 2005).

Orange River mudfish *Labeo capensis* (A. Smith, 1841) and smallmouth yellowfish *Labeobarbus aeneus* (Burchell, 1822) are both large cyprinids endemic to the westward flowing Orange–Vaal drainage basin (Jubb & Farquharson 1965; Skelton 2001). In 1975, the completion of the Orange–Fish River inter-basin transfer scheme caused a southward extension of their distribution into the Fish River and Sundays River (Cambray & Jubb 1977). With increased interest in their invasion biology, further studies, including aspects on age and growth, were conducted in the invaded Fish River and its impoundments (Laurenson *et al.* 1989; Weyl *et al.* 2009). In earlier studies, interpretation of scales was commonly employed to determine age and growth of these species (Mulder 1973a,b; Hamman 1981), whereas Tómasson *et al.* (1985) and Laurenson *et al.* (1989) based their results on the interpretation of whole lapillus otoliths. In recent years, however, astericus otoliths have become the primary hard structure used in ageing studies on temperate populations of large cyprinids in South Africa (Potts *et al.* 2006; Richardson *et al.* 2009; Weyl *et al.* 2009). Within the Cyprinidae, astericus otoliths are the largest of three otolith pairs and were therefore considered the most suitable hard structure for ageing (Vilizzi & Walker 1999; Brown *et al.* 2004; Phelps *et al.* 2007). To date, only two studies (Tómasson *et al.* 1985; Weyl *et al.* 2009) have validated the periodicity of growth zone formation using edge analysis. Both found that the deposition rate was annual.

As growth zone deposition rates can vary between localities, this study attempts to validate

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the deposition rate of growth zones in astericus otoliths of *L. capensis* and *L. aeneus* in Lake Gariep. Chemical marking and edge analysis was used to test the hypothesis that a single growth zone is deposited on the astericus otoliths of the two species each year.

Materials & Methods

The study was conducted on Lake Gariep, a 364 km^2 impoundment of the upper Orange River (30°38′S, 25°46′E; 1250 m above mean sea level). The climate in this region is considered as semi-arid and rainfall is seasonal at about 400 mm per annum, with most precipitation occurring in summer (Keulder 1979). The dam's water level is a function of the inflow from the Orange River, which peaks in spring and summer, and the release of water for power generation. Although fluctuations occur, water level is generally highest during the early summer months and lowest by the end of winter (Ellender 2009). The mean surface water temperature in summer was 21.4°C (range: 16.6–26.0°C) and in winter was 10.2 °C (range: 8.7–11.3°C). Annual average surface water temperature between May 2007 and May 2008 was 15.9°C.

The vast surface area of the dam and the low exploitation rates of the two species by anglers (Ellender *et al.* 2009) precluded the use of mark-recapture of chemically tagged wild fish as a suitable method. Chemically marked fish were, therefore, released into four earthen ponds under ambient conditions situated at the Lake Gariep State Fish Hatchery, located 3.2 km below the dam wall on the banks of the Orange River (30°37′S, 25°28′E). Four ponds were used. Two ponds were 40 m long × 20 m wide × 1 m deep and two were 50 m long × 25 m wide × 1.5 m deep. Wild fish were caught by angling during March and April 2007 from Lake Gariep and from the Orange River below the dam wall (30°37′S, 25°28′E). A total of 48 *L. aeneus* ranging from 199–545 mm fork length (L_F) and two *L. capensis* of 338 and 405 mm L_F were used. On capture, fish were placed in a water-filled canvas bag and carried to an oxygenated holding tank that contained 0.2 ml/l of the anaesthetic 2-Phenoxyethanol (Sigma-Aldrich Chemicals, Steinheim, Germany) to minimize post-capture stress until transported to the Lake Gariep Fish Hatchery. On site, fish were injected with 60 mg/kg fish mass Oxytetracycline hydrochloride solution (OTC; HiTet 120; Bayer, Leverkusen, Germany) prior to release into the ponds. OTC is a calcium-chelating chemical that is rapidly incorporated into otoliths and produces a fluorescent mark when viewed under ultraviolet light (Campana 1999). As a control and to monitor the growth rates during the course of the experiment, 17 *L. aeneus* were tagged with T-bar anchor tags (model TBA-2) and exclusively released into one of the bigger ponds, which also contained 20 common carp (*Cyprinus carpio*) that were held there for the purpose of a different experiment. Stocking density was kept well below one fish per 90 m^3 and no supplementary feeding was conducted. Fish were re-captured after 13–14 months in May 2008, measured to nearest millimetre L_F, sacrificed, sex was determined and the astericus otoliths removed and stored dry. Otoliths were stored in the dark to prevent the degrading effect that UV light has on OTC.

Otoliths were examined submerged in methyl salicylate and viewed whole under reflected fluorescent (460–490 nm and 510–550 nm) and transmitted white light to determine position of fluorescent mark and number of opaque zones distal to the mark, respectively. To count the total number of growth zones, otoliths were optically assessed under transmitted light using varying magnifications (×10–40). Growth zones were visible as alternating translucent and opaque zones (Fig. 1).

For edge analysis a total of 386 *L. aeneus* and 564 *L. capensis* otolith pairs were sampled from Lake Gariep. Most were collected during bi-monthly gillnet surveys conducted between March 2007 and May 2008. Additional samples were obtained from anglers during bank angling competition events (November 2006, January 2007, April 2007 and October 2007). All fish were sacrificed, measured to the nearest millimetre fork length (L_F) and astericus otoliths were removed and stored dry. The optical appearance of the edge of the otolith was assessed (under ×10–40 magnification and submerged in methyl salicylate) and categorized as opaque zone present or absent. Results were noted as Bernoulli variables (1 = present, 0 = absent). Otoliths containing more than eight growth increments were not considered for edge analysis because the width of individual increments at the edge of the otolith became too narrow to accurately discern the optical composition of the margin.

Edge analysis is based on the assumption that the relative frequency of edge zones follows a yearly sinusoidal cycle when plotted against time (Campana 2001). As a result, binary results were

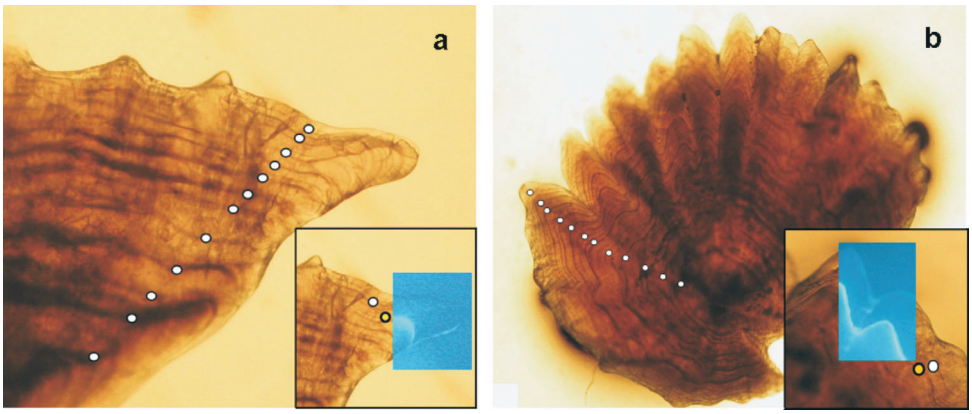

Fig. 1. Photomicrographs using transmitted light showing whole astericus otoliths of *Labeobarbus aeneus* (**a**) and *Labeo capensis* (**b**). Inserts show magnified margins with overlaid portions of the same sections viewed with fluorescent light. White dots represent opaque zones and yellow dots in magnified inserts indicate the position of the OTC marks.

expressed as the proportion of otoliths with an opaque zone present per month and modelled using a periodic logistic regression (Flury & Levri 1999) of the form:

$$Logit\,(\hat{O}_i) = \beta_0 + \beta_1 \sin\left(2\pi\left(\frac{MOY_i}{PE}\right)\right) + \beta_2 \cos\left(2\pi\left(\frac{MOY_i}{PE}\right)i\right),$$

where *logit* is the link function for the binomial distribution, $\hat{O}_i$ is the expected proportion of otoliths with an opaque zone present at the margin for each angular transformed month of any year MOY_i (with January being assigned a value of 0 and December 11), *PE* is the assumed monthly periodicity of growth deposition (i.e. 12 for an annual cycle) and β_0, β_1, β_2 the regression coefficients (Beamish *et al.* 2005). Regression parameters were estimated by minimizing the binomial negative log-likelihood function of the form:

$$-LL = -\sum_{i=0}^{11} [m_i \ln(\hat{O}_i) + (n_i - m_i)\ln(1-\hat{O}_i)]\ ,$$

where n_i is the number of otoliths examined per month and m_i represents the number of otoliths with an opaque zone present on the margin. To test the null hypothesis (H_0) that growth zone deposition is annual, we then conducted a likelihood ratio test $\chi^2_k = 2(LL_{full} - LL_{reduced})$, where $LL_{reduced}$ is the log-likelihood for the *reduced* model with the constraint that *PE* is fixed at 12, LL_{full} is the log-likelihood for the full model where *PE* is estimated, and *k* is difference in estimated parameters of the two models. Similarly, we tested the alternative hypothesis (H_a) that growth zone deposition is bimodal where *PE* was fixed at six. A significance level of $P \leq 0.05$ was used for all tests.

Results & Discussion

Of the 47 *L. aeneus* and two *L. capensis* that were injected with OTC, a total of 23 *L. aeneus* and one *L. capensis* were recaptured. In January 2007, two *L. aeneus* were caught from the ponds and successful incorporation of OTC, visible as a strong fluorescent mark, was confirmed. All other fish were recaptured in May 2008 after 13–14 months (Table 1). Only three of the 17 tagged fish (17%) were recaptured, of which only two retained the T-bar tag (Table 1). In contrast, 15 out of the 19 *L. aeneus* (78%) that were not tagged were recaptured. It could not be uncoupled whether the low survival rate of tagged fish was a direct consequence of the tagging, or was as a result of the presence of common carp in the pond. Common carp can increase turbidity and nutrient cycling in ponds through their bottom grubbing feeding behaviour. This has been shown to have significant impacts on the zoobenthos and zooplankton communities (Zambrano & Hinojosa 1999; Khan *et al.* 2003). *Labeo aeneus* is known for its visual prey selection (Eccles 1986) and it was suggested that decreased water transparency has negative effects on their foraging success and therefore survival (Tómasson *et al.* 1985). It is, however, also likely that the high mortality rate could have been a result of tagging and it is therefore recommended that survival rates of tagged *L. aeneus* are assessed prior to conducting larger mark–recapture studies on this species in the future. The two tagged specimens

Table 1. Summary of recaptured *Labeobarbus aeneus* and *Labeo capensis* that were injected with oxytetracycline (OTC). The summary includes the total number of observed growth increments and those that were deposited prior (pre-F) and posterior (post-F) to the fluorescent mark.

Species	Date injected	Date of recapture	Time at liberty (month)	L_F (mm)	Sex	OTC mark	Growth zones		
							Pre-F	Post-F	Total
L. aeneus	Mar/Apr '07	Jan '08	9–10	458	f	Yes	9	1	10
	Mar/Apr '07	Jan '08	9–10	361	m	Yes	6	1	7
	Mar/Apr '07	May '08	13–14	387	f	Yes	7	1	8
	Mar/Apr '07	May '08	13–14	412	f	Yes	10	1	11
	Mar/Apr '07	May '08	13–14	433	m	No	–	–	–
	Mar/Apr '07	May '08	13–14	400	m	No	–	–	–
	Mar '07 *	May '08	14	515	f	Yes	13	1	14
	Mar/Apr '07	May '08	13–14	472	f	Yes	10	1	11
	Mar/Apr '07	May '08	13–14	407	f	Yes	8	1	9
	Mar/Apr '07	May '08	13–14	399	m	Yes	8	1	9
	Mar/Apr '07	May '08	13–14	414	f	Yes	9	1	10
	Mar/Apr '07	May '08	13–14	475	f	Yes	10	1	11
	Mar '07 *	May '08	14	480	f	Yes	12	1	13
	Mar/Apr '07	May '08	13–14	420	f	Yes	9	1	10
	Mar/Apr '07	May '08	13–14	385	m	Yes	8	1	9
	Mar/Apr '07	May '08	13–14	421	f	Yes	9	1	10
	Mar/Apr '07	May '08	13–14	400	m	Yes	10	1	11
	Mar/Apr '07	May '08	13–14	425	f	Yes	9	1	11
	Mar/Apr '07	May '08	13–14	407	m	Yes	10	1	10
	Mar/Apr '07	May '08	13–14	442	f	Yes	–	1	11
	Mar/Apr '07	May '08	13–14	440	f	Yes	8	1	–
	Mar/Apr '07	May '08	13–14	405	f	Yes	10	1	9
	Mar/Apr '07	May '08	13–14	416	f	Yes	11	1	11
	Mar/Apr '07	May '08	13–14	467	f	Yes	12	1	12
	Mar/Apr '07	May '08	13–14	416	m	Yes	10	1	10
L. capensis	Mar '07	May '08	14	407	f	Yes	11	1	12

*Recaptured fish that retained the T-bar tag.

that were recaptured at 480 mm and 515 mm L_F and had grown by 16 and 24 mm, respectively.

A fluorescent mark was visible in 21 of the 23 marked *L. aeneus* and in the single recaptured *L. capensis* (Fig. 1). A visible OTC band in 92% of the marked specimens can be considered as a high rate of success. In a similar study on African sharptooth catfish (*Clarias gariepinus*), Weyl & Booth (2008) found that there was no discernible fluorescent mark in 29% of their sample. They attributed this to either insufficient OTC administration or to unfavourable combination of optical properties on the margin of the otolith examined. While the reasons for a lack of a fluorescent zone in two *L. aeneus* specimens remain unclear they may be similar to those hypothesized by Weyl & Booth (2008).

The total number of growth increments on otoliths ranged from seven to 12 for *L. aeneus* and was estimated at 12 for the *L. capensis* specimen. In all fish where a fluorescent band was visible on the otolith, a single growth increment containing one opaque zone and at least one translucent zone was visible distal to the fluorescent band (Table 1).

These results were consistent with the results from edge analyses (Table 2). For both species, we failed to reject the null hypothesis that one opaque deposition occurred annually in otoltiths of *L. aeneus* ($\chi^2 = 0.047$, $k = 1$, $P = 0.84$) and *L. capensis* ($\chi^2 = 1.89$, $k = 1$, $P = 0.17$) but we rejected the alternative hypothesis that growth zone deposition was bimodal, *L. aeneus* ($\chi^2 = 58.53$, $k = 1$, $P < 0.05$) and *L. capensis* ($\chi^2 = 107.93$, $k = 1$, $P < 0.05$).

For both species, the unimodal periodic regression models best described the temporal proportion of opaque zone deposition on the edge of otoliths over a one year period (Fig. 2). Observed and predicted data indicated that the highest proportion of opaque zone deposition in the otoliths of both species occurred in winter (June–September),

Table 2. Parameter estimates from the logistic periodic regression analysis predicting the temporal proportion of opaque zone deposition over a one year period for *Labeobarbus aeneus* and *Labeo capensis* in Lake Gariep, South Africa. The periodicity (*PE*) was estimated for the full models and fixed for the unimodal and bimodal models. *LL* = log-likelihood estimates

Parameter	*Labeobarbus aeneus* models			*Labeo capensis* models		
	Full	Unimodal	Bimodal	Full	Unimodal	Bimodal
β_0	0.73	0.76	0.89	–1.12	–1.43	–1.06
β_1	–0.36	–0.46	–0.09	–0.77	0.27	0.13
β_2	–1.51	–1.49	–0.07	–1.62	–1.93	0.66
PE	12.28	12	6	10.12	12	6
d.f.	4	3	3	4	3	3
LL	–175.34	–175.36	–204.60	–223.17	–224.11	–277.13

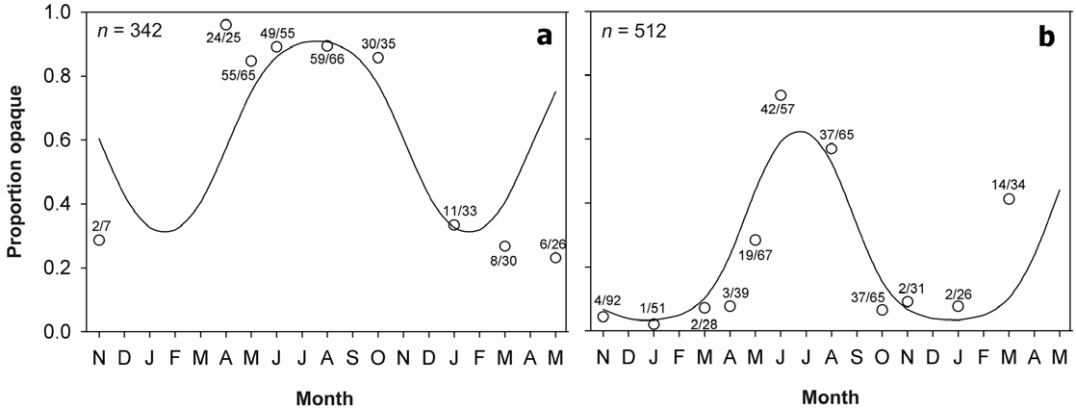

Fig. 2. Proportion of otoliths with an opaque zone on the margin for *Labeobarbus aeneus* (**a**) and *Labeo capensis* (**b**) based on data collected between November 2006 and May 2008 in Lake Gariep, South Africa. The solid line represents the predicted binomial periodic regression model. Opaque margins and total number of otoliths examined per month are denoted as numerator and denominator, respectively.

when water temperatures were at a minimum.

Mark–recapture of chemically tagged fish is considered as one of the best validation methods available, whereas indirect validation techniques such as edge analysis and marginal increment analysis have been criticized for relying on subjective optical criteria for the interpretation of the composition of the otolith margins (Campana 2001). Although, the OTC experiment in the current study had the constraint that marked fish grew under ambient conditions in earthen ponds and not at liberty in their natural environment, it provides evidence for an annual deposition of a single growth zone in the otoliths of both species. This was corroborated by the results from edge analyses and is consistent with earlier studies by Tómasson *et al.* (1985) and Weyl *et al.* (2009) that were based on marginal increment analysis and edge analysis, respectively. Under comparable environmental conditions, growth zones in asteriscus otoliths of both species can therefore be interpreted as annuli.

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REFERENCES

BEAMISH, C.A., BOOTH, A.J. & DEACON, N. 2005. Age, growth and reproduction of largemouth bass, *Micropterus salmoides,* in Lake Manyame, Zimbabwe. *African Zoology* **40**: 63–69.

BROWN, P., GREEN, C., SIVAKUMARAN, K.P., STOESSEL, D. & GILES, A. 2004. Validating otolith annuli for annual age determination of common carp. *Transactions of the American Fisheries Society* **133**: 133–196.

CAMBRAY, J.A. & JUBB, R.A. 1977. Dispersal of fishes via the Orange–Fish tunnel, South Africa. *Journal of the Limnological Society of Southern Africa* **3**: 33–55.

CAMPANA, S.E. 1999. Chemistry and composition of fish otoliths: pathways, mechanisms and applications. *Marine Ecology Progress Series* **188**: 263–297.

CAMPANA, S.E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology* **59**: 197–242.

CAMPANA, S.E. 2005. Otolith science entering the 21st century. *Marine and Freshwater Research* **56**: 485–495.

CAMPANA, S.E. & THORROLD, S.R. 2000. Otoliths, increments, and elements: keys to a comprehensive understanding of fish populations? *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 30–38.

ECCLES, D.H. 1986. Diet of the cyprinid fish *Barbus aeneus* (Burchell) in the P.K. le Roux Dam, South Africa, with special reference to the effect of turbidity on zooplanktivory. *South African Journal of Zoology* **21**: 257–263.

ELLENDER, E.R. 2009. The impact of angling on smallmouth and largemouth yellowfish, *Labeobarbus aeneus* and *Labeobarbus kimberleyensis,* in Lake Gariep, South Africa. MSc thesis, Rhodes University, Grahamstown, South Africa.

ELLENDER B.R., WEYL, O.L.F. & WINKER, H. (2009). Who uses the fishery resources in South Africa's largest impoundment? Characterising subsistence and recreational fishing sectors on Lake Gariep. *Water S.A.* **35**: 679–684.

FLURY, B.D. & LEVRI, E.P. 1999. Periodic logistic regression. *Ecology* **80**: 2254–2260.

FOWLER, A.J. 1990. Validation of annual growth increments in the otoliths of a small, tropical coral-reef fish. *Marine Ecology Progress Series* **64**: 25–38.

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

JUBB, R.A. & FARQUHARSON, F.L. 1965. The freshwater fishes of the Orange River drainage basin. *South African Journal of Science* **61**: 118–126.

KHAN, T.A., WILSON, M.E. & KHAN, M.T. 2003. Evidence for invasive carp mediated trophic cascade in shallow lakes of western Victoria, Australia. *Hydrobiologia* **506–509**: 465–472.

KEULDER, P.C. 1979. Hydrochemistry of the upper Orange River catchment. *Journal of the Limnological Society of Southern Africa* **5**: 39–46.

LAURENSON, L.B.J., HOCUTT, C.H. & HECHT, T. 1989. An evaluation of the success of invasive fish species of the Great Fish River. *Journal of Applied Ichthyology* **1**: 28–34.

LOU, D.C. 1992. Validation of annual growth bands in the otolith of tropical parrotfishes (*Scarus schlegeli* Bleeker). *Journal of Fish Biology* **41**: 775–790.

MULDER, P.F.S. 1973a. Aspects of the ecology of *Barbus kimberleyensis* and *Barbus holubi* in the Vaal River. *Zoologica Africana* **8**: 1–14.

MULDER, P.F.S. 1973b. Aspects on the ecology of *Labeo capensis* and *Labeo umbratus* in the Vaal River. *Zoologica Africana* **8**: 15–24.

PHELPS, Q.E., EDWARDS, K.R. & WILLIS, D.W. 2007. Precision of five structures for estimating age of common carp. *North American Journal of Fisheries Management* **27**: 103–105.

POTTS, W.M., BOOTH, A.J., HECHT, T. & ANDREW, T.G. 2006. The life history and fishery potential of *Labeo umbratus* (Teleostei: Cyprinidae) in five small South African reservoirs. *African Journal of Aquatic Science* **31**: 285–295.

RICHARDSON, T.J., BOOTH, A.J. & WEYL, O.L.F. 2009. Rapid biological assessment of the fishery potential of Xonxa Dam, near Queenstown, South Africa. *African Journal of Aquatic Science* **34**: 87–96.

SKELTON, P. 2001. *A Complete Guide to the Freshwater Fishes of Southern Africa.* Struik Publisher, Cape Town, South Africa.

TÓMASSON, T., BRUTON, M.N. & HAMMAN, K.C.D. 1985. The demography and management of large cyprinids in a reservoir on the Orange River, South Africa. *Fisheries Research* **3**: 279–308.

VILIZZI, L. & WALKER, K.F. 1999. Age and growth of common carp, *Cyprinus carpio,* in the River Murray, Australia: validation, consistency of age interpretation, and growth models. *Environmental Biology of Fishes* **54**: 77–106.

WEYL, O.L.F. & BOOTH, A.J. 2008. Validation of annulus formation in otoliths of a temperate population of adult African sharptooth catfish *Clarias gariepinus* using fluorochrome marking of wild fish. *Journal of Fish Biology* **73**: 1033–1088.

WEYL, O.L.F. & HECHT, T. 1998. The biology of *Tilapia rendalli* and *Oreochromis mossambicus* (Pisces: Cichlidae) in a subtropical lake in Mozambique. *South African Journal of Zoology* **33**: 178–188.

WEYL, O.L.F., STADTLANDER, T. & BOOTH, A.J. 2009. Establishment of translocated populations of smallmouth yellowfish, *Labeobarbus aeneus* (Pisces: Cyprinidae), in lentic and lotic habitats in the Great Fish River system, South Africa. *African Zoology* **44**: 93–105.

ZAMBRANO, L. & HINOJOSA, D. 1999. Direct and indirect effects of carp (*Cyprinus carpio* L.) on macrophyte and benthic communities in experimental shallow ponds in central Mexico. *Hydrobiologia* **408/409**: 131–138.

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