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Adult African Sharptooth Catfish, Clarias gariepinus, Population Dynamics in a Small Invaded Warm-Temperate Impoundment

Adult African sharptooth catfish, *Clarias gariepinus,* population dynamics in a small invaded warm-temperate impoundment

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African sharptooth catfish, *Clarias gariepinus,* is a successful aquatic invader as it has a eurytopic physiology, is highly fecund, grows quickly and has an omnivorous diet. Despite possible threats that include predation of and competition with indigenous species, habitat degradation, and the spread of diseases and parasites, there is a lack of knowledge regarding its ecology and population dynamics within invaded systems. This study presents a mark–recapture experiment to investigate its population structure, natural mortality rate, population size and density within a population inhabiting a small, 76 ha invaded water supply reservoir in the temperate Eastern Cape region, South Africa. The adult population was found to be old ($\bar{x}$ = 12.0 ± 2.9 years) and male-dominated (1.76♂:1♀ for fish <100 cm TL and 3.77♂: 1♀ for fish > 100 cm TL) with its maximum age estimated at one year less than the age of the reservoir. Adult abundance and density (in terms of numbers and biomass) was relatively low at 1655 fish (CV = 18%), 94.32 kg/ha (CV = 18%) and 21.78 fish/ha (CV = 16%), respectively. The estimated mean natural mortality rate was high at 0.80/year (CV = 82%). The skewed length- and age-structure suggests that the adult population is dominated by the fish that were either the initial colonizers during the reservoir filling phase or were the first internally reproduced recruits. The predominance of old, large fish in the population is also probably suppressing recruitment of younger fish. Despite the population being small, the fish are mobile and feed aggressively. Manual removal using baited longlines could be a feasible removal method.

Key words: mark–recapture, Cormack-Jolly-Seber model, Glen Melville Reservoir, invasive species, natural mortality.

INTRODUCTION

African sharptooth catfish, *Clarias gariepinus* (Burchell 1822), is a potamodromous species that is naturally distributed from Turkey to the Orange River, South Africa (Skelton 1993). It is omnivorous, feeding on plankton, vegetation, invertebrates, carrion and fish (de Moor & Bruton 1988) and may exhibit pack-hunting behaviour when foraging for small fish (Bruton 1979; Merron 1993). *Clarias gariepinus* is a large (>150 cm TL, >30 kg; Bruton 1976), long-lived (validated to at least 15 years, Weyl & Booth 2008) and fast-growing (Bruton & Allanson 1980; Quick & Bruton 1984; Richardson *et al.* 2009) fish that attains sexual maturity within two years of age (de Moor & Bruton 1988). It is eurythermic (80–35°C), mesohalic (0–10 ppt) and has the ability to air-breathe. These attributes predispose it to surviving in all but the most adverse of conditions

and have directly contributed to its wide use as an aquaculture species. These attributes have also contributed to its ability to invade waterbodies beyond its natural range (de Moor & Bruton 1988) and after inadvertent introductions such as by escape from aquaculture facilities or through water transfer schemes, *C. gariepinus* has established populations in many non-native environments. Such invasions include the Philippines (Mercene 1997), Bangladesh (Arthur & Ahmed 2002), Thailand (Vidthayanon 2005), India (Bhakta & Bandyopadhyay 2007) and Brazil (Cambray 2005; Vitule *et al.* 2006; Rocha & Schiavetti 2007). In South Africa, *C. gariepinus* invaded the temperate Great Fish River catchment after the species was translocated from the Orange River through a Interbasin Water Transfer (IBWT) scheme (Laurenson *et al.* 1989). Potential threats include predation of and competition with indigenous species, habitat degradation, and the spread of diseases and parasites (Dudgeon *et al.* 2006).

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In South Africa *C. gariepinus* is highly invasive outside its natural range which includes the warmer east flowing drainages and the Orange-Vaal River system. Transferred both unintentionally by IBWT schemes and escapement from fish farms as well as intentionally through illegal stocking by anglers, extralimital populations have now established in many major river systems. An IBWT scheme was responsible for the introduction of this fish into the Great Fish and Sundays River systems in the Eastern Cape (Laurenson *et al.* 1989) and by the mid 1980s this species had also been introduced, illegally, into the Keiskamma, Kei, Bushmans, and Buffalo River systems in the Eastern Cape and into the Eerste River and Kuils River systems in the Western Cape (de Moor & Bruton 1988). Since then, this fish has been widely distributed and has also been reported from many rivers and dams in the coastal drainages from the Mtata River in the Eastern Cape to the Berg River in the Western Cape (Cambray 2003). Despite these documented invasions the consequences of the establishment of this large, omnivorous fish are poorly understood (Cambray 2003).

Despite growing concerns over the effects that this species may have (Cambray 2003, 2005), there is a paucity of directed research into their ecology and population dynamics in invaded systems. This study presents a mark–recapture experiment that investigates aspects of its population dynamics, including its population structure, natural mortality rate, and abundance within an invaded small man-made reservoir in the Eastern Cape, South Africa. Quantifying population size and understanding its structure and dynamics could provide the necessary information required to manage, and possibly control, invasive *C. gariepinus* populations.

MATERIALS & METHODS

Study area

The 76 ha and 6 million m³ (at full capacity) Glen Melville Reservoir (33°11′–42.13′S, 26°38′–45.80′E) is situated in the Eastern Cape Province, South Africa, approximately 17 km northeast of Grahamstown. The reservoir provides water for domestic, industrial and agricultural use. It is filled via a water transfer tunnel biannually in March and August, and the draw-down phase results in water levels dropping to approximately a tenth of full capacity (Department of Water Affairs and Forestry, unpubl. data). The climate is warm-temperate with day length ranging from 10 h in June to 14.5 h in December. Water surface temperature over the study period ranged from 12°C in July to 27°C in February. The maximum depth of the reservoir is 25 m at the wall (Department of Water Affairs and Forestry, unpubl. data).

General sampling

Sampling was planned to coincide with all hydrological phases (low, filling, flooded and receding). This experimental approach allowed for many mark–recapture occasions within a two-year period and to allow for marked fish to mix within the impoundment. Ten sampling events were carried out between 9 March 2005 and 23 February 2007, with each sampling event lasting between two and four consecutive days. Fish were sampled using surface set longlines and angling. All sampling occurred during the day. A 400 m longline with approximately 100 size 5/0–9/0 Mustad© circle hooks, each baited with either fish fillet or chicken offal, was deployed at each sampling event. Longlines were patrolled either by boat or by wading. Fish were removed within one hour of being hooked. Angling occurred in the vicinity of the longlines and during periods when no fish were hooked on the longlines. If a fish was hooked on a longline it was clearly noticeable by the movement of the longline floats.

Once a fish was captured it was measured to the nearest 0.5 cm on a soft, wet foam measuring mat, sexed (as males have a prominent urogenital papilla), injected with oxytetracycline hydrochloride (for a separate age validation study by Weyl & Booth (2008) and to reduce secondary infection) at a dosage of 0.5 ml/kg body weight (calculated from a length-dosage chart), tagged and released. If the fish was previously tagged, it was measured, sexed, the tag number noted and released. Fish were double-tagged with PDL plastic-tipped dart and/or TBA-2 T-bar anchor tags manufactured by Hallprint©, Australia. Fish larger than 60 cm TL were tagged with either double dart tags, double T-bar anchor tags or one dart tag and one T-bar anchor tag dart for a separate tag loss study (Booth & Weyl 2008). One of the tags was inserted into the left dorsal side, just below the midpoint of the dorsal fin, whilst the other tag was inserted into the right dorsal side, about 5 cm posterior to the first tag. Smaller fish were tagged with two T-bar anchor tags.

With the exception of 17 fish, all fish that were tagged or recaptured were released alive. On the

Table 1. Maximum likelihood estimates and coefficients of variation (in brackets) from four different models applied to a Cormack-Jolly-Seber mark–recapture model of *Clarias gariepinus*. The different models refer to the combinations temporally independent or dependent (denoted by ($\cdot$) and (*t*) probabilities of capture and survival, respectively. The model weighted average of the number and density of adult fish is also provided. The number of estimated parameters in each model is *k*, –ln*L* is the negated log-likelihood, n_e is the effective sample size, *AICc* is the small sample adjusted Akaike Information Criterion that measures model fit, and w_i are the Akaike weights used in the model averaging procedure.

	Model				
	$p(\cdot)\phi(\cdot)$	$p(\cdot)\phi(t)$	$p(t)\phi(\cdot)$	$p(t)\phi(t)$	Model average
p^2	0.03 (25.59%)	0.05 (23.28%)	0.11 (39.48%)	0.3 (59.93%)	0.23 (75.9%)
p^3	0.03 (25.59%)	0.05 (23.28%)	0.05 (59.85%)	0.05 (58.67%)	0.05 (59.39%)
p^4	0.03 (25.59%)	0.05 (23.28%)	0.01 (100.99%)	0.01 (99.93%)	0.01 (100.57%)
p^5	0.03 (25.59%)	0.05 (23.28%)	0.06 (43%)	0.11 (52.84%)	0.09 (58.5%)
p^6	0.03 (25.59%)	0.05 (23.28%)	0.04 (40.65%)	0.05 (41.51%)	0.05 (43.29%)
p^7	0.03 (25.59%)	0.05 (23.28%)	0.00 (–)	0.00 (–)	0.00 (–)
p^8	0.03 (25.59%)	0.05 (23.28%)	0.03 (51.84%)	0.06 (62.32%)	0.05 (73.58%)
p^9	0.03 (25.59%)	0.05 (23.28%)	0.01 (76.44%)	0.02 (78.38%)	0.02 (84.37%)
p^{10}	0.03 (25.59%)	0.05 (23.28%)	0.11 (52.84%)	1.00[a] (–)	0.66 (65.19%)
ϕ_1	0.60 (32.87%)	0.06 (252.59%)	0.37 (43.45%)	0.00 (351.1%)	0.14 (145.56%)
ϕ_2	0.60 (32.87%)	1.00 (0.07%)	0.37 (43.45%)	1.00 (0.03%)	0.76 (42.21%)
ϕ_3	0.60 (32.87%)	0.10 (248.42%)	0.37 (43.45%)	1.00 (0.21%)	0.76 (42.21%)
ϕ_4	0.60 (32.87%)	0.13 (161.24%)	0.37 (43.45%)	0.02 (176.13%)	0.16 (127.61%)
ϕ^5	0.60 (32.87%)	1.00 (1.87%)	0.37 (43.45%)	1.00 (0.47%)	0.76 (42.22%)
ϕ^6	0.60 (32.87%)	0.00 (314.66%)	0.37 (43.45%)	1.00 (0.36%)	0.76 (42.22%)
ϕ^7	0.60 (32.87%)	0.69 (144.64%)	0.37 (43.45%)	0.02 (182.02%)	0.15 (130.24%)
ϕ^8	0.60 (32.87%)	1.00 (0.25%)	0.37 (43.45%)	1.00 (0.47%)	0.76 (42.22%)
ϕ^9	0.60 (32.87%)	1.00 (0.03%)	0.37 (43.45%)	0.01[a] (88.56%)	0.15 (138.54%)
$\overline{W}$ (kg)	4.33	4.33	4.33	4.33	4.33
$\overline{N}$	1827.9 (17.56%)	1331.2 (16.97%)	1669.3 (20.1%)	1647 (17.27%)	1655.47 (18.43%)
Density (fish/ha)	24.05 (17.56%)	17.51 (16.97%)	21.97 (20.1%)	21.67 (17.27%)	21.78 (18.43%)
Density (kg/ha)	104.14 (17.56%)	75.84 (16.97%)	95.11 (20.1%)	93.84 (17.27%)	94.32 (18.43%)
M/yr	0.08 (64.74%)	0.42 (91.16%)	0.15 (43.78%)	1.19 (44.08%)	0.80 (82.37%)
–ln *L*	219.18	211.51	198.99	191.05	
k	2	9	9	16	
n_e	419	419	419	419	
AICc	442.39	441.45	416.43	415.45	
w_i	0.00	0.00	0.38	0.62	

[a]As $\phi_9\, p_{10}$ is confounded, p_{10} is set to 1 and ϕ_9 is estimated by the model.
[b]p_7 was inestimable.

eighth sampling trip, one fish was noted to have been recently killed. The cause of death was suspected to be a Cape clawless otter, *Aonyx capensis.* On the last sampling trip, 16 fish were sacrificed to collect their otoliths. These fish were aged according the methods outlined in Weyl & Booth (2008).

Cormack-Jolly-Seber model

Description

The open-population Cormack-Jolly-Seber model (CJS) (Pollock *et al.* 1990), as parameterized by Cowen & Schwarz (2006), that uses the marking and recapturing of live animals was chosen to estimate the probabilities of capture and survival for each sampling occasion, together with population size and density.

At the end of the experiment, a capture history was constructed for each fish where, for each sampling occasion, a fish was given a '1' if it was captured and a '0' otherwise. For example, in a three-sample experiment, a fish with a capture history of '101' denotes that it was captured, tagged and released at sampling occasion 1, not observed at sampling occasion 2, and recaptured and released at sampling occasion 3.

Given the probability that a fish alive at sampling

occasion survives to sampling occasion $j + 1$, ϕ_j, and the probability that a fish is captured at sampling occasion $j + 1$, p_j, the probability associated with a fish with capture history '101' is $P(101) = \phi_1(1 - p_2)\phi_2 p_3$. Given n_ω specific capture histories and s different sampling occasions, the maximum likelihood estimates of $\{\phi_1, \phi_2, ..., \phi_{s-1}; p_2, p_3, ... p_s\}$ are obtained by maximizing a Multinomial likelihood of the form

$$LL = \prod_{i=1}^{n_\omega} \chi(l_i) \prod_{j=f_i}^{l_i-1} \phi_j \prod_{j=f_i+1}^{l_i} p_j^{\omega_{ij}} \left(1 - p_j\right)^{1-\omega_{ij}}$$

where f_i is the first sampling occasion fish i was observed, l_i is the last sampling occasion fish i was observed, and ω_{ij} is an indicator variable given a value '1' if fish i was captured at sampling occasion j and a value '0' if not captured. The probability that a fish is not observed after sampling occasion j, given that it was alive at sampling occasion j, $\chi(j)$, is calculated recursively as

$$\chi_j = \begin{cases} (1-\phi_j) + \phi_j \left(1 - p_{j+1}\right)\chi(j+1) & j < s \\ 1 & j = s \end{cases}.$$

As the time elapsed between sampling occasions were both different and less than one year, all survival probabilities were estimated as annual probabilities and rescaled accordingly, such that $\phi_j = \hat{\phi}_j^{t_j}$, where $\hat{\phi}_j$ refers to the survival parameter being estimated, and t_j the time in years between sampling occasions j and $j + 1$.

Abundance and density

Fish abundance for each sampling occasion j was estimated using the Chapman's (Seber 1982) adjusted estimate as

$$N_j = \frac{(M_j + 1)(n_j + 1)}{(m_j + 1)} - 1,$$

where $M_j = \dfrac{m_j + z_j}{1 - (1 - p_j)\chi_j}$ are the number of marked fish prior to sampling period j, and z_j are the number of fish in the population caught before sampling occasion j, not at sampling occasion j, but sometime afterwards.

The average number of fish in $s - 1$ sampling occasions is calculated as

$$\overline{N} = \frac{1}{s-1}\sum_{j=2}^{s} N_j.$$

Fish biomass was estimated as the product of mean weight of fish sampled by the estimated population size. Fish density was estimated by dividing the estimated fish biomass by the size of the reservoir as

$$Density = \frac{\overline{N} \times \overline{W}}{Area}.$$

To reduce handling time and stress individual fish were not weighed during tagging. Thus, fish mean weight, $\overline{W}$, was estimated from the converting the size of each fish to weight using the length–weight relationship obtained from Darlington Dam (Wartenberg 2009), a reservoir situated 200 km from Glen Melville Reservoir that also receives water from the Great Fish River. It has a similar altitude and temperature regime. The relationship is $W(g) = 0.00003\,L\,(mm\,TL)^{2.771}$ ($r^2 = 0.93$).

Natural mortality

The mean mortality rate over the study period was estimated directly from the adjusted survival probabilities as

$$\overline{Z} = -\frac{1}{s-1}\sum_{j=1}^{s-1}\left[\ln(\phi_j)\right].$$

As the Glen Melville population is unfished, the mortality rate was considered to be the natural mortality rate.

Modelling scenarios and parsimony

Different modelling scenarios were considered based on the different combinations of temporally independent, denoted as (·), or dependent, denoted as (t), capture and survival probabilities.

The four models were considered in the analyses and are denoted as $\{p(\cdot)\phi(\cdot)\}$, $\{p(\cdot)\phi(t)\}$, $\{p(t)\phi(\cdot)\}$ and $\{p(t)\phi(t)\}$.

Following the suggestions by Lebreton *et al.* (1992) and Burnham & Anderson (2002), model parsimony was assessed using a small sample size modified Akaike's Information Criterion statistic as

$$AICc = -2\ln LL + 2k + \frac{2k(k+1)}{n_e - k - 1}$$

where $\ln LL$ is the log-likelihood of the model, n_e is the effective number of fish sampled and k is the number of model parameters.

Only sexually mature fish (>40 cm TL) were included in the analyses.

Parameter variability and redundancy

The model was programmed in AD Model Builder (Otter Research Ltd 2000) and standard errors were calculated from the inverse Hessian matrix – the matrix of second partial derivatives of the likehood function with respect to the estimated parameters. Standard errors of the derived quanti-

ties, such as mean abundance, density and natural mortality, were calculated using the Delta method and converted to coefficients of variation as $CV = \dfrac{\sigma_{\bar{x}}}{\bar{x}}$, where $\sigma_{\bar{x}}$ is the standard error of the mean $\bar{x}$. *CV*s were presented to compare relative variability of parameters and derived quantities that are of different magnitudes. Parameter redundancy was assessed using the Hessian matrix as advocated by Giminez *et al.* (2004).

Multi-model inference

A model averaging approach was taken to estimate a weighted average of the derived estimates of population abundance and density. This approach, advocated by Burnham & Anderson (2002) and Johnson & Omland (2004), assumes that no model should be considered to be exact and the results of the different models considered, that share a common dataset and likelihood, can be averaged through the degree of support each model has, given the data.

Deviance of any model from the most parsimonious model, is calculated as $\Delta_i = AICc_i - AICc_{min}$ and then converted to reflect the likelihood of each model i M_i given a set of common *data* such that

$$L(M_i \mid data) = \exp\left(-\frac{1}{2}\Delta_i\right).$$

The model likelihoods are normalized across all models considered (in this study $M = 4$ models) to calculate the individual model 'Akaike weights' as

$$w_i = \frac{\exp\left(-\dfrac{1}{2}\Delta_i\right)}{\displaystyle\sum_{j=1}^{M}\exp\left(-\dfrac{1}{2}\Delta_j\right)}.$$

The Akaike weighted model average for an estimated quantity, $\bar{\theta}$, and its associated variance, is calculated as

$$\hat{\bar{\theta}} = \sum_{i=1}^{M} w_i \hat{\theta}_i \quad \text{and}$$

$$\hat{\text{var}}\left(\hat{\bar{\theta}}\right) = \sum_{i=1}^{M} w_i\left[\text{var}\left(\hat{\theta}_i \mid data\right) + \left(\hat{\theta}_i - \hat{\bar{\theta}}_i\right)^2\right], \text{ respectively.}$$

RESULTS

General

A total of 443 *C. gariepinus* were caught and tagged over the ten sampling events. Of these, 37 individuals were recaptured (two fish thrice, nine fish twice and 26 fish once), giving an observed recapture rate of 8.4%.

Population structure

Fish sampled ranged in size from 28 to 131 cm TL (mean = 84.8 ± 18.0 cm TL), corresponding to a mass ranging between 0.14 and 14.7 kg (mean = 4.4 ± 2.4 cm TL). Sacrificed fish averaged 12.0 ± 2.9 years of age (Fig. 1). The maximum age, 15 years, was found to be a year younger than the age of the reservoir which was constructed in 1992. Both the length- and age-structure of the population were left-skewed with the adult population being dominated by older, longer fish.

For all mature fish, and for those 5 cm size classes with >5 fish, the population was significantly male biased at 1.76 males:1 female under the null hypothesis of an equal sex ratio ($\chi^2 = 78.38$, d.f. = 15, $P < 0.001$)). Fish above 100 cm TL were overwhelmingly male biased at 3.77 males: 1 female ($\chi^2 = 47.37$, d.f. = 4, $P < 0.001$).

Capture and survival probabilities

Of the four models investigated, the best model fits were obtained when capture probability was estimated for each sampling occasion (Fig. 2, Table 1). The most parsimonious model was the fully saturated model $\{p(t)\phi(t)\}$ with the additional inclusion temporally dependent estimates of survival probabilities. The model fit of the model with temporally dependent capture but temporally independent survival probabilities, $\{p(t)\phi(\cdot)\}$, was marginally worse than the saturated model despite having seven fewer parameters. These two models accounted for *c.* 100% of the Akaike weights. The two other reduced parameter models considered, $\{p(\cdot)\phi(\cdot)\}$ and $\{p(\cdot)\phi(t)\}$, had poor fits to the data and had almost no contribution to the model averaged estimates.

Both capture and survival probabilities were estimated between 0.01 and 0.06 per sampling occasion and 0.0 and 1.0/year, respectively (Table 1). The multi-model average estimated the capture probabilities to range between 0.01 and 0.66 (mean = 0.14)/sampling occasion, and the survival probabilities between 0.14 and 0.76 (mean = 0.49/year, respectively (Table 1).

Population abundance, density and natural mortality

Absolute population estimates ranged between 1296–1819 adult fish and density between 75 and 106 kg/ha. The model average for population abundance was 1655 fish. Population density corresponded to 21.78 fish/ha and 94.32 kg/ha, respectively. The model estimates of natural
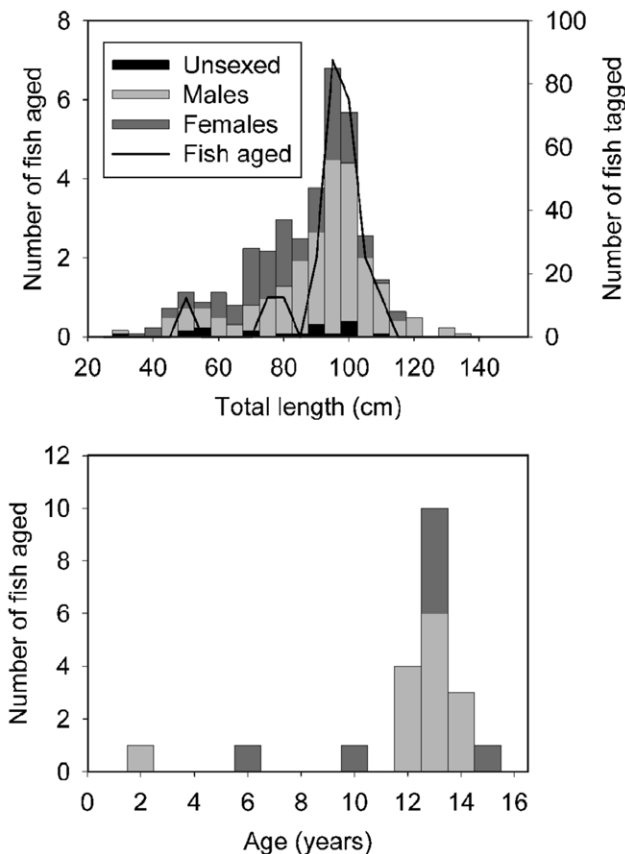
Fig. 1. Population structure of *Clarias gariepinus* in terms of length and age inhabiting the Glen Melville Reservoir in the Eastern Cape, South Africa.

mortality ranged between 0.32 and 0.98/year. The model average was 0.80/year.

DISCUSSION

The impact of invasive species on native species and ecosystems has been recognized for decades and is now viewed as a significant component to global change (Sakai *et al.* 2001). Effectively managing an invasive species is therefore necessary if the integrity of the aquatic environment is to be conserved. Understanding the population biology of an invasive organism is an important step in managing its invasiveness as it includes a synthesis of fundamental life history studies and demographic models and allows for the identification of key life history stages where management interventions would be the most technically or financially feasible. This study investigated adult population structure, natural mortality rate, abundance and density within a small invaded impoundment on the Orange-Great Fish IBWT scheme. The

adult population was dominated by old, male fish that were subjected to a high rate of natural mortality. The population was found to be small and the density, either in terms of number or biomass, low. The highly left-skewed length- and age-structure of the population, together with the maximum age determined to be a year younger than the age of the reservoir (15 and 16 years, respectively) suggests that the adult population is dominated by the original colonizing fish that either hatched from eggs transported into the reservoir when it was originally filled, or from eggs that hatched from the first spawning of established mature fish.

The adult population was found to be male-dominated, a finding similar to Cochrane (1987) and Gaigher (1977). Both studies also showed that the population became even more skewed at lengths >1 m TL. This finding was in contrast to that of Wartenberg (2009), who found no evidence for a departure from an expected 1:1 sex ratio
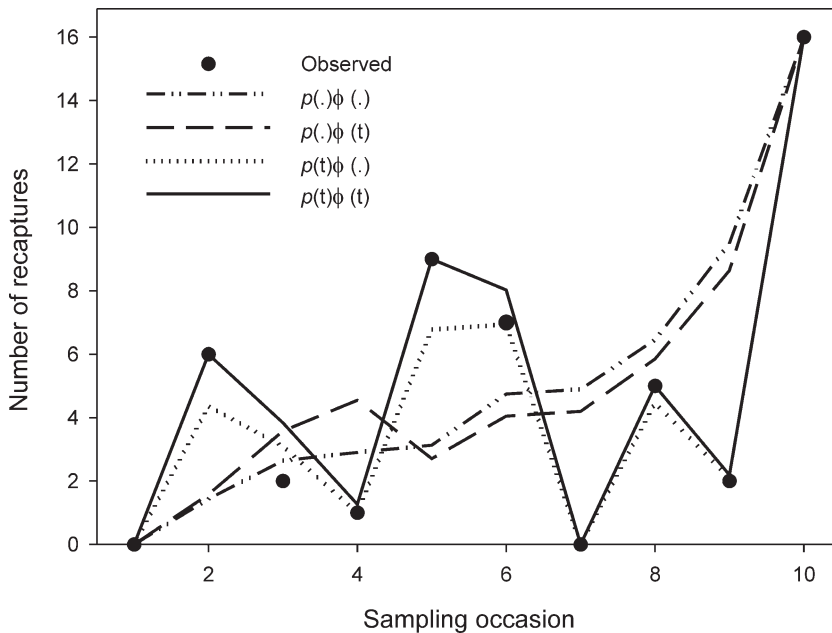
Fig. 2. The observed (dots) and the predicted number of tag recaptures (lines) for four different Cormack-Jolly-Seber models applied to the adult *Clarias gariepinus* population inhabiting the Glen Melville Reservoir in the Eastern Cape, South Africa.

across the full size and age ranges of fish sampled in Darlington Dam, another IBWT scheme impoundment. A 1:1 sex ratio would be expected if equal numbers of fish hatched as either sex, there were no differences in growth between sexes and that sex-specific mortality rates were similar. Male *C. gariepinus* have, however, been shown to grow to larger sizes than females (Willoughby & Tweddle 1978; Wartenberg 2009). In the Darlington Dam population, an equal sex ratio was noted despite the differences in growth between sexes. Differences in sex-specific mortality rates, particularly if the mortality rates are high, could therefore possibly explain the larger differences in sex ratio in older fish.

The natural mortality rate in Glen Melville Reservoir was found to be high (0.8/year) when compared to those of other freshwater predatory fish species (0.15–0.94/year; Pauly 1980) and the empirical estimate of Hoening (1980) that uses the maximum recorded age in Glen Melville Reservoir of 15 y at 0.24/year. Unfortunately there are no direct estimates of *C. gariepinus* natural mortality available for comparison but winter temperatures in Glen Melville that approach the lethal limit for this species (8–10°C; Kłyszejko *et al.* 1993) may contribute to the high mortality rate. In cold water conditions, metabolic rate would decrease

dramatically and fish would become increasingly susceptible to additional biotic and abiotic stressors. At low temperatures and during low water levels, fish could be increasingly susceptible to bird and/or otter predation. The high mortality rate observed could also be as a result of abiotic variability. Glen Melville Reservoir is drained and refilled at least biannually to meet Grahamstown's potable water supply requirements. The reservoir is filled rapidly with water levels rising from approximately a tenth to full capacity within three days. Even in winter *C. gariepinus* was observed to be rheotaxic – migrating *en masse* from the dam wall to the affluent water source. This innate potamodrometic behaviour when already metabolically stressed could potentially decrease survival over the winter filling phase of the reservoir.

Clarias gariepinus in Glen Melville Reservoir was found to be relatively short-lived with a maximum observed age of 15. The population was dominated by fish >12 years of age. The age structure found in the Darlington Dam population by Wartenberg (2009) was also found to be dominated by older fish between 12 to 17 years of age. In both reservoirs, cannabilism and/or interspecific competition are the likely factor(s) reducing the likelihood of young fish establishing and dominating the population. Longevity in the Glen Melville

population differed from both Darlington Dam (validated to 25 years; Wartenberg 2009) and Lake Gariep (>35 years, A.J.B. & O.L.F.W. unpubl. data). These differences are likely to be attributed the age of the reservoirs. Glen Melville Reservoir was completed in 1992 and if it is assumed that only eggs were translocated via the IBWT scheme, the oldest fish could only have been approximately 15 years old at the time of sampling. Similarly, Darlington Dam has been operational since 1978 and longevity of 25 years was noted. The oldest fish were sampled in the oldest reservoir that dams South Africa's largest river. This longevity estimate probably represents that found within its natural distribution range.

In the Glen Melville Reservoir, a mark–recapture experiment was considered to be the most appropriate demographic approach to estimate population size. The validity of the results from any mark–recapture estimator are, however, strongly dependent on the sampling design fulfilling certain statistical assumptions. The CJS estimator used in this study assumes that i) all fish present prior to a sampling occasion have the same probability of being captured, ii) all fish present immediately following any sampling occasion have the same probability of surviving to the next sampling occasion, iii) no tags are lost and all tags are correctly identified, and iv) sampling occurs instantaneously and fish are released immediately compared to the time intervals used in the experiment (Seber 1982; Pollock et al. 1990). The first two assumptions were assumed to hold due to the manipulated hydrological regime within Glen Melville Reservoir and the potamodrometic, flood-induced spawning behaviour (Gaigher 1977; Clay 1979; Skelton 1993) of C. gariepinus. Because of the fluctuating water levels, marked and unmarked adult animals are, therefore, forced to mix – a requirement for any mark–recapture study. The adult population under investigation was assumed to be geographically closed due to the entry of water into the reservoir. The only intake of water into Glen Melville Reservoir is via the Ecca tunnel, and this tunnel is protected by both a service grate that reduces the amount of flotsam moving through the tunnel and a 1 m weir where the tunnel enters the reservoir. In effect, this grate limits the movement of larger fish from one system to another (Department of Water Affairs and Forestry, unpubl. data). Small individuals can still pass through this grate, but adults are unable to do so. Immigration of adults and juve-

niles from the population is then restricted by the upstream weir. The incorrect identification of all tags and tag loss has been shown to negatively bias the estimated capture and survival probabilities. As these estimates are used in the estimation of abundance, then any tag loss or non-reporting would result in a positively biased estimated population size (Arnason & Mills 1981; McDonald et al. 2003; Cowen & Schwarz 2006; Booth & Weyl 2008; Dicken et al. 2008). In this study, each recaptured animal was examined by scientists for tag loss. It was therefore assumed that all tags were correctly reported. For all the fish tagged, on no occasion did any fish lose both tags (as tag scars are easily noticeable) and tag retention was estimated at 94% over the duration of the study (Booth & Weyl 2008). The last assumption was satisfied as the sampling occasions generally occurred over a three-day period compared to a between sampling period ranging between 54 and 161 days.

The density of fish both in terms of number (22 fish/ha) or biomass (94 kg/ha) was either considerably higher or lower than other C. gariepinus populations. Cochrane (1987) noted that Hartebeespoort Dam had a density of 88 fish/ha which corresponded to 147 kg/ha and the population in Lake Kariba was 5.5 kg/ha (and 14.1 kg/ha for all littoral species) (Marshall & Langerman 1988). These differences are most likely a consequence of the productivity of the different systems. In comparison with the hypertrophic Hartebeespoort Dam (Twinch 1986) and the oligotrophic Lake Kariba (Marshall & Junor 1981), Glen Melville Dam can be considered mesotrophic. As a result, fish biomass within Glen Melville is likely to be intermediate between these two systems.

To conclude, the population of C. gariepinus in Glen Melville Reservoir is small and is dominated by large, old fish of at least 12 years of age. Juveniles and young adults appear to be depressed by the presence of old, large adult fish and can be identified as the most vulnerable life history stage in the population. The high mortality rate and low abundance implies that this population may be vulnerable to overfishing. This potential vulnerability to overfishing could be exploited as a potential removal mechanism for invaded environments. Fish are mobile and feed aggressively suggesting that they could be removed using baited longlines. Removal using ichthyocides, such as rotenone, would be infeasible given that the reservoir is used for potable water and the volume of water that would need to be poisoned would be large to be

financially affordable. Removing many large fish would probably increase the number of small fish in the population through competitive release.

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