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Carp Population Biology in Victoria

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February 2003

Victoria
The Place To Be

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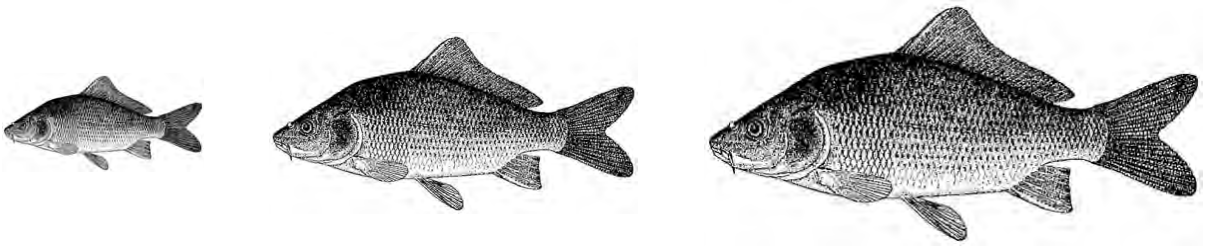

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1 Executive Summary

Towards the end of the 1990s, there was no doubt that the majority of public opinion, and a mounting degree of scientific evidence, suggested that carp-control should be a primary concern for all agencies managing the fresh waters of southern Australia. There is now a realisation that when carp dominate a waterway, there are negative social, economic and ecological consequences. In attempting to address such problems we received enormous community support. We acknowledge the assistance and support of a wide range of the community in delivering the science contained in this report. Natural resources managers, Fisheries Officers, commercial fishers, recreational fishers, and private landowners all contributed to the completion of this project. This science is simply one of the early steps in the long-term management of feral carp populations. Certainly, as subsequent steps are taken to solve the carp problem, further consultation and engagement with the community will be necessary.

In the light of this ground-swell of scientific conviction and public opinion, DNRE Victoria launched a major research project to determine the population dynamics of carp, *Cyprinus carpio* L. (Family: Cyprinidae) as an invasive species—with the aim to evaluate and determine the most suitable control strategy.

Objectives of the project were:

- To determine key characteristics of carp populations, including population estimates, growth, survival and reproductive rates at selected locations.
- To develop population models for carp to allow *what-if* type simulation of a range of potential management strategies.
- Through fieldwork and modelling, trial the feasibility of various capture, exclusion and control measures.

The research project was funded during 1999–2001 by Fisheries Victoria, then a division of the Department of Natural Resources and Environment of Victoria, now within the Department of Primary Industries. The objectives of this final report are to introduce the main research findings and discuss the relevance of these findings to management of feral carp populations. Whilst the results are particularly applicable to carp stocks in Victoria and the southern Murray-Darling basin, this contribution also helps fill some of the knowledge gaps pertaining to feral stocks of carp elsewhere in Australia and overseas where similar climatic and hydrological conditions may exist.

The study centred around five main locations:

- Murray River at Barmah
- Lake Eildon
- Campaspe irrigation channels
- Gippsland Lakes
- Barwon River

These locations were chosen to represent important habitat areas where carp are found in Victoria:

- large Murray–Darling basin rivers and associated wetlands
- large lakes and reservoirs
- irrigation channels

- coastal freshwater/brackish lakes
- coastal rivers and associated wetlands

The sampling design was to visit each location at monthly intervals and attempt to sample at least 50 carp for studies of age, growth and reproduction. Where they were easily obtainable, larger samples were measured to obtain length frequency data.. In addition, less frequent samples were obtained when opportunities arose, such as *ad-hoc* commercial carp-removals around Victoria.

Sampling methods were site-dependant due to the varying physical characteristics of each site. However, sampling efforts were standardised for each site to enable temporal comparisons. Commercial fisheries operating in the Gippsland Lakes and the Barwon River enabled samples to be largely drawn from the commercial catch at these sites.

The estimation of growth, mortality and maturity rates, essential for the present study, relies on determination of age for carp. Otolith sections of common carp were examined to validate their utility for age determination.

For the 1999 year-class in Hut Lake near Barmah the absolute age at first annulus formation was confirmed as age-1 year, by repeated sampling of a discrete young-of-year cohort.

The annual periodicity of annulus formation for common carp was confirmed in a mark-recapture experiment when 19 recaptured adult common carp, from an original stocking of 141 marked by injection with oxytetracycline (OTC), showed visible fluorescent marks on their otoliths. Time at liberty for these fish ranged from 6 to 25 months and their ages on recapture ranged from 3 to 14 years. There was complete agreement between increment counts outside the OTC mark and time at liberty.

Precision estimates on age-determinations were calculated as average percent error (APE) between readers and for each of two readers over time. Precision was assessed by re-reading sub-samples and APE was <5% in all cases. It is concluded that examination of thin otolith sections is a suitable method for the determination of annual age estimates for common carp aged 0–14 years and we are confident that the method is also applicable to fish older than 14 years. The maximum age observed for carp was 32 years.

The reproduction of carp from Victorian waters in Australia, was studied with detailed analysis of gonad maturation, spawning season, fecundity and oocyte diameter.

Results show that carp have a high annual fecundity (AF) (0.12 to 1.54 million oocytes per fish) which is positively correlated with caudal fork-length (L, mm) and total weight (W, kg) but not age. The relationships between length or weight and annual fecundity were statistically significant and best described with the simple linear or quadratic regressions:

- $AF = (0.00359\ L) - 1.269$
- $AF = (3.47 \times 10^{-4})W - (2.1 \times 10^{-8})W^2 - 0.309$.

Mean relative fecundity was 0.163 million eggs kg^{-1} whole weight.

Egg size was estimated from oocyte diameter in carp from eight stocks. Egg size was proportional to maternal size but not age.

Seasonal trends in gonadosomatic indices, together with the changes in the macroscopic and microscopic condition of ovaries, demonstrated that spawning generally peaks during Spring–early Summer, but also occurs through until Autumn and can even start in late Winter at some sites. In Victoria, this species is a multiple spawner with asynchronous oocyte development and a protracted spawning season. Stocks generally contain both females that spawn once, and females that spawn repeatedly, within a spawning season.

Two Murray–Darling carp populations– in the Campaspe irrigation system and the mid-Murray River at Barmah, were studied in further detail including estimation of growth, mortality and maturity rates.

Patterns of spatial and temporal abundance of carp in the irrigation channels indicate that juvenile recruitment by immigration was common. Estimates of standing stock range from 0 to 619 kg ha^{-1} with a mean of 144 kg $ha^{-1.}$

Maximum age of 17 years was observed. The largest male and female measured 570 mm and 680 mm caudal fork length respectively and growth in mean length-at-age and heterogeneity in length-at-age are described for males and females and both channels.

Seasonal variation in gonad and oocyte development indicates that spawning occurred during spring and autumn at temperatures of 16.5 – 22.6 ^{o}C. Relationships between length, weight and age-at-maturity are described for males and females separately. The overall sex-ratio was not significantly different from 1:1. The mean annual fecundity ranged from 400,000 to 1,170,000 eggs in carp 2–5 years of age.

Natural mortality (M), total mortality (Z) and a composite fishing and operational mortality (F+O) were estimated for each irrigation channel. The comparatively high rate of herbicide treatment and regularity of winter water-level draw-down experienced by carp in the eastern irrigation channel may have conferred characteristics of an exploited stock on that population.

In the main channel of the mid-Murray River we observed indices of adult carp abundance that dropped as soon as carp had access to floodplain environments. In the Barmah–Millewa Forest floodplain wetlands, indices of juvenile abundance were elevated in a year with sustained and extensive flooding, relative to the previous year of short-term and minor flooding.

Maximum observed age was 28 years. Strong and weak year-classes in the age-structure were associated with greater than average and less than average flooding in the Barmah–Millewa Forest respectively.

Average growth in length for males and females was described with the von Bertlanffy growth model and heterogeneity in length-at-age was described with a lognormal error distribution of the growth parameter k. Mean total mortality rate (Z) was estimated for yearlings and adult males and females greater than 7 years old from age-frequency data using both Chapman and Robson's maximum likelihood method and least squares estimation of a catch curve gradient. Natural (M) and Fishing mortality rates (F) were estimated for males and females separately, using empirical methods.

An approximate estimate (≅190 kg ha^{-1}) of standing stock biomass is proposed based on commercial harvesting of a mass-stranding after de-watering a known area.

Seasonality and timing of reproductive biology is described for the 3-year period 1999–2001. Rates of initial maturation of carp are described in terms of length, mass and age. Median values for initial maturation were 307 mm LCF, 584 g and 1.1 years for males; and 328 mm LCF, 688g and 2.7 years for females, respectively. Juvenile sex ratio was 1male:1 female although at maturity there was a significantly male-biased sex ratio.

Mean fecundity was relatively low at 0.33 million eggs, or 0.11 million eggs kg^{-1} for females 8–15 years of age. Implications of the observed protracted spawning season and low adult mortality rates are discussed along with the influence of the Barmah–Millewa Forest environmental watering allocation and flooding on carp pest-management prospects.

Using biological parameters derived from detailed study of carp populations discussed above, we developed CARPSIM, a simple age-based model to simulate the effects of a range of

management scenarios. The model simulates change in population biomass by age and sex-specific growth and simulates change in population abundance through recruitment and sex-specific mortality. Using empirical stock-recruitment data and stochastic components derived from local hydrological data or the southern oscillation index, the model simulated the population dynamics of carp populations over 200 years.

Carp management scenarios simulated included:

- effects of fishing the spawning stock
- fishing the whole stock
- spawning or recruitment sabotage
- driving the population sex ratio towards male dominance

Model predictions suggests that faster growing, shorter-lived populations may be better controlled by molecular methods inducing male-dominance, or spawning sabotage type methods whereas slower growing, long-lived populations may respond best to removal type approaches. Unselective removal, such as poisoning or trapping all age-classes is more likely to cause pseudo-extinction at levels of instantaneous fishing mortality (F) >0.7; while size-selective removal at similar F levels may only be useful to reduce the biomass below 60% of virgin biomass. CARPSIM simulations show that the probability is small for any removal-based method achieving <10% of virgin biomass when F <1.4.

Further implications for management are discussed on p28–31

2 Introduction

The common carp (*Cyprinus carpio* L.) is found throughout Australia except the Northern Territory (Kailola *et al.* 1993). Below 500 m altitude in the Murray-Darling River basin that drains approximately one-fifth of mainland Australia, carp are now the dominant fish species (Harris and Gehrke 1997; Koehn *et al.* 2000)(Figure 1). They were first introduced into Australia over 100 years ago (Brown 1996) and there have subsequently been at least three separate introductions of distinct strains or genetic-types (Kailola *et al.* 1993) including Koi, a colourful variety of the same species (Davis *et al.* 1999a). It was not until the early 1960s when the "Boolarra" strain that was originally introduced into the Gippsland waterbodies and subsequently translocated into the Murray-Darling basin, is believed to have caused the recent upsurge in carp abundance (Shearer and Mulley 1978).

Carp are perceived to have significant impacts upon aquatic systems. They are seen as causing extensive habitat and water quality degradation including the demise of native fish populations and species diversity (Bomford and Tilzey 1996). There is, however, still debate as to what extent carp are the cause of major disturbances in freshwater systems and to what extent they are a response to disturbance (Harris and Gehrke 1997).

In the 1990s southern Australia saw a renewed scientific and public interest in carp as both an environmental vandal and an increasing target for commercial (Hopkins 1998; Woods 1998) and recreational fishing (Waldock 1998).

In the same decade there were three national workshops (MDA 1995; Nannested 1994; Roberts and Tilzey 1996); two national committees or working-groups[1]; around 50 major publications[2] and countless research dollars allocated to the issue of carp in Australia. Meanwhile, the distribution of carp spread to new horizons such as lakes Sorell and Crescent in Tasmania (IFC 1995); Deep Lake[3], Lake Toolondo (Brown and Hall 2001) and the Glenelg River catchment in Victoria[4] and yet there was still little understanding of what limits their population growth, reproduction and death rates, and how abundant they really are (Thresher 1997).

Towards the end of the 1990s, there was no doubt that the majority of public opinion, and a mounting degree of scientific evidence, suggested that carp-control should be a primary concern for all agencies managing the fresh waters of southern Australia. In the light of this ground-swell of scientific conviction and public opinion, DNRE Victoria launched a major research project to determine the population dynamics of carp as an invasive species in order to evaluate and determine the most suitable control strategy.

Objectives of the project were:

- to determine key characteristics of carp populations, including population estimates, growth, survival and reproductive rates at selected locations.
- to develop population models for carp to allow *what-if* type simulation of a range of potential management strategies.
- through fieldwork and modelling, some trials of the feasibility of various capture, exclusion and control measures were also planned.

The research project was funded during 1999–2001 by Fisheries Victoria a division of the Department of Natural Resources and Environment of Victoria. The objectives of this final report are to introduce the main research findings and discuss the relevance of these findings to management of feral carp populations. Whilst the results are particularly applicable to carp stocks in Victoria and the southern Murray-Darling basin, this contribution also helps fill

[1] CCCG ~ Carp Control Coordination Group; NCTF ~ National Carp Task Force
[2] see bibliography
[3] Marine and Freshwater Resources Fish Survey, 30 November 1998
[4] specimen identified by P.Brown in a personal communication with Paul Shea, NRE Fisheries Officer, 9 September 2002

some of the knowledge gaps pertaining to feral stocks of carp elsewhere in Australia and overseas where similar climatic and hydrological conditions may exist.
An excellent review of collected knowledge on carp biology, ecology and management in the 1990s was published during this study. As such, a formal literature review of the subject will not be included with this report, other than literature cited in the text. Readers seeking further background information on carp in Australia are directed to read Koehn *et al.*(2000).

Figure 1. Carp are often a highly visible feature of many Victorian waterways, whether during surface-basking behaviour, or as a stranded mono-specific fish-kill in a dried up lake

3 Methods

This report will largely be confined to a summary of research results and a discussion of their implications for management. Much of the detailed descriptions of methods and results is contained within the relevant appendices 2–6 at the end of this report.

3.1 Field Sampling and Study Area

Sites where carp have been collected as part of various Fisheries Victoria or Marine and Freshwater Resources Institute surveys since 1989 are shown in Figure 2, along with locations where carp were collected as part of this study.

Populations are often defined as reproductively-discrete biological units (Milner *et al.* 2002). Practically nothing is known of carp movement rates, or rates of exchange within or between populations. Furthermore, the distribution of carp is such that there is a high possibility of biologically-important sub-structure in populations at the level of catchments, river-reaches or individual wetlands. A more useful definition is that of *stocks* as discrete groupings having broadly similar biology and genetics. Economic and practical reasons usually dictate that fisheries management is practised at this level, and this is the definition of *stock* that we have used throughout this study.

The sampling-design for our major sites (i.e. Murray River at Barmah, Lake Eildon, Campaspe irrigation channels, Gippsland Lakes and the Barwon River), was to visit each location at monthly intervals and attempt to sample at least 50 carp for studies of age, growth and reproduction. Where easily obtainable, large samples were measured to obtain length frequency data.. In addition, less frequent samples were obtained when opportunities arose, such as *ad-hoc* commercial carp-removals around Victoria.

Sampling methods were site-dependant due to the varying physical characteristics of each site. However, sampling efforts were standardised for each site to enable temporal comparisons. Commercial fisheries operating in the Gippsland Lakes and the Barwon River enabled samples to be largely drawn from the commercial catch.

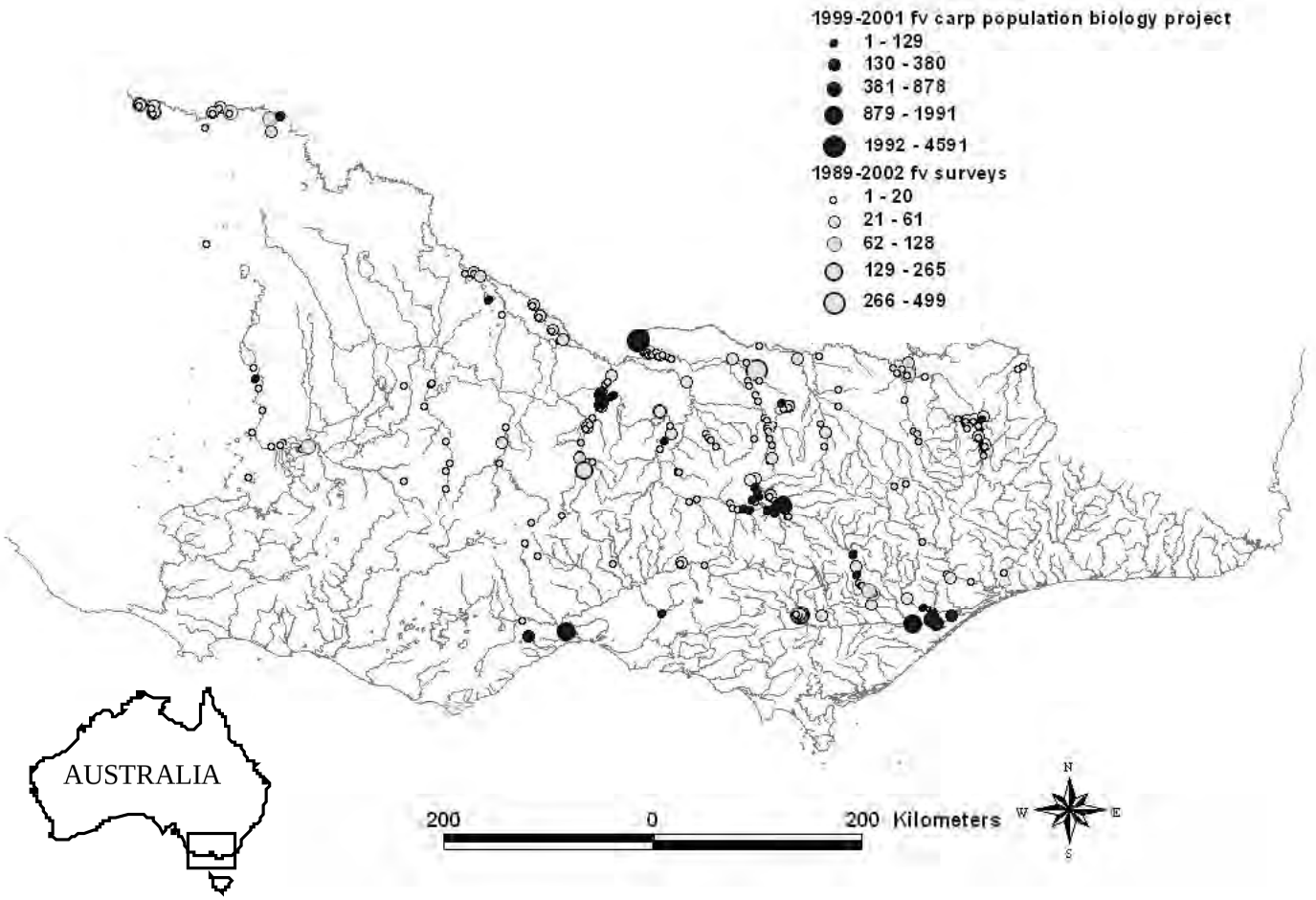

Figure 2 Locations within Victoria where carp have been captured as part of various surveys by Fisheries Victoria or the Marine and Freshwater Resources Institute from 1989–2002 (yellow) and as part of the current carp research project 1999–2001 (dark blue). Symbol size indicates sample size at each location. Box on inset map of Australia locates position of main map.

3.2 Age, Growth and Mortality

3.2.1 Age Validation and Precision (see Appendix 2 for details)

The age structure of carp populations was investigated using otoliths, the calcified structures within the inner-ear of fish, to estimate the age in years of 6110 individuals. Some validation of the use of otoliths and other hard-parts of carp has been published (Vilizzi *et al.* 1998; Vilizzi and Walker 1999). However, the degree of reliance on age-estimation necessary for this project justified further investigation and the use of robust methods for validation.
The two essential requisites of an age validation study are to ensure that fish *are* aged 1-year at the formation of the first increment; and that subsequent increments are deposited with annual frequency (Campana 2001). Length frequency analysis of young-of-year carp sampled from Barmah Forest wetlands was used to establish the absolute age of juveniles as the first increment was deposited in their otoliths. Mark-recapture of fish was used to establish the periodicity of increment formation discernible within the sectioned otoliths. Carp were marked with an antibiotic (i.e. oxytetracycline, or OTC) which is taken up in calcified structures causing a fluorescent mark, and held in a Goulburn River billabong over a two-year period. Injection of carp with oxytetracycline (OTC) (50 mg kg^{-1}) produced a fluorescent mark visible under ultra-violet light (UV) as a yellow band on the otolith-section.
Highly experienced otolith readers from MAFRI's Central Ageing Facility were used and precision of age-estimation was assessed using the average percent error (APE) method (Beamish and Fournier 1981; Campana 2001). Consistency was assessed with APE estimates between readers and drift in accuracy was assessed using APE estimates repeated over time.

3.2.2 Growth (see Appendices 4 & 5 for details)

Growth was studied in detail for two populations in the mid-Murray River and two Campaspe irrigation channels. Mean growth in length by sex, and for each channel, was estimated for sub-samples (Campaspe, n=455; Barmah, n=1193) using standard non-linear models (Von Bertalanffy 1938). Variability of length at age was estimated using the stochastic growth model of Troynikov (1998) that describes length-at-age given individual variability in growth rate. Mean growth in weight by sex, was described by fitting a linear-exponential regression of the form $W=aL^b$, where *a* and *b* are parameters fitted using a minimum sum of squares method. Testing of statistical significance in differences in growth relationships among male and female groups was accomplished using Kimura's (1980) log-likelihood method.

3.2.3 Mortality

For the mid-Murray River and Campaspe channel sites, age estimates were used to create age-length keys (ALK) to predict the age distribution of whole samples from subsamples of aged fish. Using the predicted age-distributions, total adult mortality rates (*Z*) were estimated by sex, and for each channel by calculating both the maximum likelihood estimator of Chapman and Robson (1960) and the linear regression estimator from the catch-curve (Ricker 1975). An empirical method was used to estimate natural mortality rate (*M*) (Pauly 1980) by channel, using average habitat temperature and estimated growth parameters. For the Campaspe irrigation channels a composite mortality rate comprising of fishing (*F*) and channel-management operations (*O*) was estimated as $F+O = Z - M$ for each channel population. *F* was estimated similarly for the mid-Murray at Barmah stock ($F=Z-M$) by sex.

3.3 Reproductive Biology (see Appendix 3 for details)

Female reproduction was studied in carp from eight geographical locations with a detailed analysis of gonad maturation and spawning season. Fecundity, the number of eggs produced– and mean oocyte diameter were also estimated. Four stocks were from the Murray-Darling Basin, the remainder from the Gippsland Lakes and Barwon River catchments or internal drainages such as Lake Modewarre or the Wimmera.

Gonad condition was estimated macroscopically in the laboratory and classified according to an eight point development scale adapted from the literature (Gupta 1975; Jankovic 1971). Gonads were dissected and weighed to calculate a gonad condition index (gonadosomatic index (GSI), which is gonad mass as a percentage of whole body mass. Gonad tissue was dissected from sub-samples and histological sections were prepared and examined microscopically to confirm oocyte development stage. Oocyte size was determined by measuring diameter of whole oocytes and sectioned oocytes. We estimated fecundity by counting the mature oocytes in a small gonad sample of known weight.

The timing and duration of spawning season was determined from seasonal trends in GSI along with changes in macroscopic and microscopic condition of the ovaries.

All carp sampled were measured for length (LCF, mm) and most for weight (g). Age was estimated from sub-samples using sectioned otoliths. Reproductive status assessed using GSI, gonad staging and histology of oocytes. The hypothesis that the overall sex-ratio was 1M:1F was tested using a chi-squared test. When this hypothesis was rejected a linear regression was fitted through the %-female data for each age-class to examine changes in sex-ratio as the population aged.

Relationships between fecundity of running-ripe carp and maternal length, weight (n=70), and age (n=55); and oocyte size and maternal length (n=396), weight (n=387)and age (n=386) were estimated using linear and non-linear regression. In the irrigation channels fecundity was estimated for 13 running-ripe, female carp aged 2–5 years. Fecundity was also estimated for three running-ripe, female carp from Barmah Lake that were aged 8–15 years.

The relationships between length, weight, age and rate of maturity were estimated by fitting a logistic curve to data arranged to describe the proportion of carp that were mature by size, weight or age classes. Parameters of the best fitting curves are estimates of the median and 95-percentile size or age at maturity.

3.4 Spatial and Temporal Abundance (for details see Appendices 4 and 5)

Carp were sampled from two irrigation supply channels near Rochester on the Campaspe irrigation system (n=1112) over two consecutive irrigation seasons.

Patterns of spatial and temporal abundance were examined by sampling fixed sites each month using a standardised boat-electrofishing methodology. Channels are managed in ways that have the potential to limit carp populations by de-watering over winter and herbicide treatment over summer. Each channel carp population in this study had been exposed to varying intensities of channel management in recent years.

Carp were also sampled from the Murray River and a range of wetlands in the Barmah-Millewa forest (n=2177) over a 28 month period.

Patterns of spatial and temporal abundance here were examined by sampling fixed sites each month using standardised boat-electrofishing and fyke-netting methodologies. Annual flow variability was such that years of minor and severe flooding were both sampled. The second year of the study also coincided with the 2nd use of the Barmah-Millewa Forest environmental water allocation (EWA) when 340 GL of water was released to extend major natural flooding throughout the river reach.

3.4.1 Population Estimates

At the end of the study in the irrigation channels an operational application of acrolein herbicide to one channel, for macrophyte control, presented the opportunity to estimate absolute population abundance at three of our fixed sites. A combination of mark-recapture and depletion methods were used to both estimate the sampling efficiency of the electrofisher and the stock density of carp in the channel.
The commercial harvest of a stranded carp population in Moira Lake also presented an opportunity to crudely estimate standing-stock in a known area of the flooded Millewa Forest.

3.5 Population Simulation Model Development (see Appendix 6 for details)

CARPSIM was developed as a simple age-based model capable of simulating the outcomes of a range of carp management scenarios. The model simulates change in population biomass by age and sex-specific growth and simulates change in population abundance through recruitment and sex-specific mortality. We used observations of population-recruitment data from Harris and Gehrke (1997) presented in Koehn *et al* (2000), as well as stochastic recruitment indces derived from local hydrological data or the southern oscillation index (SOI) (B.O.M. 2002), to simulate the population dynamics of carp populations over 200 years. SOI, is a climatic indicator derived from the ratio of air-pressures measured at Darwin & Tahiti and is correlated to rainfall in Eastern Australia. Sustained negative values of the SOI often indicate El Niño episodes. These negative values are usually accompanied by sustained warming of the central and eastern tropical Pacific Ocean, a decrease in the strength of the Pacific Trade Winds, and a reduction in rainfall over eastern and northern Australia. The most recent strong El Niño was in 1997/98.
Positive values of the SOI are associated with stronger Pacific trade winds and warmer sea temperatures to the north of Australia, popularly known as a La Niña episode. Waters in the central and eastern tropical Pacific Ocean become cooler during this time. Together these give an increased probability that eastern and northern Australia will be wetter than normal.
Biological parameters from the profiles of two Victorian populations within the Murray-Darling basin are used to parameterise the model.
Carp management scenarios simulated included the effects of fishing the spawning stock; of fishing the whole stock; of spawning or recruitment sabotage; and of driving the population sex ratio towards male dominance.

4 Summary of Main Results

4.1 Age, Growth and Mortality

4.1.1 Age Validation and Precision (details in Appendix 2)

By repeatedly estimating the ages of young-of-year (0 year old) carp sampled from Hut Lake, a north-central Victorian wetland near Barmah, it was shown that the first increment formation was in late Spring to early Summer at an absolute age of approximately 1-year. Samples of OTC marked carp were recaptured (n=19) after periods of 0.5, 1 and 2 years. Inspection of otoliths under UV light and normal transmitted light, revealed the relative location of OTC bands and annual increments deposited during time at liberty in the billabong. There was complete agreement between the number of years at liberty and the count of annual increments deposited subsequent to the OTC bands. Thus for carp aged 3–14 years the frequency of otolith increment deposition was confirmed as annual.
Precision of age-determinations for large samples of carp from 15 locations around Victoria (n= 6110) was assessed by re-reading sub-samples (~20%) and calculating the average percent error (APE) (Beamish and Fournier 1981). Estimated bias-corrected mean APE (95% confidence interval) for re-read samples from the primary reader (n=1068) was 4.56% (4.14–4.97%); for the secondary reader (n=230) was 4.04% (2.67–5.42%); and between readers (n=229) was 4.98% (4.18–5.79%). The mean APE values of <5% suggest that precision in age-determination using otolith thin-sections is acceptable (Campana 2001; Morison *et al*. 1998). The overlapping 95% confidence intervals suggest that although the secondary reader was less precise, there was no significant difference in precision of age-determination between readers.
Results of this study suggest that examination of thin otolith sections is a suitable method for the accurate and precise determination of annual age estimates for common carp aged 0–14 years. Furthermore, there were no changes to the appearance of the outer increments on fish aged at older than 14 years that would suggest that the process of increment formation was different to that which produced them annually on younger fish. Therefore the method is also likely to be reliable for carp older than 14 years.

4.1.2 Growth

Growth was described in detail for two populations. For the Campaspe channel population and the mid-Murray population, we described growth in mean length at age and heterogeneity in length-at-age for males and females. Growth in mean weight for length was also described for males and females (Table 1). Mean length-at-age, and weight-for-length was significantly different for each gender and mean length-at-age also differed between irrigation channels. The oldest carp sampled was 32 years old from Gippsland in Victoria's south-east and was a male that was sampled from within a group of fish actively spawning. However, several carp 25 years or older were also sampled from the Murray River at Barmah, the Kerang lakes and the Barwon River as well as the Gippsland Lakes indicating that longevity is a widespread phenomenon.

4.1.3 Mortality

Mortality rates are presented in Table 1. In the Campaspe irrigation channels, male and female mortality rates were similar and so these were pooled to calculate rates for each channel. The comparatively high rate of herbicide treatment and regularity of winter water-level draw down experienced by carp in the eastern irrigation channel may explain the comparatively high total mortality rate estimated for the eastern channel (Z=0.625) versus the

western channel (*Z*=0.326). This demonstrates resilience and variability in this carp population, as despite this very large difference in total mortality rates, our sampling detected no difference in mean relative abundance between channels and this is likely to be related to the large sampling-variability associated with the relative-abundance estimates.
In the mid-Murray carp population, adult female total mortality rates (Z) were over 1.5 times higher than that estimated for males. In males the estimated natural mortality (M) rate matched Z almost completely while for females, M was lower and therefore an additional mortality component could be identified, traditionally known as fishing mortality (F).

4.2 Reproductive Biology (details in Appendix 3)

Estimates of fecundity for female carp show that as maternal size (length and weight) increases, egg production increases. However, there is no relationship between age and egg-production in mature fish. The relationships between length (L) or weight (W) and annual fecundity (AF) were statistically significant and best described with the simple linear regression:

$$AF = 0.00359\ L - 1.269$$

Or the quadratic linear regression:

$$AF = 3.47 \times 10^{-4} W - 2.1 \times 10^{-8} W^2 - 0.309.$$

Relative fecundity is a measure of egg production that is standardised to a unit of body-weight or length. Although larger females produce more eggs, they do not produce more per kg of bodyweight than smaller females. Thus, mean relative fecundity was 0.163 million eggs kg^{-1} whole weight, and did not show any significant relationship with maternal size or age.
Egg size was also proportional to maternal length and weight but not age. Body condition declined significantly in older fish and this may explain why it is large fish, but not necessarily old fish, that produce the biggest eggs. The carp in a small sample (n=35) from Lake Modewarre, were extremely large and heavy for their age and produced the largest eggs of all.
Histological preparations of ovarian tissue were important in accurately identifying spawning and post-spawning stages. Seasonal trends in gonadosomatic indices, together with observed changes in the macroscopic and microscopic condition of ovaries, demonstrated that extended spawning seasons are common. Spawning generally peaks during spring – early summer, but also occurs through until autumn and can even start in late winter at some sites.
In Victoria, carp are multiple spawners with asynchronous oocyte development (i.e. batches of developing oocytes with different developmental status, mature at different rates or according to different schedules within the ovary). Carp in Victoria also have a protracted spawning season and stocks generally contain a mix of females that spawn only once, and females that may spawn repeatedly within a spawning season.

4.3 Campaspe Irrigation Channel Stock (details in Appendix 4)

Feral common carp, *Cyprinus carpio* L., were sampled from two irrigation supply channels in central Victoria, south-eastern Australia over two summer irrigation seasons as part of a broader population dynamics study. The total electrofishing sample of fish from the Campaspe eastern and western channels was dominated by catches of exotic fishes: 1114 carp, 1040 goldfish (*Carassius auratus*), 4 carp x goldfish hybrids, 366 redfin perch (*Perca fluviatilis*). Native fish were comparatively rare and comprised 2 golden perch (*Macquaria ambigua*), 7 Australian smelt (*Retropinna semoni*) and 16 flathead gudgeon (*Philypnodon grandiceps*). Although small species such as smelt and gudgeon may be somewhat under-

represented in the samples, broadly speaking these figures represent the rarity of fish species other than carp or goldfish.

Patterns of spatial and temporal abundance indicate that juvenile recruitment by immigration was common. Sampling efficiency with a single pass of the boat-electrofisher varied from 6–13% and estimates of standing stock range from 0 to 619 kg ha^{-1} with a mean of 144 kg $ha^{-1.}$

A maximum age of 17 years was observed for *C. carpio.* The largest male and female measured 570 mm and 680 mm caudal fork length respectively.

Seasonal variation in gonad and oocyte development indicates that spawning occurred in spring and autumn at water temperatures of 16.5 – 22.6 ^{o}C.

Relationships between length, weight and age at maturity are described for males and females in terms of median and 95-percentile size and ages (Table 1). Males and females mature at similar ages and sizes in their second or third year.

The overall sex-ratio was not significantly different from 1:1. The mean annual fecundity ranged from 400,000 to 1,170,000 eggs in carp 2–5 years of age.

Table 1 Carp population parameters

Description	Parameter (units)		Campaspe		Barmah	
			males	females	males	females
Maximum observed length	L_{max}	(mm)	570	680	570	623
Mean growth in length	L_{inf}	(mm)	495	538	489	594
	t_0	(year)	-0.291	-0.391	-0.519	-0.609
	K	($year^{-1}$)	0.475	0.380	0.249	0.177
Heterogeneity in growth in length	L		576	689	575	629
	T_0		-0.006	-0.768	-0.01	-0.008
	E(k)		0.003	0.002	0.001	0.002
Parameter of Lognormal distribution	*p*		-1.226	-1.595	-1.927	-1.921
Parameter of Lognormal distribution	*a*	(n x 10^{-3})	3.919	3.491	3.18	3.21
Weight for length	*A*	(n x 10^{5})	3.726	4.109	1.739	1.669
	B		2.902	2.902	3.000	3.000
Maturity						
Length at which 50% are mature	Lm_{50}	(mm)	287	273	307	328
Length at which 95% are mature	Lm_{95}	(mm)	344	310	379	392
Weight at which 50% are mature	Wm_{50}	(g)	556	490	584	688
Weight at which 95% are mature	Wm_{95}	(g)	872	825	932	1032
Age at which 50% are mature	Am_{50}	(years)	1.3	1.4	1.1	2.7
Age at which 95% are mature	Am_{95}	(years)	2.4	2.6	1.2	4.7
Mortality						
Total mortality rate	Z	($year^{-1}$)	0.540	0.474	0.268	0.426
Natural mortality rate	M	($year^{-1}$)	0.404	0.341	0.262	0.199
Fishing mortality rate	F	($year^{-1}$)	†0.136	†0.133	‡0.006	‡0.227

† based on Z from age-at-full-recruitment = 2 years

‡ based on Z from age-at-full-recruitment = 7 years for males & 9 years for females

4.4 Mid-Murray River and Barmah-Millewa Forest Wetlands Carp Stock (details in Appendix 5)

Carp were sampled from 1999–2001 in the Murray River at Barmah and associated Barmah-Millewa Forest wetlands (n=7357), along with eight other species (Table 2).
Note that while targeting carp, with fishing intensity sufficient to remove ~ 2 tonnes of carp, we encountered a low but significant by-catch of native species all of which are listed as part of the threatened lower Murray fish-community. However, by busing non-destructive fishing methods such as electrofishing and fyke netting, almost all the valuable native fish species were able to be released alive.

Table 2 Research catch when targeting carp during 1999–2001 in the mid-Murray River and associated wetlands in the Barmah-Millewa forest.

Name	Species	Electrofisher		Netting[5]	
Exotic species		Count	Weight (kg)	Count	Weight (kg)
common carp	*Cyprinus carpio*	1129	1662	6034	552
goldfish	*Carassius auratus*	63	7	1115	11
goldfish x carp hybrid	*C. carpio x C. auratus*			3	3
redfin	*Perca fluviatilis*	18	1	57	4
weatherloach	*Misgurnus anguilicaudatus*			3	
mosquitofish	*Gambusia affinis*			1	
Native Species					
golden perch	*Macquaria ambigua*	53	44	30	21
Murray cod	*Maccullochella peelii peelii*	13	12		
silver perch	*Bidyanus bidyanus*	4	2	4	3

Carp relative abundance increased in spring 1999 at a fixed site close to access to Barmah Lake and remained high through spring as limited flooding restricted carp access to floodplain habitats. Changes in carp reproductive status suggested that spawning occurred, starting in September as river temperatures rose to ~17^{o}C and was widespread. However, all through that summer and autumn, catch rates of juvenile carp remained low indicating that little successful recruitment had occurred.
The following year (ie. 2000), the aggregation had developed in the river channel by June. In July, the hydrograph rose at the start of what was to become significant and widespread flooding including the 2nd use of the Barmah-Millewa Forest environmental water allocation (EWA). The carp aggregation in the river channel quickly broke-up as carp swarmed onto the floodplain. Again, observed changes in reproductive status indicated that spawning occurred, peaking in October 2000 with river temperatures of ~17 ^{o}C. However, this time mid-summer saw a large peak in the catch-rate of juvenile carp indicating, by comparison, that recruitment was much greater in 2000 than in 1999.
Age-determinations from large samples of carp in 1999–2001 (n=767, 361 and 65 respectively) enabled analysis of the age-structure of the carp population. Analysis of trends in year-class strength suggests that years with greater-than-average flooding produce the strong year-classes; while years with less-than-average flooding produce poor year-classes. The largest male carp was 3200 g and 570 mm, LCF and the largest female carp was 4060 g and 623 mm. The oldest male and female carp were 23 and 28 years respectively.

[5] majority of sampling used fyke-nets (ie. hoop-nets) but some limited gill-netting was deployed in the flooded forest

Relationships between length, weight and age at maturity are described for males and females in terms of median and 95-percentile size and ages (Table 1). Males generally mature in their second year while most females delay maturation for a further 1–3 years until they are between 3 and 5 years old

The sex ratio of mature carp was significantly male-biased in the overall sample. However examination of the relationship between age and sex ratio shows a significant decline in the proportion of females with age. In fact the sex ratio of carp aged 0-years was not significantly different to 1:1.

Commercial trapping of stranded carp (K&C Fisheries) as they attempted to leave Moira Lake in autumn–winter 2001 successfully removed 76 tonnes of carp. Under the assumption that at least these 76 tonnes of carp were present in the flooded Millewa Forest in January (3,431 ha) we can estimate a minimum average biomass estimate of $\cong$22 kg ha^{-1} for the Millewa Forest wetlands. However, when this mass of carp were confined to Moira Lake the carp density was $\cong$ 190 kg ha^{-1}. A sub-sample (n=265) of the carp within the catch was measured and the size distribution (200 – 590 mm, LCF) suggests that the catch mainly contained fish older than 1 year. A smaller sub-sample was randomly chosen for laboratory analysis (n=20) and all were mature with 19 males and 1 female. Substantial biomass of juvenile cyprinids was also obtained but on examination these were shown to be goldfish, *C. auratus* . No large native fish species were trapped as by-catch.

4.5 CARPSIM: Results of simulating carp management scenarios (details in Appendix 6)

Model predictions suggest in general that faster growing, shorter-lived populations may be better controlled by genetic methods inducing male-dominance, or spawning sabotage type methods whereas slower growing, long-lived populations may respond best to removal type approaches.

Deterministic models are those where outputs are always the same for a given set of inputs and there is no variability expressed in the outputs. Note the contrast with *stochastic* models where a range of outputs is possible for each set of inputs and the variability of these outputs is an integral part of the models usefulness in risk-assessment

Population trajectories in deterministic models developed stable cycles with a frequency of 9–14 years that were driven by cycles in recruitment strength. Such cycles were also discernible in simulations with stochastic variation in recruitment. Variation in the frequency of this cycling seemed related to variation in age at maturity.

The equilibrium biomass is simulated at the end (year 200) of the deterministic model run as the cycles damp-down to a stable value. Deterministic simulations predict equilibrium biomass of 570 kg ha^{-1} and 550 kg ha^{-1}; egg production at equilibrium of 114 x 10^6 eggs ha^{-1} and 116 x 10^6 eggs ha^{-1} and average generation times of 10 and 5 years for Barmah and Campaspe channel stocks respectively.

Unselective removal, such as poisoning, trapping or otherwise culling all age-classes is more likely to cause quasi-extinction at annual fishing mortality rates (F) > 0.7 (Table 23, Appendix 5). Quasi-extinction is regarded as an endpoint in population viability; it means a reduction to a pre-set value of extremely low population abundance, but not zero. The terminology is also useful because mathematical models of populations often deal theoretically with fractions of an individual.

Size-selective removal (eg. commercial seine netting) or targeting mature fish, such as a spawning aggregation, at similar F levels may only be useful to reduce the biomass below 60% of virgin biomass (Table 24, Appendix 5). Although, *virgin biomass*, usually means biomass present before a stock was fished. In this sense, it has been defined as carp biomass simulated after 30 years of population growth from the founding population. CARPSIM simulations show that the probability is small of any removal-based method achieving <10% of virgin biomass when F <1.4.

Spawning-sabotage is a term used to describe any carp-management technique that effectively causes total juvenile mortality and therefore prevents recruitment—for instance when water-levels are drawn-down to strand eggs. We simulate this in the model using the parameter, $R_{fail.}$ ~the proportion of years in which recruitment is prevented. Simulations of spawning sabotage or recruitment prevention suggest that when sabotage can only be achieved at low rates (eg. $R_{fail} \leq 80\%$) carp populations will persist although quasi-extinction was achieved rapidly at extremely high rates of simulated spawning sabotage (eg. 99 years in 100, R_{fail} =99%). Furthermore, low rates of spawning sabotage produced highly variable responses in biomass trajectories ranging from an effective complete fish-down, to almost doubling the virgin biomass (Table 25, Appendix 5). For example, at R_{fail}=50%, spawning-sabotage would be an extremely risky management policy with a much greater than 5% risk of ending up with a greater biomass of carp than you start with.

Our simulations of male-dominance (eg. via a daughterless carp genome) as a management strategy suggest that given realistically parameterised populations, driven to a 1% female sex-ratio over 50 years, we can expect an 80% success rate at achieving quasi-extinction within 75 – 90 years (Table 26, Appendix 5). Results seem more sensitive to the initial biological parameters than to the source of stochastic recruitment variability. The simulations

parameterised for the faster-growing Campaspe population with a shorter generation time are slightly more optimistic than those for the slower-growing, Barmah population.

5 Implications for Management

5.1 Age and Longevity

This contribution extends the recognised longevity of carp in Australia to 32 years which doubles the previous known longevity of 16 years from the lower Murray River (Vilizzi and Walker 1999). Previous authors have considered life-spans of 15 years as adequate when modelling potential control methods (Davis *et al.* 1999b). Extended longevity has implications for the time scale over which management activities may have to perform in order to achieve lasting impact on carp populations. It is perhaps a sobering thought to those considering the prospects for control, that some of the carp swimming in Victorian waters today are likely still to be part of the first generation of invaders that colonised these waters in the late 1960s and early 1970s.

This study confirms that examination of otolith thin sections is an accurate method for determining annual age in common carp at least up to 14 years of age. Furthermore, there were no changes to the appearance of the outer increments on fish aged at older than 14 years that would suggest that the process of increment formation was any different to that which produced them annually on younger fish.

Estimates of average percent error on age-determinations were generally < 5% confirming that otolith thin sections can provide precise, replicable estimates of age-structure in carp populations.

5.2 Reproduction

Fecundity is potentially high and proportional to maternal size but not age. Mean relative fecundity (per kilogram of maternal bodyweight) was constant across all sizes and ages examined. Therefore, the weight of mature females in the population determines egg production and for a given mature-biomass of any age or size structure, similar quantities of eggs will be produced. Egg size (mean oocyte diameter) also increased proportionally with maternal size. Large eggs confer a survival advantage in many fish species. Carp-control methods that cause the removal of large females may also be advantageous if these fish would potentially have contributed better quality eggs than the remaining smaller females. Management actions such as size-selective harvesting at levels that reduce the average size of spawning females in the stock may cause some reduction in average egg-quality. However, if recruitment compensation occurs as a density-dependant process when a share of the mature-biomass is removed, then the number of eggs produced may not decline.

Spawning seasons were prolonged often for six months or more and contained multiple spawning events. Usually there was a main spawning period during spring as river temperature reached 17^{o}C followed by a series of minor spawnings over summer and autumn and occasionally into early winter. Note that water temperatures across much of Victoria rarely exceed the suggested upper thermal-limits of carp spawning. Carp management strategies relying on sabotaging spawning activities should concentrate efforts on periods when water temperature first reaches 17 ^{o}C in the spring. However, if the management activity cannot be maintained over a prolonged period it is likely that subsequent minor spawnings will occur. Furthermore, if spring spawning is simply prevented without the removal of the spawning stock, it is likely that many mature adults will simply delay their main spawning activity until later in the season. Wherever possible, the removal of female spawning biomass in late winter is probably the best way of preventing subsequent recruitment.

5.3 Recruitment and year-class strength

In the mid-Murray River and Barmah Forest wetlands there was evidence that year-class strength was proportional to annual flows and juvenile abundance was highest in a year when significant wetland flooding occurred. However, note that 19 consecutive age-classes were present in this stock during the study. This suggests that significant recruitment had occurred at least in each of the preceding 19-years despite variation in hydrology.
Evidence of spawning was detected in the irrigation supply channels in the Campaspe irrigation system. However, an important component of recruitment was by immigration of juveniles ~100–200 mm LCF from the Campaspe River. Carp of this size could potentially be screened out of inflows to the system as a preventative measure.

5.4 Campaspe Irrigation supply-channel stock

Carp are the dominant fish species in this irrigation supply network. Despite extensive sampling of the channels using electrofishing and observations of fish-kills after herbicide treatment, few native fish or macro-crustacean species were captured or observed. Those that were, are regionally and nationally common (eg. yabby, flat-headed gudgeon and Australian smelt). The channel system draws its water from the Campaspe River, which has a slightly more diverse fish community, but generally offers a source-community that is currently of low biodiversity. Therefore management activities targeting carp control that are contained within the network of supply channels offer little threat to local or regional biodiversity or fisheries. Note that this *may not* apply to other irrigation supply systems, that source water from natural systems of higher biodiversity or fisheries value.
It should be noted that the Campaspe irrigation supply channels return little, or no, water to the Campaspe river system once it is extracted. Combined with the physical structure of the water-control structures, this suggests that juvenile carp emigrating from the system would be unlikely to form a source of recruitment for the river system. Any emigrating juveniles from the downstream-end of each channel are likely however, add to the stock in the main Waranga-Mallee supply channel.
The experimental observations made in parallel with acrolein herbicide treatment indicate that boat-electrofishing is comparatively inefficient as a control method in channels, as it sampled only 6–13% of carp present.
Standing stock estimates were variable and although a high biomass was occasionally present of up to 650 kg ha^{-1}, the average was only 144 kg ha^{-1}. Carp population density in the Campaspe irrigation supply channels was usually well below the level at which significant environmental impact is said to occur. Studies that have identified such critical levels of biomass have however, been mainly concerned with impacts on water-quality and vegetation communities. It is possible that physical damage to channel banks identified by the irrigation industry (Jackel 1996) does occur with the observed carp population biomass and structure.
Current channel-management activities with the potential to negatively impact carp include acrolein treatment and water draw-down. An apparent doubling of the total mortality rate observed in one channel relative to another was probably due to a 3-fold increase in acrolein treatments and a winter draw-down in water-levels. Note however, that despite this our sampling showed no detectable difference in indices of carp abundance or biomass between these two channels. Escalating the channel-management strategy to mandatory annual water-draw-downs and annual acrolein treatment may further increase carp mortality rates. However, we are uncertain whether this would significantly reduce abundance or biomass without additional control measures such as screened inflows (see comments above regarding recruitment *via* immigration).

5.5 mid-Murray River carp stock

Carp are again the dominant fish species in the fish community. During three years of sampling one-day per month mainly using electrofishing and fyke-nets, over 2 tonnes of carp were captured from a 500 m reach adjacent to Barmah Lake compared to less than 100 kg of native fish species. In the river channel boat-based electrofishing was a practical method to harvest carp. Most carp in the river channel were large enough to be sexually-mature and abundance was high during low-water periods when access to the floodplain was limited. By-catch did contain small numbers of native fish species that are listed in Victoria, as threatened (ie. silver perch), or part of the threatened lower-Murray fish community (ie. golden perch & Murray cod). However, electrofishing was used as a non-destructive sampling tool and all threatened or high value specimens were returned alive to the water. Use of fyke-nets was effective only as a sampling tool for relatively small numbers of juvenile carp inhabiting the shallow floodplain wetlands. Most of the native fish by-catch from netting came when gill nets were set in the flooded forest targeting spawning carp.

The approximate standing-stock estimates made for Millewa Forest and Moira Lake are low in comparison to densities said to have ecological impact. Commercial harvesting of stranded carp stocks from Moira Lake in autumn 2001 was successful in removing a large biomass (ie. 76 tonnes). Again observations indicated that the majority of the catch was sexually mature carp and no significant by-catch of native fish species was recorded.
Estimates of average adult mortality rates (Z) are lower than those used in previously published models of potential pest-control methods. Lower mortality rates have implications in terms of potentially increasing the likelihood of persistence and the resilience of populations in the face of management actions designed to control them in comparison with previously modelled simulations.
Recent radio-telemetry studies of a small number of carp in the Barmah area suggest that small males may be the most mobile component of the population (Stuart and Jones 2002). However, the current study of the age-structure of the population suggests that this does not equate to greater loss-rates for males in the Barmah stock, in-fact the reverse is true. Carp from the mid-Murray River show sexual-dimorphism in growth, maturation and mortality rates. One of the manifestations of these characters is a changing sex-ratio over time whereby older age-classes are male dominated. This knowledge is critical in developing realistic population models of carp stocks and if carp control methods such as *daughterless carp* are deployed where population sex-ratio's may be used as a performance measure for the technology.

5.6 CARPSIM simulation of management activities and population effects

Previous estimates of population reduction on application of daughterless-carp pest-control methods may be overly optimistic. Scenarios tested with CARPSIM assumed reduction to a 1% female population over a 50-year period. Results are expressed within a risk assessment framework, derived from 1000 replicate runs of each scenario of the model. Models were run with hydrological and climate-based recruitment variability, and with starting parameters from both (Campaspe & Barmah) populations to produce estimates of time to quasi-extinction. If *success* is defined here as the population reaching quasi-extinction, depending on the combinations of recruitment variability and starting population, CARPSIM simulations suggest an 80% chance of success after 75–97 years. That is 80% of model runs simulated quasi-extinction after 75–97 years.
Spawning sabotage is a risky strategy and is only appealing when extremely high probabilities of recruitment failure (eg. 99 years in 100 years) could be achieved. Furthermore, when

recruitment failure could only be achieved at low rates (up to 8 years in every 10 years) there was a >5% chance that virgin biomass was exceeded in the long-term.

Unselective removal controls (eg. trapping of all age-classes) applied to feral carp stocks have potential to drive the population to quasi-extinction when the fishing mortality rate (*F*) can be raised, by the control-efforts, to over 0.7 $year^{-1}$. It should be noted that current maximum estimates of fishing mortality rate within the actual populations that were simulated are significantly less than this (ie. 0.3 $year^{-1}$ for Barmah and 0.2 $year^{-1}$ for Campaspe).

Size-selective removal controls (eg. fishing mature adults only) even when exerted at a fishing mortality rate (*F*) of greater than 2.1 $year^{-1}$, are unlikely to drive a stock to quasi-extinction levels. However, useful levels of biomass reduction may be achieved when *F* can be maintained at 0.7–1.4 $year^{-1}$. Very high rates of fishing mortality (>2.1 $year^{-1}$) are necessary to reduce biomass to less than 10% of the original unfished biomass.

Simulated carp population trajectories show cyclic behaviour that seems related to sexual dimorphism in rates of maturity. With perturbations in recruitment driven by stochastic environmental events, these cycles persist throughout the modelled period (200 years). It is unlikely that any current data sets exist to test whether such cycles are a real characteristic of feral carp stocks. However, if feral carp stocks do undergo cycles in abundance, the detection of trends in abundance due to any management strategy will be more difficult and will need to take such abundance-cycles into account.

In the populations that were simulated the estimates of natural mortality rate (*M*) ranged from 0.2 – 0.3 $year^{-1}$. The fishing mortality rates (*F*) applied in simulated fishing scenarios only begin to have significant effects on the populations when they are 2–3 times estimates of total mortality (*M*). More significant effects of fishing were achieved with *F* set at four-times and six-times *M*.

CARPSIM outputs are clearly sensitive to the parameters that dictate the scale and shape of the stock-recruitment relationship. In the Ricker stock-recruitment relationship these parameters are α and β. While empirical stock and recruitment density data was used to estimate α and β in the current simulations, the better estimation of the parameters describing the stock-recruitment relationship is a clear knowledge-gap. Direct estimation of α and β from observation of stock-recruitment data for a given carp stock is practically a very difficult task, normally requiring long-term data on densities or absolute abundances of fish various life-history stages. However, given reliable population density estimates (biomass or abundance) CARPSIM can be fitted to estimate α and β, perhaps achieving more realistic outputs for a given stock. This may be a more fruitful area of research than attempting to directly measure the stock-recruitment relationship.

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7 Appendix 1 – List of Additional Project Outputs

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FRESHWATER FISHING

CONSERVATION

Eildon Fisheries Surveys

Since December 1998, the **Marine and Freshwater Resources Institute (MaFRI)**, on behalf of Fisheries Victoria, has been undertaking research into the carp population of Lake Eildon. This is part of a much larger Victorian project focusing on carp. The Victorian Carp Project Team is based at **MaFRI**, Snobs Creek, and has been undertaking monthly netting surveys in various parts of Lake Eildon. It won't surprise some anglers that over nine hundred carp have been caught. What is interesting, however, is the relative abundance of valuable recreational species being caught as by-catch.

The data in the Lake Eildon Survey table gives some indication of the size and relative abundance of species caught during Lake Eildon surveys between December 1998 and March 2000.

Photo: Paul Brown

Technical officer Dan Stoessel holds four kilos of prime Lake Eildon brown trout.

LAKE EILDON: SURVEY - 12/98 TO 3/00

Species	No.	Max Lgth (cm)	Mean Lgth (cm)	Max Wght (kg)	Mean Wght (kg)
Redfin	475	42	17	1.415	0.112
Brown trout	261	69	35	4.065	0.752
Golden perch	103	53	41	3.315	1.409
Rainbow trout	4	38	30	0.385	0.244
Macquarie perch	3	39	36	0.765	0.664
Murray cod	2	61	58	4.400	3.715
Roach	1053	23	18	0.417	0.084
Carp	988	70	39	5.819	1.105
Goldfish	88	43	25	1.530	0.341
Goldfish x Carp hybrids	20	46	39	2.044	1.112

It should be noted though that the nets were set to maximise the catch of carp and therefore the relative abundance figures may be misleading. Nets are often set in fairly shallow water, close to grassy banks and away from thick stands of emergent timber. One would expect that structure-loving species, such as golden perch and redfin, may be more abundant closer to the timber, and in deeper water. This may help to explain the low number of Murray cod in the catch to date, although it may also indicate that the abundance of this species is low.

The capture of healthy golden perch in these surveys is confirmation that the Departmental stocking program of the last 5 years is beginning to yield results. Whilst golden perch have been caught in the Howqua Arm and Gough's Bay areas of the lake for many years, Fisheries Victoria anticipates a further increase in the number of golden perch caught as part of the summer anglers' bag. Based on the growth rates of golden perch in other waters, the 1996 and 1997 releases of this species into Lake Eildon should enter the fishery as takeable fish this coming summer.

The table below outlines the departmental stocking program for golden perch in Lake Eildon. There was no departmental stocking of golden perch prior to 1995.

The release of golden perch fingerlings by the Futurefish Foundation, the Victorian Fishing Tackle Association, the Australian Fishing Tackle Association and the Australian Fishing Network in 1999/2000 is not included in the above figures. Other native fish and salmonid releases are planned by the Futurefish Foundation.

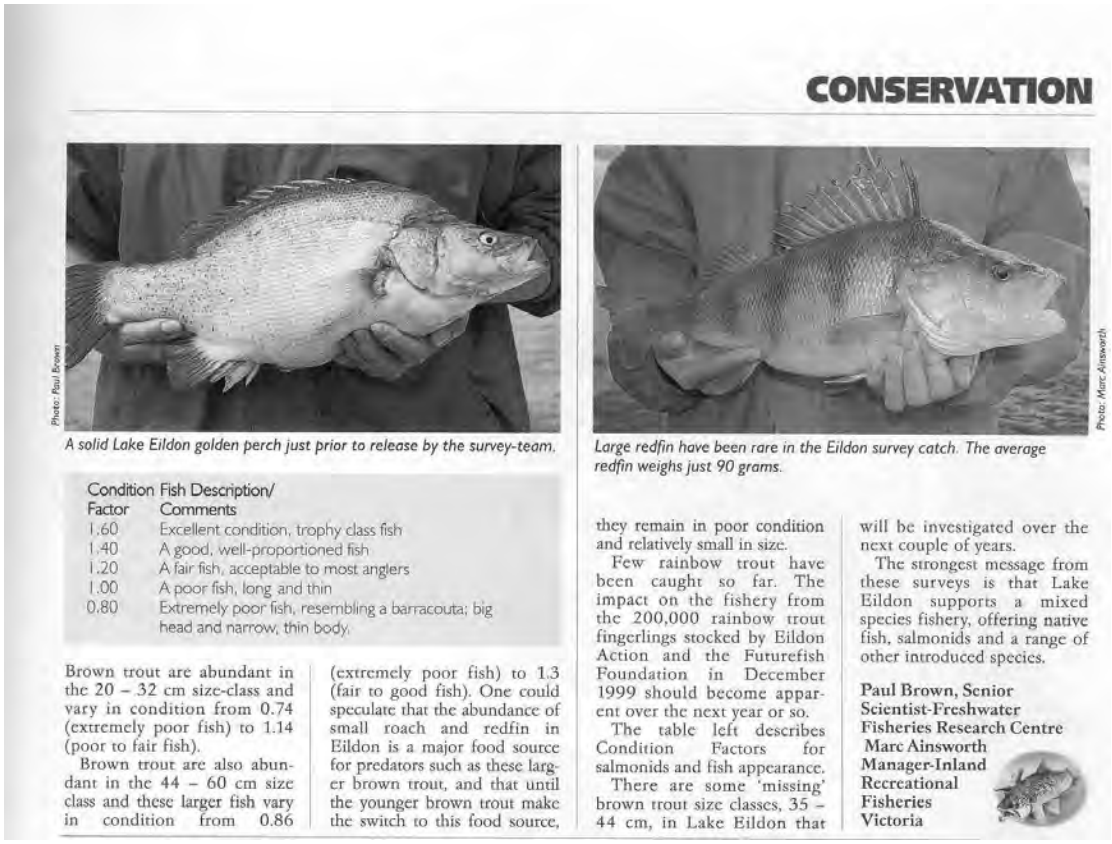
Month & Year of Release	No. fingerlings
3/1995	50,000
2-3/1996	50,000
3/1997	50,000
3-4/1999	120,000

The low water levels of Lake Eildon in 1999/2000 have seen the lake below 20 per cent capacity. The subsequent reduction of habitat and increase in fish concentration may be unfavourable for juvenile fish survival and development. On the upside, however, when rain does come and the lake level increases over the now fertile banks, fish condition and growth rates are likely to improve.

The Carp Project surveys have captured brown trout to over 4 kg, with an average weight of around 800 grams.

Photo: Marc Ainsworth

Roach, an introduced species, has been abundant in the Eildon survey catch.



CONSERVATION

Photo: Paul Brown

A solid Lake Eildon golden perch just prior to release by the survey-team.

Photo: Marc Ainsworth

Large redfin have been rare in the Eildon survey catch. The average redfin weighs just 90 grams.

Condition Factor	Fish Description/ Comments
1.60	Excellent condition, trophy class fish
1.40	A good, well-proportioned fish
1.20	A fair fish, acceptable to most anglers
1.00	A poor fish, long and thin
0.80	Extremely poor fish, resembling a barracouta; big head and narrow, thin body.

Brown trout are abundant in the 20 – 32 cm size-class and vary in condition from 0.74 (extremely poor fish) to 1.14 (poor to fair fish).

Brown trout are also abundant in the 44 – 60 cm size class and these larger fish vary in condition from 0.86 (extremely poor fish) to 1.3 (fair to good fish). One could speculate that the abundance of small roach and redfin in Eildon is a major food source for predators such as these larger brown trout, and that until the younger brown trout make the switch to this food source, they remain in poor condition and relatively small in size.

Few rainbow trout have been caught so far. The impact on the fishery from the 200,000 rainbow trout fingerlings stocked by Eildon Action and the Futurefish Foundation in December 1999 should become apparent over the next year or so.

The table left describes Condition Factors for salmonids and fish appearance.

There are some 'missing' brown trout size classes, 35 – 44 cm, in Lake Eildon that will be investigated over the next couple of years.

The strongest message from these surveys is that Lake Eildon supports a mixed species fishery, offering native fish, salmonids and a range of other introduced species.

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Sivakumaran, K.P. and Brown, P. (2001) Barmah–Millewa Carp Population Biology, Appendix F, pp206–232. *In*: Barmah–Millewa Forum: Report on Barmah–Millewa Flood of Spring 2000 and the second use of Barmah–Millewa Forest Environmental Water Allocation, Spring/Summer 2000/2001. July 2001. Barmah Millewa Forum

Brown P. (2002) Carp in Gippsland: What will it take to make them go away? p13–19 *In*: Proceedings of the Gippsland Lakes Carp Management Workshop, 21 February, (Ed) Angie Gutowski. Gippsland Coastal Board, pp58.

In addition, note that the details in Appendices 2 – 6 have been submitted for publication in international scientific journals

8 Appendix 2 – Validating otolith annuli for annual age determination of carp

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8.1 Summary

Common carp (*Cyprinus carpio* L.) are an important pest species in Australia. As part of a broader study of common carp population-dynamics reliant upon age estimates, otolith sections of common carp were examined to validate their utility for age determination. For the 1999 year-class in Hut Lake near Barmah the absolute age at first annulus formation was confirmed as age-1 year, by repeated sampling of a discrete young-of-year cohort.
The annual periodicity of annulus formation for common carp was confirmed in a mark-recapture experiment when 19 recaptured adult common carp, from an original stocking of 141 marked by injection with oxytetracycline (OTC), showed visible fluorescent marks on their otoliths. Time at liberty for these fish ranged from 6 to 25 months and their ages on recapture ranged from 3 to 14 years. There was complete agreement between increment counts outside the OTC mark and time at liberty. Precision estimates on age-determinations were calculated as average percent error (APE) between readers and for each of two readers over time. Precision was assessed by re-reading sub-samples and APE was <5% in all cases. It is concluded that examination of thin otolith sections is a suitable method for the determination of annual age estimates for common carp aged 0–14 years.

8.2 Introduction

Previous studies of the age and growth of common carp in Australia have used scales (Hume et al. 1983), otoliths and cleithra (Vilizzi 1998; Vilizzi and Walker 1999a; Vilizzi et al. 1998) to estimate annual and daily age. Johal et al. (1984) used scale structure to determine the age of common carp in northern India and found that a lack of seasonal resorption made the recognition of true annuli difficult. Conversely, reabsorption at the scale edge also caused problems for Carlos (1990) who noted partial loss of the last annulus in 7% of his common carp specimens from Spain. In several fish species otoliths provide a better record of age in older and slower-growing individuals, whereas scales of these individuals may fail to grow regularly or even decay via absorption or erosion (Casselman 1990). For this reason in current studies of the population biology of wild common carp in Victoria, otoliths were chosen to determine age.

Validation of daily annulus periodicity in common carp has been achieved through using laboratory reared, chemically marked larvae (Vilizzi 1998) up to 5 weeks of age. Validation of annual age determination has been limited to analysis of marginal increment formation (Vilizzi and Walker 1999a) in fish 1–15 years of age. However, in his recent review of accuracy, precision and quality control in age determination, Campana (2001) was very critical of marginal increment analysis as a validation method and considered absolute age to be the true goal of validation studies, although he conceded that this was often impossible. His recommendation was that if absolute age could not be determined then two steps were necessary for annual age validation:

1. Determination of the age of first annulus formation
2. Verification that annulus formation has annual periodicity throughout the age-range of interest

This study is part of a broader study of common carp population biology around Victoria that will rely on age-estimates of large sample sizes for the calculation of age-at-maturity, growth and mortality rates. For this future project, thin sections of otoliths (Morison et al. 1998b) are the preferred method for production aging and it was felt that greater certainty was required regarding the validation of common carp age determination from otolith sections. Previous common carp ageing studies using otoliths, either whole or sectioned, have reported low levels of precision (Vilizzi et al. 1998). Lack of precision in age determination can indicate problems in the inherent periodicity or clarity of increments within a structure or can simply reflect the level of experience of readers. Therefore highly experienced otolith readers were used in this validation study to minimise one of the possible sources of reduced precision. This study aims to validate the age at the formation of the first annulus, determine the periodicity of annulus formation in a range of age-classes under natural conditions, and quantify the precision of the age estimates produced.

8.3 Methods

Asterisci (referred to simply as otoliths from here on) were collected from fresh or frozen common carp using the “up through the gills method” (Secor et al. 1991). Details of the further preparation and age-determination process are given in Anderson (1992a; 1992b) and Morison (1998b).

8.3.1 Description of otolith sections

Transversely sectioned common carp otoliths are complex in both morphological characteristics and annulus structure. The primordial regions of otoliths are relatively opaque, which can impede the clarity and definition of the presence of the first annulus. Interpretation of annuli becomes easier toward the edge of otoliths of larger common carp, as a broad pattern of otolith structure is visible.

Before ages were assigned to samples, both a primary (CG) and secondary reader (KKG) first became familiar with the morphology and annuli structure of the otolith. Both readers were highly experienced with the interpretation of increments in otoliths working full-time in a dedicated ageing laboratory and determining ages from tens-of-thousands of otoliths from a wide range of species each year. A sample of approximately 100 otoliths from fish of various sizes was studied to establish interpretation criteria. Terminology used follows the glossary for otolith studies (Secor et al. 1995). Production of an annual increment was defined as the completion of an opaque zone following a translucent zone. Hence the annulus used to mark of each year was the completion of an opaque zone. Measurements of samples were made using the image analysis software Optimate^{TM}. Annuli were marked 'onscreen' along a transect from the primordium to the edge of the ventral lobe (Figure 4). The distance between each annulus was extracted for the first 10 annuli. Even though the ventral lobe was used to provide a consistent measurement axis, the entire preparation was used to assist in interpretation. To avoid biasing age determinations, otolith readers were not informed of the collection dates of the common carp specimens.

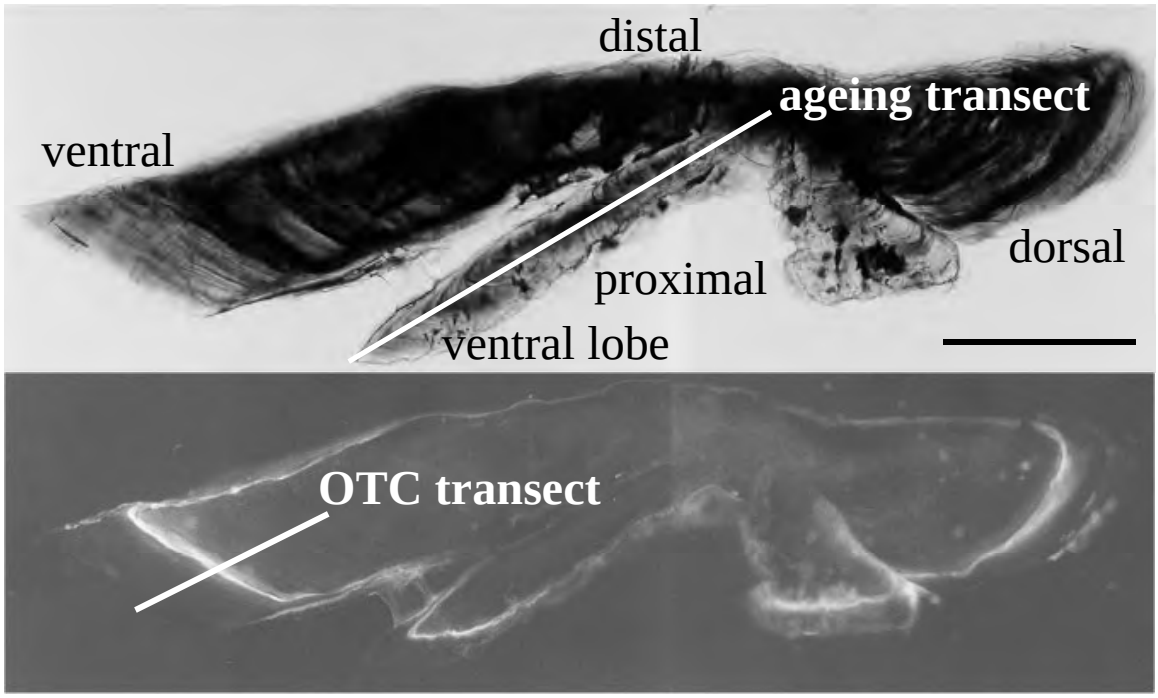

Figure 4 Photomicrograph using transmitted light, showing orientation of thin-section of common carp otolith and transect used for counts of annuli (upper); scale bar = 300 µm. The same otolith section under incident UV light showing OTC mark and transect used for measuring its position (lower)

8.3.2 First Annulus Formation

Strong juvenile recruitment was observed in Hut Lake, a wetland in the Barmah Forest associated with the Murray River (Figure 5; Latitude -35.9120, Longitude 144.9931) during 1999. As this wetland remained flooded for a prolonged period these juveniles were sampled eight times in 12 months using fyke nets (5-m single wing, 10-mm mesh bag). The age at which the first otolith annulus was formed was confirmed by examination of otoliths, sampled over the 12-month period, from a single cohort apparent in length frequency distributions.

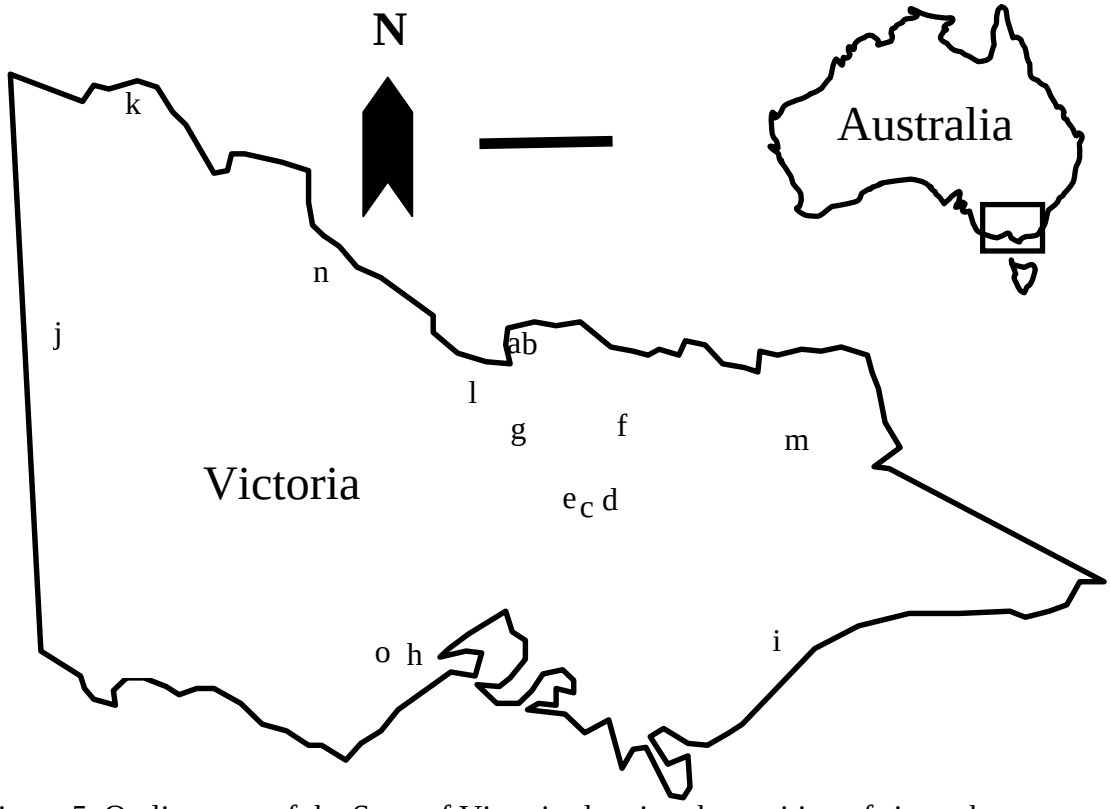

Figure 5. Outline map of the State of Victoria showing the position of sites where carp were sampled for the present age-validation study: a = Murray River at Barmah, b = Hut Lake, c = Elliotts Lagoon, d = Lake Eildon, e = Meggitts Lagoon, f = Lake Mokoan, g = lake Nagambie, h = Reedy Lake, i = Gippsland Lakes, j = Lake Hindmarsh, k = Murray River at Mildura, l = Campaspe irrigation channels, m = Lake Dartmouth, n = Kerang Lakes and o = Lake Modewarre. Scale bar = 100 km. Box on inset map of Australia shows location of State of Victoria

8.3.3 Annuli Periodicity

The frequency with which common carp deposit otolith annuli was determined using the mark-recapture of chemically marked fish. The technique uses a fluorescent mark "time-stamp" produced by administering a fluorochrome chemical to the fish (Kobayashi et al. 1964). Chemically marked common carp were released into a system of enclosed natural lagoons and recaptured up to two years after marking.

For this study, 141 common carp were captured from a range of local Victorian waterways . During January, February and June 1999 carp were electrofished from 6 locations (Figure 5); Meggitts Lagoon (n=12), Elliotts Lagoon (n=46), Lake Mokoan (n=2), Lake Eildon (n=68) and Lake Nagambie (n=13). They were transported back to the laboratory and maintained in

tanks for 2 days to ensure that no fish had sustained injuries or died as a result of capture. The adult common carp were anaesthetised by immersion in a solution of 1:3000 MS222 (Sandoz®). The length (LCF, mm) and weight (g) of each fish were measured. All fish were of unknown age and ranged in fork length from 200–700 mm and in total weight from 150–8250 g. Each fish was then given an intra-peritoneal injection of oxytetracycline hydrochloride (OTC) (as Terramycin/MA, injectable solution, Pfizer®) at a dose of 50 mg/kg body mass. Chemically marked common carp were given an externally identifiable tag to discriminate them from wild, untreated ones. A numbered dart tag (Hallprint®) was inserted into the dorsal muscle just below the dorsal spine and the tag number recorded.
Batches of common carp were injected on three occasions in January, February and June 1999. The tagged and injected fish were kept under observation for up to a week to ensure no adverse affects were caused by the treatment and handling. A salt bath (NaCl) was given the day after the treatment to reduce the likelihood of subsequent infections. OTC-marked common carp were stocked into a permanent lagoon system on the Goulburn River floodplain known as Elliott's Lagoon (Latitude -37.2470, Longitude 145.8050). The OTC-marked common carp shared Elliott's Lagoon with an existing naturally reproducing, wild stock of common carp.
Approximately 2000 young-of-year common carp were also seined in February from Hut Lake and transferred to laboratory tanks. The daily mortality rate of these captive juveniles was initially high so they were maintained on artificial diets for three months until mortalities had stabilised.
As injection was impractical for so many small fish, marking of these fish was done by immersion in a buffered oxytetracycline hydrochloride solution (0.5 g/l) for 12 hours (McFarlane and Beamish 1987). A single exposure to OTC was carried out in two batches, one in March, the other in June. Following marking approximately 1000 young-of-year common carp were also stocked into Elliot's lagoon system. Due to their small size (~50-80 mm, LCF) these fish were stocked without any external mark.

8.3.4 Initial sampling to confirm mark status

During June 1999, approximately six months after OTC marking and releasing the first batch of common carp, two adult common carp were recaptured and sacrificed. The otoliths were sectioned, mounted, and photographed under ultraviolet light to verify that adequate marking had occurred. An obvious fluorescent mark could be observed near the otolith edge of both specimens.

8.3.5 Sampling one year after marking

During January and February 2000 electrofishing, gill nets and a seine were used to catch 45 common carp from Elliott's Lagoon. Of these common carp, six were identified as being OTC-marked fish by their tags. However, tag loss appeared to have been high. An additional six common carp in this sample were putatively identified as OTC-marked fish by the presence of tagging scars, although some of these were faint. To be certain, the otoliths were collected from all 45 common carp including untagged fish.

8.3.6 Sampling two years after marking

During February 2001 angling was used to catch 40 common carp from Elliot's Lagoon. Four of these were identified as being originally OTC-marked fish by their tags. An additional 3 common carp in this sample were putatively identified as OTC-marked fish by the presence of apparent tagging scars. To be certain, the otoliths were collected from all 40 common carp including un-tagged, presumably wild fish.

8.3.7 OTC-Mark Analysis

At the end of the present study, over 2 years after the initial marking-and-release of the OTC treated common carp, otolith thin-sections were prepared using the method of Anderson et al. (1992b) The presence of OTC marks were assessed by examination for fluorescence under a Leitz Labourlux compound microscope fitted with an incident light 100 w ultraviolet light source, and a Lietz I2 block (exciting filter 450 – 490 nm) to suit the fluorescent properties of OTC (Birk 1984). Assessment of the location of OTC marks and age determinations were all done "blind", that is the reader never knew the sampling date of any specimens. Where present, the OTC mark appeared as a bright yellow band. Increment measurements are often made from the primordium to the otolith edge, however this was not suitable in this study due to the low magnification required and the difficulty in replicating the exact transect when ageing the fish. An alternative method was adopted. Using fluorescent light, the position of the OTC was determined by measuring the distance between the mark and the otolith edge on the proximal-ventral side. The measurement was used to determine the position of the OTC mark in samples viewed using transmitted light. Under transmitted light, the position of an OTC mark can appear as a growth discontinuity within the otolith, probably reflecting the stress of the capture and marking process. Once the position of the OTC mark had been located under transmitted light a more accurate measurement was made from the mark to the edge using a compound microscope at 40x magnification (Figure 4). All measurements were taken along a transect perpendicular to the increments. The distance between the otolith edge and the outer edge of each opaque increment outside the OTC mark was measured. Up to four increments were measured. The number of increments present after the OTC mark was then calculated.

8.3.8 Precision of Age Determination

Otoliths from a total of 6110 common carp from 15 locations around Victoria (Figure 5) were used for age-determination over a three-year period as part of a broader study of common carp population biology. The primary reader (CG) determined 5257 and a secondary reader (KKG) determined a further 853. To assess any drift in precision over time, about 20% of samples were re-read by the primary (n=1068) and secondary (n=230) readers. Also, to assess the level of consistency between readers a random sub-sample of age-determinations (n=229) were re-read by both readers. For statistical comparison of the consistency of age-determinations both within and between readers, we calculated bias-corrected mean average percent error (APE) (Beamish and Fournier 1981) and 95% confidence intervals on the mean using a boot strapping procedure (Efron and Tibshirani 1993) suggested in Morison (1998a).

8.4 Results

8.4.1 First Annulus Formation

Young-of-year (YOY) common carp were first sampled in Hut Lake in March 1999. The length-frequency distribution and age determination for this sample (Figure 3) showed predominantly YOY fish. The only fish that showed a single annulus (aged 1) were > 200 mm LCF. By June 1999 the sample length frequency suggested the YOY cohort had a modal length of ~85 mm LCF, again some fish aged 1 year were present and were larger than 120 mm LCF. By August and September 1999, only YOY fish remained in the sample, ranging in size from 70 – 160 mm LCF. By November, there was a significant proportion of fish showing their first increment. By December the first annulus was observed on the majority of individuals within the sample. In January 2000, in addition to the original cohort (now > 90 mm and 1 year old) the presence of a new YOY cohort of fish <80 mm was evident. Therefore the first increment began to form by 30 November 1999 and was almost complete by 21 December.

Figure 6. Elliott's Lagoon, on the Goulburn River floodplain, was stocked with carp chemically marked with oxytetracycline to assist in the validation of age determination methods

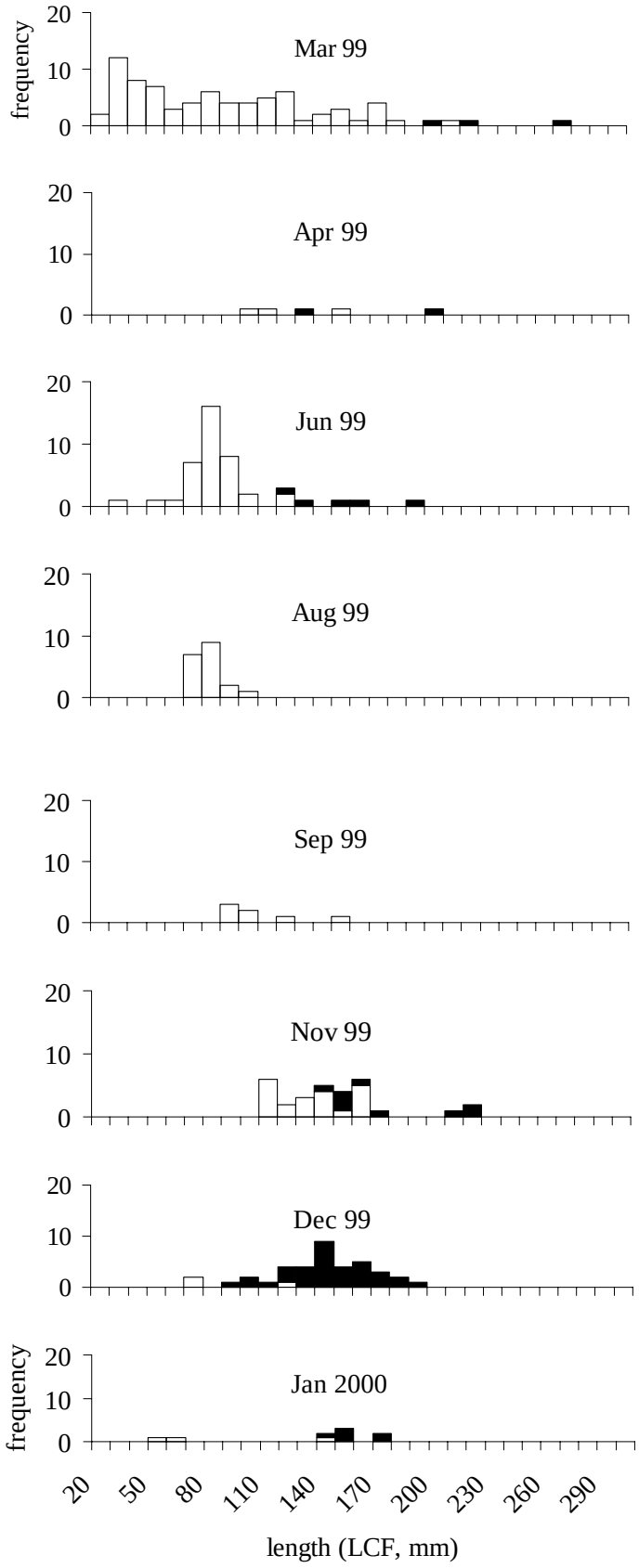

Figure 7. Time series of length frequency distributions for monthly samples of carp <300 mm, LCF from Hut Lake in the Barmah Forest in 1999. Clear bars are carp aged 0 years and solid bars are fish with their first annulus, aged 1 years.

8.4.2 Annuli Periodicity

Two years after the initial marking procedure examination of the otoliths from recaptured common carp showed OTC marks in a total of eight that were tagged and a further six that had a recognisable tag-scar. In addition, five common carp that had no tag or recognisable tag-scar also had OTC marks. Presumably these had simply shed their tags and the scar had healed. None of the un-tagged individuals aged as 2 years-old, and therefore potentially from the immersion experiment, had visible OTC marks. This suggests that the immersion method for 0 juveniles may have been unsuccessful.
Common carp sacrificed 1-year after OTC injection all had a single increment outside the OTC mark. Common carp sacrificed 2-years after OTC injection all had two increments outside the OTC mark (Table 3). The total age of these fish was estimated to be in the range of 3 to 14 years. This confirms that annulus-counts made from thin-sections are a reliable indicator of age for common carp aged 3–14 years.

8.4.3 Precision of Age Determination

Estimated bias-corrected mean APE (95% confidence interval) for re-read samples from the primary reader (n=1068) was 4.56% (4.14–4.97%); for the secondary reader (n=230) was 4.04% (2.67–5.42%); and between readers (n=229) was 4.98% (4.18–5.79%). The mean APE values of <5% suggest that precision in age-determination using otolith thin-sections is acceptable (Campana 2001; Morison et al. 1998b). The overlapping 95% confidence intervals suggest that although the secondary reader was less precise, there was no significant difference in precision of age-determination between readers.

Figure 8. Hut Lake, in the Barmah forest, provides an ideal temporary habitat for carp during flood periods

Table 3 Details of common carp observed with OTC mark in otolith sections. For recaptured common carp that had shed their tags, time at liberty can be estimated from the three injection-dates.

Age determination (years)	Date Injected	Date of Recapture	Tag No. on Recapture	Time at Liberty (months)	No. of Annuli outside OTC-mark
4	January 1999	January 2000	1053	12	1
5	Jan, Feb or June 1999	January 2000	?	6–12	1
8	Jan, Feb or June 1999	January 2000	?	6–12	1
10	January 1999	January 2000	1713	12	1
12	Jan, Feb or June 1999	January 2000	?	6–12	1
14	February 1999	January 2000	1710	11	1
3	Jan, Feb or June 1999	February 2000	?	7–13	1
4	Jan, Feb or June 1999	February 2000	?	7–13	1
5	Jan, Feb or June 1999	February 2000	?	7–13	1
7	January 1999	February 2000	0679	13	1
7	February 1999	February 2000	1703	12	1
10	Jan, Feb or June 1999	February 2000	?	7–13	1
11	Jan, Feb or June 1999	February 2000	?	7–13	1
5	Jan, Feb or June 1999	February 2001	?	20–25	2
6	January 1999	February 2001	1077	25	2
7	Jan, Feb or June 1999	February 2001	?	20–25	2
9	June 1999	February 2001	1825	20	2
10	January 1999	February 2001	1063	25	2
10	Jan, Feb or June 1999	February 2001	?	20–25	2

8.5 Discussion

8.5.1 First Annulus Formation

Despite comprehensive sampling of several common carp stocks over a three-year period in which spawning and recruitment occurred regularly, only one strong juvenile cohort was consistently sampled from recruitment until first increment formation. In many cases juvenile cohorts disappeared from the samples, either through mortality, gear-selection or emigrations prior to first increment formation.
This method corresponds somewhat to Campana's (2001) description of discrete length modes sampled for age-structure and is a rational method for validating the interpretation of annuli in young fish. The assumption that the 1999 juvenile cohort from Hut Lake was indeed of young-of-year fish is supported by many studies of juvenile common carp growth and ontogeny (Chakrabarti and Jana 1992; Hume et al. 1983; Szumiec 1990; Szumiec 1997; Vilizzi 1998; Vilizzi and Walker 1999c) and by the absence of any visible annuli on the otoliths of any of these fish. Having accepted this assumption, the method essentially is that of validation of absolute age for age-1 common carp. This is one of the key-requisites of age-validation (Campana 2001).

8.5.2 Annuli Periodicity

Of the two OTC marking methods used, administering OTC by injection was the most successful (McFarlane and Beamish 1987). However, it is uncertain whether the lack of recaptures from the batches of juveniles marked by immersion was a result of a failure of the marking-process itself, poor survival of stocked fish, a low proportion of marked juveniles among a much larger number of naturally-recruited fish, or some combination of these factors. Immersion in tetracycline hydrochloride was used successfully to mark common carp larvae by Vilizzi (1998) who subsequently validated daily increment periodicity in common carp larvae up to 5-weeks old, from the Murray River in South Australia.
Several authors have successfully used OTC mark-and-recapture methods to validate the annual periodicity of annulus formation in marine fishes (Cappo et al. 2000; Ferreira and Russ 1992; Ferrell et al. 1992; Fowler and Doherty 1992). Many of these recent Australian studies have relied on at least some captive tank (Ferreira and Russ 1992; Ferrell et al. 1992) or cage-reared individuals (Cappo et al. 2000). In all of these studies the periodicity of annulus formation was close to annual. Some researchers simply reported the coincidence of years at liberty with the number of annuli outside the OTC mark. Others also used a model of otolith growth to resolve issues of variability and report periodicity and it's confidence limits (Cappo et al. 2000). Although logistically more challenging, this method is at its most robust when used with fish growing in a natural environment, and at liberty for several years (Campana 2001). Common carp in this study were obtained from a variety of locations and habitats prior to marking and were released into a natural lagoon system on the Goulburn River floodplain. All but one recaptured common carp that had retained tags had shown positive growth-in-length increments similar to fish of their ages in other wild stocks. Tagged fish that were recaptured were 4 – 10 years old. One 10-year old common carp showed no growth in length during the two years it was at liberty. However, given the growth rates and variability previously observed in other common

carp stocks (Lorenzen 1996; Soller et al. 1965; Vilizzi and Walker 1999a; Vilizzi and Walker 1999b), the fish in our study appeared to be growing normally.
Common carp in our study ranged in age from 3 to14 years. This somewhat under represents the age-structure of many wild stocks in Victoria where ages <3 years and >14 years are common (authors' unpublished data). The previous section provides evidence for validation of the method of age determination for common carp of up to 1 year-old. Unfortunately we could not be certain of including older common carp within the trial until marked fish were recovered. This study provides good evidence that the periodicity of annulus formation, in adult common carp aged 3 –14 years, was annual. There were no changes to the appearance of the outer increments on fish aged at older than 14 years that would suggest that the process of increment formation was different to that which produced them annually on younger fish.

8.5.3 Precision of Age-determination

Previous common carp ageing studies using otoliths have reported relatively low precision. Vilizzi (1998) reported mean APE values >12% and ~ 6% for within and between-reader reproduceability in whole common carp otoliths. In validation studies such as these it is difficult to separate the causes of high APE. It might be to do with the variability in otolith structure or a lack of clarity of increments, but it may also reflect the skill of the reader. As suggested by Campana (2001) and Morison (1998b) variation between species and structures being aged makes it is difficult to assign a target level of precision *a priori*. However, Morison (1998b) goes on to say that repeated application to a variety of species, and results from other published (unspecified) studies suggests that APE values of around 5% should be expected. Based on a review of literature Campana (2001) reports that many ageing studies are carried out with a precision level corresponding to an APE of <5.5%. Common carp age-determinations in this study were therefore carried out with acceptable levels of precision both within and between readers.

8.6 Acknowledgments

Part of this work was carried out under New South Wales Fisheries collecting permit F98/452. The Elliott family is thanked for allowing us to put even more common carp in their lagoon. From MAFRI, thanks to Kyne Krusic-Golub for being our secondary otolith reader and to Peter Grant for ably assisting to manage our data. Thanks also to Sandy Morison and Wayne Fulton for their useful comments assisting the development of this manuscript.

8.7 References cited in Appendix 2

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9 Appendix 3 – Maturation and reproductive biology of female wild carp in Victoria, Australia

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Submitted to: Environmental Biology of Fishes, 2002

9.1 Summary.

The reproduction of carp *Cyprinus carpio* L. (Family: Cyprinidae), from Victorian waters in Australia, is studied with detailed analysis of gonad maturation, spawning season, fecundity and oocyte diameter. Results show that carp has a high annual fecundity (AF) (0.12 to 1.54 million oocytes per fish) which is positively correlated with caudal fork-length (L, mm) and total weight (W, kg) but not age. The relationships between length or weight and annual fecundity were statistically significant and best described with the simple linear or quadratic regressions: AF = (0.00359 L) – 1.269 or AF= $(3.47x10^{-4})W – (2.1x10^{-8})W^2 – 0.309$. Mean relative fecundity was 0.163 million eggs kg^{-1} whole weight. Egg size was estimated from oocyte diameter in carp from eight stocks. Egg size was proportional to maternal size but not age. Seasonal trends in gonadosomatic indices, together with the changes in the macroscopic and microscopic condition of ovaries, demonstrated that spawning generally peaks during Spring–early Summer, but also occurs through until Autumn and can even start in late Winter at some sites. In Victoria, this species is a multiple spawner with asynchronous oocyte development and a protracted spawning season. Stocks generally contain both females that spawn once, and females that spawn repeatedly, within a spawning season. Implications for management for the control of feral carp stocks are discussed.

9.2 Introduction

Determination of fecundity and the development of sexual maturity is fundamental to fishery science. Due to the importance of these parameters in the dynamics of populations (Hunter et al. 1992) they are commonly estimated for species of economic significance.

The most suitable method of determining the reproductive cycle in female fishes is to observe seasonal developmental changes in the gonads (Sivakumaran 1991, Karlou-Riga & Economidis 1996, Karlou-Riga & Economidis 1997). This maturation cycle has been described as morphological changes that gonads undergo to attain full growth and ripeness.

Methods of identifying spawning seasons of fishes are reviewed by West (1990) who suggested that histological studies, while expensive and time consuming, yield the most reliable, objective information on spawning cycles. Histological examination is considered essential for detecting details within the maturation cycle such as: maturing females, partially spawned fish, postovulatory follicles, and atretic oocytes (Hunter & Macewicz 1985a, Hunter & Macewicz 1985b, Schaefer 1987, West 1990, Davis & West 1993, Marshall et al. 1993).

The carp (*Cyprinus carpio* L.) (Cyprinidae), also referred to as common carp or European carp, is one of the most extensively translocated and domesticated fish species in the world. Carp originated in central Asia and spread east and west to China and the Danube (Balon 1974). The species was successfully spread throughout Asia and Europe, and was domesticated as an ornamental and aquaculture species. Carp are now established on every continent except Antarctica. They are widely distributed throughout south-eastern Australia, with smaller populations in Western Australia and Tasmania (Koehn et al. 2000) where they are generally regarded as an exotic pest species.

Several studies on the reproductive biology of carp have been previously undertaken in several regions of the northern hemisphere, including eastern Europe, the United Kingdom, India, Israel and South Africa (Sarig 1966, Parameswaran et al. 1972, Hulata et al. 1974, Gupta 1975, Toor & Chauhan 1975, Bieniarz et al. 1977, Bieniarz et al. 1979, Fouche et al. 1985, Dubost et al. 1997). In particular, Alikunhi (1966), Fida (1988), Dobriyal (1990) and Guha (1991) published information on reproductive aspects of carp (*C. carpio*) from India. Swee (1966) described the reproductive biology of carp in eastern Canada. Crivelli (1981) studied maturation and spawning in southern France, and Jankovic (1971) recorded oogenesis of carp from Lake Skadar on the border of Montenegro and Albania. However, only limited information is available on reproductive biology of carp from Australia. What does exist is mainly derived from Hume et al. (unpublished data[6]), Brumley (1996) and Adamek (unpublished data[7]) in New South Wales and Victoria, none of which used histological analysis.

Consequently, little is known of some of the most basic elements of the biology and ecology of carp in Australia (Vilizzi et al. 1998).

This study therefore aims to go some way in filling this knowledge gap through the histological study of carp from several sampling sites throughout Victorian waters in Australia. The spawning cycle of carp is delineated based on the state of maturation of

[6] Hume, D.J., A.R. Fletcher & A.K. Morison. 1983. Carp program - final report. Arthur Rylah Institute for Environmental Research, Fisheries & Wildlife Division Ministry for Conservation Victoria, Melbourne, Australia.

[7] Adamek, Z. 1998. Breeding Biology of Carp (*Cyprinus carpio* L.) in the Murrumbidgee Irrigation Area. Visiting Scientists Report, CSIRO Land and Water, Griffith. 38pp.

ovaries resulting in a detailed analysis of the reproductive season (using gonadosomatic indices), ovarian developmental stages, and also fecundity.

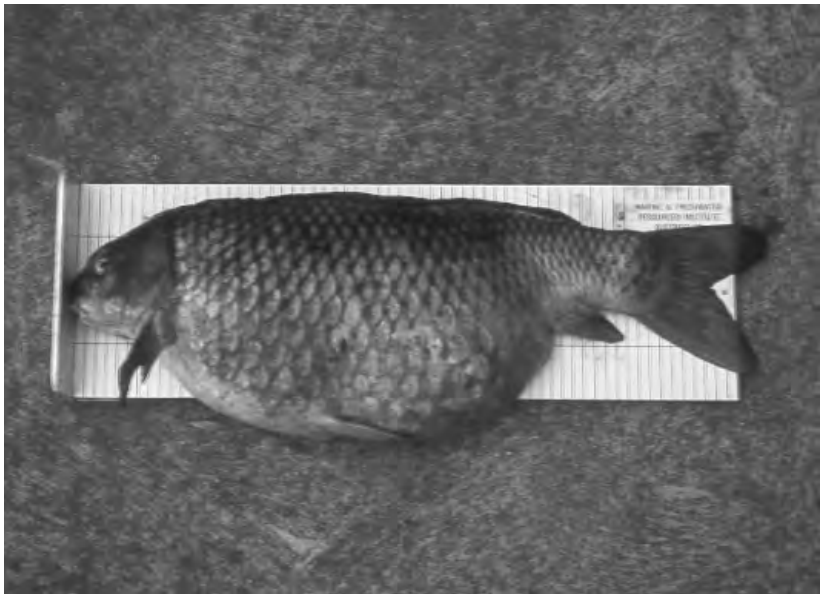


Figure 9. This large female from the Barwon River wetlands shows the species' potential for high fecundity

9.3 Materials and methods

Carp in eight geographical locations were sampled for this reproductive study (Figure 10). Four separate sub-stocks in Lake Eildon, Lake Dartmouth, the Murray River and the Campaspe irrigation districts can all be considered part of a genetically contiguous Murray-Darling basin stock (Davis et al. 1999). Two sub-stocks were also regularly sampled in separate coastal catchments, the Barwon River and the Gippsland Lakes. Occasional samples were obtained from the internal drainage catchments of the Wimmera River and Lake Modewarre.

Details of locations, coordinates, sampling frequency and methods used are listed in table 4. In Lake Eildon although gill nets were the main method, carp were sampled using multiple gears to ensure all available size classes of carp were susceptible to capture. Gill nets were negatively buoyant, 25m long and 2.5m deep. Lake Dartmouth was also sampled occasionally for carp using similar gill nets. The Murray River was sampled using electrofishing only. A boat mounted electrofishing unit (Smith Root ^{TM},

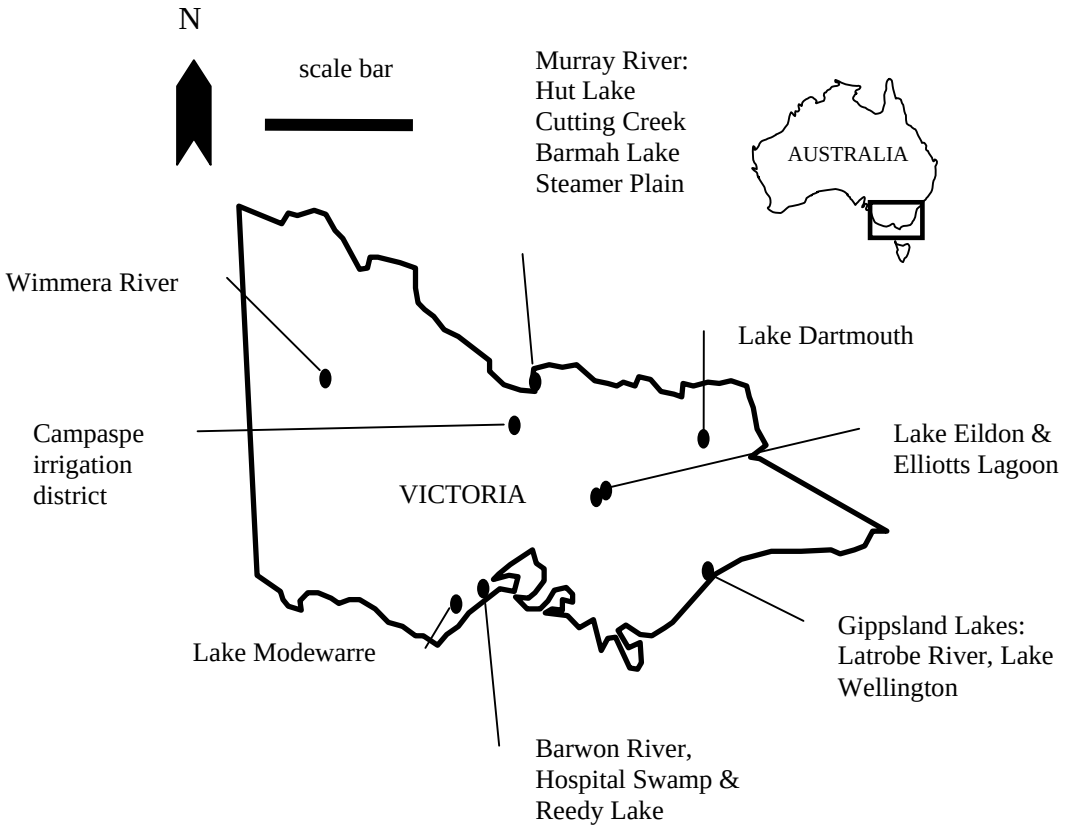


Figure 10 Map showing the State of Victoria and its location within Australia (inset) and identifying locations where carp were sampled for this study (scale bar =200 km)

Table 4 Details of location, timing of sampling and gear used to sample carp for analysis of reproductive biology. GN=gill nets (knot-to-knot mesh size in parenthesis), FN=fyke net, BS=beach seine, EF=boat electrofishing, A=angling.

Location	Latitude	Longitude	Frequency / Timing	Gear details
Lake Eildon	-37.2347	145.9899	Monthly (1999–2001)	GN (51,76, 89,102,127,152); FN, BS, EF
Lake Dartmouth	-36.5947	147.5454	Occasionally (1999-2001)	GN (51, 76, 102, 127, 152)
Murray River	-35.9595	144.9549	Monthly (1999–2001)	EF
Barmah Lake	-35.9470	144.9599	Monthly (1999–2001) when flooded	FN, GN (51,76, 89,102,127,152)
Hut Lake	-35.9116	144.9918	Monthly (1999–2001) when flooded	FN
Cutting Creek	-35.9244	144.9585	Occasionally (1999–2001) when flooded	EF
Steamer Plain	-35.9382	144.9745	Occasionally (1999–2001) when flooded	FN, GN (51,76, 89,102,127,152)
Campaspe Irrigation channels	-36.3631	144.7003	Monthly (1999–2000)	EF
Hospital Swamp	-38.2279	144.3985	Occasionally (1999–2000)	EF
Reedy Lake	-38.2041	144.4336	Monthly (1999–2001)	EF, FN
Lake Wellington	-38.0920	147.3190	Monthly (1999–2001)	BS
Latrobe River	-38.1519	147.1083	Occasionally (1999–2001)	EF
Wimmera River	-36.2231	141.9742	August (1999)	BS
Lake Modewarre	-38.2454	144.1090	October (2000)	EF
Elliotts Lagoon	-37.2531	145.8307	Occasionally (2000–2001)	A, GN, EF

GPP 5) was used to sample a fixed site of approximately 500 m of river at Barmah each month. The Barmah wetlands associated with the Murray River site were also sampled including; Barmah Lake, Hut Lake, Cutting Creek and Steamer Plain. All were sampled with a standard fleet (20) of fyke nets (13 mm knot-to-knot mesh in the wings and the cod-end). The Campaspe Irrigation district was sampled at six sites in two channels; Campaspe East supply channel and Campaspe West supply channel near Rochester.

The commercial fishery catch from two Barwon River wetlands; Hospital Swamp and Reedy Lake was sampled. This included catches from electrofishing operations and carp by-catch from the eel fishery (fyke nets). Commercial catch sampling also enabled data collection from carp in Lake Wellington and the Latrobe River as part of the Gippsland Lakes carp stock. A sub-sample (n=50) was taken from a sample of 200 randomly selected carp from a day's commercial electrofishing or seine-net haul. These were returned on ice to the laboratory for biological sampling. Single samples were obtained from commercial electrofishing operations in the Wimmera River and Lake Modewarre and occasionally by angling, gill-netting and electrofishing from Elliotts Lagoon, a billabong on the Goulburn River Floodplain.

All sample processing was completed in the laboratory. Wherever practical other species of fish of recreational, commercial or conservation value were returned alive to the water, or used to benefit other approved fisheries research programs.

Carp were weighed in grams and their caudal fork length measured to the nearest millimetre. Carp otoliths (asteriscii) were removed and stored dry. Age was determined by counting annual growth increments on examination of thin otolith-sections (Vilizzi & Walker 1999, and see Appendix 2– this report). Fulton's (1902) condition factor was calculated for each carp.

Where possible, the sex (male, female) of each fish was determined and the macroscopic reproductive stage assessed (Sivakumaran 1991, Knuckey & Sivakumaran 1999, Knuckey & Sivakumaran 2001) according to an appropriate set of stage descriptions developed (Table 5) by adaptation from published literature (Jankovic 1971, Gupta 1975). Fish too young for macroscopic determination of sex were classed as indeterminate. Gonads were removed, weighed and preserved in 10% neutral buffered formalin. The gutted weight was noted and the gonadosomatic index (GSI) calculated on both whole and gutted weight (Knuckey & Sivakumaran 2001). Subsequent analysis will use GSI calculated from whole body weight, as this is the more widely used method in the literature (Cailliet et al. 1986). The dissected gonads were left in formalin for 4 to 10 weeks. A transverse medial sub-sample of about 30g of the fixed gonad was then removed and preserved in Davidson's solution. These sub-samples were blocked in paraffin wax and 6 µm sections were cut, mounted and stained in Harris' haematoxylin and eosin (Lunar 1968). Analysis of sexual staging relied on histological interpretations, that were deemed by West (1990) to be the most appropriate in determining spawning cycles in the ovary. Thus we have followed the histological guidelines presented by Knuckey & Sivakumaran (1999) for Blue Warehou and Gupta (1975) and Jankovic (1971) for carp. Histological examination of ova facilitated an understanding of cellular processes occurring during the reproductive cycle. This enabled the confirmation of our macroscopic estimates of reproductive stage, and improved the accuracy of estimates of fecundity at size and age.

Ovaries were staged on the basis of the most advanced type of oocytes present, regardless of their abundance (Wallace et al. 1987, West 1990, Baelde 1996). Oocyte development and maturation is a continuous process, which has been subdivided into various stages to simplify histological classification of ovaries. Description of

microscopic stages of oocyte development for female carp is shown in Table 6 and Figure 11.

Table 5 Macroscopic Description of Gonad Stages in Female Reproductive Development

Stage	Stage description	Appearance
1A	Immature (virgin)	Ovaries ribbon-like, flesh-coloured and occupy one-half of the body cavity, no oocytes visible. (F1a).
1B	Resting	Strip-like, yellowish-white or light pinkish ovary with lobular structure. No oocytes visible. (F1b).
2A	Developing (virgin)	Ovaries finger-like and yellowish and occupy three-fourths of the body cavity. Mass of small eggs visible to naked eye. (F2a).
2B	Redeveloping	Ovaries opaque and light yellowish and occupy three-fourths of the body cavity. Mass of small eggs visible to naked eye.(F2b)
3	Mature	Ovaries quite long and yellowish and fill almost the whole of the body cavity. Ova, big, appear yellow with a greenish halo, or light greenish-yellow, when seen under the microscope. (F3).
4	Running ripe	Ovaries, large and fill the cavity completely. Eggs pass out on a slight pressure applied to the abdomen. Just before breeding takes place the mature ova increase considerably in size with accumulation of yolk, and at this stage they are ripe. The greenish-white ovaries have attained their maximum volume and occupy the entire length of the body cavity; sometimes covering the alimentary tract, and bulging with closely packed ova.. Many ova are above 60 micro-divisions (ie. 1.035 mm). Gonad / genital aperture often inflamed. (F4).
5	Partially spent	Ovaries flaccid, blood-shot and contain ova of all sizes. Limp, grey ovary with non-ejected eggs or at this stage the ovary does not differ greatly in colour and appearance from the previous stage. Remaining ova not as closely packed together. Gonad/genital aperture often inflamed. (F5).
6	Fully spent	Ovaries, very much flaccid, blood-shot, light pinkish. A watery fluid passing out on pressing. The larger ova completely discharged, or sometimes grey ovary with black spots, the non-ejected eggs being resorbed, and small, new, white eggs. Gonad/genital aperture often inflamed. (F6).

Table 6 Description of microscopic stages in oocyte development of female carp.

Stage	Stage description	Histological Appearance
I	Chromatin nucleolar	Very small oocytes, nucleus surrounded by a thin layer of dark-blue-stained cytoplasm (<70 m)
II	Perinucleolar	Oocyte size increases slightly as dark-blue-stained cytoplasm thickens, nucleoli appear at the periphery of nucleus (58 - 410 µm; n = 365, 71 ovaries)
III	Cortical alveoli	Appearance of cortical alveoli in pale-blue-stained cytoplasm, pink-stained zona radiata distinguishable, oil vesicles appearing, lampbrush chromosomes often visible in the nucleus (73 - 1014 m; n = 590, 115 ovaries)
IV	Yolk	Marked increase in oocyte size, cytoplasm filled with pink-stained yolk granules, cortical alveoli and oil vesicles increase in size and number (441 - 1570 m; n = 2860, 499 ovaries)
V	Nuclear migration	Migration of nucleus to periphery of oocyte, fusion of yolk granules into yolk plates; fusion of oil vesicles into the oil droplet (733 - 1627 m; n = 460, 91 ovaries)
VI	Hydration	Further increase in size of oocytes, all yolk granules fused into a few plates (893 - 1772 m; n = 230, 41 ovaries)
POF (old)	New postovulatory follicle	Remaining follicle soon after ovulation. It is large, highly convoluted with an obvious lumen, and may contain fine granular material. The layered nature of both cell types (thecal and granulosa) remains intact in lumen
POF (new)	Old postovulatory follicle	Convoluted nature much less apparent, lumen much reduced, even closed, and the thecal and granulosa cells no longer retain their orderly arrangement
α	α~-atretic oocyte	Zona radiata dissolves, oocyte shape loses integrity, yolk globules begin to disintegrate and are less regular in shape
β	β~-atretic oocyte	Numerous disorganised granulosa cells surrounded by a thin thecal and blood vessel layer. Contents of nucleus of some granulosa cells is contracted to a deep staining irregular mass (ie. pyknotic) and many cells contain a large intracellular vacuole that may be empty or contain amorphous particles

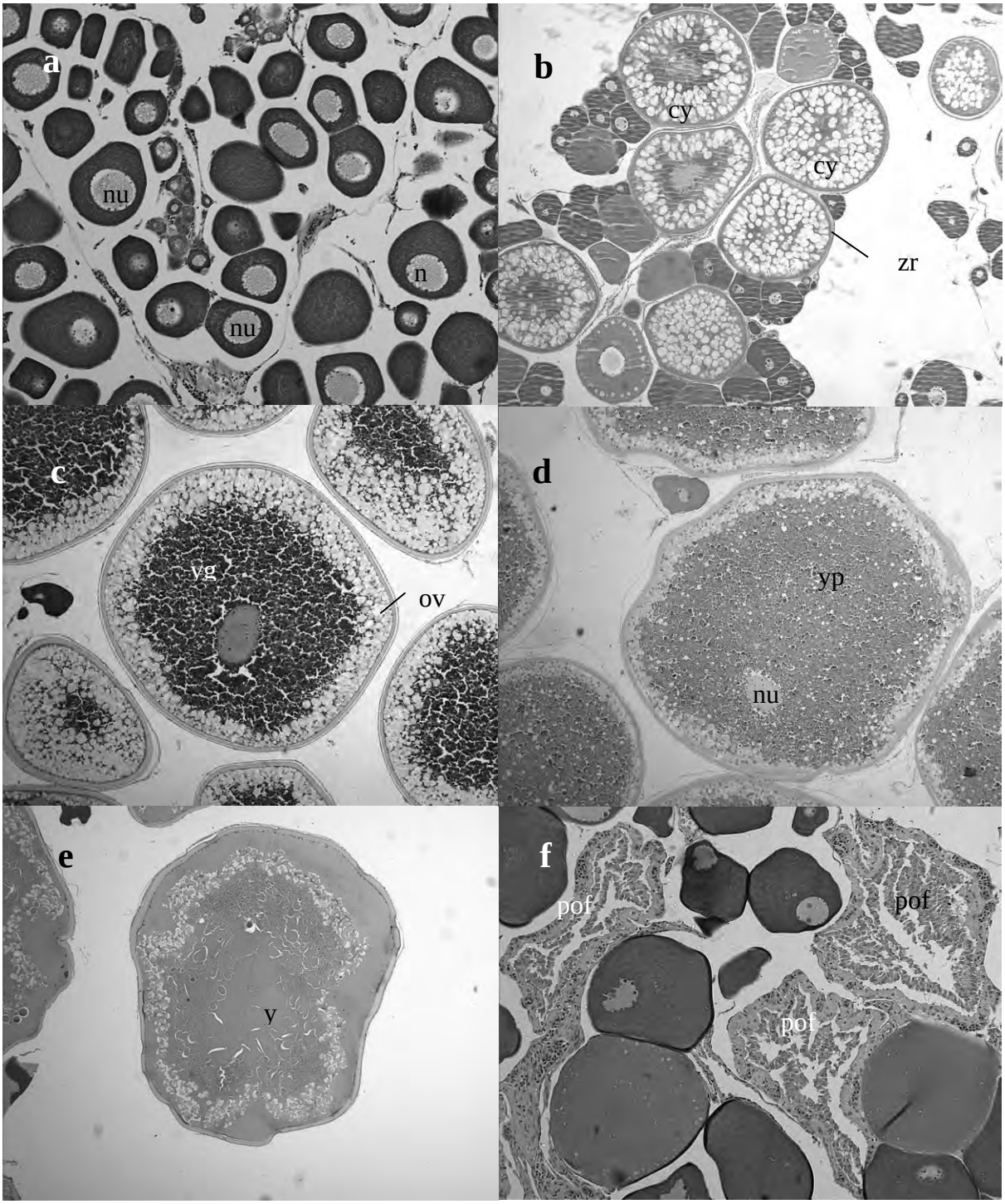


Figure 11 Histological sections showing the maturation stages of common carp oocytes. (a) Stage II, perinucleolar stage shows perinucleolar oocytes with large central nucleus (nu) and nucleoli appear at the periphery of nucleus. (b) Stage III, cortical alveoli stage, cortical alveoli appear in pale blue stained cytoplasm (cy) and pink stained zona radiata (zr) are present. (c) At stage IV yolked stage, there is a marked increase in oocyte size and the cytoplasm is filled with yolk granules (yg), cortical alveoli and oil vesicles (ov). (d) At stage V, nuclear migration stage, the nucleus migrates to the periphery of oocyte and the yolk granules begin to fuse into yolk plates (yp). (e) The onset of hydration and the appearance of yolk granules fused into fewer yolk plates mark stage VI, hydration stage. (f) Stage VII, the postovulatory follicle stage is apparent after spawning when postovulatory follicles (pof) are clearly visible.

Histological analysis was based on the following features: Endogenous vitellogenic (V) oocytes (i.e. accumulation of yolk globules in cytoplasm); exogenous vitellogenic (EV) oocytes (i.e. appearance of yolk granules); oocytes showing germinal vesicle migration (GVM) (i.e. peripheral movement and breakdown of nucleus); mature (M) oocytes (i.e.. coalescence of yolk plates and hydration); post-ovulatory follicles (POF) (i.e..ruptured, empty follicles marking positions of ovulated mature oocytes with the degenerating follicle showing fewer loops and reduced in size) and atretic mature (AM) oocytes (i.e.. resorption of unused mature oocytes).

The presence of postovulatory follicles (POF) in ovaries was used to identify females that had begun to spawn (Hunter & Macewicz 1985a, Hunter & Macewicz 1985b, Schaefer 1987). Individuals with POF, or with oocytes developed at least to the stage of exogenous vitellogenesis, were considered either to have spawned or to be capable of spawning (Bell et al. 1992). Oocytes undergo the same basic pattern of growth in all teleost species studied (Coward & Bromage 1998).
Atresia is reabsorption of residual oocytes after spawning and it's function is to remove unwanted material (Macer 1974, Hunter & Macewicz 1985b, Marshall et al. 1993). Atretic oocytes were recognised by their irregular shape, breakdown in fine structure (disintegration of the nucleus and liquefaction of yolk granules), and hypertrophy of the granulosa cells (Davis 1977). The process of atresia is rapid where the amount of yolk resorption is minimal and the remaining corpora atretica soon disappear. Oocytes where the early stages of atresia were detected (stages alpha and beta as described by Hunter & Macewicz 1985a,b) were considered atretic.
Staging and measurements of whole oocytes were used to assess whether the fecundity of carp is determinate or indeterminate, and whether yolk formation is completed before spawning starts or continues after (Hunter et al. 1985). Sub-samples of ovaries preserved in Davidson's solution were mixed in small jars with water and shaken manually to dissociate the oocytes. All ovaries used had been previously staged histologically, and histological sections were used to stage corresponding whole oocytes under the microscope (Table 7) adapted from Horvath (1985), West (1990) and Knuckey and Sivakumaran (1999). One hundred oocytes were measured along the maximum diameter for 65 females at various stages of maturity.

Table 7 Description of whole carp oocytes

Stage description	Oocyte Appearance
Unyolked oocytes	Very small oocytes, nucleus surrounded by a thin layer of dark-blue-stained cytoplasm. Cytoplasm homogeneous, brownish and transparent, comparatively large dark nucleus. Oocytes more or less spherical cytoplasm thickened, dark, granular, but still translucent, nucleus still visible
Yolked oocytes	Oocytes dark, completely opaque, size increasing with development, nucleus occluded
Nuclear migrated oocytes	Occurrence of partly translucent oocytes (hydrating), yolk plates visible
Hydrated oocytes	Occurrence of very large, almost totally translucent oocytes, oil droplet visible

Annual fecundity is the number of eggs in the ovaries that will mature during a particular spawning season. Annual fecundity data is used to calculate the reproductive potential of a population. Annual fecundity is determined from the standing stock of advanced oocytes (yolked oocytes, nucleus migrated oocytes and hydrated oocytes) at the beginning of the spawning season (Hunter & Macewicz 1985a). Ovaries with yolked oocytes, nucleus migrated oocytes and hydrated oocytes on macroscopic examination (Stage IV) were potentially suitable for the estimation of annual fecundity. Further, examination of fixed samples was carried out in the laboratory and all ovaries used in the estimation of annual fecundity were also examined histologically for recent spawning activity, as indicated by the presence of fresh postovulatory follicles. Only ovaries that showed no signs of previous spawning in that season were used to estimate the annual fecundity of carp. In such ovaries yolked oocytes, nuclear migrated oocytes and hydrated oocytes were observed and there was no sign of postovulatory follicles or of major atresia. Thus, the annual fecundity estimates for female carp were made from the standing stock of advanced oocytes at stage IV (running-ripe ovaries) collected during 1999 and 2000 spawning season.
For the annual fecundity estimation, 5 to 10 random samples of 0.1 to 0.2 g each were taken from the anterior, middle and posterior regions of each ovary of each specimen. These sub-samples were pooled to form a single composite sample of approximately 1 g. The weight of this sample was determined to the nearest 0.001 g. The number of ova in each sample was counted under a binocular microscope and the total numbers of eggs in each ovary was estimated using the method of Bagenal (1978), Cailliet (1986) and Knuckey & Sivakumaran (1999), Equation 1.

Equation 1
$$AF = \frac{c}{s} \times OW$$

Where AF = Annual fecundity, c = Number of eggs counted in sample, s = weight of sample (g), OW = weight of both ovaries (g).
The relationships between annual fecundity and other parameters such as fish weight, length and age were obtained by plotting the data as a scatter-plot and fitting linear regressions up to the cubic polynomial form.
The term relative fecundity (Bagenal 1978) was used in order to make observations on fish of different size more comparable. It is defined as the annual fecundity per unit

fish-weight or length just prior to spawning. In the current study relative fecundity was calculated per kilogram of whole fish weight.
Oocyte diameter for each fish (n=396) was estimated by calculating the mean of the maximum and minimum diameter (µm) of the largest oocytes (n = 5 to 15) that had been sectioned through the nucleus. This procedure has been shown to be representative of the true oocyte diameter by Foucher (1980).
Correlations (Pearsons) were examined between the variables mean oocyte diameter, fish length (LCF), whole weight, condition factor and age. Where significant correlations existed with mean oocyte diameter, linear, quadratic and cubic regressions were fitted to describe the relationship. The best fitting regression was identified from the adjusted coefficient of determination statistic (R^2adj).

9.4 Results

Over 6800 carp determined as male or female and 1561 carp of indeterminate sex were collected from fifteen locations within Victoria for analysis of their reproductive condition. The size range of male and female carp sampled in this study was 95–770 mm.
During the present study, temperatures of the individual waters surveyed ranged between 10 to 25°C for the months of August to March, and 18 to 9°C between April and July. Victoria receives its highest rainfall over the winter months. Photoperiod seasonality for Victoria is such that greatest day lengths occur from September to April (11–15 hours light, 13–9 dark) peaking in mid December; and shortest day lengths from May to August (10–11 hours light, 14–13 dark) with a minimum in mid June.
Gonads were staged macroscopically and GSI values calculated for 2424 female carp. As expected, a clear relationship was apparent between mean GSI and reproductive stage in females (Figure 12). GSI values were low for females with ovaries assigned to Stages I to II, reflecting their immature status, and slowly increased in fish with ovaries allocated Stages III to IV, coinciding with the maturation of the ovary. Maximum GSI for females was variable (6 - 35%). GSI in Stage V ovaries showed considerable variability owing to some individuals having already shed an unknown number of oocytes, resulting in loss of ovary mass (partially spent). Seasonal maturation of ovaries begins in August and continues through to March.

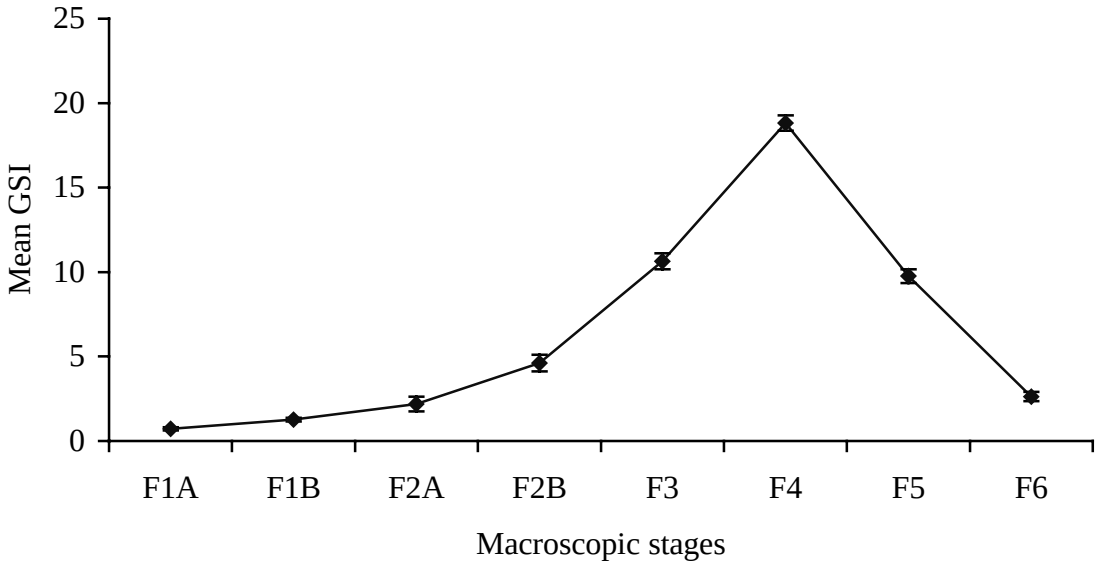


Figure 12 Mean gonadosomatic index (GSI) ±1 S.E for female carp plotted against macroscopic stage of the gonad (for stage descriptions see Table 5) Analyses performed on data collected between February 1999 and June 2001 and pooled over area.

Over 1556 ovaries were collected for histological analysis from February 1999 to 2001 and were used to assess changes in the reproductive state of carp throughout the study period. In mature ovaries, the cytoplasm of the largest oocytes is full of yolk granules and lipid droplets. Just prior to spawning, the hydration process continues until ovulation, when the follicular epithelium surrounding the oocyte breaks and the egg is released. The follicular cells then form strings, which are folded in the space left by the egg. These postovulatory follicles undergo a rapid degeneration. Except for atretic mature oocytes, examples of the histological appearance of maturing oocytes can be seen in Figure 12.

The oocytes in sectioned material with a mean diameter less than 410 µm constitute the reservoir of oocytes that are present year round in ovaries. Out of 1451 indeterminate carp, twenty fish were sub-sampled for histological examination. The results showed three were female and, belong to perinucleolar and cortical alveoli stages. Based on histological analysis of the ovaries collected and staged macroscopically as spent (stage VI), 30% of these ovaries had new and old postovulatory follicles. The mean diameter ranges of oocytes in sectioned material belonging to microscopic stages II to VI were 58-410 µm, 73-1014 µm, 441-1570 µm, 733-1627 µm and 893 -1772 µm respectively.

The yolked oocytes were present throughout the year from all the sites. Some of the variance in mean diameter of hydrated oocytes can be attributed to the distortion that occurs during histological processing (Rickey 1995). Histological processing is known to cause shrinkage of oocytes (West 1990); therefore oocytes diameters determined from processed tissue sections should only be considered an index rather than an absolute measurement of oocyte size (Rickey 1995).

The rates of atresia for both unyolked and yolked oocytes were generally low to medium and when present, atretic oocytes represented between 10 to 80% of all oocytes. However, few ovaries presented a high level of atresia (about 95%) of their yolked oocytes. Histological examination revealed that 31% of the ovaries sampled were in the stage of atresia and about 27% belong to first type of atresia (alpha stage atresia). Ovaries with atretic oocytes were observed throughout the year and

occurrence noted in all the macroscopic ovarian maturity stages (Table 8). Alpha atretic oocytes belong to histological oocyte stages of cortical alveoli and yolk and hydration. Only fifty-seven females presented the second type of atretic ovaries (beta stage atresia) and five were in the very advanced stage of atretic ovaries. Neither alpha nor beta atretic oocytes could be detected macroscopically, but they were recognisable microscopically in the preserved samples. Atresia becomes noticeable as the spawning season draws to a close and the remaining advanced oocytes in the ovary are reabsorbed. In many individuals at the partially spent stage (V) yolked oocytes in atresia were the most advanced type observed, indicating that spawning was over for these fish and reabsorption had started (Table 8).

Figure 13. Targeting small groups of spawning carp in Avon River wetlands, in Gippsland using a seine net (left). A spawning group typically contained one or two females, and several males (right).

Table 8 Distribution of the most advanced microscopic stages observed after macroscopic classification in carp ovaries.

Microscopic stages	Macroscopic stages									
	Immature	Resting	Developing	Redeveloping	Mature	Running-ripe	Partially spent	Spent	Indeterminate	Total
Perinucleolar stage	38	20	1					14	2	75
Cortical alveoli stage	21	46	15	5	3			25	1	116
Yolk stage		5	20	43	226	144	96	42		576
Nuclear migration stage		1		1	32	42	13	3		92
Hydration stage			1	3	2	37	2	1		46
New POF stage		4	1	2	4	4	11	23		49
Old POF stage		5	2	6	17	9	37	37		113
Cortical alveoli oocytes in atresia		8	2	1				11		22
Yolk oocytes in atresia		14	2	25	65	59	206	68		439
Hydrated oocytes in atresia		1			3	3	17	4		28
Total	59	104	44	86	352	298	382	228	3	1556

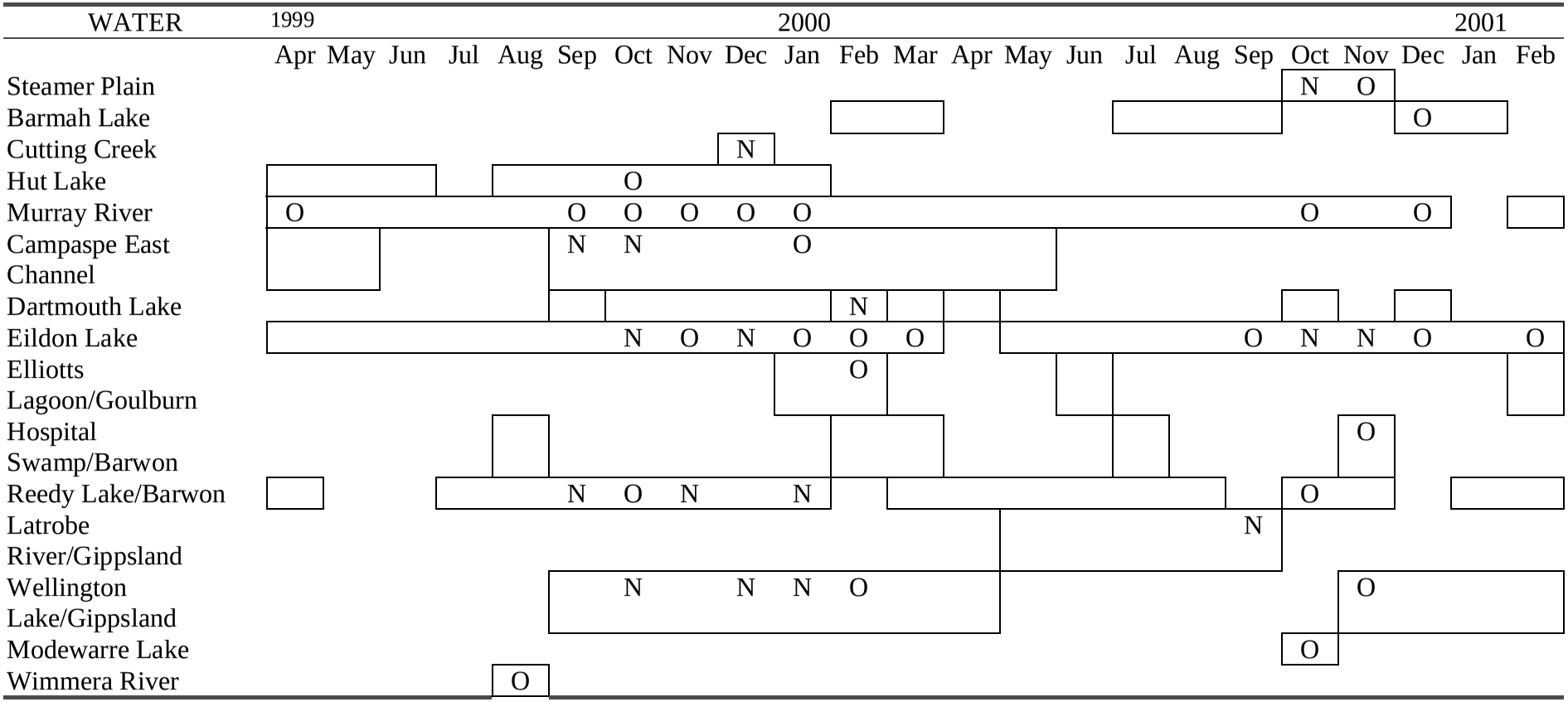
The presence of hydrated oocytes was detected by histological analysis from 49 ovaries collected from study sites at Lake Eildon, Reedy Lake, Hospital Swamp, Modewarre Lake and Wellington Lake. Hydrated oocytes were notably absent from the running ripe ovaries (stage IV) collected from Murray River. The occurrence of hydrated and atretic stage oocytes together was only observed from Barmah Lake and the Latrobe River.

Postovulatory follicles were found in 162 (10.4%) of all ovaries histologically examined. They were never found in ovaries at an early stage of yolk formation. New and old postovulatory follicles were present in ovaries belonging to macroscopic stages IV, V and VI. New and old POF were found during the period September to April. These females were partially spent yet capable of spawning again that season.

Some ovaries collected during the study period were staged macroscopically as spent (stage VI). Based on subsequent histological analysis, neither new nor old POF's were observed although these ovaries showed cortical alveoli, yolked and hydrated oocytes in atresia (Table 9).

A number of distinct groups of oocytes at different developmental stages were observed during oocyte measurement for running-ripe ovaries of carp. The size-frequency distribution of whole oocytes in ovaries shows the developmental sequence of maturation. Oocyte diameter clearly shows a polymodal distribution, with peaks corresponding to size ranges shown in the macroscopic stages, with some overlap between stages. As maturation progressed, there was no clear gap between size-modes of unyolked and yolked oocytes (Figure 14), showing that the fecundity of carp is indeterminate. This continuous, polymodal size distribution is confirmed in histological preparations of oocytes in running-ripe ovaries (Figure 15).

Table 9 Evidence of spawning of Carp from Victoria. Boxes show sampling months. Presence of new (N) and old (O) postovulatory follicles is indicated



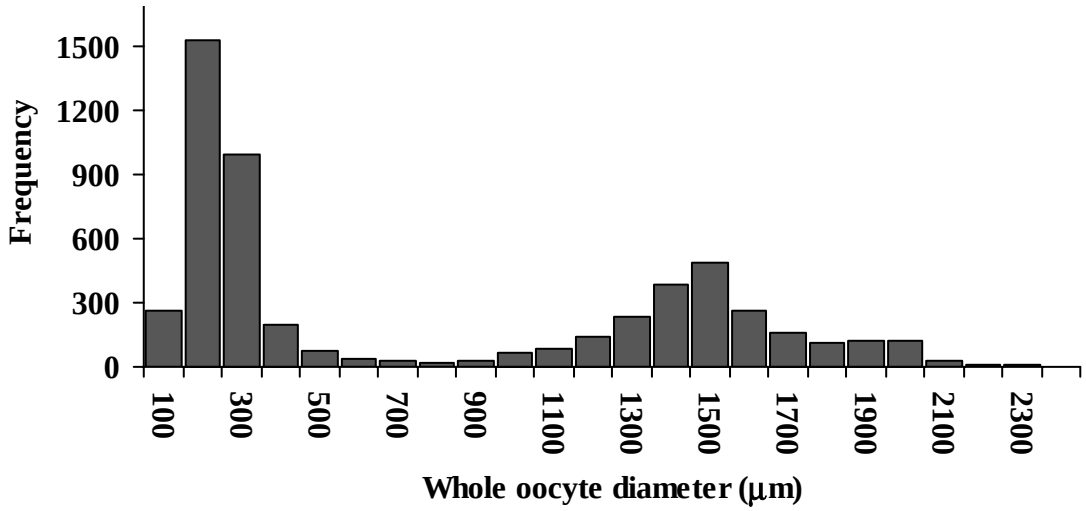


Figure 14 Frequency distribution of Carp whole oocyte diameter (µm) of carp at the running-ripe stage of maturity. Data pooled from carp (n=50) collected from different regions.

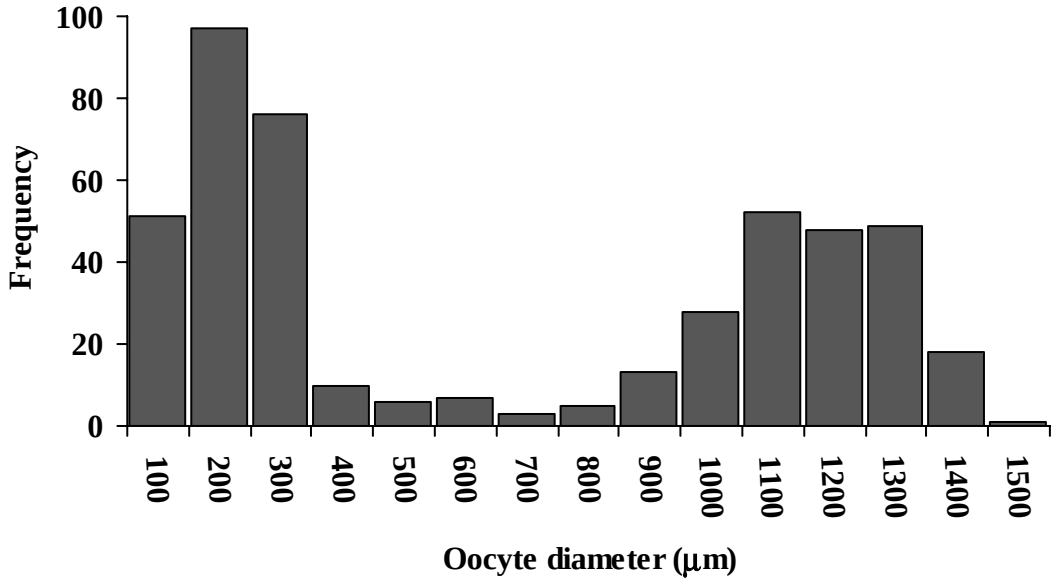


Figure 15 Frequency distribution of carp oocyte diameter (µm) measured in running-ripe stage of maturity. Data pooled from carp collected from different regions (n=3)

Based on the present study, fecundity was indeterminate. The annual fecundity (AF) was estimated from the standing stock of yolked oocytes, nuclear migrated oocytes and hydrated oocytes in 70 ovaries belonging to carp macroscopically staged as running-ripe (IV). The annual fecundity (AF) for fish combined from different stocks is presented in Table 10. The AF ranged from 0.12 to 1.54 million oocytes per fish, and mean AF was 0.764 (± 0.363 s.d.) million oocytes per fish, although varying considerably at given length (Figure 17), weight (Figure 18) and age (Figure 19).

Figure 16. After carp were observed spawning in Avon River wetlands, eggs were easily observed (circled) adhering to benthic detritus and vegetation in the littoral zone.

Table 10 Annual Fecundity estimates for running-ripe Carp of different stocks

Stock	Number of samples	Annual fecundity range (x 10^6, eggs)	Relative annual fecundity range (x 10^6 kg^{-1} of whole fish weight)
Barwon	31	0.23 - 1.35	0.12 - 0.26
Campaspe	3	0.65 - 1.17	0.18 - 0.23
Elliotts Lagoon	1	0.51	0.14
Eildon	2	0.17 - 0.20	0.12 - 0.12
Gippsland	11	0.12 – 0.77	0.08 - 0.15
Modewarre	21	0.61 - 1.54	0.08 - 0.23
Murray	1	0.33	0.12

The relationship between length and annual fecundity was statistically significant and best described with the simple linear regression:

$$AF = 0.00359\ L - 1.269 \qquad (F=106,\ p<0.001,\ df=1,68,\ R^2adj=0.58).$$

Where annual fecundity (AF) is in millions of eggs and length (L) is in millimetres. The relationship between weight and annual fecundity was statistically significant and best described with the quadratic linear regression:

$$AF= 3.47x10^{-4}W - 2.1x10^{-8}W^2 - 0.309 \qquad (F=82,\ p<0.001,\ df=1,68,\ R^2adj=0.70)$$

Where weight (W) is whole weight in grams and annual fecundity is as above. The simple linear regression of weight on annual fecundity, was also significant but was a slightly less adequate description of the data (R^2 adj=0.61).The relationship between age and annual fecundity was not significant.
Relative fecundity (RF) ranged from 0.075 to 0.262 million eggs kg^{-1} with a mean of 0.162 (± 0.046 s.d.) million eggs kg^{-1}. There was no significant relationship between RF and maternal size or age.

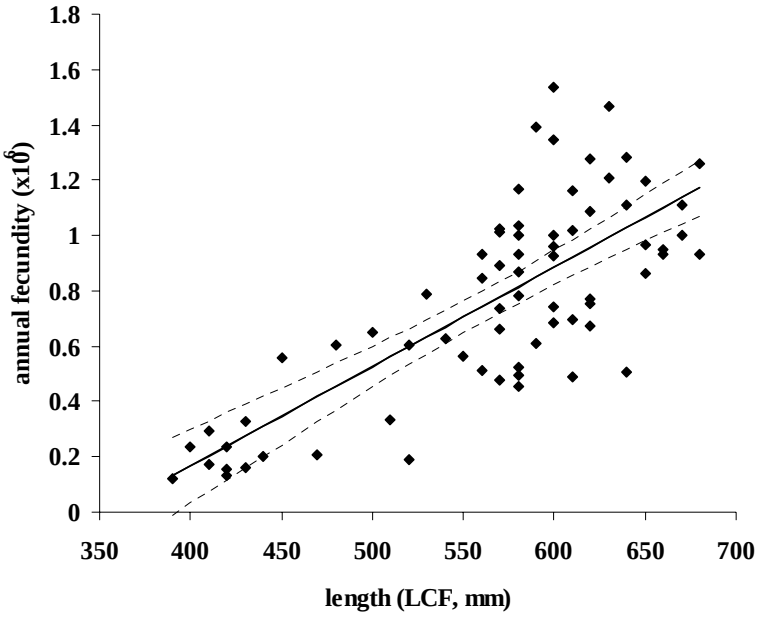


Figure 17 Annual fecundity estimates and linear relationship between annual fecundity and females length (LCF, cm) for carp at the running-ripe stage (n=70). Solid line is the predicted annual fecundity at length, dotted lines show upper and lower 95% confidence estimates on the mean

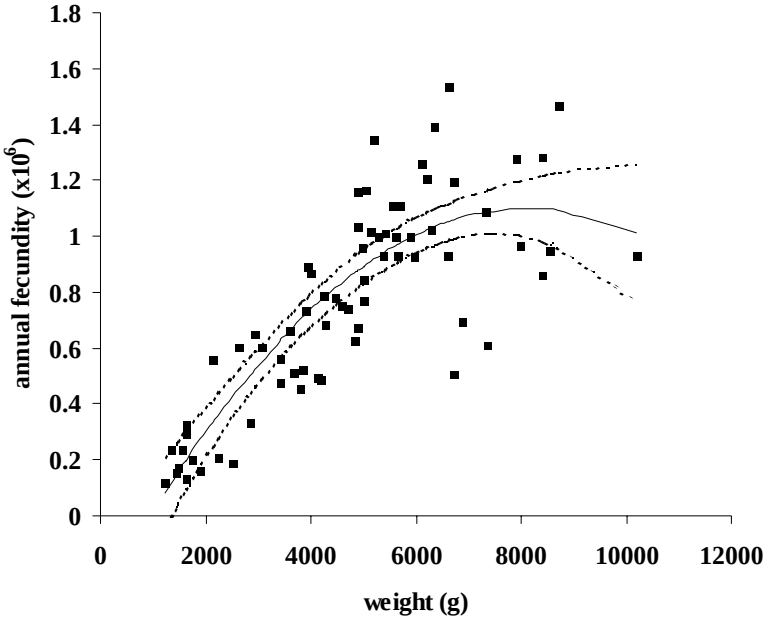


Figure 18 Annual fecundity estimates and quadratic linear relationship between annual fecundity and females weight (g) for carp at the running-ripe stage (n=70). Solid line is the predicted annual fecundity at weight, dotted lines show upper and lower 95% confidence estimates on the mean

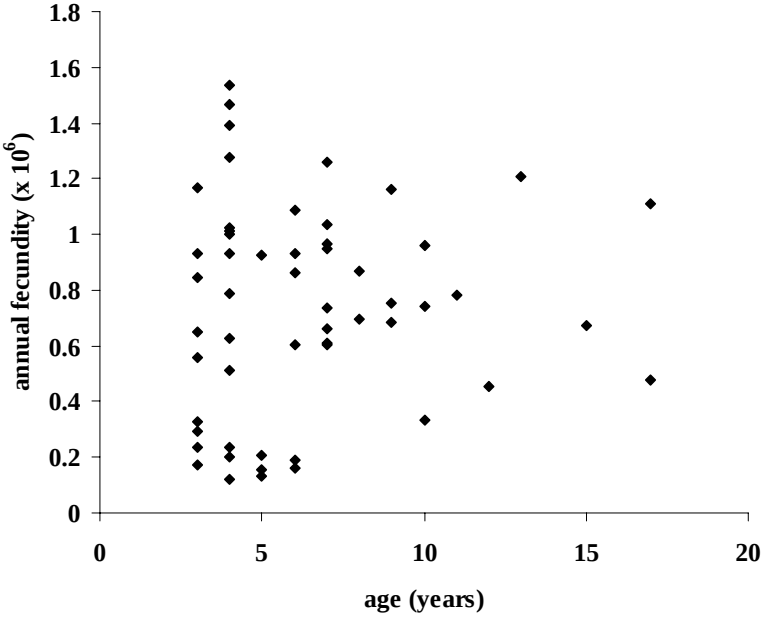


Figure 19 Annual fecundity estimates at age for female carp at the running-ripe stage (n=55).

Oocyte diameter ranged from 441 – 1569 µm. Significant positive correlations were determined between mean oocyte diameter and length (r=0.17, p<0.001, n=396); and between mean oocyte diameter and weight (r=0.18, p<0.001, n=387). However, there was no significant correlation between age or condition factor and mean oocyte diameter. There was also a significant negative correlation between age and condition factor (r = -0.17, p<0.001, n=386).
The relationship between length (L, LCF mm) and mean oocyte diameter (MOD, µm) was statistically significant and best described with the cubic regression:

$$MOD = 2.03 \times 10^{-5} L^3 - 3.10 \times 10^{-2} L^2 + 15.65 L - 1515.47$$
(F=7.79, p<0.0001, df=3,391, R^2adj=0.05)

The relationship between weight (W, kg) and mean oocyte diameter was statistically significant and best described with the cubic regression:

$$MOD = 1056.24 + 20.18 W + 1.44 W^2 - 0.25 W^3$$
(F=4.45, p=0.004, df=3,384, R^2adj=0.03)

9.5 Discussion

Early stages of development, such as chromatin nucleolar oocytes (stage I) are difficult to determine macroscopically. Ovaries of 59 individuals were classed macroscopically as stage I, and subsequent histological analysis was completed for these specimens. Microscopically these samples were found to be at the perinucleolar (stage II) and cortical alveoli (stage III) stages. This suggests that reproductive development had already started at the minimum size observed (70 mm. LCF).

The reproductive biology of carp around the world, shows them to be a very adaptable species. In Europe, soon after spawning carp re-initiate gonadal growth under the long photoperiod and warm temperatures of late summer (Bieniarz et al. 1978). Ovarian recrudescence is completed, except for final maturational stages, within about 2 months before the temperature drops to a lower critical threshold. The gonads remain at this stage throughout autumn and winter prior to final maturation (Hontela & Stacey 1995). During this resting period up to 30% of the oocytes may undergo atretic resorption (Bieniarz et al. 1978). In the River Cayumapu in cool-temperate Chile carp gonadal growth occurs from late spring until Autumn and stabilizes during winter before spawning begins in early spring (Prochelle & Campos 1985). In South Africa, carp has protracted spawning seasons that are associated with the rainy portion of the year (Fouche et al. 1985). In tropical Brazil (Welykochatko 1976) and Bangaladesh (Tweb et al. 1989) spawning seasons extended for 5–6 months and included multiple spawnings. In the present study, histological observation showed some ovaries containing oocytes in atresia and ovaries containing yolked oocytes throughout the year in all stocks. This implies that in Victoria, any resting phase is very short and there are always some females with ovaries close to maturation

Even in reproductively active carp populations in Victoria, a comparatively low occurrence of hydrated oocytes was observed. This may be explained by the short lifespan of this stage of oocyte development, prior to spawning. The appearance of translucent (hydrated oocytes) is usually taken as an indication that spawning is imminent within a day or perhaps hours (West 1990). Therefore we would only expect to encounter this oocyte stage in samples collected within a few hours of a spawning event. Since sampling occurred, in the present study, at approximately monthly frequency the chances of this occurring were slim.

In the present study, the GSI of carp was quite variable with running-ripe ovaries that constituted 6 to 36% of the body weight of the fish. These values overlap and slightly extend the range encountered in comparable Australian studies. Hume et al. (unpublished data[1]) reported that GSI of carp sampled from Lake Cooper in Northern Victoria was highest in winter 1980 and 1981, averaging 20–28%. Adamek (unpublished data[2]) also reported that maximum values of GSI in mature female were 10 – 25% during September – October in the Murrumbidgee Irrigation Area, New South Wales.

GSI of carp shows greater variation in some international studies. In Russia, the ovaries constituted up to 15% of the body weight of mature fish (Nikolsky 1963) while in Japan it formed 3.1 to 16.4% of body weight with an average of 10.4% (Matsui 1957). Carp in India seem to have better developed ovaries, with the gonads of healthy, ripe, female carp constituting 26 to 38 % of the body weight of the fish (Parameswaran et al. 1972). In the present study, histological examination of gonad from females used in GSI studies validated the macroscopic stage estimates. Although there were some females with mature gonads appearing throughout the year, partially spent females were only recorded during September to April reflecting the spawning season.

It must be noted that this peak GSI value on its own may not indicate the peak spawning time, but rather a later developing stage for most females. However, high values of this index can be used to determine the spawning period when hydrated oocytes can be identified (Hunter & Macewicz 1985a).

In the present study, spawning females contained ovaries with histological characteristics of past spawning (postovulatory follicles) or imminent spawning (hydrated oocytes or migratory nucleus stage oocytes) (Karlou-Riga & Economidis 1996, 1997). Hunter (1980) suggested that the best indicator of the time of spawning was occurrence of both hydrated eggs and postovulatory follicles.

The evidence from GSI data, histological analyses, presence of nuclear migrated oocytes, hydrating oocytes and new and old postovulatory follicles, suggests that the spawning season of carp in Victoria can last seven–nine months with a peak of seven months from September–March, and does not differ markedly in duration across all sites. The only notable extremes being the season beginning one month earlier in the single sample obtained from the Wimmera River (August) and closing a month later in the Murray River (April).

Such combined evidence, from observations of GSI and the presence of macroscopic and microscopically identified maturity stages, suggests that spawning occurred at most sites in two consecutive spring–early summers (1999 and 2000). However, spawning also occurred at some sites in Autumn 1999 and 2000; and even occurred in Winter 1999 at one site.

Conditions at the time of spawning that maximize the survival of the progeny are the ultimate factors regulating reproductive effort. If the ultimate requirements are not satisfied, some species spawn to produce a weak year class, whereas others fail to spawn and resorb their gonads (Gaigher 1984, Tomasson et al. 1984).

In many tropical cyprinids, spawning is associated with seasonal rains, flooding of rivers or the monsoons and this is also the case in temperate cyprinids. When temperature reaches critical values in the spring in Europe, the final maturational stages of oocyte development are completed and carp may spawn, providing the appropriate spawning stimuli are present (Billard 1995, Hontela & Stacey 1995). Photoperiod is also considered an important ultimate factor regulating the timing of spawning and recrudescence in Japanese carp (Davies et al. 1986, Munro et al. 1995). In Victoria, spawning occurs under shorter day length conditions than that used to stimulate carp spawning under experimental conditions in Japan (Davies et al. 1986).

Temperature is an important ultimate factor influencing spawning success, survival of the larvae and growth of juvenile fish (Hontela & Stacey 1995). In Australia, carp preferred spawning temperatures of 17–29 ^{o}C (Hume et al., unpublished data[1]; Adamek, unpublished data[2]). These temperatures overlap the temperature for maximum growth and food conversion (24–30^{o}C) (Coutant 1977, Suzuki et al. 1977, Goolish & Adelman 1984). Water level, water quality, nutrients, temperature, breeding substrate, and vegetation are also ultimate factors which may determine the spawning success in cyprinids (Hontela & Stacey 1995).

In a range of studies reported worldwide, the general requirement for carp spawning in a wide range of environments appears to be the maintenance of a water temperature greater than 15-18°C for a prolonged period (Huet 1975). In Europe, under pond conditions the optimum spawning temperature for carp is between 18°C and 22°C, although in colder areas, spawning may take place as low as 14°C according to Horvath (1985). In Canada, carp spawned between 16.5 and 28 ^{o}C, with a peak of spawning activity between 17 and 23 ^{o}C, while spawning activity decreased above 26°C and ceased entirely above 28°C (McCrimmon 1968). In the present study, during the peak

spawning months (September–April), the daily average of the water temperature range was 16.5–22.6^{o}C, with maximum daily water temperatures of 20–25^{o}C. Therefore, the present study confirms that carp-spawning activity in Victoria corresponds well with the previously known preferred temperature range for carp spawning. The Victorian climate provides temperatures potentially adequate for an extended spawning season.

The variability of fecundity in Victorian carp is similar to that encountered in a range of studies worldwide and slightly extends the known range of fecundities reported previously in Australia.

Reviews of carp biological data for Asia and the far east (Alikunhi 1966), and for Europe and the near east (Sarig 1966) report absolute fecundity ranges of 0.01– 0.860 million eggs and 0.086 –2 million eggs respectively. In terms of relative fecundity this is 0.097–0.264 million eggs kg^{-1} for Asian and 0.01– 0.438 million eggs kg^{-1} for European carp. In the Mississippi basin, USA, Lubinski (1986) reported relative fecundity of 0.22 million eggs kg^{-1}. Australian studies previously cited relative fecundities of 0.12–0.25 million eggs kg^{-1} (*see* Hume et al., unpublished data [1]).

Absolute fecundity was proportional to age, length and weight in wild Amur carp (*C. carpio haemopterus*) (Gromov 1979a) and was best described by quadratic curvilinear regression relationships. Variability in absolute fecundity of individual fish with the same length, weight and age is possibly due to differences in food supply, temperature and other environmental effects (De Vlaming 1972, Bagenal 1978).

In the present study, the increase in annual fecundity with female size suggests, not surprisingly, that larger females are relatively more important for egg production. In the heaviest females there is some suggestion that fecundity declines, although for most of the range of weights observed (1222–10205g) the relationship is linear. The lack of relationship between annual fecundity and age is perhaps more surprising although this may be due to the large variation observed in size-at-age for carp in Australia (Vilizzi & Walker 1999, also see Appendices 4 and 4, this report).

In Victorian carp, mean oocyte-diameter generally increased as female length and weight increased. As older fish could not maintain body condition, this may explain why mean oocyte-diameter was not also proportional to age. In salmonids, larger and older females have been shown to produce larger eggs (Pitman 1979, Springate & Bromage 1985). Schrank & Guy (2002) noted that egg diameter was proportional to female length in bighead carp, *Hypophthalmichthys nobilis.* Zonova (1973) found oocyte diameter and variability in oocyte diameter in carp was positively correlated to age but not with length, weight or condition.

Larger eggs may confer an early survival advantage in fishes for a range of reasons including increased larval size at hatching (Pitman 1979, Springate & Bromage 1985, Lobón-Cerviá 2000, Vøllestad & Lillehammer 2000); higher larval and juvenile growth rates (Pitman 1979, Sehgal & Toor 1991, Ojanguren et al. 1996, Lobón-Cerviá 2000); larger yolk-size and longer survival times under starvation conditions (Vøllestad & Lillehammer 2000). It seems likely however, that this is most advantageous under harsh environmental conditions. Lobón-Cerviá (2000) observed that the size of parr in wild brown trout (*Salmo trutta*) up to two months old was related to initial oocyte diameter, while Springate (1985) showed that the growth advantage of large oocyte diameter was no longer apparent in rainbow trout (*Oncorhynchus mykiss*) after 4-weeks of feeding in a hatchery.

Fish species that have extended spawning seasons are usually multiple spawners, individual females producing several clutches of eggs (Hontela & Stacey 1995). Wherever they are found carp are adaptable and show extremely plastic life-history strategies (Balon 1974, Balon 1995). Multiple spawnings may be observed within

populations despite individuals only spawning once. For example, if environmental stimuli, such as floods occur in pulses throughout the potential spawning season, a fraction of the breeding biomass may spawn on each pulse. The resulting observations of larval presence and juvenile recruitment would be similar to those in stocks where individuals may have spawned repeatedly (Vilizzi 1998). However, in the present study of the histology of atresia, the frequency of observations of atresia in yolked oocytes and hydrated oocytes suggest that in Victoria carp stocks contain both females that spawn once, and females that spawn repeatedly within a spawning season.

In carp, development of individual oocytes within their follicles is synchronised only in the early stages of development. It gradually becomes asynchronous to the degree that oocytes in all stages can be found in the ovary at any time. This allows a very rapid completion of development by those in an advanced stage, in order to replace ova which have been released, so rapid re-ripening is possible (Horvath 1985). In the present study, each carp ovary had oocytes belonging to all stages of development. This was initially observed while studying the whole oocytes measurements and later confirmed by histological study. Histological analyses of some ovaries showed simultaneous occurrence of nuclear migrated oocytes, hydrated and new postovulatory follicles with other oocytes but without any oocytes in atresia. Therefore, carp in Victorian waters are a multiple spawning species with asynchronous oocyte development.

Gromov (1979b) observed that in wild carp populations of central Amur, when environmental conditions promoted an early start to the spawning season, asynchronous oocyte development allowed female carp to spawn some of their oocytes immediately and the remainder intermittently, as they developed throughout the season. Whereas when spring-flooding was late, spawning was delayed allowing the majority of oocytes to ripen and most of the spawning population to spawn completely with the onset of spawning conditions. Similarily, under Victorian temperate conditions there is a protracted spawning season, during which the individual females may spawn once, or repeatedly under exceptionally good conditions. The protracted spawning season and multiple spawning characteristics that are described may restrict the effectiveness of management strategies aimed at limiting spawning opportunities by environmental manipulation (e.g.. water draw-downs etc.) or the targeted fishing of pre-spawning aggregations.

Previous authors have assumed density-dependent recruitment and growth effects will dominate the population dynamics of Australian feral carp stocks (Thresher 1997, Koehn et al. 2000). This study shows that although big, old, females certainly produce more eggs, the lack of relationship between relative fecundity and maternal size or age suggest that the size and age composition of a carp spawning biomass would have little effect of the quantity of eggs produced. Commercial fishing with nets can select for larger, older fish. However, if compensatory growth and recruitment occurs in the remaining stock this may not reduce the overall quantity of eggs produced. However, through producing larger, and thus higher quality eggs, the larger females do have the potential to contribute proportionally more to future generations than a similar biomass of smaller females.

In terms of feral carp management strategies, the size-selective harvesting of the largest, and oldest females in a population has the potential to impact larval survival and recruitment of future year-classes in a manner disproportionate to that suggested by simple fecundity relationships between spawning biomass and egg-production. Models simulating control strategies for feral carp populations should take into account the relationships between maternal size, age and egg quality for it’s potential to effect recruitment.

9.6 Acknowledgments

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10 Appendix 4 – Population dynamics of carp in irrigation channels subject to acrolein® herbicide treatment for plant control

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10.1 Summary

Feral common carp, *Cyprinus carpio* L., were sampled from two irrigation supply channels in central Victoria, south-eastern Australia, over two summer irrigation seasons as part of a broader population dynamics study. Patterns of spatial and temporal abundance indicate that juvenile recruitment by immigration was common. Estimates of standing stock range from 0 to 619 kg ha^{-1} with a mean of 144 kg $ha^{-1.}$ Maximum age of 17 years was observed. The largest male and female measured 570 mm and 680 mm caudal fork length respectively and growth in mean length-at-age and heterogeneity in length-at-age are described for males and females and both channels. Seasonal variation in gonad and oocyte development indicates that spawning occurred during spring and autumn at temperatures of 16.5 – 22.6 ^{o}C. Relationships between length, weight and age-at-maturity are described for males and females separately. The overall sex-ratio was not significantly different from 1:1. The mean annual fecundity ranged from 400,000 to 1,170,000 eggs in carp 2–5 years of age. Natural mortality (M), total mortality (Z) and a composite fishing and operational mortality (F+O) were estimated for each irrigation channel. The comparatively high rate of herbicide treatment and regularity of winter water-level drawdown experienced by carp in the eastern irrigation channel may have conferred characteristics of an exploited stock on that population.

10.2 Introduction

World-wide, carp have many different roles in irrigation systems. Irrigation channels are used as aquaculture sites for carp (*Cyprinus carpio* L.) and related species (Redding and Midlen 1990), and in many countries, cyprinids such as grass carp (*Ctenopharyngodon idella*), are routinely used for macrophyte control (Beyers and Carlson 1993; Dall Armellina *et al.* 1999; Redding-Coates and Coates 1981; van Weerd 1985). In Argentina, where carp are seen as beneficial for controlling submerged plant-growth of nuisance-species (eg. *Potomogeton pectinatus*), the relationship between carp (*C. carpio*) biomass and turbidity in a Rio Colorado irrigation system was predictable (Fernandez *et al.* 1998). Indeed, the enhancement of carp abundance was investigated (Sidorkewicj *et al.* 1998) as possible control agents for aquatic macrophyte infestations.
In Australia however, feral carp are considered a pest (Anonymous 2000). Carp (*C. carpio*) were possibly introduced to Victoria, New South Wales (NSW) and Tasmania (Clements 1988) during the 1860s and 1870s by acclimatisation-societies. They were certainly held at the government hatchery in Prospect, NSW, in 1908 and occasional captures showed them to be present in the lower Murray Darling basin (MDB) until the late 1960s, without showing signs of developing populations of particularly high-density. However, it was in the 1960s that the colonisation of major-waterways began with the illegal stocking of carp across south-eastern Victoria and the draining of Lake Hawthorn into the River Murray (Clements 1988; Shearer and Mulley 1978). Carp in the Campaspe River are likely to have originated from upstream colonisation from the River Murray in the early 1970s (Shearer and Mulley 1978). The Campaspe irrigation system has maintained a continuous connection with MDB waterways via the Campaspe River and inter-connecting irrigation systems sourcing water from the neighbouring Goulburn River catchment since its construction in 1963.
Carp in Australian irrigation supply and drainage channels have been considered a problem on many levels (Brown and Harris 1994b). Fernandez (1998) noted that their erosive feeding behaviour (i.e. mumbling) causes undermining and slumping of channel-banks and Jackel (1996) documented such damage to Australian irrigation channel banks and cited carp as the main cause. It has been suggested that mumbling can cause re-suspension of sediment (Gehrke and Harris 1994) and that high carp biomass may increases the discharge of nutrients from the channels via re-mobilisation of particle-bound phosphorous, although Meredith (1995) found little evidence to support this. Increases in suspended solids may exacerbate physical wear of pumping machinery (Koehn *et al.* 2000).
Irrigation channels and storage systems may act as a source of carp for recruitment to the natural waterways or act as a sink, with favourable habitat harbouring stocks of carp that can then further infest the natural waterways (Brown and Harris 1994a). Populations of carp in Campaspe irrigation channels can be regarded as open, sub-populations of a larger reproductively isolated MDB stock. At the start of each irrigation season, as the channels are filled there may be ample opportunity for immigration of all age-classes. Likewise at the end of each irrigation season, most channels are drained to a series of unconnected shallow (<30 cm deep) pools, which provide opportunities for emigration, and presumably exposure to a relatively high predation risk for those carp remaining.
The management of excessive macrophyte growth with acrolein has been conducted in open channels in North America and Australia since the 1960s (Eisler 1994). A side effect of this treatment is the associated fish mortality. In Australian channels carp are

an unwanted pest species and mortality of carp from acrolein treatment is regarded as beneficial although the herbicide is not used directly as a piscicide.

There has been a resurgence of interest in carp in Australia, as a pest species, since the 1990s (Koehn *et al.* 2000). However, as Thresher (1997) suggested, only limited data are available on population characteristics of wild carp stocks. Studies of carp in Australian irrigation systems have largely concentrated on determining their physical effects on the channel environment and water quality (Roberts and McCorkelle 1995). Although the biology of carp in Australian irrigation channels is largely unknown, some estimates of age and growth and cohort composition of carp are available for the lower Murray River (Vilizzi 1998; Vilizzi and Walker 1999) and Lake Sorell in Tasmania (Vilizzi *et al.* 1998). Earlier Victorian studies concentrated mainly on the effects of carp on their environment (Fletcher *et al.* 1985); age and growth studies using scale age-estimates and reproductive studies in some populations (Hume *et al.* 1983). A fish survey of four New South Wales Rivers from 1992 to 1995 (Gehrke *et al.* 1995) provided some indication of mortality rate and its variability. Further surveys of multiple sites in NSW Rivers during 1996 (Harris and Gehrke 1997) were used to fit a Ricker stock-recruitment relationship. Adamek (1998) provides some information on carp breeding biology within a NSW irrigation system.

The present study formed part of a wider ranging investigation designed to provide detailed biological information on carp populations in a range of Victorian habitats. Irrigation channels are a significant component of Victorian surface waters. Most channels contain carp stocks and possess a characteristic range of habitat features that may shape the population dynamics of the carp that inhabit them. Jackel (1996) suggested that resident carp populations could be effectively controlled or even eradicated in channel systems, using repeated acrolein treatments. We hypothesise that past and present management practices, including winter draw-downs and acrolein treatments, may have unintentionally imposed the characteristics of an exploited population on carp stocks within the Campaspe irrigation district. As heavily fished populations of carp are rare in Australia, such irrigation channel stocks present an opportunity to learn more about how these populations function.

10.3 Materials and Methods

10.3.1 Study Area

The Campaspe irrigation district is centred on Rochester in central Victoria (Lat 36.3631^{o} South, Long 144.7003^{o} East). Water is supplied mainly for dairy-pasture irrigation and broad-acre vegetable horticulture from two irrigation channels that are gravity-filled from a large weir-pool on the Campaspe River. Flow is regulated through the eastern (Campaspe #1) and western (Campaspe #2) channels via a system of drop-board regulator gates. Both channels terminate in outfalls to the main Western Waranga-Mallee irrigation channel that carries water west, from the neighbouring Goulburn river catchment, to irrigation districts west of the Campaspe catchment. The eastern irrigation channel is 6.14 km long and the western irrigation channel is 6.15 km long. Channel dimensions vary along their lengths although depth is reasonably uniform (0.8–1.0 m). Three sites were selected in each irrigation channel near the inflow, middle and outfall areas (Figure 20). Width of our sample sites is typical of each irrigation channel. The western irrigation channel varies from 11.3 m wide at the inflow end to 4.6 m near the outflow, and the eastern irrigation channel is 7.0 –7.5 m wide throughout (Table 11).

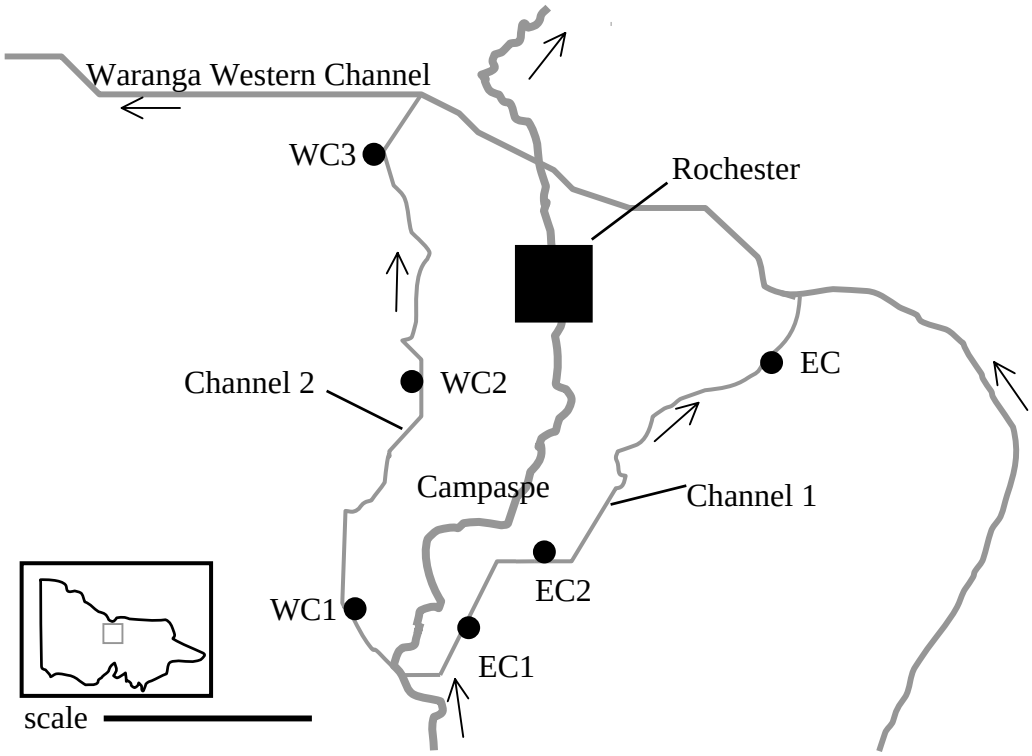

Figure 20. Map showing Campaspe River and Irrigation supply channels No.1. (eastern irrigation channel) and No. 2 (western irrigation channel) direction of flow is shown by arrows. Carp sampling sites are shown (•). Location of Rochester district within Victoria is shown inset. Scale bar = 5 km.

The irrigation supply system is filled and operated from September to March or April each year and the standard operations procedure is to allow residual water to drain out of the system when the irrigation season closes in April. During the winter of 1999, due to unusual circumstances, the water was maintained in the eastern irrigation channel

after inflows ceased. This provided an additional opportunity to observe any differences in carp distribution, abundance and biological parameters during the 1999 irrigation season that may be associated with the watering regime of each irrigation channel. Water temperature was continuously monitored at a single site on the eastern irrigation channel from September 1999 to May 2000. These data were used for a linear regression of average water temperature against local air temperature (Bureau of Meteorology). The relationship between the variables determined from the regression was later used to predict the mean annual habitat (water) temperature, discussed later in calculations of natural mortality.

The irrigation channel riparian vegetation is a dense pasture community dominated by *Paspalum* spp. In these channels macrophytes were observed in varying densities both within and between sites. Ribbonweed (*Vallisnaria* spp) and floating-pondweed (*Potamogeton* sp) were the dominant species although other species such as *Nitella* sp. were also present.

The managing authority for the Campaspe irrigation system uses Acrolein ® herbicide to manage aquatic macrophyte infestations in supply channels. Acrolein® is toxic to fish. Treatment of the western irrigation channel during 1993 and of the eastern irrigation channel during 1993, 1994 and 1997 caused substantial mortality of carp (Jackel 1996). Treatment during March 2001, subsequent to our sampling activity provided us with an excellent opportunity to calculate our electrofishing efficiency rate and thus express samples in terms of standing-stock estimates.

Table 11. Summary of main carp sampling site dimensions on the Campaspe Channels. Sites prefixed with WC are on the western channel; those with EC are on the eastern channel. Sites are numbered in upstream to downstream order and locations are shown in Figure 20

Site	Width (m)	Length (m)	Mean Depth (m)	Area (Ha)
WC1	11.3	2071	1.5	2.34
WC2	11.0	510	1.2	0.56
WC3	4.6	650	1.2	0.30
EC2	7.0	886	0.6	0.62
EC1	7.0	1566	1.0	1.10
EC3	7.5	787	1.0	0.59

10.3.2 Spatial & Temporal Distribution

Carp were sampled approximately monthly at each site during the irrigation season with a single pass of a boat-based electrofisher (Smith–Root, Model V, 5.0 GPP) using pulsed AC output at a frequency of 120 Hz. Near vertical channel batters and regular obstructions to navigation within the channel, meant that trailer launching for the electrofishing boat was impractical. A four-wheel drive, four-wheel steer crane was employed to facilitate easy and frequent launches and retrievals of the boat.

10.3.3 Sampling Procedures for Standing Stock Estimation

Efficiency of electrofishing depends on many factors including biological, technical and environmental factors including the size and shape of the water body relative to the electric field area (Mann and Penczak 1984; Reynolds 1996). Occasionally during

sampling, carp were observed avoiding the electrofishing boat by escaping between the boat and bank behind the boat. At some sites, fish were trapped at the end of the site by a weir, whereas at other sites they could escape under a bridge. Sampling efficiency was therefore estimated independently for each site at the end of our series of monthly samples. The estimate of sampling efficiency was then used to calibrate the time series of relative density samples and convert to a time series of standing stock estimates. Sampling-efficiency trials took place over five days during March 2001 at the end of the irrigation season. Carp were sampled using standard electrofishing methodology at each of three main sites in the eastern irrigation channel. Acrolein ® could not be used in the western irrigation channel. All carp sampled were marked by clipping the caudal fin, and released into the section of channel from which they were sampled.

10.3.4 Population Estimation

Carp population size was estimated at each site in the eastern irrigation channel using the daily mortalities after herbicide treatment as successive samples in a removal experiment. After acrolein treatment, the carp in a site died progressively over several days. During previous attempts at carp-control, floating dead carp have been observed to sink and then re-float over several days (Jackel 1996); hence, the individual probability of "capture" for carp collected after acrolein treatment may have varied over time. Seber (1986) recommended two methods as the best estimators of population size: the generalised removal estimator (M_{bh}) (Otis *et al.* 1978) and the generalised jackknife estimator (M_h) (Pollock and Otto 1983). Both methods allow different capture probabilities on successive occasions. Model M_{bh} allows capture probability to vary between individuals and by behavioural response to capture. The jackknife estimator (M_h) only allows capture probability to vary between individuals; however, it is a more robust and generally more precise estimator than the removal estimator when the number of removal-occasions is low (Pollock and Otto 1983).

Prior to the injection of Acrolein ®, stop-nets (25-mm knot-to-knot mesh size) were set at the downstream end of each site to prevent immigration or emigration of carp between the electrofishing and herbicide treatments. Acrolein ® was injected at the upstream end of each site at a nominal concentration of 0.25 mg L^{-1} , where the actual concentration varied from 0.2 to 0.3 mg L^{-1}.

Site inspections were maintained for 4 days to collect dead carp as they appeared in each site, and to clear debris and bycatch from the stop nets. Each day dead carp that were recovered after Acrolein treatment were counted and weighed. For other fish species the total weight for each species was noted.

Population estimates ($\hat{N}_i$) were calculated using the jackknife estimator within the program CAPTURE (Rexstad and Burnham 1991; White *et al.* 1982). Electrofishing sampling-efficiency at site i, (e_i) was calculated as the electrofishing sample size (n_i), divided by the population estimate ($\hat{N}_i$) (Equation 2).

Equation 2

$$e_i = \frac{n_i}{\hat{N}_i}$$

The assumption that stop-nets imposed closure on area a_i at each site (i) and that Acrolein ® treatment accounted for all fish within this area, and therefore gave an unbiased estimate of total population density, was intended to be tested by observing the tag-return rate for each site. A tag return rate of 100% would indicate that the assumptions of a closed population and total mortality had been upheld. For each previous month (j) at each site (i), the standing stock (S_{ij}) was estimated from the electrofishing sample (c_{ij}), the efficiency (e_i) for that site derived from Equation 2, and the site area (a_{ij}) for that month and site (Equation 3), as follows:

Equation 3

$$S_{ij} = e_i \times \frac{C_{ij}}{a_{ij}}$$

10.3.5 Age & Growth

For age and growth study, carp sampled each month were stored on ice and returned to the laboratory. Carp ≥ 50 mm caudal fork-length (LCF) were weighed to the nearest gram, and measured to the nearest 5 mm. Carp < 50 mm LCF were weighed to the nearest 0.1 g and measured to the nearest millimetre. Otolith pairs (asteriscii) were dissected from all carp sampled. The otoliths were dried, weighed (to the nearest 0.001 g), mounted in blocks using clear polyester casting resin and sectioned for age-estimation (Morison *et al.* 1998). Daily increment formation for juvenile carp has been validated (Vilizzi 1998) and annual cycles of otolith edge-growth noted in some age-groups from whole otoliths and thin otolith sections for fish aged from 0+ to 17+ years-of-age from the lower Murray River (Vilizzi and Walker 1999) suggests that annual age-estimation is also reliable. Data from juvenile carp cohort-progression and oxytetracycline marking of carp with between 0 to 14 growth increments confirms that a single increment is laid down each year and the initial increment is laid down at approximately 1 year of age (Appendix 2).

Mean length-at-age was described by applying a deterministic growth model (Von Bertalanffy 1938). The von Bertalanffy parameters were estimated by non-linear least squares regression. Comparing mean length-at-age between females and males, and for each of the eastern and western channels was accomplished using a likelihood ratio test (Kimura 1980).

Heterogeneity of growth in length-at-age was described by a four parameter, stochastic growth model (Troynikov 1998). The three von Bertalanffy parameters of the deterministic model are; t_0 the age at zero length, L_∞ the predicted asymptotic mean maximum length, and K the growth coefficient or rate at which average length-at-age approaches L_∞. The four Troynikov parameters in the stochastic model are similar, except that K is replaced by two parameters and is estimated with random error from one of the three non-normal probability distributions Weibull, Gamma, or Lognormal, depending on which best fit the data. The parameter (L_∞) that in the Von Bertalanffy model represents the asymptotic *average* length achieved by a fish of infinite age is interpreted differently in the Troynikov model where L symbolises the asymptotic maximum length.

10.3.6 Mortality

In potentially open populations such as this the decline in numbers of fish from a particular life-history stage over a period of time cannot strictly be interpreted as mortality. Such changes are more correctly referred to as loss-rates (sensu Elliott 1985) as they include elements of immigration and emigration as well as mortality. However to enable useful comparisons with other studies, and because the purpose of the present study is to consider the Campaspe irrigation channels as a discrete, manageable system, the standard terminology of fisheries literature will be used in considering loss-rates as "mortality" from the system in question.

Age estimates from carp (n=455) were used to generate an age-length key (ALK) to estimate the age of the total carp catch (n=1112). Two methods were used to estimate the instantaneous rate of total annual mortality (Z). The maximum likelihood estimator (Chapman and Robson 1960) and the least squares estimator (Ricker 1975) were both calculated for total catch and catch pooled by channel and sex. In comparative simulations (Dunn *et al.* 2002; Jensen 1985) the Chapman and Robson estimator has proved to be the least biased and most precise. The age at full recruitment to the sampling method (electrofishing) was set from 1 to 3 and Z calculated for each case. Natural mortality (M) was also calculated from empirical models (Pauly 1980; Rikhter and Efanov 1976) for comparison and to allow the estimation of fishing mortality (F) from the relationship Z=F+M. Mean water temperature for 1999 and 2000 was used as our estimate of average habitat temperature for an empirical estimation of natural mortality (Pauly 1980). Age at 95% maturity was used as an estimate of age at "massive maturation" (T_{mass}) for Rikhter and Efanov 's empirical method (1976).

10.3.7 Reproductive Biology

All fish samples were dissected in the laboratory. The sex (male or female) of each fish was determined where possible. Where sex could not be determined due to immaturity the fish was classed as indeterminate. The macroscopic reproductive stage of each fish was assessed according to an appropriate set of stage descriptions developed by adaptation from published literature (for testes see Table 12 and for ovaries see Appendix 3).

The gonads were then removed, weighed and preserved in 10% neutral buffered formalin. For each fish the gutted weight was recorded and the gonadosomatic index (GSI) was calculated on both whole and gutted weight (see Equation 4). The overall patterns of gonadal development shown by both whole-weight GSI and gutted-weight GSI were similar. To assist comparison with other studies, subsequent analysis for this report will use GSI calculated from whole body weight, as this is the more widely used method in the literature (Cailliet *et al.* 1986).

Equation 4
$$GSI = \frac{g}{W} \times 100\%$$

where GSI is gonadosomatic index, g is gonad weight (g) and W is either whole body weight or gutted body weight (g).

Figure 21. Structures obstructing the continuous navigation of irrigation channels, such as bridges and regulators, are common. During carp sampling, a crane was used to facilitate the frequent launching and retrieving of the electrofishing boat around these structures

Table 12. Macroscopic stage descriptions of testes. Criteria used to describe gonadal development and recrudescence in *Cyprinus carpio* modified after (Gupta 1975; Jankovic 1971).

Stage	Stage description	Male
1A	Immature (virgin)	Thin strip-like or strap-like, white-rimmed testes (M1a).
1B	Resting	The testes are grey, white or brownish, limp, and small. Sometimes rubbery. No milt present (M1b).
2A	Developing (virgin)	The testes enlarging, occupying the greater part of the abdominal cavity. Their colour is mostly milky-white. Creamy or white milt sometimes present (M2a).
2B	Redeveloping	The testes occupying the greater part of the abdominal cavity. Their colour is mostly white to reddish white. Creamy or white milt sometimes present (M2b).
3	Mature	Milky-white or creamy-white testes almost fill whole body-cavity. Sometimes milt ejected on pressure. Pronounced hyperemia (M3).
4	Running ripe	Milky-white or creamy-white testes tinged with pink because of pronounced hyperemia. The testes very large and fill the entire body cavity. Milt ejected on the slightest pressure. (Genital/gonad aperture often inflamed) (M4).
5	Partially spent	Milt running. Testes decreasing in size and weight and therefore no-longer fill whole body-cavity. Genital/gonad aperture often inflamed (M5).
6	Fully spent	Small amount or no milt on pressure. Testes relatively small; creamy/white/pale pink; mottled appearance; walls of testes are loose; sometimes many distinct small blood vessels on surface. (Genital/gonad aperture often inflamed) (M6).

The dissected gonads were fixed in the formalin for 4–10 weeks. A transverse medial sub-sample of about 30g of the gonad was then removed and preserved in Davidson's solution (Knuckey and Sivakumaran 2001). These sub-samples were sent to a commercial pathology service for sectioning and then returned for subsequent histological examination. The transverse medial material was blocked in paraffin wax and 6-μm thin sections were cut, mounted and stained in Harris' haematoxylin and eosin (Lunar 1968). This enabled an understanding of the processes occurring at the cellular level during the reproductive cycle by histological examination of ova and sperm.

The histological sections were used to describe the different stages of oocyte development. The macroscopic and histological characteristics of maturity stages of testis and ovary of common carp are presented in chapters 4 and 5 of this report. Description of histological sections has allowed the verification of our macroscopic estimates of reproductive stage, and thus enabled accurate estimates of fecundity at size and age.

10.3.7.1 Fecundity

Annual fecundity is considered determinate in species where the stock of oocytes that are destined to be spawned in a season is identifiable at the beginning of the spawning season, even though the fishes may spawn repeatedly during the season (Hunter and

Macewicz 1985a; Hunter and Macewicz 1985b; Knuckey and Sivakumaran 2001; Yamamoto 1956).
The annual fecundity of common carp was estimated from the standing stock of yolked oocytes (Stage IV) from samples collected during 1998 spawning season using gravimetric method (Hunter and Macewicz 1985b). To ensure that the correct weighting factors were used for determination of annual fecundity, the gonads of 13 fish were carefully dissected. From the left gonad of each fish, 10 random samples of tissue weighing 0.1 g each were taken to provide a 1 g composite sample of eggs from each fish. These were stored for 1–2 months in Davidson's fluid and then Gilson fluid to separate the oocytes in the tissue. This sample was used for fecundity estimation and to determine the size distribution of oocytes. The average relative fecundity was measured as the number of oocytes per kilogram (whole fish weight). NB: Whole fish weight is used, as this then becomes a simple predictor of egg production.

10.3.7.2 Size and Age-at-maturity

Female carp were categorised as mature if they were macroscopically staged as mature (F3), running ripe (F4), partially spent (F5), or fully spent (F6). These stages corresponded to those where >99% of the histology preparations contained yolked-oocytes. Males of the same macroscopic gonad developmental stages (M3 to M6) were regarded as mature to enable useful comparisons of size at maturity for both sexes. Size at maturity was estimated by counting the proportion of mature fish in each 10-mm length-class. A logistic curve was fitted to the data using a non-linear least-squares procedure weighted by the sample size for each length-class. In a logistic regression the probability of an animal being mature at length *l* is determined from a random dichotomous variable taking the value 1 with a probability of *p* for the mature condition and the value of 0 with a probability of 1–*p* for the immature condition. The form of the logistic equation used is shown in Equation 5, where *a* is the 10-mm length-class, *b* is the length (LCF, mm) at 50% maturity (Lm_{50}), and *c* is the length (LCF, mm) at 95% maturity (Lm_{95}). Weight at maturity was estimated from the proportion of mature fish

Equation 5
$$\%mature = 100/(1+e^{-[Ln(19).\frac{a-b}{b-c}]})$$

in each 100-g weight-class. Using these weight data in Equation 5; *a* is the 100-g weight-class, *b* is the weight (g) at 50% maturity (Wm_{50}), *c* is the weight (g) at 95% maturity (Wm_{95}). As we had age estimates for most fish sampled, age-at-maturity was also estimated by fitting a logistic curve to the proportion of fish mature in each age-class. Using the age-data in Equation 5; *a* is the age-class in years, *b* is the age at 50% maturity (Am_{50}), *c* is the age at 95% maturity (Am_{95}).

10.3.7.3 Sex Ratio

The overall sex ratio was calculated from mature carp larger than the Lm_{50} and was tested with a chi-squared test against the null hypothesis that the sex ratio was 1:1

10.4 Results

The total electrofishing sample of fish from the Campaspe eastern and western channels was dominated by catches of exotic fishes: 1114 carp, 1040 goldfish (*Carassius auratus*), 4 carp x goldfish hybrids, 366 redfin perch (*Perca fluviatilis*). Native fish were comparatively rare and comprised 2 golden perch (*Macquaria ambigua*), 7 Australian smelt (*Retropinna semoni*) and 16 flathead gudgeon (*Philypnodon grandiceps*). As the objective of our electrofishing was to sample carp, the relative abundance of other species may have a slight negative bias although broadly speaking these figures represent the rarity of fish species other than carp or goldfish.

10.4.1 Spatial & Temporal Distribution

Relative abundance indices for the western irrigation channel (Figure 22) and standing stock measures for the eastern irrigation channel (Figure 23) give an indication of the changing abundance patterns over almost two irrigation seasons. In the western irrigation channel there was a strong pattern of low carp abundance for all three sites at the start of the 1999/2000 irrigation season compared with the end of the previous season (Figure 22). The overall mean relative abundance (carp ha^{-1}) for the samples in the western channel from the 1999/2000 irrigation season was significantly lower than that from the previous season (t=2.76, p=0.02). This pattern was not as strong when the biomass of carp is considered (Figure 2) (t=1.51, p<0.1), as early catches from the 1999/2000 season were mostly composed of large fish. Mean abundance count for the whole 1999/2000 irrigation season was higher in the eastern channel (t=1.39, p<0.1) than in the western channel, but there was no significant difference between the mean biomass' in the two channels (Figure 23).

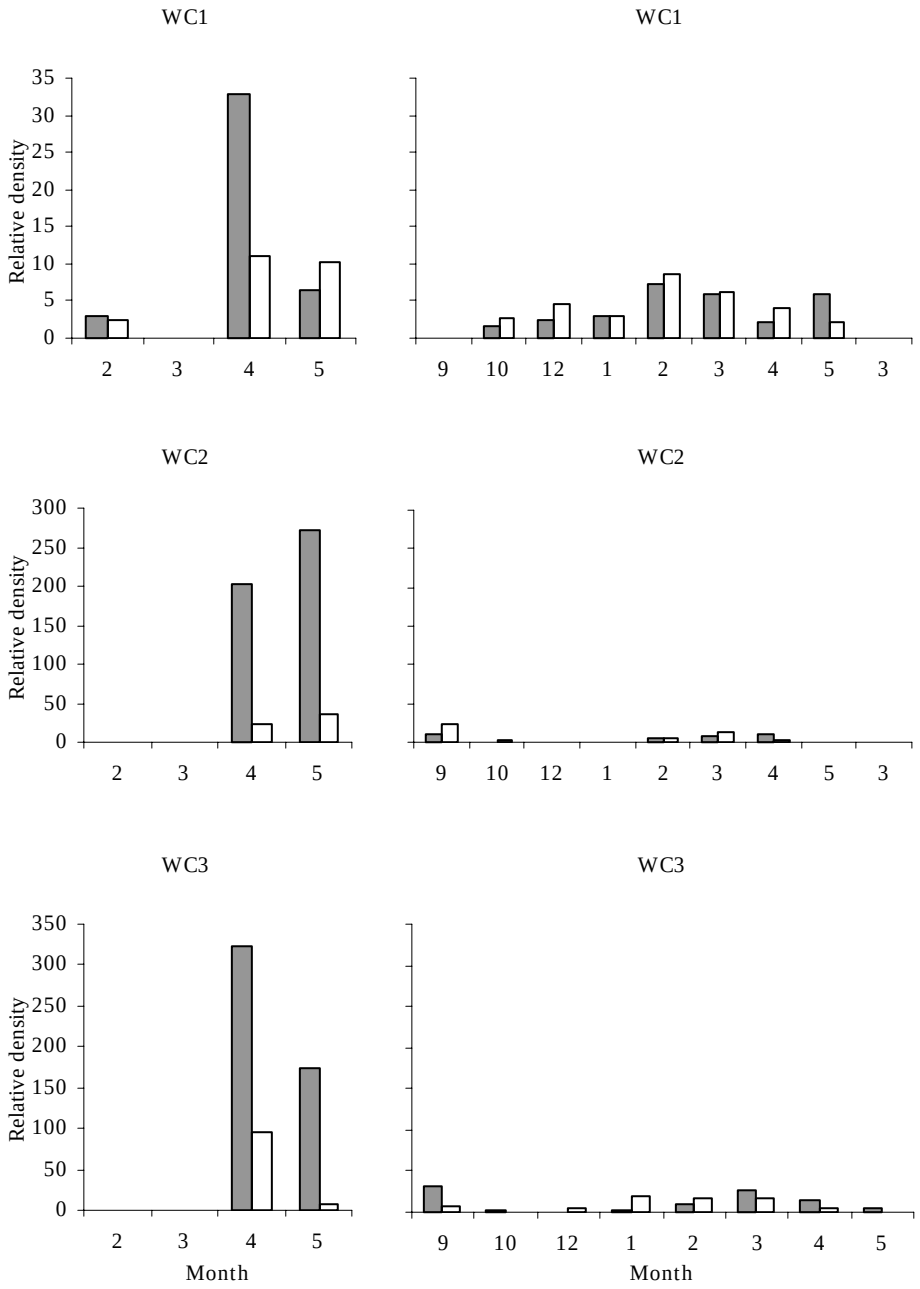

Figure 22. Time series of carp relative abundance for three sites in the western Campaspe irrigation channel (WC1, WC2 and WC3). Solid bars = density (carp ha^{-1}). Open bars = biomass (kg ha^{-1}). Samples are from the 1998/99 irrigation season (left) and 1999/2000 irrigation season (right).

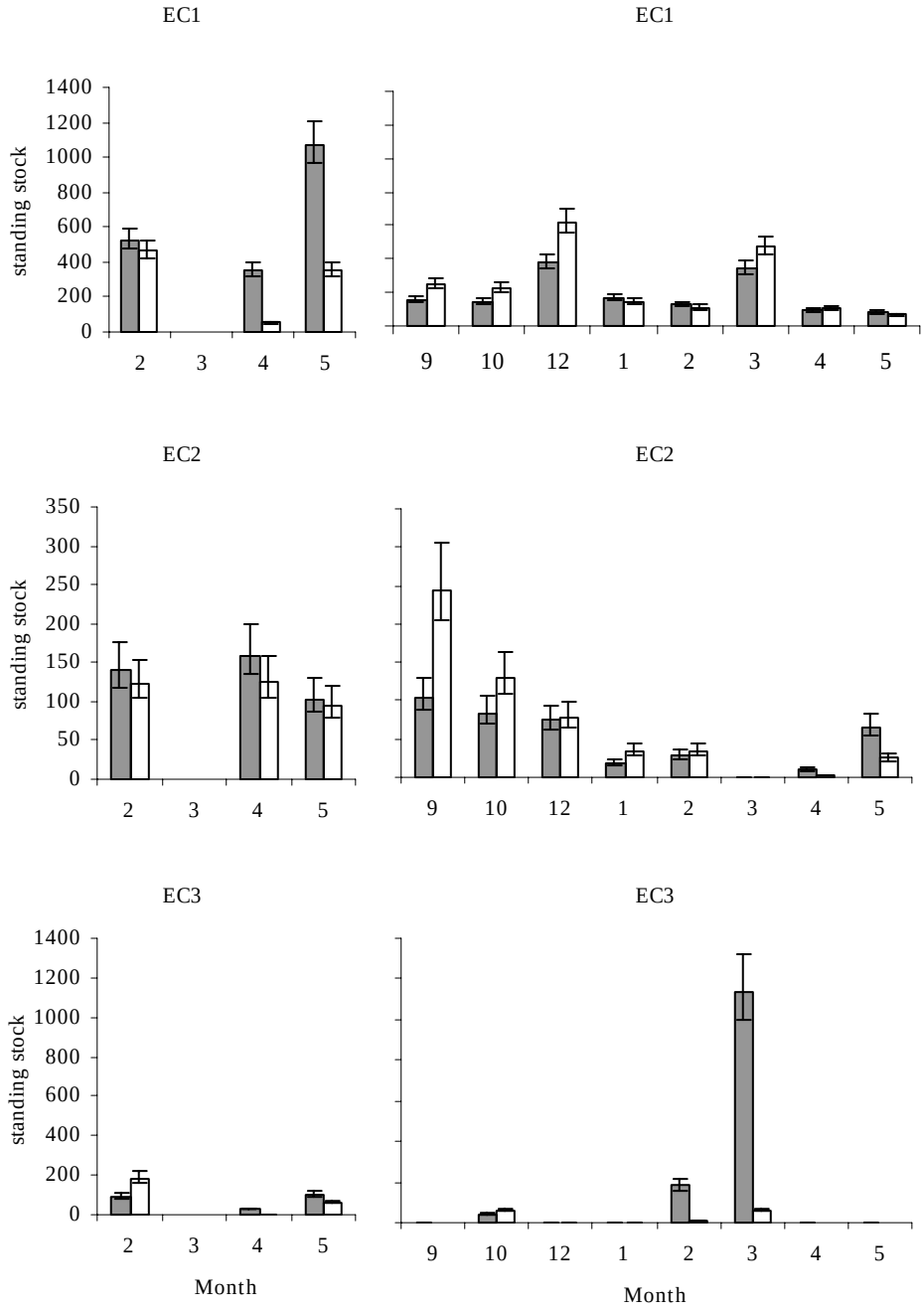

Figure 23. Time series of estimates of carp standing stock density (mean and 95% CI) in the Eastern Campaspe irrigation channel for three sites (EC1, EC2 and EC3) over eleven months during two irrigation seasons 1998/99 (left) and 1999/2000 (right). Solid bars = density (carp ha^{-1}). Open bars = biomass (kg ha^{-1})

At all sites in the eastern channel the pattern of abundance, both numerically and by weight, was similar between the end of the 1998/99 irrigation season and the beginning of the 1999/2000 irrigation season and there was no significant difference between overall means for the two seasons (Figure 22).
The standing stock estimates for the eastern channel varied from 0 to 619 kg ha^{-1} with an average of 144 kg ha^{-1} and standard deviation of 152 kg ha^{-1}.
There was no overall pattern in changes of abundance between sites and times that may have indicated movement within each channel. However during April of the 1998/99 irrigation season, the sudden one-off change in abundance of a strong juvenile cohort with modal length ~180 mm mainly in the western channel, suggests that this represents recruitment by immigration into the channels as this cohort was comparatively rare in the previous February samples (Figure 24). This juvenile cohort is completely absent again at the start of the following irrigation season, indicating total loss by either emigration or mortality.
The more complete sampling of the following 1999/2000-irrigation season indicated a similar phenomenon occurred again. There was a sudden brief juvenile abundance during March at a modal length of ~130 mm LCF suggesting juvenile immigration.

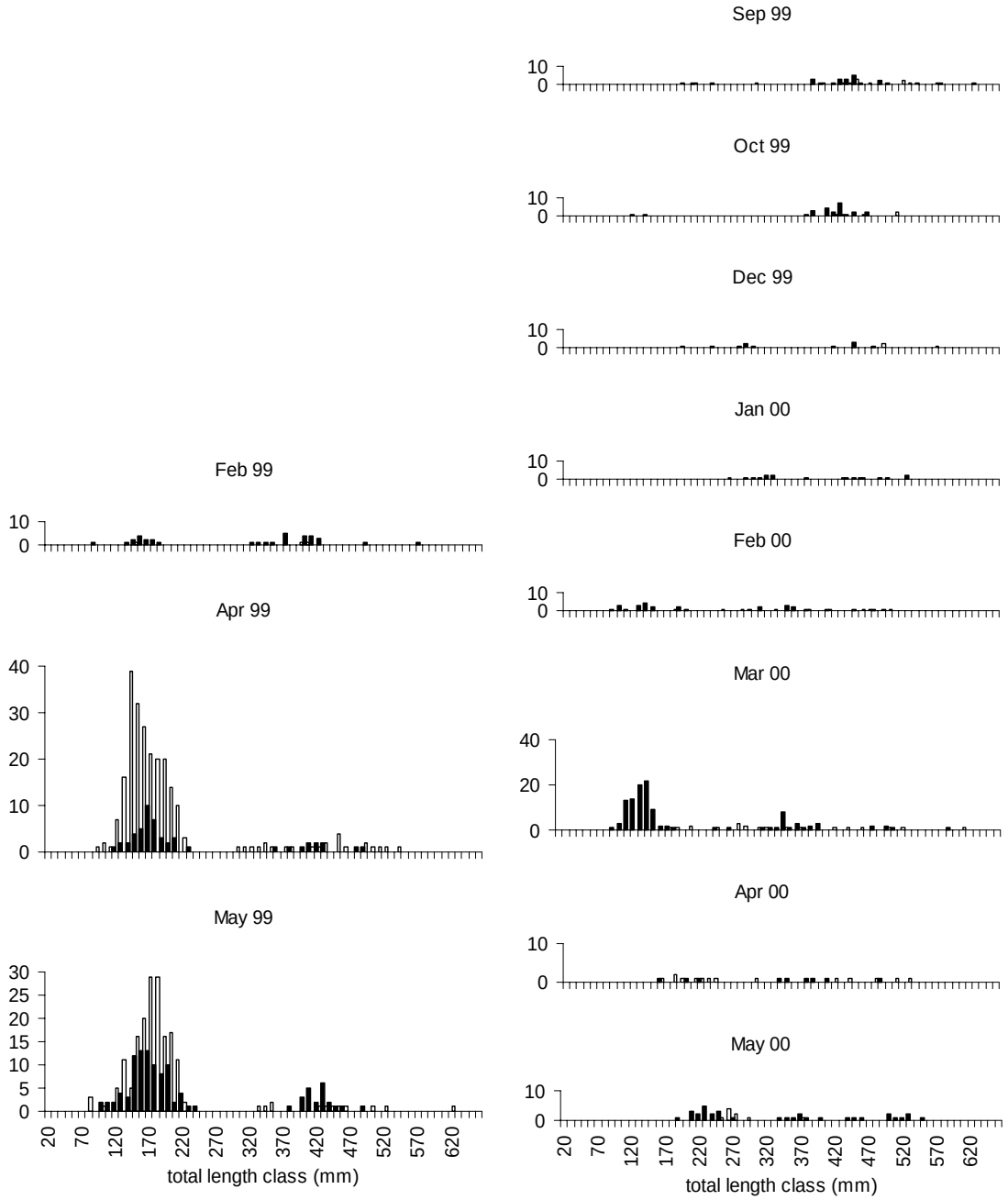

Figure 24. Length-frequency plots for carp from Campaspe irrigation channels during 1998/99-irrigation season (left) and 1999/2000-irrigation season (right). Samples from three sites pooled on each irrigation channel. 10-mm (LCF) length-classes are shown for the eastern irrigation channel (solid bars) and western irrigation channel (open bars).

10.4.2 Population Estimates

During the collection of carp poisoned by acrolein treatments from three sites in the eastern channel totals of 262 kg of carp and 89 kg of goldfish were collected along with less than 50 specimens of other fish species, including Australian smelt, flat headed gudgeon and redfin. The number of individual carp captured each day after acrolein treatment was used to calculate the generalised removal estimator and the jackknife estimator, regardless of whether individuals were marked (Table 13). However, the

initial marking of individuals provided a check on the accuracy of the removal-methods. In theory for a closed population, under conditions where all fish were successfully removed, all marked fish would have been recovered. In all cases the tag-return rate was less than 100%. However, observations of carp behaviour after Acrolein ® treatment suggested that that this was due to incomplete recovery of dead carp, rather than incomplete mortality or lack of closure. Carp died over several days after acrolein treatment. Moribund carp could be seen at the water surface for several days after treatment. Some became trapped in sub-surface vegetation or simply sank and were therefore difficult to recover.

Table 13. Results from mark recapture experiments on three sites on the Campaspe Eastern irrigation channel.

Site	Initial number marked	Day	Number of recovered carp		
			Unmarked	Marked	Total
EC1	49	1	106	11	117
		2	160	9	169
		3	75	4	79
		4	5	1	6
EC2	35	1	10	0	10
		2	49	7	56
		3	40	2	42
		4	8	1	9
EC3	55	1	173	10	183
		2	51	1	52
		3	8	1	9
		4	0	0	0
Grand Total	139		685	47	732

For the removal estimator, population estimates for each site were lower than the combined total of the number of carp removed plus any marked carp that were not recovered, suggesting that this estimator negatively-biased the population estimate. Using the more robust jackknife estimator all population estimates were higher than the total of the number of carp recovered plus un-recovered, marked carp and are therefore preferred for use in subsequent calculations (Table 14).

Table 14. Population estimation using the generalised jackknife estimator (Pollock and Otto, 1983). Sites are shown in Figure 20. Summary statistics and results including numbers of carp initially marked and released are shown (n_1) along with total carp catch after acrolein treatment (C), recaptures (R) also show as % of original number marked in parenthesis, the total catch plus the number of marked carp still missing (C+m), the Generalised jackknife estimator or population estimate ($\hat{N}$) and the standard error (SE) and upper and lower 95% confidence intervals on the estimate. The sampling efficiency is also given ($\hat{N}$: n_1) along with 95% confidence intervals

Site	n_1	C	R (%)	C+m	$\hat{N}$	SE	Lower 95%	Upper 95%	$\hat{N}$: n (95% CI)
EC1	49	371	25 (51 %)	395	647	37.30	584	730	13.2 (11.9, 14.9)
EC2	35	117	10 (29 %)	142	203	20.95	171	254	5.8 (4.9, 7.3)
EC3	55	244	12 (22 %)	287	424	30.25	375	494	7.7 (6.8, 9.0)

At EC3 there was potential for a breakdown of the assumption of population-closure when the upstream stop-net was stolen overnight on one occasion. It is possible that during this period the carp population within EC3 increased due to immigration. For a period of several hours, moribund carp remained present upstream of the site. Emigration from the site was unlikely, as the downstream stop-net remained intact. Although we cannot be sure, it is doubtful that carp could have moved upstream in their moribund state. Thus, if immigration occurred then the bias would be towards *over*estimating the population.
The initial recovery rate for EC3 was higher than for the other sites. However, this was already observed before the stop-net was stolen (<24 h elapsed). Carp recovery rates after replacement of stop net (>35 h elapsed) were similar to those at other sites. Therefore, there is little evidence to suggest a lack of closure while the stop-net was missing and we regard the jackknife population estimator for EC3 as valid.

10.4.3 Standing-Stock Estimation

The ratio of $\hat{N}$ to n_1 is the sampling efficiency (e) of our standard electrofishing method for a site (Equation 2) in the eastern channel (sites in the western channel were not treated with Acrolein ®). This ratio is also the factor by which the relative abundance from the monthly electrofishing samples from the same sites has to be multiplied, in order to calibrate relative abundance to absolute abundance estimates.
Using this calibration the absolute population abundance (carp per hectare) of carp at each site was estimated from the relative abundance in the known area sampled each month. The biomass of the estimated population each month was also estimated by multiplying the observed mean carp weight by the estimated abundance (Figures 22 and 23).

10.4.4 Age & Growth

Growth in mean length-at-age was described by the von Bertalanffy growth model and parameter estimates for $L\infty$, K and t_0 are presented (Table 15) for groups of males plus juveniles, females plus juveniles and in each of the eastern and western channels. Likelihood ratio tests (LR) between males and females, and between eastern and western channels showed that there was a significant difference in mean length-at-age, between pairs of groups.
Heterogeneity in length-at-age was best described by fitting a lognormal error distribution to the values of the growth coefficient K (Troynikov 1998). Confidence intervals, encompassing 90% of the variability of length-at-age, and the median length-at-age are shown (Figures 25 and 26) for groups shown with LR to have a significant difference in mean length-at-age.

Table 15. Parameter estimates for mean growth in length-at-age (Von Bertalanffy 1938) for carp from the Campaspe channels Estimates are given by the gender groups males +juveniles (Male) and females +juveniles (Female) and for each channel. Estimates were obtained by non-linear least squares regression. Standard deviations are shown in parenthesis. n, sample size; SS, sum of squares; ***=P<0.001. Differences in length-at-age between groups were tested using the log likelihood test (Kimura 1980).

Group	n	L∞ (mm)	K ($year^{-1}$)	t_0 (mm)	Error SS	Significance
All	456	510 (± 0.001)	0.480 (± 0.003)	-0.237 (± 0.127)	3371925	
Eastern	287	525 (± 0.002)	0.484 (± 0.004)	-0.228 (± 0.218)	680819	
Western	169	521 (± 0.002)	0.350 (± 0.003)	-0.458 (± 0.207)	35028	*** E vs W
Male	259	495 (± 0.002)	0.475 (± 0.003)	-0.291 (± 0.186)	690351	
Female	267	538 (± 0.002)	0.380 (± 0.003)	-0.391 (± 0.209)	375459	*** M vs F

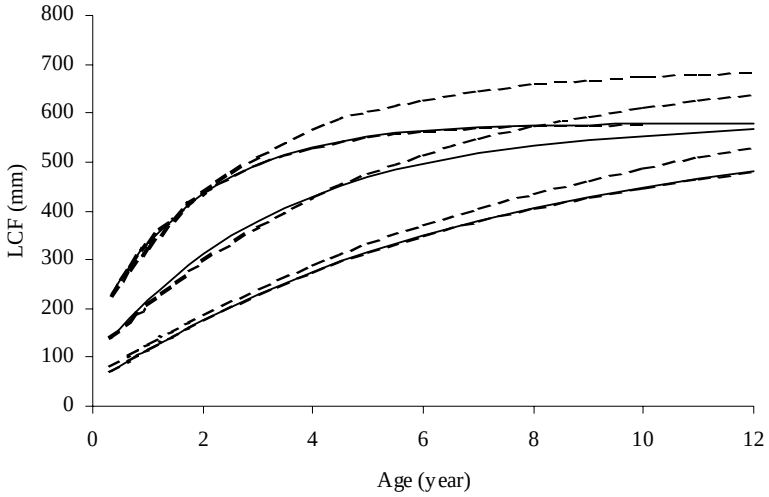

Figure 25. Heterogeneity of length-at-age described by the stochastic growth model (Troynikov 1998) for two groups males and juveniles (solid lines, n=259) and female and juveniles (dashed lines, n= 267). Curves are (from top to bottom) 95%, 50% and 5% quantiles. Thus for each group the outer lines encompass 90% of the variability in length-at-age and the centre line is median length-at-age. Mean length-at-age is significantly different between groups (*P<0.001*)

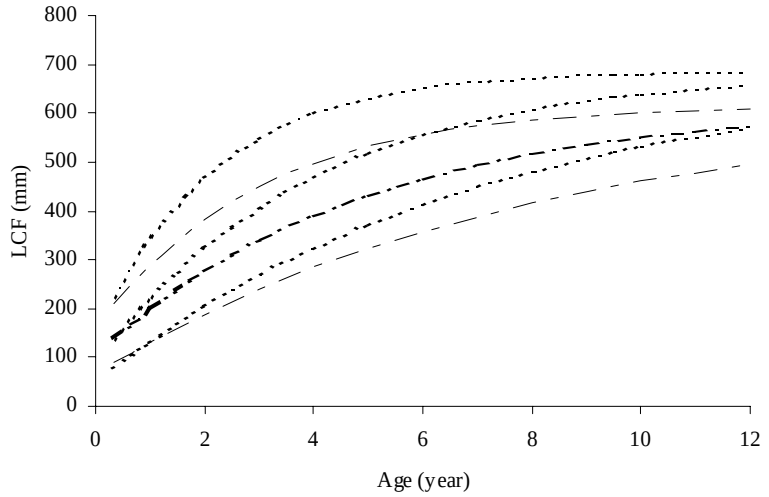

Figure 26. Heterogeneity of length-at-age described by the stochastic growth model (Troynikov 1998) for two groups from eastern (dotted lines, n=287) and western (dashed lines, n= 169) channels. Curves are (from top to bottom) 95%, 50% and 5% quantiles. Thus, for each group the outer lines encompass 90% of the variability in length-at-age and the centre line is median length-at-age. Mean length-at-age is significantly different between groups (*P<0.001*).

10.4.5 Mortality

Carp age-frequencies were estimated using ALK for total catch by sex and for each channel. Each age-frequency distribution was used to calculate estimates of total mortality rate (Z) (Table 16).

Estimates of Z are provided for ages-at-full-recruitment (Tc) from age 1– 3 years, as we are uncertain of the size-selectivity function for electrofishing carp. However, studies of electrofishing selectivity (Jackson and Noble 1995), including our own observations, indicate that selection bias is likely to occur for sizes less than that of 1 year-old carp. Therefore estimates of Z using Tc=1 are probably the most appropriate for all groups (Table 16) except males and females. Estimates for males and females do not include fish that were too immature to determine sex. This mainly includes fish aged 0+ and some 1+ individuals. Therefore Z for male and female groups (Table 16) is only estimated for Tc = 2 and 3 years and estimates using Tc=2 are probably the most appropriate for each sex.

Mean estimates of Z from both methods were higher for the eastern channel than for the western channel (CR; t=4.8, p=0.02 and CC; t=16.9, p>0.001). In three (Tc) cases out of four, estimates of Z were slightly higher for males than for females although the mean difference over all Tc cases was not significant. Male and female samples were therefore pooled to produce an estimate of Z of 0.625 for the eastern channel and of 0.326 for the western channel.

Natural Mortality (M) was estimated using empirical methods (Pauly 1980) based on parameters of the von Bertalanffy growth models. For comparison with total mortality estimates, using an estimate of mean environmental temperature (17.6 ^{o}C) and growth parameters for eastern and western channel groups and each gender, M was estimated as 0.402 for the eastern channel, 0.326 for the western channel, 0.404 for males and 0.341 for females. For an alternative estimate of M we used our estimate of age at which 95% of females are mature (t_{m95}=2.6 years) as T_{mass} in Rikhter and Efanov's (1976) empirical relationship between rate of maturity and mortality to calculate M=0.261.

10.4.6 Reproductive Biology

Of the carp sampled to investigate the reproductive biology, 158 were males, 177 females and 779 of indeterminate sex. Carp of indeterminate sex ranged in size from 70 to 260 mm LCF, and were from 0 to 2 years old.

10.4.6.1 Seasonal fluctuations in GSI

The relationship between GSI and gonad stage enabled GSI to be used as a broad indicator of common carp maturity. Generally, mature individuals had GSI values > 4% and these fish were usually > 350 mm for males and > 360 mm for females.

Most of the females > 400 mm had a GSI > 10% and some up to 24%. GSI values in spawning fish were variable because some individuals had already shed an unknown number of oocytes, resulting in loss of ovary weight (partially spent). Generally GSI values for spawning females were considerably higher than for spawning males, which rarely exceeded 14%.

Gonadal development in females from both channels was minimal during February 1999. Monthly changes in mean GSI of females (Figures 27 and 28) revealed an overall increase in reproductive activity during spring 1999. Mean GSI peaked during October from specimens from the western channel and during September in specimens from the eastern channel. Female GSI was reduced over summer and a second peak in GSI was observed in females during April and May 2000 from both the western and eastern channels.

For males, mean GSI peaked during September 1999 in both channels then declined over the summer. In the eastern channel a further increase was also observed during April 2000 although in the western channel male GSI dropped to a minimum during April and May 2000 (Figures 29 and 30).

Table 16. Estimates of total mortality rates (Z).Chapman-Robson (CR) maximum likelihood method (Chapman and Robson 1960) and least-squares regression catch curve analysis (CC) for carp sampled 1999/2000 for a range of age-at-full-recruitment (Tc). Age frequencies were derived for the full samples from age-length keys (ALK). Figures in parenthesis are variance for CR and R^2 for CC. n= sample size. Mean Z estimate for Eastern is significantly greater than Western, CR; t=4.8, p=0.02 and CC; t=16.9, p>0.001.

Method	Tc	All	Eastern	Western	Males	Females
CR	1	0.488 (0.0005) n=467	0.625 (0.0013) n=322	0.326 (0.0008) n=131	Not estimated	Not estimated
CR	2	0.542 (0.0010) n=311	0.837 (0.0035) n=210	0.297 (0.0010) n=88	0.540 (0.0025) n=118	0.474 (0.0017) n=131
CR	3	0.462 (0.0014) n=160	0.991 (0.0106) n=101	0.270 (0.0012) n=60	0.398 (0.0030) n=54	0.414 (0.0024) n=74
CC	1	0.319 (0.759) n=467	0.590 (0.919) n=322	0.252 (0.753) n=131	Not estimated	Not estimated
CC	2	0.298 (0.709) n=311	0.597 (0.895) n=210	0.228 (0.690) n=88	0.294 (0.609) n=118	0.248 (0.658) n=131
CC	3	0.257 (0.653) n=160	0.549 (0.852) n=101	0.202 (0.602) n=60	0.228 (0.503) n=54	0.208 (0.592) n=74

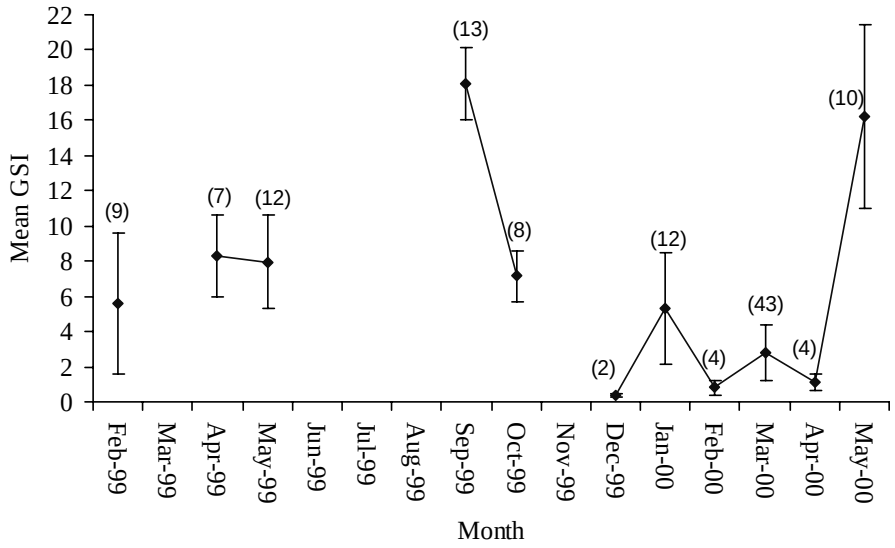

Figure 27. Monthly change in mean GSI (± 1 s.e.) for female carp from eastern Campaspe irrigation channel. Sample size in parenthesis.

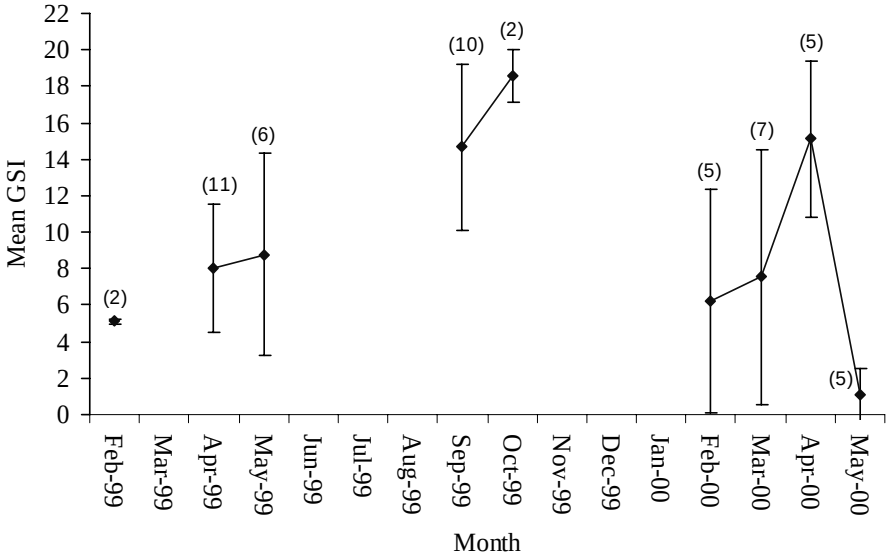

Figure 28. Monthly change in mean GSI (±1 s.e.) for female carp from western Campaspe irrigation channel. Sample size in parenthesis.

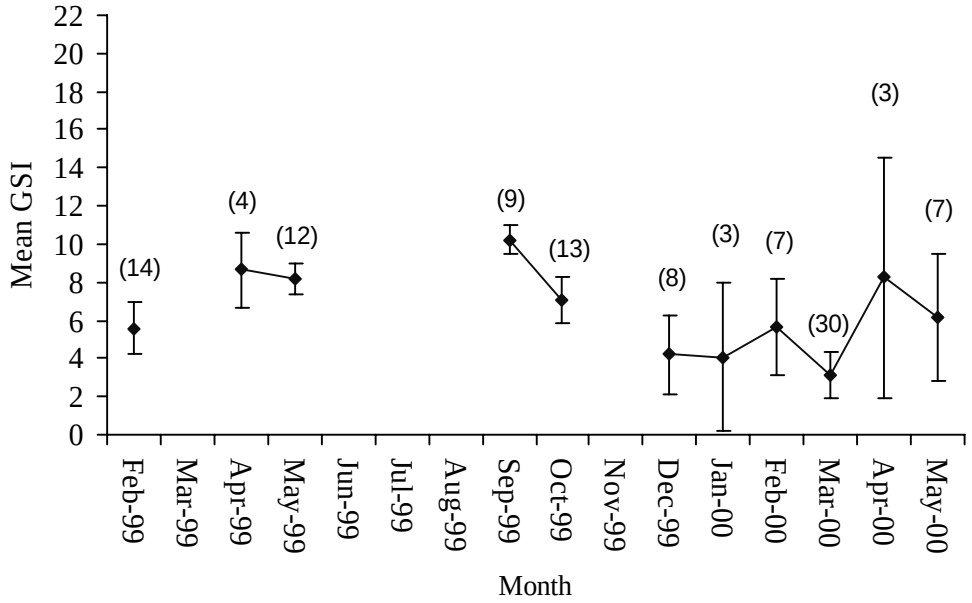

Figure 29. Monthly change in mean GSI (±1 s.e.) for male carp from the eastern Campaspe irrigation channel. Sample size in parenthesis.

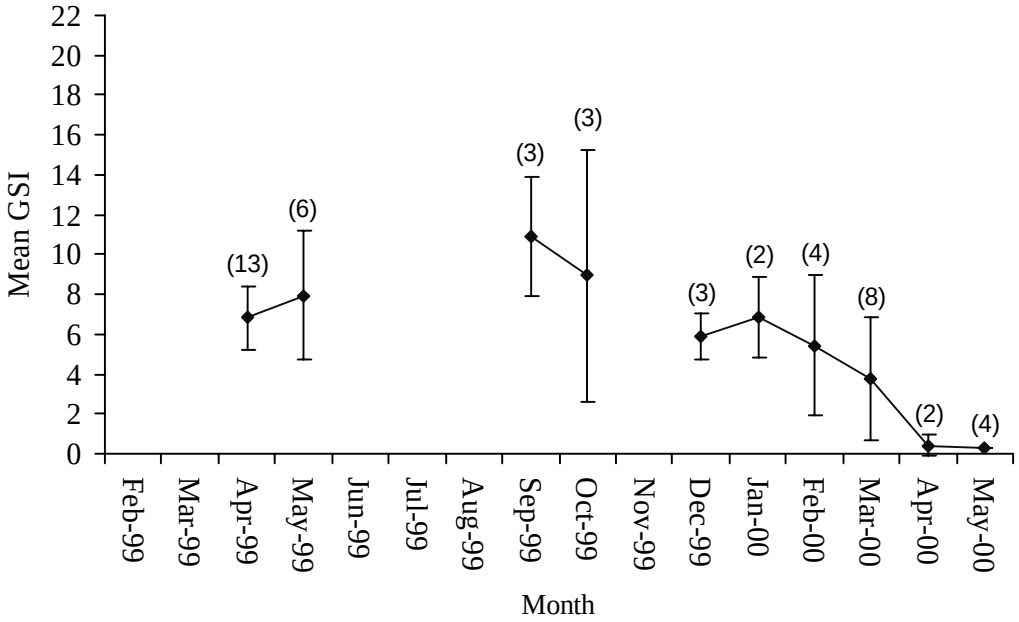

Figure 30. Monthly change in mean GSI (±1 s.e.) for male carp from the western Campaspe irrigation channel. Sample size in parenthesis.

10.4.6.2 Seasonal distribution of maturity stages

The majority of females observed during September–October 1999 from both channels were either running-ripe (F4) or partially spent (F5). In the eastern channel running-ripe (F4) females were observed during February 1999, September 1999, March 2000, and May 2000 (Figure 31). In the western channel, F4 females were observed during September–October 1999 and during March 2000 (Figure 32). From the eastern channel partially spent females (F5) were collected during February 1999, October 1999, and January 2000 (Figure 11). In the western channel F5 females were observed during October 1999 and February–April 2000 (Figure 32). Fully spent (F6) females were observed during February 1999 and March 2000 in both channels.

The majority of males observed were running ripe (M4) during September–October 1999 in both channels (Figures 33 and 34). Partially spent males (M5) were collected during October 1999 and December 1999–March 2000 from the eastern channel (Figure 33). In the western channel, partially spent males (M5) were only sampled during February–March 2000 (Figure 34). Spent males (M6) were observed during October 1999 in both channels, during January–March 2000 in the eastern channel, and during February–March 2000 in the western channel.

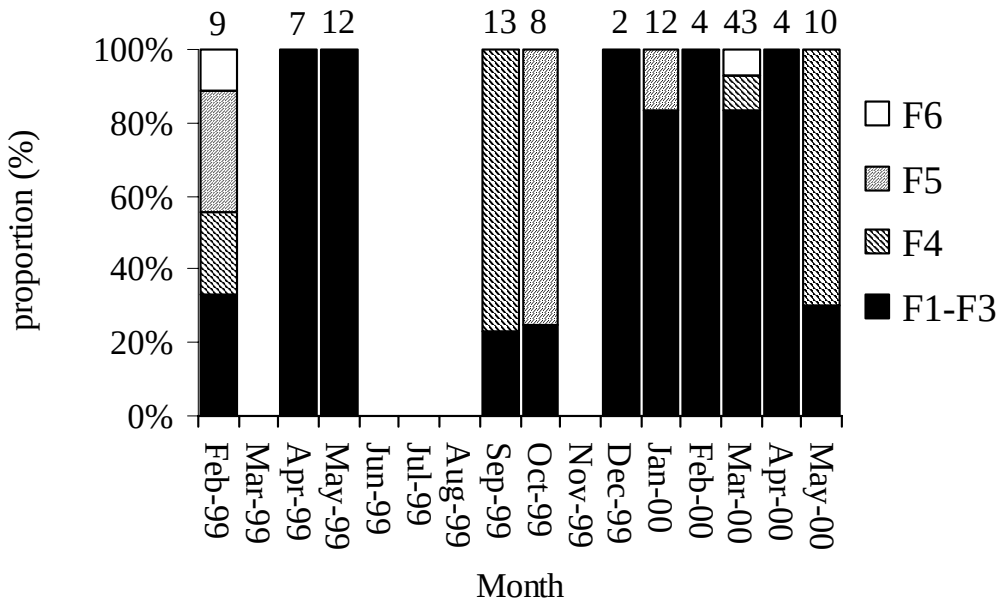

Figure 31. Percentage of female carp in each monthly sample from the eastern Campaspe irrigation channel with gonads that were immature to mature (F1–F3), running ripe (F4), partially spent (F5) or spent (F6). Sample size is shown above each bar.

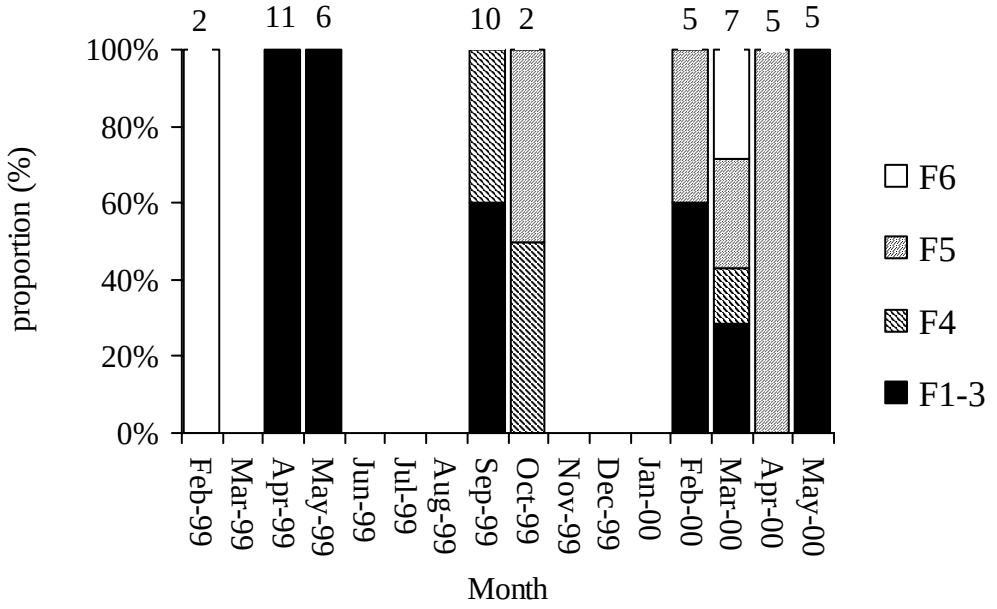

Figure 32. Percentage of female Common Carp in each monthly sample from the western Campaspe irrigation channel with gonads that were immature to mature (F1-F3), running ripe (F4), partially spent (F5) or spent (F6). Sample size is shown above each bar.

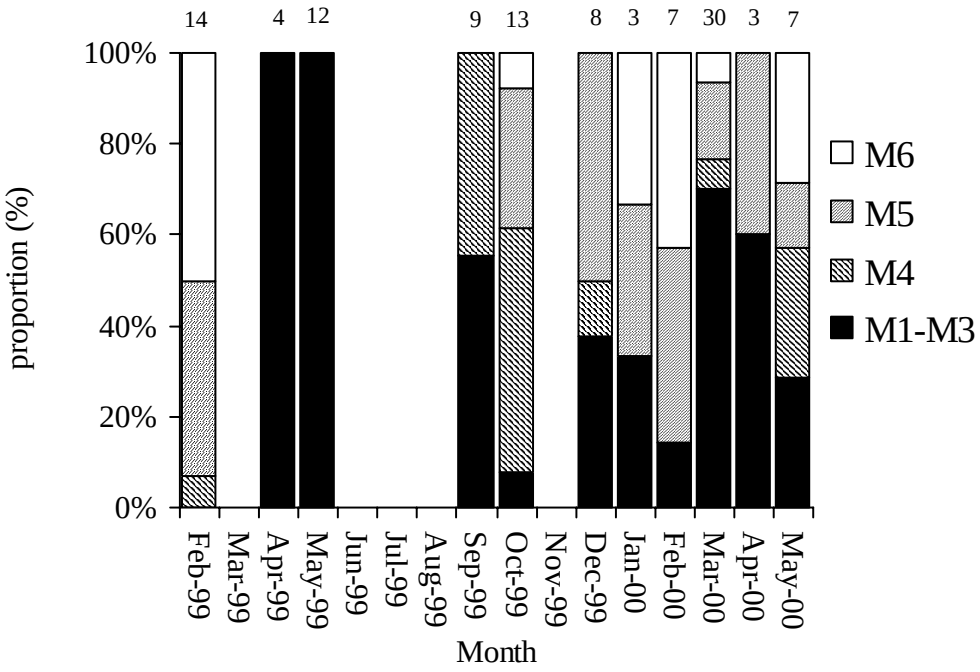

Figure 33. Percentage of male carp in each monthly sample from the eastern Campaspe irrigation channel with gonads that were immature to mature (M1–M3), running ripe (M4), partially spent (M5) or spent (M6). Sample size is shown above each bar.

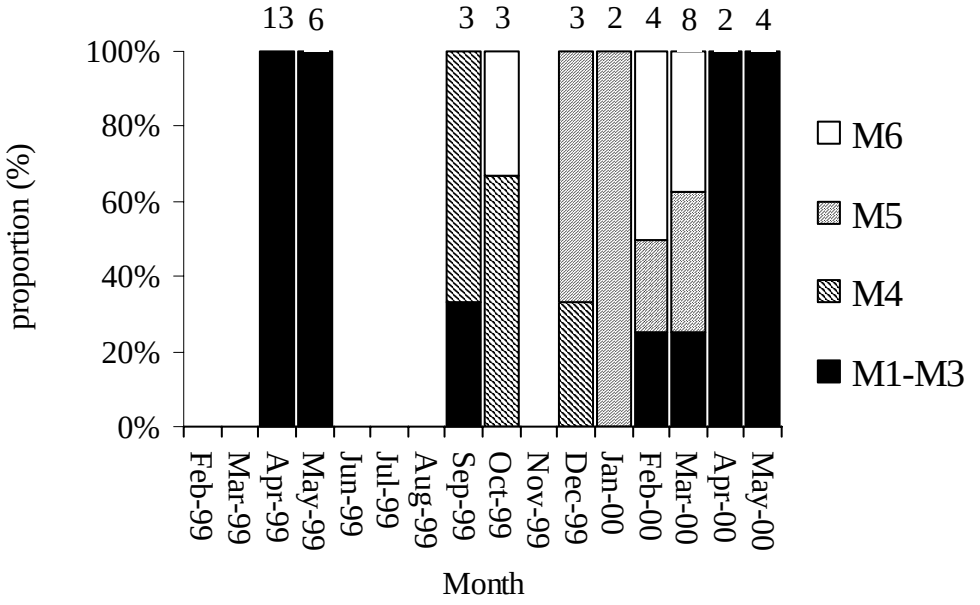

Figure 34. Percentage of male carp in each monthly sample from the western Campaspe irrigation channel with gonads that were immature to mature (M1–M3), running ripe (M4), partially spent (M5) or spent (M6). Sample size is shown above each bar.

10.4.6.3 Histological Stages

Histological examination revealed the types of oocytes present in each macroscopically identified stage of gonads. Details of the appearance of the ovarian stages and of the corresponding stage of the oocytes in histological sections were presented in chapter 5 of this report. The histological samples collected during the study period were used to assess changes in the reproductive status of carp throughout the year. Histological sections from the gonads of 347 carp were analysed.

Of the females with running ripe ovaries (macroscopically staged as F4), 74% had yolked oocytes, 4% contained postovulatory follicles (POF), and 11% had yolked oocytes in the atresia stage.

Partially spent ovaries (F5) sampled in October 1999, January and February 2000 contained POF, degenerating POF and yolked oocytes in atresia that indicated these fish had spawned recently. Examinations of histological sections showed that ovaries identified macroscopically as spent (F6) contained only yolked and unyolked oocytes and not any POF. However one spent ovary was found to contain a few yolked eggs in the atresia stage.

10.4.6.4 Size and Age-at-maturity

All females < 240 mm or males <280 mm LCF were immature. Fitting the logistic equation for the female maturity ogive gave an estimate of Lm_{50} = 273 mm and Lm_{95}=310 mm (Table 17 and Figure 35). For males, the estimate of Lm_{50} was 287 mm; however, the slightly broader logistic ogive fitted to male date suggests that 95% are mature at 344 mm (Table 17 and Figure 36).

All males of weight <400g and females <200 g were immature. Fitting the female maturity ogive to the weight data gave an estimate of Wm_{50} = 490 g with Wm_{95} = 825 g. Similarly the male weight data gave an estimate of Wm_{50} = 556 g and Wm_{95} =872 g (Table 17).

The youngest mature male and female were < 1 year old. The logistic maturity ogive fitted to the proportion of females mature-at-age gave an estimate of Am_{50} = 1.4 years with Am_{95}= 2.6 years of age. The corresponding estimate of Am_{50} for males was 1.3 years also with 95% mature at 2.4 years of age (Table 17)

Table 17. Estimates of size and age-at-maturity for male and female carp from the Campaspe irrigation channels. Data were arranged in 10-mm length-classes, 100-g weight-classes or whole year-classes as appropriate.

Sex	parameter	Length (mm)	Weight (g)	Age (y)
Female	Initial maturity	240	200	0+
	50% maturity	273	490	1.4
	95% maturity	310	825	2.6
Male	Initial maturity	280	400	0+
	50% maturity	287	556	1.3
	95% maturity	344	872	2.4

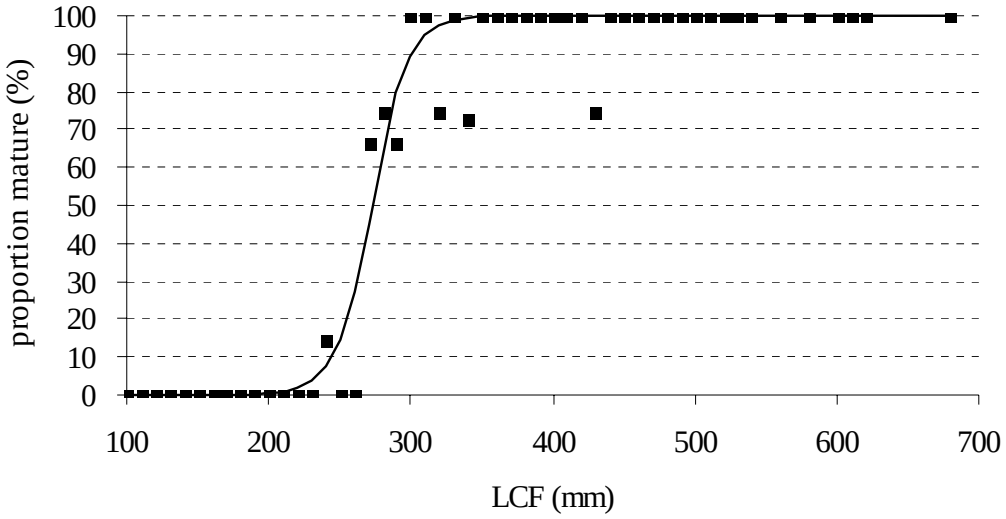

Figure 35. Maturity ogive for female carp plotted against total length (LCF, mm). Data points represent the percent mature in 10-mm length-classes. Analysis was for data pooled over both irrigation channels and two irrigation seasons. Female Lm_{50}=273 mm LCF, Lm_{95}=310 mm LCF

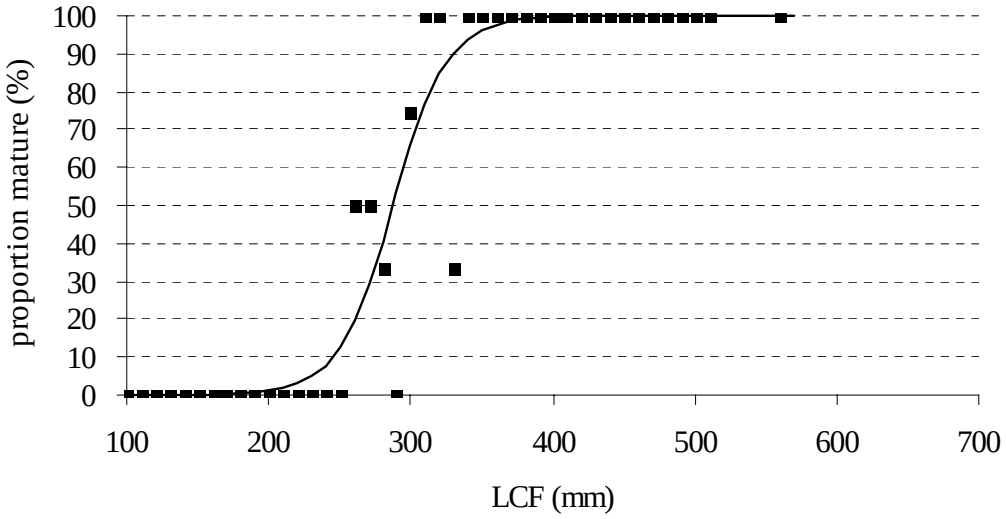

Figure 36. Maturity ogive for male carp plotted against total length (LCF, mm). Data points represent the percent mature in 10-mm length-classes. Analysis was for data pooled over both irrigation channels and two irrigation seasons. Male Lm_{50}=287 mm LCF, Lm_{95}=344 mm LCF

10.4.6.5 Sex ratio

The overall sex-ratio of carp larger than L_{m50} (n=264) was 1.10 females per male. This is not significantly different from an equal sex ratio.

10.4.6.6 Fecundity estimates

The fecundity was estimated from 13 running ripe female carp, with GSI values > 17 %, sampled during September 1999, March 2000 and May 2000 (Table 18). Ten females were sampled ripe and prior to spawning as histological examination showed no postovulatory follicles or evidence of atresia. However, two fish were partially spent (i.e. had degenerating POF) and a third showed evidence of reabsorption without spawning (i.e. atresia in yolked eggs). Female size range was 440–620 mm LCF and individuals were 2–17 years old. The annual fecundity range of running-ripe females was 0.40–1.17 million eggs in carp 2–5 years of age. This represents average egg production of 0.79 million per female sampled from this population. The relative fecundity range of carp was 0.13–0.27 million eggs per kg whole fish weight with and average of 0.22 million eggs per kg of whole fish weight.

Table 18. Fecundity estimates for running ripe and partially spent carp from the Campaspe irrigation channels. Fish length is given as caudal fork length (L), weight given is whole weight (W), absolute fecundity (AF) and relative fecundity are scaled in millions and gonadosomatic index =GSI . Gonad stage descriptions are as listed in Appendix 3.

L (mm)	W (kg)	Age (years)	AF (10^6 x N)	RF (10^6 x N) / W	GSI %	Gonad stage
440	2.100	4	0.48	0.23	20.48	Run-ripe
440	1.940	2	0.40	0.21	20.93	Resorption
490	2.915	4	0.80	0.27	22.85	Run-ripe
500	2.930	3	0.65	0.22	18.43	Run-ripe
500	2.838	4	0.68	0.24	18.39	Run-ripe
510	3.180	3	0.87	0.27	21.95	Run-ripe
520	3.250	4	0.73	0.22	20.92	Run-ripe
520	3.010	4	0.74	0.24	21.46	Run-ripe
540	3.520	4	0.85	0.24	20.57	Run-ripe
580	5.032	3	1.17	0.23	21.18	Run-ripe
600	5.622	-	1.00	0.18	21.45	Run-ripe
610	5.484	17	0.69	0.13	17.32	Resorption
620	5.930	5	0.82	0.14	24.52	Resorption

10.5 Discussion

Carp and other exotic fish species dominate the fish community in the Campaspe irrigation supply channels. Native fish are extremely rare. The carp population can be characterised as a reproductively active, open population with relatively low longevity and high growth and loss rates.

10.5.1 Density Effects

It has been suggested that carp are a direct threat to the physical integrity of irrigation channels (Jackel 1996) and riverbanks (McFarland 1994) due to their benthivorous, erosive feeding habits. However, the low to moderate densities observed during most of this study period seem unlikely to present a physical threat to the eastern and western Campaspe irrigation supply channels. Around the world, the soft-bodied attached algae (e.g. *Chara* sp) and the soft-stemmed pondweeds (e.g. *Potamogeton* sp) are often the first to disappear as a result of carp infestation (Koehn *et al.* 2000). Both types of macrophytes were habitually observed during the course of this study in the Campaspe irrigation channels.
Biomass densities that we estimated for the Campaspe eastern channel during 1999 and 2000 (mean 144 kg ha^{-1}, standard deviation 152 kg ha^{-1}) were often below those recognised in Australia as causing significant detrimental effects via turbidity or vegetation damage. Hume (1983) recommended that carp should be considered a pest in Victoria when their biomass density exceeded 450 kg ha^{-1}. Carp densities of 226–1180 kg ha^{-1} have been shown to have significant detrimental effects on turbidity in experimental ponds (Roberts *et al.* 1995) and on sediment re-suspension in billabong-scale experiments (King *et al.* 1997; Robertson *et al.* 1997). In Argentina, carp at densities similar to those encountered in this study, significantly reduced growth of the dominant vegetation (*Chara* sp and *Ruppia* sp) (Sidorkewicj *et al.* 1998).

10.5.2 Recruitment and Reproduction

The sudden appearance and disappearance of juvenile cohorts in our samples suggests that immigration and emigration may be an important process structuring the populations within irrigation channels. As such, this population may act as a “sink” (Brown 1996) for carp recruitment from the Campaspe River population and the irrigation channels may act as extra nursery grounds for the riverine stock in times of drought.
The breeding cycles of fishes are usually determined with aid of parameters such as gonadosomatic index (GSI), fecundity and gonadal histomorphology (De Vlaming 1972; 1974).
The presence of post ovulatory follicles (POF) within the ovaries of running ripe and partially spent female fish is regarded as evidence of very recent spawning activity (Karlou-Riga and Economidis 1997; West 1990). Carp with POF were sampled in the Campaspe irrigation channels confirming that spawning occurred during September–October 1999 and January 2000.
There is strong agreement between the preferred temperature range for carp spawning and the time when evidence of spawning was observed in carp in the Campaspe irrigation channels. From histological observation, spawning was known to have occurred in spring 1999 (September and October) and summer 2000 (January). However, combined evidence from observations of GSI and the presence of macroscopic and microscopically identified maturity stages suggests that initially spawning occurred at the end of summer (February) 1999; then

the following spring (September–October) 1999 and again the following late summer–autumn (January–April) 2000. During these months the daily average of the water temperature range was 16.5–22.6°C with maximum daily water temperatures of 20–25°C. In a previous Victorian study, carp spawned during September–December in water temperatures of 17–25°C (Hume *et al.* 1983). In Poland, the spawning season of carp begins when the water temperature reaches 18 °C (Bieniarz *et al.* 1978). Sarig (1966) suggested that spawning occurs across the Near East and Europe when daytime temperatures reach 18–20 °C with a night time minimum of ~15 °C. In tropical regions spawning generally occurs throughout the year, although it will cease when water temperatures exceed 34–39 °C (Alikunhi 1966). Temperatures greater than 25 °C may be detrimental to carp larval development (Penaz *et al* 1983 cited in Koehn *et al* 2000). Adamek (1998) also suggests that an upper temperature limitation may have been important in restricting the spawning period in the Murrumbidgee Irrigation Area, New South Wales during 1997 to less than two months from October to early November, when the water temperatures range was 19–29 °C. In the Campaspe irrigation channels such high temperatures were never attained during the period of the present study. Useful comparisons of size or age-at-maturity are often confounded by the inconsistent way in which they are reported. Some authors report the age or size at initial maturation (i.e. the smallest or youngest observed mature fish) (Hume *et al.* 1983). Hume (1983), for example uses a description of gonad development using four stages to report the smallest mature male (125 mm) and female (150 mm) as somewhat smaller than the 280 and 240 mm in the present study. Our inclusion of four additional developmental stages may have had greater resolution. Other authors report the size or age range of mature fish. Swee (1966) reported the age composition of carp "on the spawning grounds" as 2–12 years with a mean age of ~6 years. Crivelli (1981) reported that in the south of France, the proportion of females "developing" was 60% in carp 1+ years and 95% in carp 2+ years of age. Thus carp in the Campaspe irrigation channels mature at a similar rate to those studied in other temperate and Mediterranean climates (Crivelli 1981) and in New South Wales (Brown 1996) although exact comparison is difficult. Within a population, individual fish become mature at a range of different sizes and ages. A mathematical function, such as the logistic ogive, that best fits this variability provides useful input for any proposed stock assessment process (Knuckey and Sivakumaran 2001). Parameters of the function provided a standardised template for comparisons between stocks (Weyl and Booth 1999) and should be used whenever possible.

10.5.3 Age and Growth

Observations of the age and growth of carp in the Campaspe irrigation system suggest that they grow relatively fast but reach a modest size compared with other Australian stocks. Although significant differences were observed between eastern and western channels, and between males and females, groups reached their asymptotic length ($L\infty$) of 500 to 540 mm (TL) at rates of 0.350 to 0.484 $year^{-1}$ (K). These are similar, if slightly higher, to growth rates observed for carp in the lower Murray River (Vilizzi and Walker 1999). Although the carp from the lower Murray River attained larger asymptotic size, this may be due to the scarcity of carp > 10 years old in the Campaspe channel stock. The species shows quite variable growth rates throughout its broad geographic range and the observed parameter values in this study are comparable with those determined for Eurasia and China (Li *et al.* 1990.; Nikolsky 1957; Yie 1988)

10.5.4 Management and Mortality

The slow-flowing, shallow, well-vegetated channels with silty substrates correspond well to the habitat requirements of carp (Brown 1996; Koehn *et al.* 2000). However, in comparison with many other Australian stocks, carp in irrigation channels are subjected indirectly to hostile and active management via manipulation of the water-supply function. Application of herbicide to control macrophyte infestation and regular de-watering of the majority of the channel system are both likely to increase carp mortality over and above natural mortality levels.

In fish stocks where there is both loss by fishing mortality (F) and loss by natural mortality (M) (i.e. senescence, predation, disease, emigration, fishing induced mortality) the total loss rate (Z) is the sum of both parts (Ricker 1975) (i.e. Z=M+F).

The total mortality rate is also reflected by the age-structure of the stock, and thus analyses of the sampled age-structure can be used to estimate the total mortality rate using regression methods (Ricker 1975) or maximum-likelihood methods (Chapman and Robson 1960).

In most feral carp stocks in Australia there is minimal fishing and therefore $M \cong Z$. The natural mortality component can be approximated using empirical methods, from the relationship between habitat temperature and mortality rate (Pauly 1980) or from size at maturity (Rikhter and Efanov 1976). In a fished stock, the difference between the estimates of Z and M would be used to calculate F. In the Campaspe irrigation channels some fishing mortality would result from our own sampling efforts, but would otherwise be minimal (i.e. there are also anecdotal reports of a small amount of collecting of stranded fish by local anglers requiring crayfish bait). Two artificial mortality "risks" are imposed on carp in irrigation channels: de-watering and Acrolein treatment. In a sense these can be considered "extra" to the risk considered by empirical methods and therefore included as fishing mortality or perhaps as the additional term "Operational mortality" (O). Thus for the Campaspe channel carp stock $Z = M + F + O$. A comparison of population characteristics in eastern and western channels supports this hypothesis. Although relative abundances, were similar among channels there are fewer carp older than five years in the eastern channel (1.7%) and none over 10 years compared with the western channel (8% > 5 years and 2% >10 years) and total mortality estimates for the eastern channel are at least double that of the carp in the western channels (Table 16). This may be due to the eastern channel having received three times as many Acrolein treatments since 1993, and being de-watered (as usual) between 1999 and 2000 irrigation seasons, whereas the western channel (unusually) was kept full.

By rearranging the above equation and by substititing for Z and M, we can estimate a mortality rate due to operational management plus fishing (O+F) of around 0.2 for the highly exploited eastern channel. Under our assumption of minimal fishing mortality and we therefore estimate that annual de-watering and repeated acrolein treatments (1993, 1994 and 1997) equate to an increase of the mean instantaneous natural mortality rate from ~0.3 to ~0.5. This equates to an increase in the average annual percentage mortality from 26% to 40% due to channel management practices.

As Thresher (1997) pointed out there is a dearth of comparable published information on mortality rates of feral carp stocks around the world. Billard (1995) presented survival data from extensive aquaculture ponds in central Europe that suggested juvenile carp mortality rates over the first year approach 50–80 %; with 20–30% in the second year; and 10–20% in the third. Hence, using logarithmic regression methods (Ricker 1975), the average

instantaneous mortality rate (Z) relating to this extensive aquaculture scenario is ~0.6 to 0.8 for the life-history period from larvae to 3 year-old carp.
Recently Koehn(2000) used length-frequency data from Gehrke(1999) pooled from samples collected in multiple habitats over three years to estimate approximate mortality rates for carp in four New South Wales rivers. As would be expected, these annual mortality estimates are higher than those reported in extensive aquaculture and ranged from 83–98% for carp < 1 year old; from 44–88% for carp < 2 years old, and ~52 % for older fish averaged across all four rivers.
Although there are examples of effective carp removal by poisoning (Hall 1988) or exclusion (e.g. Pilby Creek in Australia (Koehn *et al.* 2000), there is no information on the effects of such management or exploitation on the dynamics of carp populations in Australia and few internationally. Crivelli (1990) suggested that the decline in the carp fisheries of northern Greek Lakes was mainly due to over exploitation and proposed a reduction of fishing-effort as a means to restore the stock. However, he acknowledged that other factors such as habitat degradation and the introduction of exotic species were also part of the problem. The carp population of the Campaspe irrigation channels is subject to fairly intensive "management" through de-watering and Acrolein treatment. In comparison with carp stocks in a less controlled or managed environment (chapters 8–10), Campaspe channel carp show some characteristics of an exploited population such as reduced longevity, and high growth rates. Consequently, the carp in the eastern channel that are subject to the most intensive management are the most intensely effected. This suggests that current management practices are indeed having a measurable impact on the population structure of carp within this system. We can hypothesis that without this burden of additional mortality rate the channel stock would contain older, large carp.
However, the adaptability of carp is illustrated by the fact that despite an apparent doubling of the natural mortality rate due to intensive channel management activities in the eastern channel, there were no detectable differences in carp relative abundance or biomass between channels. The resilience of this carp population is such that through emigration and rapid recruitment they have recolonised and repopulated over 12 km of irrigation channels despite up to three virtually complete fish-kills due to acrolein treatment in the past eight years.

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11 Appendix 5 – Population biology of carp in the mid-Murray River and Barmah Forest wetlands, Australia

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11.1 Summary

Feral common carp (*Cyprinus carpio* L.) dominate the biomass and abundance of fish communities across much of south-eastern Australia. Despite this, little detail is known of carp population dynamics in Australia. This study describes biological attributes of an important carp stock in the main channel and Barmah–Millewa Forest floodplain wetlands of the mid-Murray River. Observed indices of adult carp abundance in the main river channel dropped as soon as carp had access to floodplain environments. Indices of juvenile abundance were elevated in a year with sustained and extensive flooding, relative to the previous year of short-term and minor flooding. Maximum observed age was 28 years. Strong and weak year-classes in the age-structure were associated with greater than average and less than average flooding in the Barmah–Millewa Forest respectively.

Average growth in length for males and females was described with the von Bertlanffy growth model and heterogeneity in length-at-age was described with a lognormal error distribution of the growth parameter k. Mean total mortality rate (Z) was estimated for yearlings and adult males and females greater than 7 years old from age-frequency data using both the Chapman and Robson maximum likelihood estimator and least squares estimation of a catch curve gradient. An approximate estimate ($\cong$190 kg ha^{-1}) of standing stock biomass is proposed based on commercial harvesting of a mass-stranding after de-watering a known area. Natural (M) and Fishing mortality rates (F) were estimated for males and females separately, using empirical methods. Seasonality and timing of reproductive biology is described for the 3-year period 1999–2001. Rates of initial maturation of carp are described in terms of length, mass and age. Median values for initial maturation were 307 mm LCF, 584 g and 1.1 years for males; and 328 mm LCF, 688g and 2.7 years for females, respectively. Juvenile sex ratio was 1male:1 female although at maturity there was a significantly male-biased sex ratio. Mean fecundity was relatively low at 0.33 million eggs, or 0.11 million eggs kg^{-1} for females 8–15 years of age. Implications of the observed protracted spawning season and low adult mortality rates are discussed along with the influence of the Barmah–Millewa Forest environmental watering allocation and flooding on carp pest-management prospects.

11.2 Introduction

Feral carp (*Cyprinus carpio* L.) are estimated to comprise the largest fish biomass and be the most numerous large fish species across Australia's largest river catchment, the Murray–Darling Basin (Gehrke *et al.* 1995). The invasive species is now found in many of the major freshwaters of Victoria and NSW (Gehrke *et al.* 1995; Gehrke *et al.* 1999; Harris and Gehrke 1997) and is continuing to expand its range in Victoria (Brown and Hall 2001; NRE 2001) and South Australia (Anonymous 1994).

Considering the distribution and prevalence of the species, relatively little is known of the biological characteristics of Australian carp populations, and from only a few locations. Most Australian studies of carp have concentrated on the impacts of carp on their environment (Koehn *et al.* 2000).

Age and growth of carp was studied in the lower Murray River wetlands (Vilizzi 1998; Vilizzi and Walker 1999b), some Victorian wetlands (Hume *et al.* 1983) and some Tasmanian Lakes (Vilizzi and Walker 1999a). Hume *et al* (1983) also studied the reproductive biology, interactions between carp and other fish, and the effects of carp on their environment. Adamek (1998) studied the breeding biology of carp in a New South Wales (NSW) irrigation district. Gehrke *et al* (1995; 1999) and Schiller (1996) explored the relationship between carp recruitment and hydrology in four NSW rivers. Some estimates of absolute population abundance have been made (Reid and Harris 1997). Movement and migration were examined by Reynolds (1983) in the lower Murray River and, more recently, by (Stuart and Jones 2002) in the Barmah-Millewa wetlands on the mid-Murray River.

A holistic approach was taken to describing carp biological characteristics such as reproductive biology, age and growth and mortality rates and to population estimation in a Victorian irrigation system (Appendix 4) using validated, otolith-based age estimates (Appendix 2).

The Barmah–Millewa Forest (BMF) at 65,000 ha is the one of the largest continuous wetland areas in the Murray–Darling Basin (Murphy 1990). Recent studies of the fish community of BMF wetlands have shown carp to be the dominant species (Gehrke *et al.* 1995; McKinnon 1997) and the wetlands to be an important centre of juvenile carp production (Stuart and Jones 2002). BMF carp can be regarded as a significant open, sub-population of a large reproductively isolated Murray–Darling Basin stock.

The present study forms part of a broader investigation designed to provide detailed biological information on carp stocks in a range of Victorian habitats as a precursor to developing an effective carp pest control strategy.

The size and location of BMF towards the upstream-end of the River Murray floodplain makes the carp stock in this area a potential keystone of any effective basin-wide management plans of the future. The objectives of the present paper are to characterise the population biology of carp in the Barmah wetlands and the mid-Murray River. Growth and reproductive biology are described; mortality rates are estimated; and the relationship between hydrology, year-class strength and relative abundance of carp is examined. The study period 1999–2001 overlapped with the release of the second Barmah–Millewa Forest environmental water allocation (EWA), which opportunely allowed the observation of carp populations under such conditions.

11.3 Methods

11.3.1 Study Area

The Barmah Forest ($145^0$00' E, $36^0$00' S) is situated in the south-east of Australia in northern Victoria, on the River Murray between the towns of Tocumwal and Barmah. Barmah Forest covers an area of ~30,000 ha and, together with the Millewa and Moira State Forests on the New South Wales (NSW) bank of the Murray, it forms the largest forest of river red gum (*Eucalyptus camaldulensis*) in Australia (MacKay and Eastburn 1990; McKinnon 1997). The mid-Murray River flows in a relatively narrow channel for several kilometres downstream from the effluence of the Edwards River, a major anabranch. As such, relatively small increases in flow cause it to overflow. These floods inundate large areas of river red gum forest and periodically reconnect numerous wetlands to the river (Figure 37). Barmah Lake in Victoria and Moira Lake in NSW are the largest of these wetlands. Hut Lake is typical of many of the smaller wetlands. Except during periods of flooding, flowing water within the forest is confined to the main mid-Murray River, a system of smaller anabranch-creeks such as Budgie Creek and major tributaries, such as the Broken Creek. Barmah Lake is free to fill and drain, through several small creeks and a large opening to the river in the southern end of the lake, depending on the river height. The flow of water to Moira Lake from the River Murray has recently been controlled through regulating structures.

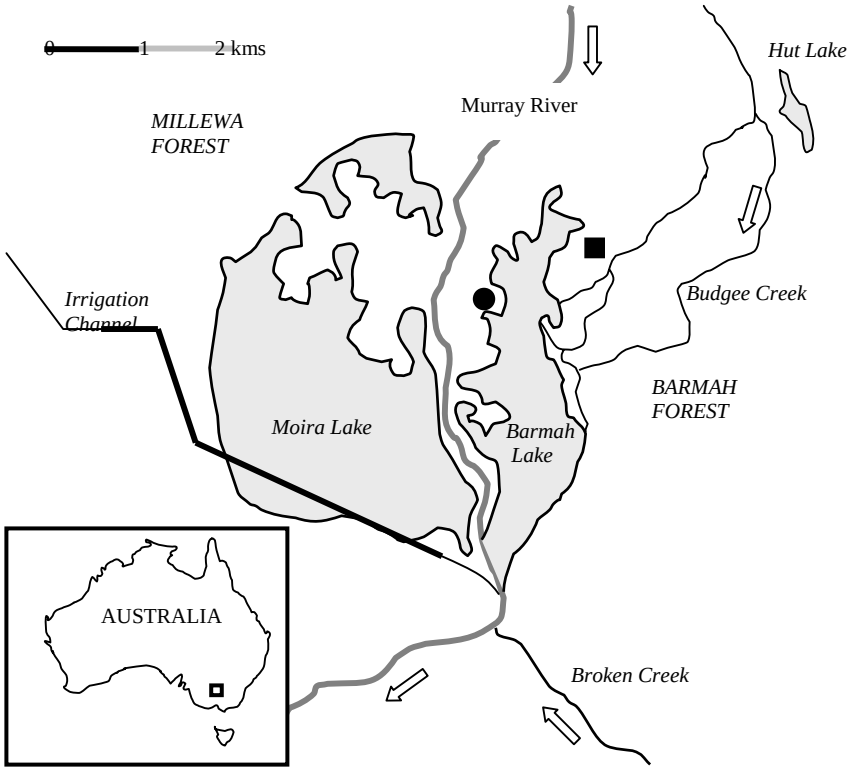

Figure 37. Map showing mid-Murray River flowing through the Barmah-Millewa Forest. Barmah Lake and Moira Lake lie to the east and west of the Murray River. Position of hydrologic recording instruments is shown by symbols (square=Budgee Creek at War plain, circle=Moira Lake outlet) Inset shows the approximate location of the Barmah-Millewa Forest within Australia.

Carp were sampled primarily from sites within the main channel of the mid-Murray River, from Barmah Lake and Hut Lake. During periods of extensive flooding, samples were also taken from open areas of floodplain within the forest adjacent to the primary sites. During commercial trapping operations, carp were also sampled from Moira Lake as the water was drained through a regulator in 2001.

11.3.2 Hydrology

Murray River daily flow and stage-height data were collated for Tocumwal (1970–2000) (Theiss Environmental Services) to provide a hydrographic time-series over a period equivalent to the life-span of carp sampled during the study.
Data on water temperature and flood stage height were collated for stations within the Barmah–Millewa Forest (River Murray water) for the period of the present study to compare with patterns of spatial and temporal patterns in carp abundance. Data from continuous recording stations Budgee Creek at War Plain (#409398A) and the Moira Lake outlet (#409232A) were chosen to indicate hydrologic conditions at major wetland access points where carp could potentially move from the River Murray into the wetlands.

11.3.3 Stock definition from movement & migration

Although the Murray–Darling Basin carp stock is genetically diverse and contains all three of the recently identified carp haplotypes in Australia, two of the haplotypes were rare. Davis *et al.*(1999a) found that sites close to our study area were occupied solely by the single most common haplotype.

Recent radio-telemetry studies of carp in the Barmah Forest have shown that adult carp make considerable movements (10s of km) between wetlands and the river channel as well as (100s of km) upstream and downstream in the river channel (Stuart and Jones 2002). This research has also shown that many juveniles originating from the wetlands of the Barmah Forest emigrate to the river when the floodwaters are receding. In terms of defining the stock boundaries, this suggests that carp from the Barmah Forest wetlands and the adjacent River Murray are certainly part of a much larger stock contiguous with much of the Murray–Darling Basin. In terms of describing the characteristics of carp from the Barmah area it makes biological sense to pool samples from the various wetlands, as these "sub-populations" have the opportunity to mix within the time-scale of a carp life span.

11.3.4 Carp Spatial and Temporal Distribution

Carp were sampled approximately monthly with several methods chosen to suit the various habitat types and environmental conditions. Electrofishing was the standard method chosen for the River Murray channel. On each occasion a fixed site upstream of the southern end of Barmah Lake was fished with a single pass of a boat-based electrofisher (Smith–Root, Model V, 5.0 GPP) using pulsed AC output at a frequency of 120 Hz. This site was immediately adjacent to the mouth of Barmah Lake and thus was potentially on a major carp access route between the river channel and the wetlands.

When the catch was small, additional nearby river sites were fished in attempts to obtain a minimum sample size of 50 fish for age and growth and reproductive studies. Site length (m) and width (m) fished was always noted and the electrofishing catch data were used to calculate a standardised index of relative abundance (CPUE) for the river (carp ha^{-1}). Preliminary sampling, and data from previous studies in the region (McKinnon 1997) and in literature from overseas (Vilizzi and Walker 1999c) indicated that small juvenile carp were more common in shallower wetland habitats than in the main channel. Therefore an additional standard fleet of fyke nets (n=20) (5 m single-wing, 10 mm mesh) was also deployed each month in shallow lakes. Fyke nets were used in Barmah Lake when there was sufficient water depth (≥25 cm). Once water receded in Barmah Lake our sampling effort switched to Hut Lake. Floodwaters once immediately prior to and once during the present study connected Hut Lake and Barmah Lake. Additional *ad hoc* sampling was conducted occasionally with gill nets, seine nets and obtaining samples from commercial trapping operations to increase the sample-sizes for reproductive and age-and-growth studies.

11.3.5 Year-Class Strength

In a comparison of strong and weak year-classes with the time-series of Murray River flow data, the effects of mortality would be expected to accumulate and weaken any existing relationships for the older age-classes. Therefore during both 1999 and 2000, our comparison was restricted to the most abundant adult age-class sampled (7-year-olds), and the least abundant of the recent year-classes (2-year-olds).

Daily flow records for the Murray River at Tocumwal (Figure 38) were summed to estimate total annual flow. Using the magnitude of total annual flows, the years from 2000 back to 1976 were simply ranked to compare with the carp relative year-class strengths.

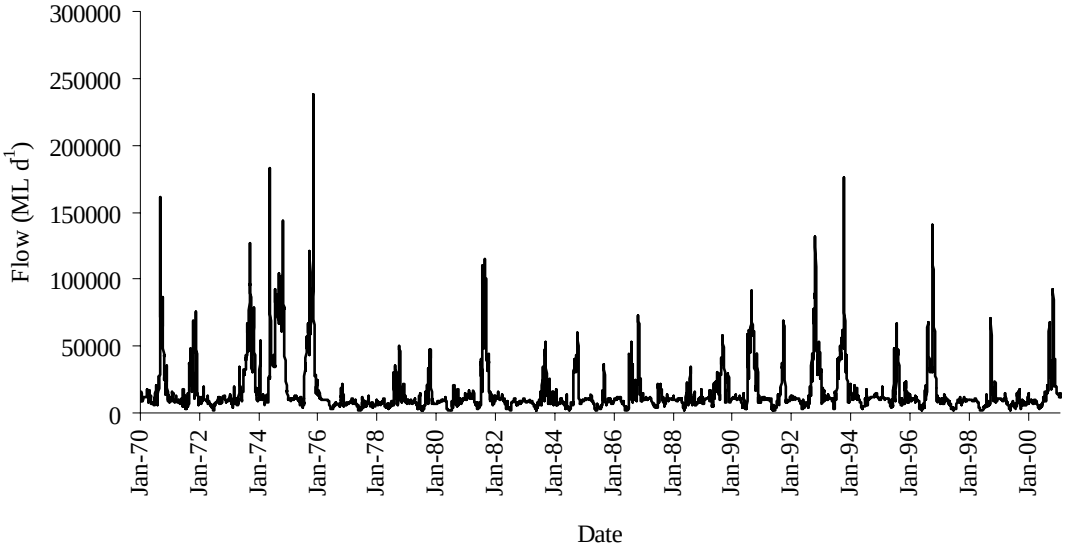

Figure 38. Flow hydrograph for Tocumwal gauge, upstream of the Barmah Forest 1970–2000

11.3.6 Age and Growth

For age and growth study, carp sampled each month were stored on ice and returned to the laboratory. Carp ≥ 50 mm caudal fork-length (LCF) were weighed to the nearest gram, and measured to the nearest 5 millimetres. Carp < 50 mm LCF were weighed to the nearest 0.1 g and measured to the nearest millimetre. Otolith pairs (asteriscii) were dissected from all carp sampled. The otoliths were dried, weighed (to the nearest 0.001 g), mounted in blocks using clear polyester casting resin and sectioned for age-estimation (Morison *et al.* 1998).
Daily increment formation for juvenile carp has been validated (Vilizzi 1998) and annual cycles of otolith edge-growth noted in some age-groups from whole otoliths and thin otolith sections for fish aged from 0+ to 17+ years from the lower Murray River (Vilizzi and Walker 1999b) suggests that the assumption of growth-increments being annual is valid. The present authors' data from juvenile carp cohort-progression and oxytetracycline marking of carp with between 2 to 14 growth increments confirms that a single increment is laid down each year and the initial increment is laid down at approximately 1 year of age (Appendix 2). Therefore, increment counts from sectioned otoliths were used to estimate age in years.
Mean length-at-age was described by applying a deterministic growth model (Von Bertalanffy 1938). The von Bertalanffy parameters were estimated by non-linear least squares regression. Comparing mean length-at-age between females and males was accomplished using a likelihood ratio test (Kimura 1980).
Heterogeneity of growth in length-at-age was described by a four parameter, stochastic growth model (Troynikov 1998). The three von Bertalanffy parameters of the deterministic model are t_0 the age at zero length, L_∞ the predicted asymptotic mean maximum length, and K the growth coefficient or rate at which average length-at-age approaches L_∞. The four Troynikov parameters in the stochastic model are similar, except that K is replaced by two parameters and is estimated with random error from one of three non-normal probability

distributions Weibull, Gamma, or Lognormal, depending on which best fit the data. The best fitting probability distribution was determined using the approximation to Kullback's mean information or information integral (Wilks 1962). Although not a hypothesis test, this helps to avoid invalid assumptions about parameter distribution and eliminates the worst models from a given set of models (Troynikov and Walker 1999). The parameter (L_∞) that in the Von Bertalanffy model represents the asymptotic *average* length achieved by a fish of infinite age is interpreted differently in the Troynikov model where L_{max} symbolises the estimated upper limit to length, in the population.

11.3.7 Mortality

Age estimates from a sub-sample of carp (n=931) were used to generate an age-length key (ALK) to estimate the age-structure of the total carp catch pooled for 1999–2000 (n=7357). Electrofishing samples were used to calculate mortality rates for the larger adults and fyke net catches were used to estimate juvenile mortality rates.

Two methods were used to estimate the instantaneous rates of total annual mortality (Z). In comparative simulations (Dunn *et al.* 2002; Jensen 1985) the Chapman and Robson estimator has proved to be the least biased and most precise. The maximum likelihood value (Chapman and Robson 1960) and the minimum sum of least squares value (Ricker 1975) were both calculated for electrofished males (n=496) and females (n=328) and for total electrofished catch including juveniles of indeterminate gender (n=862).

Mean juvenile mortality (Z) was estimated by calculating the negative slope of the change in log-transformed age-frequency data over ages 0–1 and 1–2 years for all fish this age sampled with fyke nets 1999–2001 (n=5524) (Ricker 1975).

Natural mortality (M) was also calculated from an empirical model (Pauly 1980; Rikhter and Efanov 1976) to allow the estimation of fishing mortality (F) from the relationship Z=F+M. Mean water temperature at the Murray River gauge at Barmah for 1978–2001 (Theiss Environmental Services) was used as our estimate of average habitat temperature for an empirical estimation of natural mortality (Pauly 1980).

11.3.8 Reproductive Biology

All fish samples were dissected in the laboratory. The sex (male or female) of each fish was determined where possible. Where sex could not be determined due to immaturity the fish was classed as indeterminate. The macroscopic reproductive stage of each fish was assessed according to an appropriate set of stage descriptions adapted from published literature (Appendix 3 and 4).

The gonads were then removed, weighed and preserved in 10% neutral buffered formalin. For each fish the gutted weight was recorded and the gonadosomatic index (GSI) was calculated on both whole and gutted weight. The overall patterns of gonadal development shown by both whole-weight GSI and gutted-weight GSI were similar. To assist comparison with other studies, subsequent analysis for this report will use GSI calculated from whole body weight, as this is the more widely used method in the literature (Cailliet *et al.* 1986).

Gonads were fixed in the formalin for 4–10 weeks. Once fixed, a transverse medial sub-sample of about 30g of the gonad was then dissected and preserved in Davidson's solution (Knuckey and Sivakumaran 2001). These sub-samples were sent to a commercial pathology service for sectioning and then returned for subsequent histological examination. The

transverse medial material was blocked in paraffin wax and thin sections (6 μm) were cut, mounted and stained in Harris' haematoxylin and eosin (Lunar 1968). This enabled an understanding of the processes occurring at the cellular level during the reproductive cycle by examination of oocytes and spermatocytes in histological sections of ovaries and testes to determine the stages of meiosis.
Description of histological sections (Appendix 3) has allowed the verification of our macroscopic estimates of reproductive stage, and thus enabled accurate estimates of fecundity at size and age.

11.3.8.1 Fecundity

Annual fecundity is considered determinate in species where the stock of oocytes that are destined to be spawned in a season is identifiable at the beginning of the spawning season, even though the fishes may spawn repeatedly during the season (Hunter and Macewicz 1985a; Hunter and Macewicz 1985b; Knuckey and Sivakumaran 2001; Yamamoto 1956). The annual fecundity of common carp was estimated from the standing stock of yolked oocytes (Stage IV) from samples collected during 1998 spawning season using gravimetric method (Hunter and Macewicz 1985b). To ensure that the correct weighting factors were used for determination of annual fecundity, the gonads of 13 fish were carefully dissected. From the left gonad of each fish, 10 random samples of tissue weighing 0.1 g each were taken to provide a 1 g composite sample of eggs from each fish. These were stored for 1–2 months in Davidson's fluid and then Gilson fluid to separate the oocytes in the tissue. This sample was used for fecundity estimation and to determine the size distribution of oocytes. The average relative fecundity was measured as the number of oocytes per kilogram (whole fish weight). NB: Whole fish weight is used, as this then becomes a simple predictor of egg production.

11.3.8.2 Size and Age at Maturity

Female carp were categorised as mature if they were macroscopically staged as resting (F1B), redeveloping (F2B), mature (F3), running ripe (F4), partially spent (F5), or fully spent (F6). Females staged thus, had all undergone at least one previous spawning. Males of the same macroscopic gonad developmental stages (M1B, M2B and M3 to M6) were regarded as mature to enable useful comparisons of size- and age-at-maturity for both sexes. Size at maturity was estimated by counting the number of mature and immature fish in each 10 mm length-class for each sex separately. A logistic curve was fitted to the data using a non-linear least-squares procedure weighted by the sample size for each length-class. In a logistic regression the probability of an animal being mature at length l is determined from a random dichotomous variable taking the value 1 with a probability of p for the mature condition and the value of 0 with a probability of $1–p$ for the immature condition. The form of the logistic equation used is shown in Equation 6, where a is the 10 mm length-class, b is the length (LCF, mm) at 50% maturity (Lm_{50}), and c is the length (LCF, mm) at 95% maturity (Lm_{95}). Weight at maturity was estimated from the proportion of mature fish in each 100 g weight-class. Using these weight data in Equation 6; a is the 100–g weight-class, b is the weight (g) at 50% maturity (Wm_{50}), c is the weight (g) at 95% maturity (Wm_{95}). As we had age estimates for most fish sampled, age at maturity was also estimated by fitting a logistic curve to the

proportion of fish mature in each age-class. Using the age-data in Equation 6; *a* is the age-class in years, *b* is the age at 50% maturity (Am_{50}), *c* is the age at 95% maturity (Am_{95}).

Equation 6

$$\rho_{mature} = \left(1 + e^{Ln(19)\left(\frac{a-b}{b-c}\right)}\right)^{-1}$$

11.3.8.3 Sex Ratio

The overall sex ratio for mature carp was calculated from carp larger than the Lm_{50} and was tested with a chi-squared test against the null hypothesis that the mature sex ratio was 1. Sex ratio (% female) was also calculated for each year-class where gender could be determined and each gender was present (0–16 years, n=692) and the slope of a linear regression of sex ratio on age was determined.

11.4 Results

11.4.1 Hydrology and Spatial and Temporal Distribution

Standardised indices of relative abundance (CPUE) for the Murray River (carp ha^{-1}) and for the Barmah forest wetlands (carp per fleet of fyke nets) (Figure 39) were plotted for comparison with time series of temperature and water-level data (Figure 40)

During the 1999 and 2000 there were two periods of high abundance for carp in the river channel site. In 1999, CPUE was initially low at <50 carp.ha–1 during January–July, but increased to >200 carp.ha–1 during September–November. The increase in CPUE was coincident with the onset of rising water temperature at Barmah and a minor elevation in water level of the wetlands (Figure 40).

During 2000, carp CPUE in the Murray River increased in April and June. In April, water temperatures were falling and significant flooding had yet to commence. In July and August, the opening of water-regulators significantly raised water levels throughout the Barmah–Millewa Forest. This flooding continued until January 2001 (Figure 40) and was sustained through the use of the Barmah–Millewa Forest environmental water allocation (EWA). Carp abundance in the Murray River site dropped to <50 carp.ha–1 at the onset of the wetland flooding and did not increase until December and February when the wetland water levels again declined.

For the same two-year period, only a single peak in juvenile carp abundance was observed (Figure 39). During all of 1999, low CPUE of <400 carp per fleet of fyke nets was observed with no apparent pattern related to seasonal fluctuations in temperature and no increase in juvenile abundance was observed associated with the minor wetland flooding of 1999. However, the following year (2000) wetland flooding started in July and August when flow-regulating structures were opened. This flooding peaked in November 2000 in the Barmah Forest wetlands (Anonymous 2001). Juvenile carp abundance increased, in a pulse lasting for two months, to over 4500 carp per fleet of fyke nets coincident with the descending limb of the hydrograph.

In January 2001, at the end of the prolonged flood peak the area remaining flooded in the Millewa Forest was 3,431 ha or 9% of the forest area as measured from aerial photography surveys (Anonymous 2001). Forest water-regulators controlling water and fish access from this flooded area to the Murray were all closed by the end of January 2001 (Anonymous 2001). Hence, by April 2001, Moira Lake (~400 ha) represented the largest wetland in the Millewa Forest.

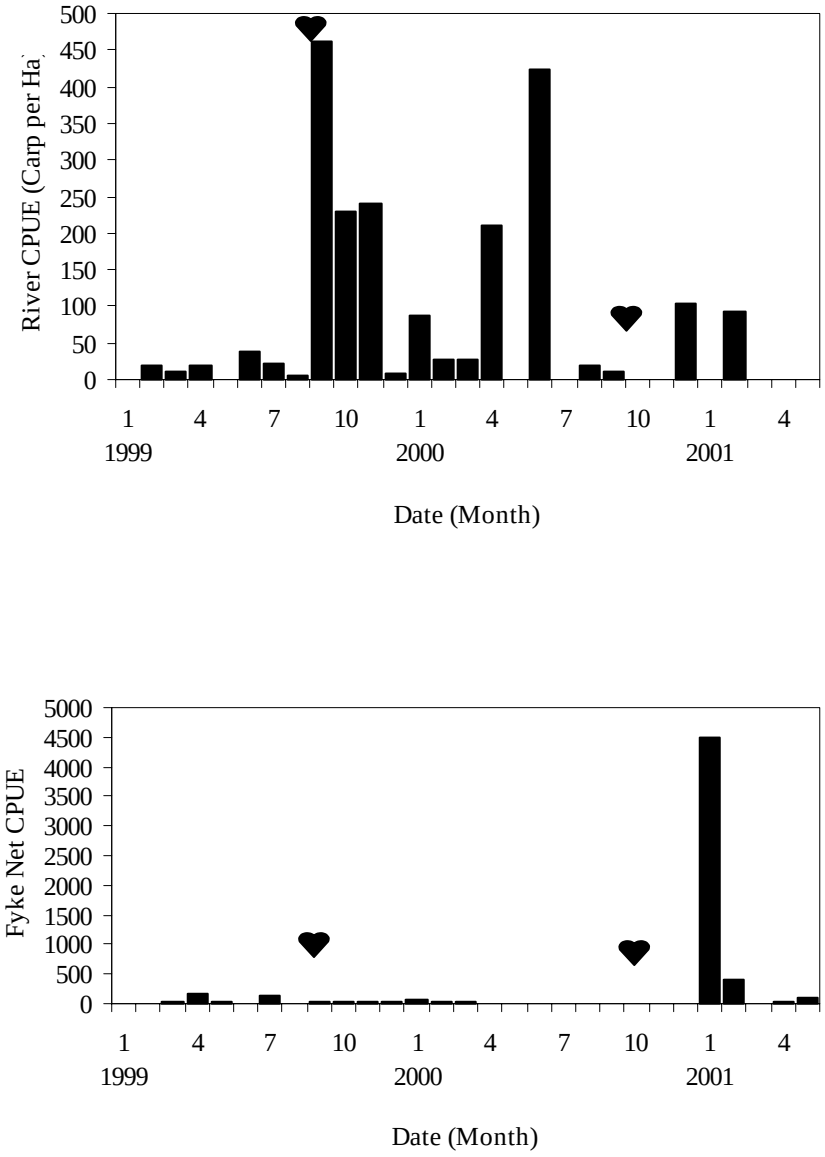

Figure 39. A standardised indices of abundance for carp in the River Murray at Barmah January 1999–February 2001 (upper) (carp ha^{-1}), and for carp in the Barmah Forest wetlands (Barmah Lake and Hut Lake) January 1999–May 2001 (lower panel) (carp per 20 fyke nets). Arrowhead indicates timing of initial drop in carp GSI each year suggesting the main spawning period.

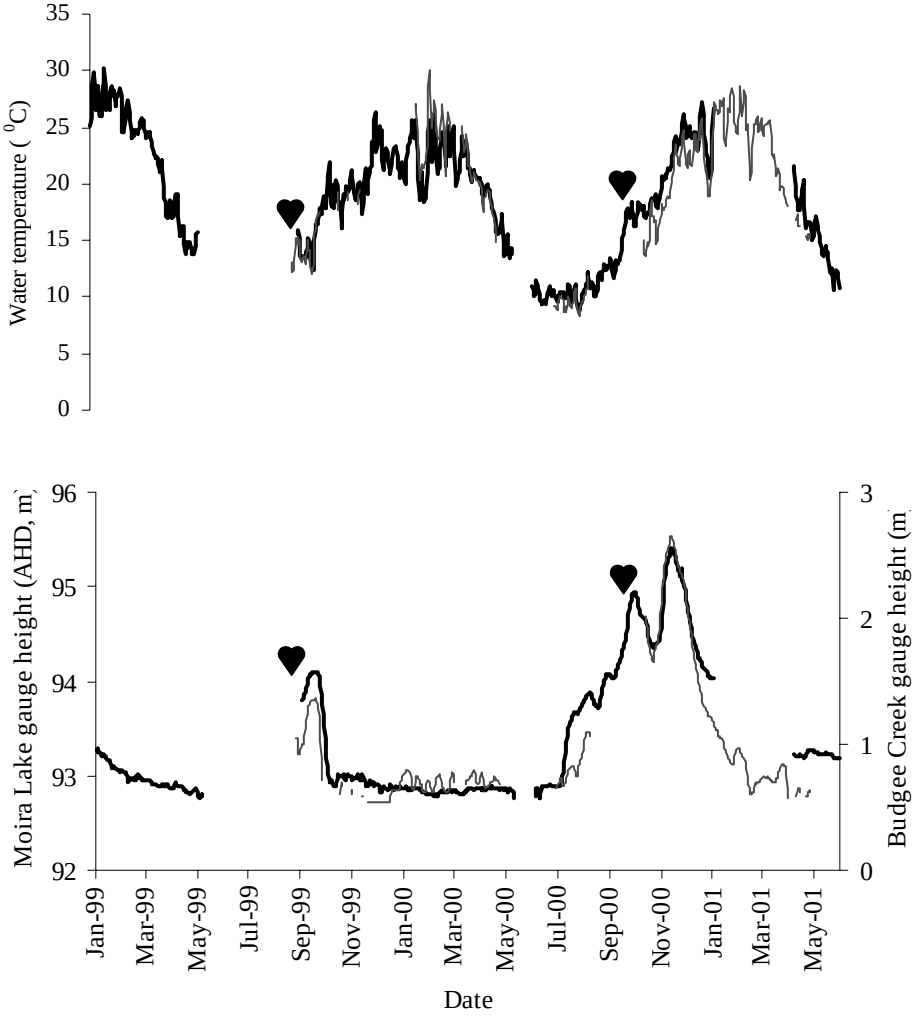

Figure 40. Time series of water temperature (upper panel) and surface level (lower panel) measured at two wetland gauging-stations. Budgee Creek at War Plain, #409398A (thin line), and Moira Lake outlet, #409232A (thick line). Arrowheads indicates timing of initial drop in carp GSI each year suggesting the main spawning period.

11.4.2 Year-Class Strength

Age was determined for each animal in large samples of carp collected by all methods during 1999 (n=767) and 2000 (n=361) and in a smaller sample collected at the beginning of 2001 (n=65). Comparison of adult year-class strength indicated that the overall population age-structure was similar in both years and had a bimodal distribution (Figure 42). Abundant juveniles of 0–1 year old were separated from the abundant adult age-classes (>7 years old) by a series of poorly represented age-classes (2–6 year olds). Juveniles (0 and 1 year olds) were abundant in 2000 but proportionally fewer young animals were sampled for age analysis and they were therefore under-represented in the data.

There is no clear pattern of progression of any strong year-classes, but rather a repeated pattern of weak and strong age-classes in each of the years 1999 and 2000 for which we have a large sample (Figure 42). The most abundant adult age-class (7 years old) in 1999 and

2000 corresponds to year-classes 1992 and 1993 — years that can be ranked as the largest and fourth largest total annual flows at Tocumwal in the present carp population-lifespan (28 years). The least abundant recent age-classes were 2-year olds in 1999 and 3-year-olds in 2000 and correspond with the 1997 year-class which was only the 18th largest total annual flow during the present carp population-lifespan.

Figure 41 Using a purpose-built trap constructed on Moira Creek, Keith Bell (K&C Fisheries)(inset) successfully harvested 76 tonnes of carp from the receding waters in Moira Lake in 2001, with no significant by-catch of native fish

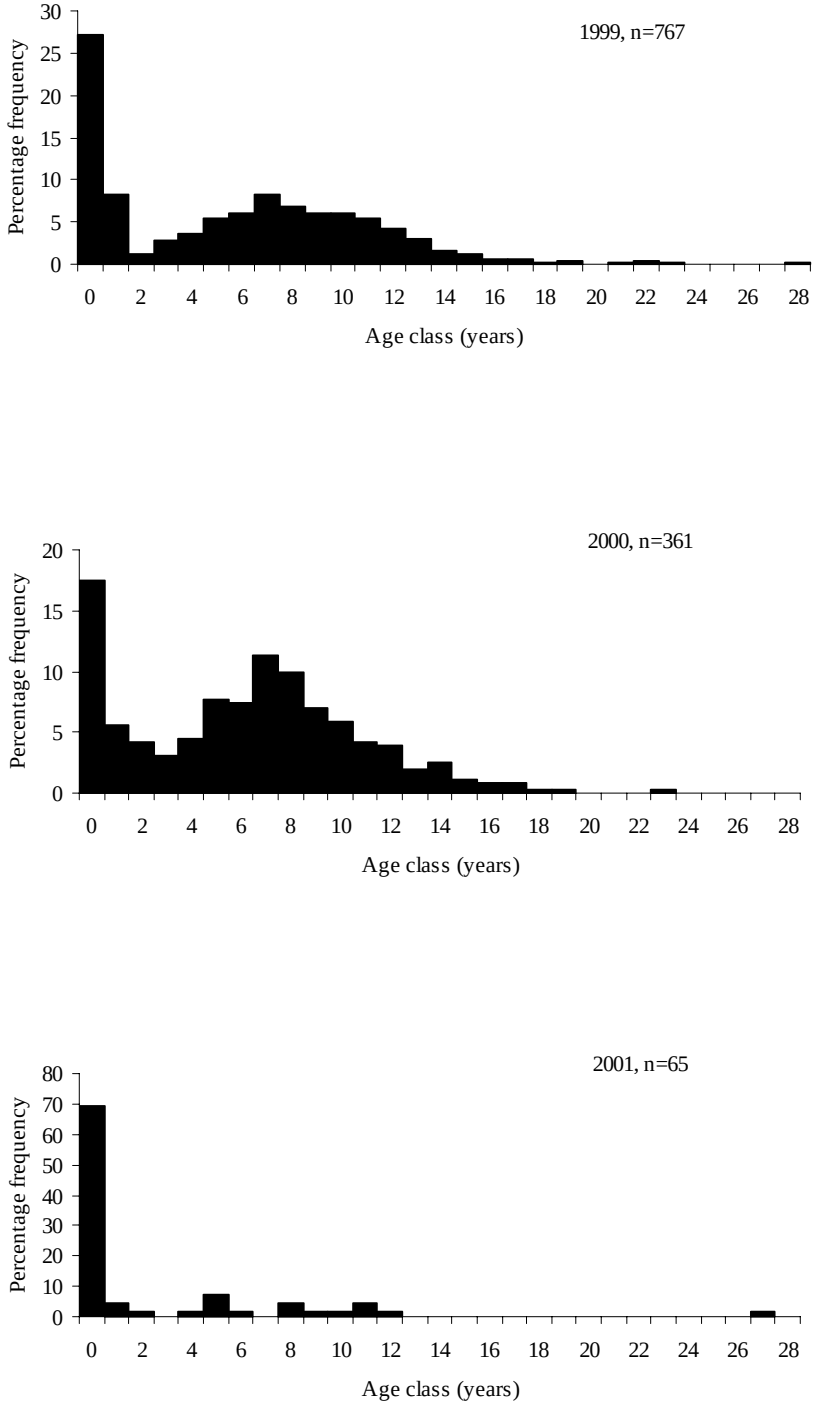

Figure 42. Percentage age frequency distributions for carp sampled for age determination from the mid-Murray River and adjacent Barmah Forest wetlands 1999 (upper) and 2000 (middle) and 2001 (lower)

11.4.3 Age and Growth

The largest male carp weighed 3200 g and measured 570 mm LCF and the largest female carp weighed 4060 g and measured 623 mm LCF. The oldest male and female carp were 23 and 28 years, respectively.
Growth in mean length-at-age was described by the von Bertalanffy growth model and parameter estimates for $L\infty$, K and t_0 are presented for groups of males plus juveniles, and females plus juveniles (Table 19). Likelihood ratio tests (LR) indicated that there was a significant difference in mean length-at-age, between these gender-groups (χ^2=1433, *p<0.001*).

Table 19. Parameter estimates for mean growth in length-at-age (Von Bertalanffy 1938) for carp from the mid-Murray River and adjacent Barmah Forest wetlands by sex. Estimates were obtained by non-linear least squares regression. Standard deviations are shown in parenthesis. n, sample size; SS, sum of squares; ***=P<0.001.

Group	n	L∞ (mm)	K (year^{-1})	t_0 (mm)	Error SS	Significance
All	1010	515 (0.070)	0.236 (0.074)	–0.542 (0.070)	37272424	
Males (plus juveniles)	724	489 (0.008)	0.249 (0.087)	–0.519 (0.079)	8720759	*** M vs F
Females (plus juveniles)	536	594 (0.163)	0.177 (0.084)	–0.609 (0.163)	2536722	

Kullback's mean information indicated that heterogeneity in length-at-age was best described by fitting a lognormal error distribution to the values of the growth coefficient K (Troynikov 1998). Confidence intervals, encompassing 90% of the variability of length-at-age, and the median length-at-age are shown (Figure 44) for each gender-group.
On average females grow faster than males; however, heterogeneity in length-at-age was high for both male and female carp in the Barmah Forest area. This variability increased to a maximum between 5 and 10 years of age then declined. For example most carp 250 mm LCF were less than 5 years old, whereas individuals ~500 mm LCF commonly ranged 5–20 years (females) or 7–25+ years of age (males).

11.4.4 Mortality

11.4.4.1 Total adult mortality

Carp age-frequencies were estimated using an ALK for total electrofished catch by sex. Each age-frequency distribution was used to calculate estimates of total mortality rate (Z) (Table 20).

Inspection of the total age-frequency distributions derived from the ALK (Figure 42) suggested that carp were not fully recruited to the Barmah Forest area until at least 7 years of age. Modal age-class in male age-frequency was 7 years and 9 years in females, respectively. Estimates of Z are provided for ages-at-full-recruitment (Tc) aged 7– 10 years (Table 20). Estimates of Z from both methods were higher for females than for males. In each case, the Chapman and Robson method produced lower estimates than the least-squares method.

Figure 43. When the Barmah–Millewa Forest floods it creates ideal carp habitat in the warm, shallow and productive wetlands

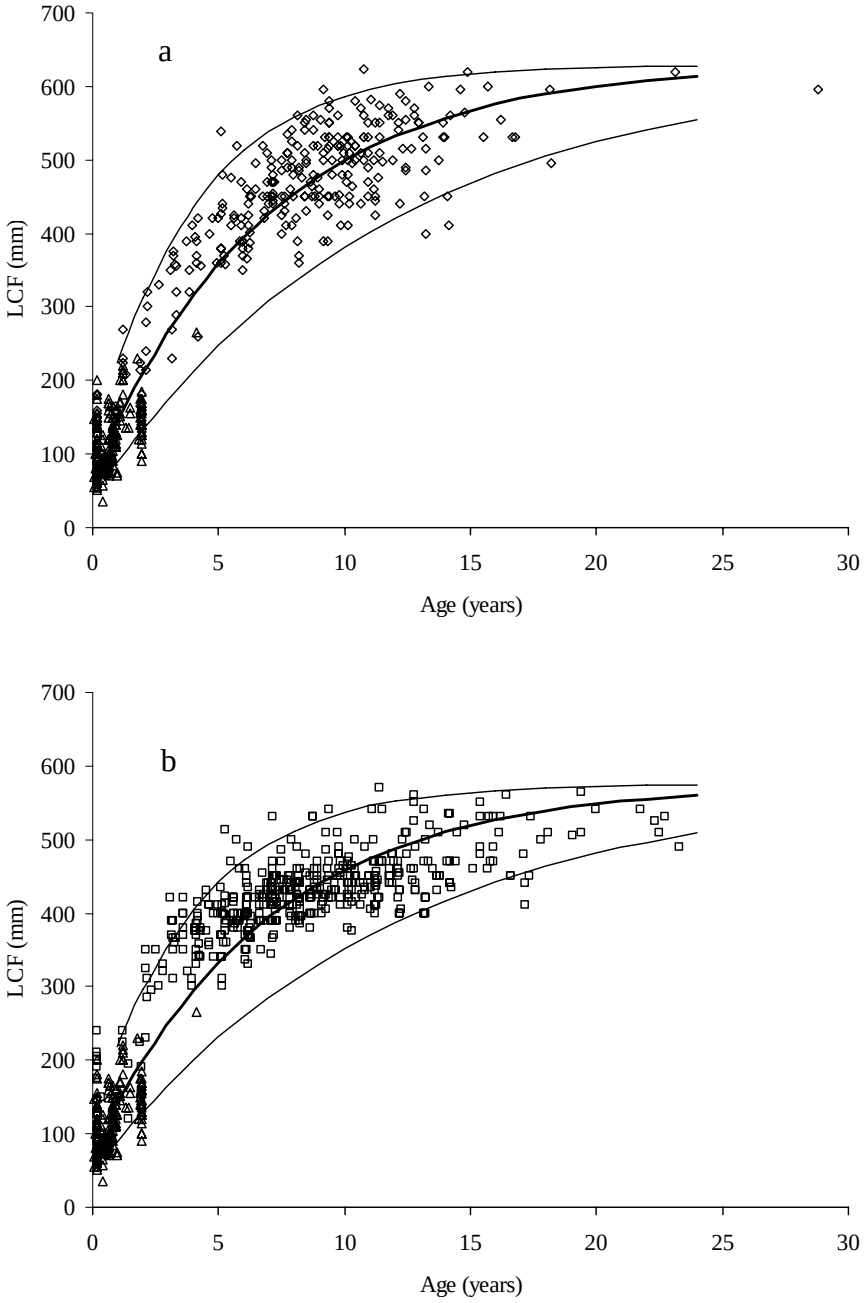

Figure 44. Length-at-age for carp sampled from the mid-Murray River and adjacent Barmah Forest wetlands. Heterogeneity of length-at-age described by the stochastic growth model (Troynikov 1998) with lognormal error distribution for the two groups (a) males (♦) and juveniles (▲) (n=724) and (b) females (■) and juveniles (▲) (n=536). Curves are (from top to bottom) 95%, 50% and 5% quantiles. Thus for each group the outer lines encompass 90% of the heterogeneity in length-at-age and the centre line is median length-at-age. Mean length-at-age is significantly different between groups (P<0.001).

Table 20. Results of mortality estimation (Z) using Chapman-Robson (CR) maximum likelihood method (Chapman and Robson 1960) and least-squares regression catch curve analysis (CC) for carp sampled by electrofishing 1999–2001 for a range of age-at-full-recruitment (Tc). Age frequencies were derived from age-length keys (ALK). Measure of uncertainty for Z is given as variance for CR method and R^2 for CC method; n=sample size

Estimation Method	Age at full recruitment (Tc)	All			Males			Females		
		Z	Variance or R^2	n	Z	Variance or R^2	n	Z	Variance or R^2	n
CR	7	0.285	0.0001	570	0.268	0.0002	336	0.311	0.0004	232
CR	8	0.303	0.0002	451	0.269	0.0003	258	0.359	0.0007	192
CR	9	0.329	0.0003	357	0.276	0.0004	201	0.426	0.0012	154
CR	10	0.370	0.0005	283	0.312	0.0006	170	0.495	0.0022	113
CC	7	0.296	0.968	570	0.316	0.871	336	0.342	0.781	232
CC	8	0.326	0.938	451	0.327	0.850	258	0.374	0.785	192
CC	9	0.350	0.945	357	0.348	0.836	201	0.406	0.785	154
CC	10	0.384	0.963	283	0.407	0.892	170	0.422	0.734	113

11.4.4.2 Total juvenile mortality

During the period 1999–2001, the average total instantaneous mortality rate (Z) was 3.24 for juveniles aged 0 year and 1.80 for 1 year olds.

11.4.4.3 Natural Mortality, Fishing Mortality and Exploitation Rate

Using the average water temperature in the Murray River at Barmah (17.08^{o}C) and the growth model coefficients L_{∞} and K in Pauly's empirical model (1980) we estimated the instantaneous natural mortality rate (M) at 0.199 for females, 0.262 for males and 0.250 for all combined.
From Chapman and Robson estimates of total mortality in and the relationship Z=F+M we can calculate that fishing mortality (F) would be negligible for males (<0.05) but noteworthy for females (0.11–0.30).
Exploitation rate (E), expresses F as a proportion of Z. For females E was 36–60% and only 2–16% for males.

11.4.5 Biomass Estimate

In April and May 2001, at the outlet regulator of Moira Lake, a commercial fishing operation was implemented by K.& C. Fisheries Ltd, to harvest carp remaining in the receding waters of Moira Lake. On a trial-and-error basis using a combination of trapping methods on the outfall, the operators harvested 75 tonnes of carp as the lake was drained and expressed the view that this represented the total stock remaining in Moira Lake at that time (Keith Bell, K&C Fisheries, *pers.com.*). By-catch comprised 48 kg of goldfish (*Carassius auratus*) and <10 redfin perch (*Perca fluviatilis*). No large native fish species were trapped.
Under the assumption that at least these 75 tonnes of carp were present in the flooded Millewa Forest in January (3,431 ha) we can estimate an approximate average biomass estimate of ~22kg ha^{-1} for the Millewa Forest wetlands, although once confined to Moira Lake the carp density increases to ~190 kg ha^{-1}.

11.4.6 Reproductive Biology

11.4.6.1 Seasonal distribution of maturity stages from macroscopic and microscopic studies

From macroscopic examination of gonads *in situ*, observed running-ripe or spent stages for males and females indicated imminent or recent spawning activity, which were predominant during February 1999, September 1999–April 2000 and October 2000–April 2001
Spent females (Stage V and VI) predominated during February 1999 with some also present during June–July 1999. They again predominated during September 1999–March 2000 and in the following season during October 2000–April 2001. It is evident that the majority of the females sampled during August–September 2000 were in the running ripe stage (Stage IV) (Figure 45).
Curiously, no running ripe males were collected, although partially spent males were collected during March 1999, September 1999–May 2000, November 2000–March 2001, and fully spent males were collected during February–March 1999, September 1999–May 2000, and October 2000–February 2001.
Monthly histological examination of gonad samples revealed what types of oocytes were present at each macroscopic stage of gonads. Details of the appearance of

ovaries and of the corresponding stage of the oocytes in histological sections are presented in Appendix 3. For the present study, histological sections from 662 gonads were analysed (330 testis and 332 ovaries.)

During February–April 1999 yolked and unyolked oocytes dominated the samples. Atretic or postovulatory oocyte types were only in the majority during September 2000–April 2001 and again during October 2000–February 2001 (Figure 46). Examination of histological sections indicated 97 ovaries staged macroscopically as spent actually contained yolked (18%), unyolked (22%), nuclear migrated oocytes (1%), oocytes in atresia (40%) and postovulatory follicles (20%). Of 19 animals with postovulatory follicles, 4 animals had new postovulatory follicles and 15 animals had both new and old postovulatory follicles. The animals with new postovulatory follicles were sampled during December 1999 and October 2000 whereas the animals with old postovulatory follicles were sampled during April 1999, September–January 1999, and October–December 2000. Yolked oocytes were present throughout the year except during October 1999, March 2000 and February 2001. In the present histological study, we observed no ovaries with any newly hydrated oocytes. However seven animals macroscopically staged as partially spent, spent and resting stage actually had hydrated oocytes in atresia stage upon histological examination. All these samples were collected in from Barmah Lake in December 2000 along with samples containing old postovulatory follicles.

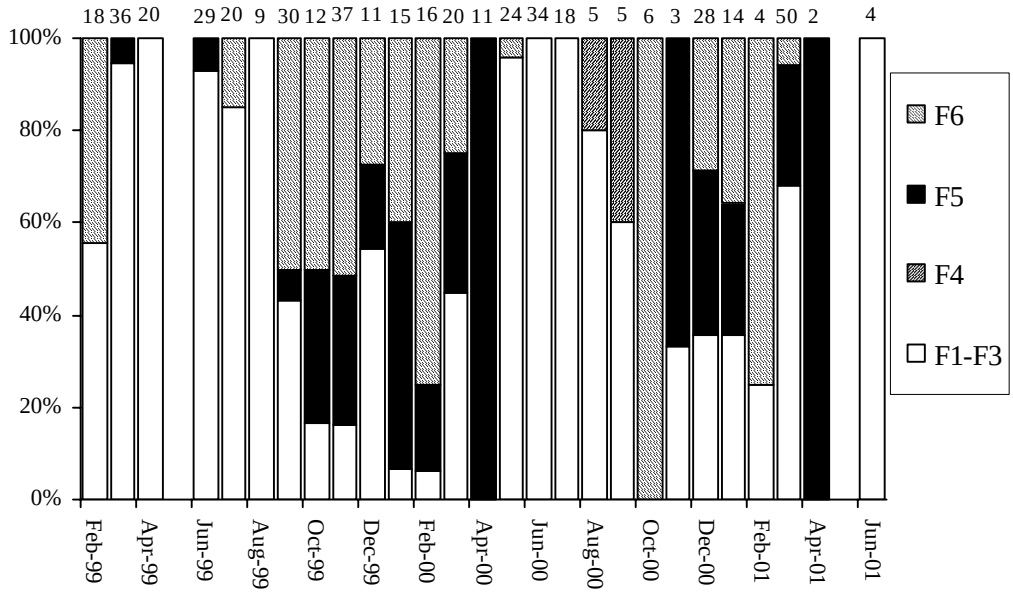

Figure 45. Percentage of female carp in each monthly sample from the mid-Murray River and Barmah Forest wetlands with gonads that were immature to mature (F1–3), running ripe (F4), partially spent (F5 or spent (F6). Sample size *n* is shown above monthly bars.

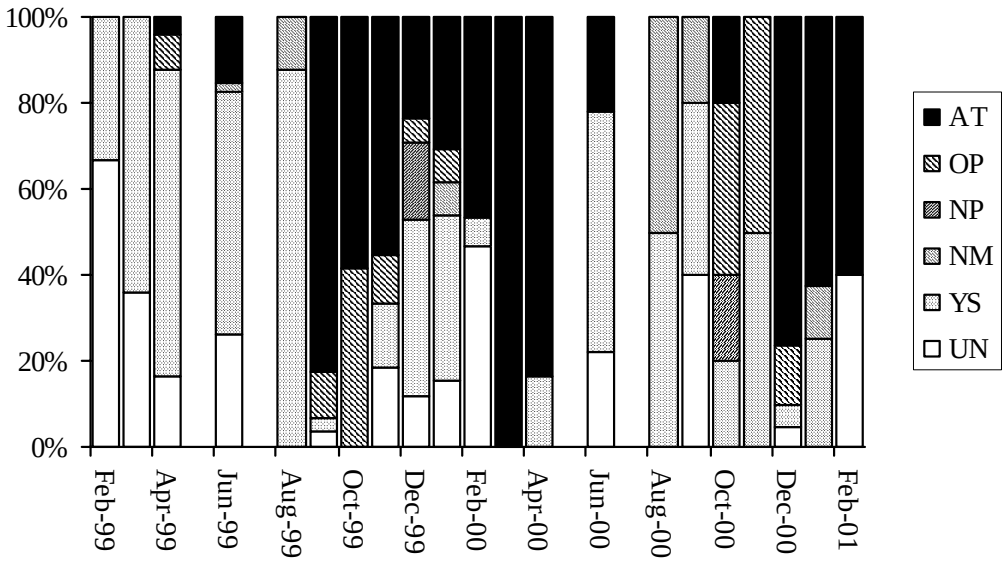

Figure 46. Monthly histological changes observed in ovarian maturity. (AT– atresia; OP– old postovulatory follicles; NP– new postovulatory follicles; HY– hydrated; NM– nucleus migration stage; YS– yolked stage; UN– unyolked stage includes chromatin nucleolar stage, perinucleolar stage and cortical alveoli stage). Analyses performed on data collected from mid-Murray River and Barmah Forest Wetlands

11.4.6.2 Size and Age at Maturity

All females < 280 mm or males <230 mm LCF were immature. Fitting the logistic equation for the female maturity ogive gave an estimate of Lm_{50} = 328 mm and Lm_{95}=392 mm (Table 21 and Figure 47). Males mature slightly smaller and the estimate of Lm_{50} = 307 mm and Lm_{95} = 379 mm (Table 21 and Figure 48).
All males and females of weight <400 g were immature. Fitting the female maturity ogive to the weight data gave an estimate of Wm_{50} of 688 g with 95% mature at 1032 g. Again the male weight data gave lower estimates of Wm_{50} = 584 g and Wm_{95} =932 g (Table 21).
The youngest mature male and female were in their first year (0+ year old) although this was rare. The logistic maturity ogive fitted to the proportion of females mature-at-age gave an estimate of Am_{50} = 2.7 years with Am_{95}= 4.7 years of age. The corresponding estimate of Am_{50} for males was 1.1 years with relatively rapid maturation so that 95% were mature at 1.2 years of age (Table 21).

Table 21. Estimates of size and age at maturity for male and female carp from the mid-Murray River and Barmah Forest Wetlands. Data were arranged in 10–mm length-classes, 100–g weight-classes or whole year-classes as appropriate.

Sex	Estimate	Length (mm)	Weight (g)	Age (y)
Female	Initial maturity	280	400	0+
	50% maturity	328	688	2.7
	95% maturity	392	1032	4.7
Male	Initial maturity	230	400	0+
	50% maturity	307	584	1.1
	95% maturity	379	932	1.2

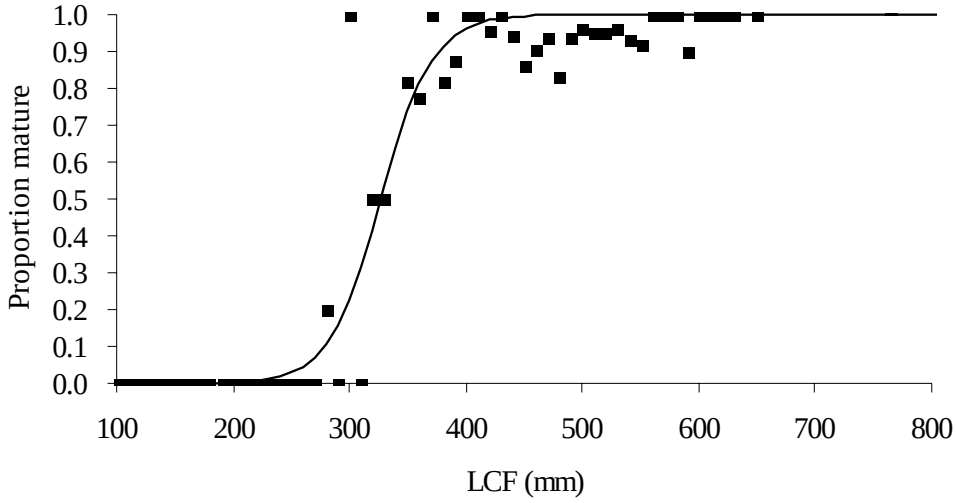

Figure **47**. Maturity ogive for female carp from the mid-Murray River and Barmah Forest wetlands plotted against length (LCF, mm). Data points represent the proportion mature in 10 mm length-classes. Analysis was for data pooled from all sites sampled during 1999–2001. Female Lm_{50}=328 mm LCF, Lm_{95}=392 mm LCF

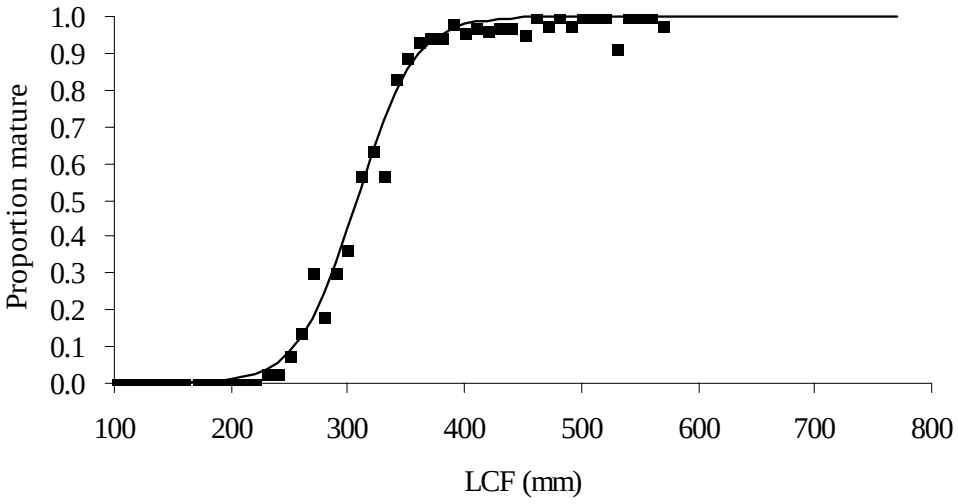

Figure **48**. Maturity ogive for male carp from the mid-Murray River and Barmah Forest wetlands plotted against length (LCF, mm). Data points represent the proportion mature in 10 mm length-classes. Analysis was for data pooled from all sites sampled during 1999–2001. Male Lm_{50}=307 mm LCF, Lm_{95}=379 mm LCF

11.4.6.3 Seasonal fluctuations in GSI

The pattern of seasonal gonad development was consistent between males and females although the pattern for 1999 differs somewhat from that in 2000 (Figure 49). Ovarian development peaked a month earlier and was lower in 1999. After an August 1999 peak, GSI dropped sharply in September suggesting that this marked the main spawning period. Redevelopment was slow, there was little development until April 2000 when ovaries were briefly ~75% of their previous peak. Gonadosomatic index rose again to peak in September 2000. The sharp drop in October marks the main spawning period for 2000. Redevelopment started slightly earlier, in March, and was much more rapid at the end of the study than had been observed in 1999. The timing of testicular development mirrored that of the ovaries although the amplitude of changes in GSI is less than for females.

Sharp drops in GSI were coincident with rising water temperature in the Murray River at Barmah that ranged 10^0–16.8^0C and 12.5^0–17.1^0C in 1999 and 2000, respectively, while rising water temperatures of adjacent wetlands ranged 12.0^0–17.8^0C and 12.4^0–18.4^0C over the same periods.

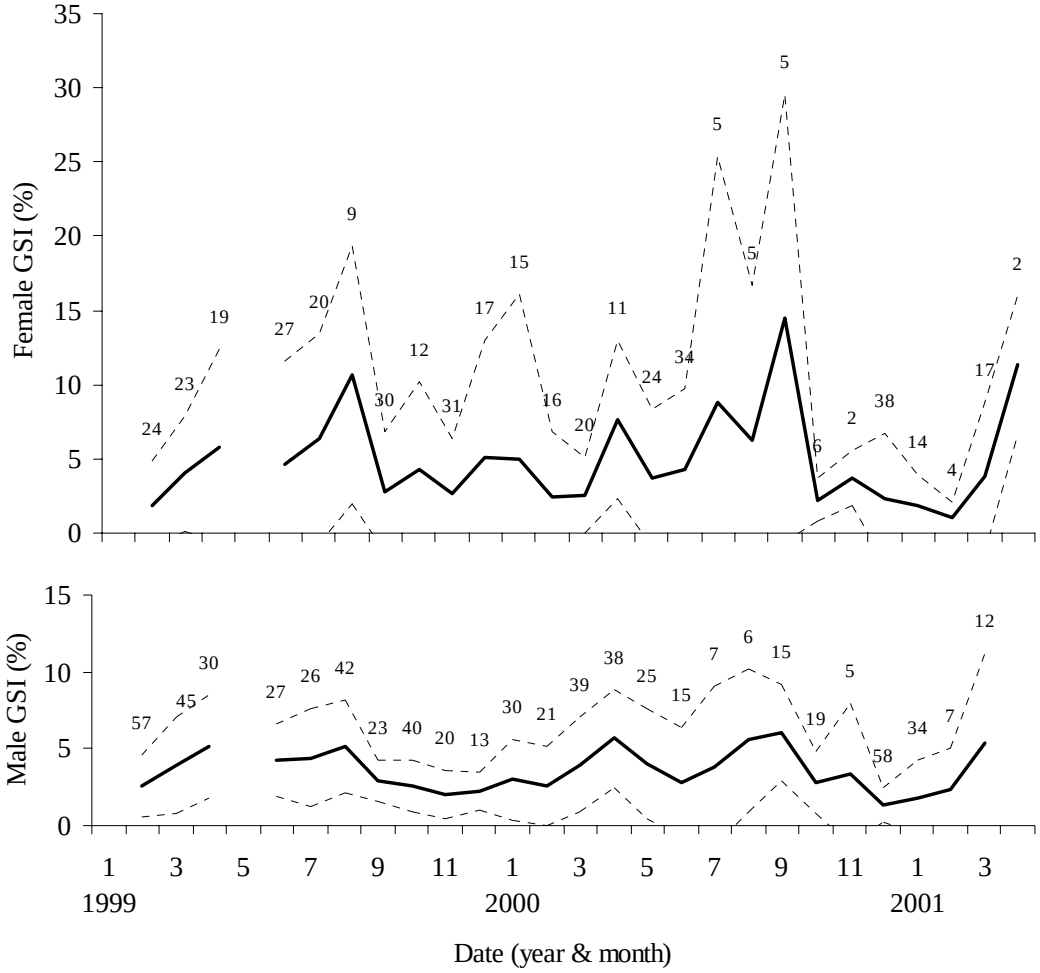

Figure 49. Changes in mean monthly gonadosomatic index (GSI, solid line) during January 1999–March 2001 in female (upper) and male (lower) carp > initial length at maturity caught in the Mid-Murray and Barmah forest wetlands. Approximate 95% confidence limits on the mean (±2 standard deviations) are shown (dotted lines) truncated at zero. Sample sizes are shown as numbers above data-points.

11.4.6.4 Sex ratio

The sex-ratio of mature carp (ie. $\geq Lm_{50}$) was 39% females (n=1127). This is a significantly male biased sex ratio (p<0.001) if the overall sample is considered. However examination of the linear relationship between age and sex ratio shows a significant decline in the proportion of females at age (F=5.7, p=0.03) from >50% females for ages < 2 years, to ≤ 40% females at ages of 12 years and older. With the 95% confidence intervals on the intercept (age=0) including the value for 50% females. Therefore the sex ratio of carp aged 0 years was not significantly different to 1:1.

11.4.6.5 Fecundity estimates

The fecundity was estimated from three running ripe female carp sampled in August and September 2000. These samples were selected as GSI values exceeded 14 %. Two carp with ovaries macroscopically staged as running ripe were collected from Barmah Lake and histological examination was not carried out for these samples. A third female carp, collected from Murray River, had ovaries macroscopically staged as running ripe. Histological examination indicated no postovulatory follicles or evidence of atresia and oocytes at the nuclear migration stage. Fish sizes were 450, 510 and 600 mm LCF and were 8, 10, and 15 years old, respectively. The individual annual fecundity estimates were 0.31, 0.33 and 0.34 million eggs respectively. This represent average egg production of 0.327 million. Considering the whole fish weight, the relative fecundity estimates were 0.08, 0.12 and 0.14 million eggs kg^{-1}. The average relative fecundity was 0.113 million eggs kg^{-1} of whole fish weight.

11.5 Discussion

Two hypotheses can be generated to explain the CPUE observations of for the 2-year period 1999–2000. The first is that aggregations of carp develop during the winter–spring in the Murray River close to access-points for the Barmah–Millewa forest wetlands. Low water levels and small-scale inundation of wetlands, as occurred in 1999, restricts the aggregation to the river channel; whereas during raised water levels and sustained wetland flooding the carp aggregation disperses onto the floodplain. This supports the assertion that radio-tagged carp shift habitat use into the wetlands when the floodplain was inundated and conversely were found in the main channel when the floodplain was dry (Stuart and Jones 2002). Other authors have observed comparable lateral movements of adult carp to and from wetlands. Sometimes such movements were associated with spawning activity (Kanitskiy 1983; Swee and McCrimmon 1966) but not always (Lubinski *et al.* 1986; Reynolds 1983).
The second hypothesis concerns recruitment. Juvenile-CPUE observed in the wetlands suggests that significant recruitment only occurs following years where wetland access was available due to raised water levels. During spring of 2000 very large numbers of juveniles (~25–30 mm, LCF) were captured in drift-nets in the Murray River downstream of the wetlands in the main channel although unfortunately similar observations were not made in 1999 (Stuart and Jones 2002). Many authors in Australia (Geddes and Puckridge 1988; Humphries *et al.* 1999; Walker and Thoms 1993) have discussed positive correlations between flooding and recruitment for endemic fish stocks. Some have suggested that exotic species such as carp benefit equally from floodplain innundation (Gehrke *et al.* 1999). However, the observed correspondence in the present study between weak and strong carp year-classes and the year ranked by total annual flow, is further evidence that flooding also enhances recruitment of feral carp stocks in the Murray River. It is likely, therefore, that hydrological data or climatic indices influencing such hydrology, such as the southern oscillation index (B.O.M. 2002), may prove useful in qualitative predictions of carp recruitment success. Ironically, the decline in Australian native fish stocks, together with the attribution of this decline to flow-regulation and development of water-storage capacity, and calls for its remediation through the use of environmental flow allocations has disturbing parallels with the decline in abundance of wild carp in Europe today (Balon 1974).
In 1993, an environmental water allocation (EWA) of 100 GL per year from NSW and Victoria, for watering the Barmah–Millewa Forest, was agreed to by the Murray–Darling Basin Ministerial Council. In 2001, this allocation was increased to 150 GL per year, in an anticipated 80% of years. The EWA can effectively be carried over if not used in a given year, up to a maximum volume of 700GL. The EWA was first used in 1998, with 97 GL used to extend the duration of minor flooding. A second greater application of the EWA came during the present study from October 2000 to January 2001, when 340 GL was released to extend a larger flood event still further. This was the largest release of water ever made to the environment in Australia[8]. The rehabilitation of environmental flows to enhance river-health in south-eastern Australia needs careful examination in the light of this contribution showing that carp population success in the mid-Murray is positively correlated to flooding. Parallel development of effective carp control strategies is necessary to prevent significant

[8] MDBC 2002. The Living Murray – a discussion paper on restoring the health of the River Murray. Murray-Darling Basin Commission, Canberra. 54p.

amounts of restored aquatic productivity, due to EWA's, being *spent* on increased production of carp, a highly competitive invasive and unwanted species. The predicted enhancement of pest fish production resulting from environmental flow rehabilitation and ecosystem-interactions with native fish and bird communities may be a fruitful area of research and subject for further modelling.

Growth of carp in the mid-Murray at Barmah was slower, and both females and males reached smaller asymptotic-maximum sizes, than those reported in the lower Murray (Vilizzi and Walker 1999b) and from other similar studies in Victoria (Hume et al, 1983; and see Appendix 4). Although the increased age-range (0–28 years) observed in the present study indicates greater longevity in this slower growing population. Indeed this study extends the known longevity of carp in Australia from the previously observed maxima of 16 years (Vilizzi and Walker 1999b) and 17 years (Appendix 4). The species shows quite variable growth rates throughout its broad geographic range and the observed parameter values in the present study are comparable with those determined for Eurasia and China (Li *et al.* 1990; Nikolsky 1957; Yie 1988).

Vilizzi and Walker (1999b) suggested that growth models should provide "precision, generality and realism" although they concluded that no model could satisfy all three criteria due to inevitable trade-offs between each attribute. *Accuracy* must be another desirable attribute. Accuracy goes hand-in-hand with precision to provide useful input to any population modelling that relies on such a growth model. To secure accuracy one can do little more than start with a broadly representative collection of good age-determinations and length measurements. However, *precision* or uncertainty and heterogeneity in length-at-age and hence *realism* can be incorporated into the growth model output by using a stochastic approach with a range of non-normal probability distributions, such as those of Troynikov (1998). In this case Kullback's mean information was used to indicate that a lognormal probability distribution fitted the data best.

Due to the unusual age-structure of the sampled animals, total mortality can only be estimated for juveniles and for adults older than 7 years. The dearth of information on mortality rates of wild carp stocks allows few comparisons. The present estimates of Z for the mid-Murray River at Barmah are generally lower than those estimated for carp aged 2–17 in Victorian irrigation channels (Appendix 4) and notably lower than the suggested mortality schedule used by Davis *et al.* (1999b) in modelling potential pest control applications for carp. Estimates of juvenile total mortality rate for Barmah during 1999 and 2000 are towards the upper end of the range determined from published length-frequency data (Gehrke *et al* 1999 in Koehn *et al* 2000). Empirical estimates of natural mortality (M) for carp in Barmah are similar to those estimated for a wild carp stock in China (Yie 1988) although about half that calculated by Nees et al. (1957) for Lake Wingra in Wisconsin , USA.

For many Australian carp populations, the assumption that fishing mortality is minimal is reasonable and therefore estimates of total mortality from biological data should be equal to estimates of natural mortality from empirical data. Carp are seldom the target of recreational anglers in Australia but they are frequent in the by-catch of recreational anglers (Koehn et al. 2000) and once caught, it is illegal to return these carp to the water. Commercial fishers do not routinely target the Barmah area of the Murray River (Kailola et al. 1993), although since 1997, Moira Lake a major wetland within the adjacent Millewa forest, has been drained annually and the carp either perished or were harvested (see below).

In the present study, the natural mortality rate estimated for males resulted in a minimal component of total mortality (Z) allocated as fishing mortality (F). This is consistent with our discussion above, about the potential for fishing mortality from either the recreational or commercial fisheries. However, because of the sex differences in growth model parameters, females were estimated, by an empirical method (Pauly 1980), to have a lower M than males. When combined with higher estimates of Z for females, this results in a greater component of Z allocated to female fishing mortality. This sex difference in mortality rates and specifically the elevated F for females raises further interesting hypotheses. Pauly's (1980) empirical model could be a poor estimator of M for carp. However, his data set was extensive and included two cyprinid species within the 175 stocks of 84 species including several other freshwater genera.

Growth parameters or Z may have been estimated inaccurately; however, the relationship between growth and mortality adequately supports the assumption of low fishing mortality for males, just not for females. It is possible that through sex-differences in behaviour the average environmental temperature experienced by females is slightly higher than Murray River temperature. For instance, it is conceivable that by seeking out warmer water, females could periodically experience habitat temperature higher by several degrees than males. Simple simulations of this effect show, however, that reasonable fluctuations in environmental temperature alone cannot explain the sex-difference in M. Under the reasonable assumption that parameters have been estimated equally accurately for both males and females, then females may actually experience a lower M and hence a higher F than males. This effect could be due to females being larger at a given age and thus experiencing less predation from gape-limited predators such as birds and fish. Stranding may be a cause of size and sex-selective mortality in fish. According to Welcomme (2001), stranding is a major source of mortality in floodplain rivers either by direct losses, increasing vulnerability to fishing gear and other predators, or starvation. Quinn and Buck (2001), showed that large male salmon during their freshwater spawning migration were more likely to strand, and more likely to be selected by predators, than smaller females. Resource management activities associated with shallow flooding and de-watering of the forest to enhance timber production (MacKay and Eastburn 1990; Murphy 1990) and de-watering Moira Lake for wetland management may therefore be considered a major potential contributor to mortality.

In the present study, assignment of macroscopic gonad stages could be compared with the histological examination of the same gonad material. Such comparisons show that for carp, careful macroscopic staging is required to provide accurate insights into the timing of reproduction. Without examination of gonad histology, confusion of pre- and post-spawning stages is likely and the correct classification as partially spent or partially atretic is risky.

Combination of evidence from CPUE, GSI, gonad staging and histology suggests that the main spawning periods during the present study of the mid-Murray River carp stock at Barmah were in August–September 1999 and September–October 2000 as water temperatures increased from about 12 to 18^0C over a one month period. This concurs with the observations of yolk-sac larvae during September 2000 at a water temperature of 15 ºC (Stuart and Jones 2002). This is slightly earlier and cooler than observed during 1997, 300 km further North in the Murrumbidgee Irrigation District (Adamek 1998), although similar to the temperature thresholds observed by Swee and McCrimmon (1966) in Canada and Crivelli (1981) in France. Koehn et al. (2000)

also report several uncorroborated accounts, based on larval occurrence, of carp spawning in Victoria at temperatures lower than those observed in this study. During 1999, only a small flow increase occurred during the spawning period, whereas during 2000 major sustained flooding occurred prior to, during and after the spawning period. Although there is evidence to suggest carp spawned during 1999, without significant access to floodplain habitat, relatively few juveniles were produced and gonad redevelopment was delayed in the spawning stock. Flooding during 2000 gave carp prolonged access to floodplain habitats that lead to successful spawning and significant recruitment of juveniles. Kanitskiy (1983) suggested that a favourable reproductive environment for carp (*C. carpio haemopterus*) in the Barguzin River relied on a complex of factors including water temperatures 18–20 ^{0}C and rising water levels giving access to inundated terrestrial or aquatic vegetation. There is also good evidence that during 1999–2001 spawning activity occurred throughout the summer and into autumn and during early winter months. However, we are uncertain whether such spawnings late in the season are due to repeat-spawning individuals or a proportion of individuals delaying their single spawning. There is histological evidence to suggest that some Victorian carp stocks contain both females that spawn once and females that spawn repeatedly within a single spawning season (Appendix 3). Implications of this information for management include that populations with extended spawning seasons may be more difficult to control with methods relying on prediction of when spawning may occur (e.g. water draw-down, trapping or fishing the pre-spawning biomass etc.) Pest control efforts to remove late-season spawners that are repeat spawning may be relatively less important than those for delayed, single-spawners, as they will produce relatively few eggs.

For several reasons it seems that the BMF carp stock is, in a sense, a spawning aggregation. Although some precocious maturation was observed in both sexes, males generally mature 2–3 years earlier than females and a similar 2–3 year period also separated the modal age-classes between males and females.

Under different rates of maturation for the sexes, the observed male-biased sex ratio on the spawning grounds may also be expected. The abundance of the youngest, mature male age-classes will have been reduced less by natural mortality than the youngest mature female age-classes. The observed differential mortality rates among sexes may amplify this. Although the sex ratio is male biased in the spawning stock there is no evidence of any such bias in the sex ratio of younger fish. In carp populations where there are no differential mortality rates by gender and males and females mature at similar ages, an even sex-ratio remains throughout the age-structure of the population (Appendix 4).

Useful comparisons of size- or age-at-maturity are often confounded by the inconsistent way in which they are reported. Hume *et al* (1983) for example uses a four-stage description of gonad development to report initial maturity for males (125 mm) and females (150 mm) as somewhat smaller than the 230 and 280 mm respectively, in the present study. Other authors report the size or age range of mature fish. Carp in the BMF mature at a similar rate to that observed in southern France (Crivelli 1981) and the Dongjiang River, China (Yie 1988) although exact comparison is difficult. Size- and age-at-maturity was generally lower for females in nearby irrigation channels (Appendix 4) although males in the BMF matured in general at larger size they were slightly younger in comparison to irrigation channel males. Within a population, individual fish become mature at a range of different sizes and ages. A mathematical function, such as the logistic ogive, that best fits this variability provides useful input for any proposed stock assessment process (Knuckey and

Sivakumaran 2001). Function parameters provided a standard template for between stock comparisons (Weyl and Booth 1999) and should be used whenever possible. Although the sample size was small, fecundity was below average in comparison with other Victorian stocks (Appendix 3). Relatively low fecundities were also reported in the upper Mississippi (Lubinski *et al.* 1986) where carp from the main river channel were often termed 'racehorse carp' due to their lean physique and poor condition. Carp in the Murray River at Barmah also fit this description. Lubinski's (1986) explanation that this state was due to the high energy-levels required to maintain their position in high velocity habitats, may also apply to the mid-Murray River carp. This detailed description of the mid-Murray River carp stock has filled some of the knowledge gaps identified by several workers (Grewe 1997; Koehn *et al.* 2000; Thresher 1997) as necessary to more effectively combat pest populations of carp. As such it is hoped that this contribution will provide useful input into the National Management Strategy for carp control (Anonymous 2000a; Anonymous 2000b) and a basis for more realistic models of carp populations.

11.6 Acknowledgement

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12 Appendix 6 – CARPSIM: Stochastic simulation modelling of wild carp population dynamics, with applications to pest control

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12.1 Summary

Common carp (*Cyprinus carpio* L.) is an important pest fish species in Australasia and North America. Carp are widely implicated in freshwater aquatic resource degradation and both the resource management and broader communities are currently seeking effective control measures. We developed CARPSIM, a simple age-based model to simulate the effects of a range of management scenarios. The model simulates change in population biomass by age and sex-specific growth and simulates change in population abundance through recruitment and sex-specific mortality. Using empirical stock-recruitment data and stochastic components derived from local hydrological data or the southern oscillation index the model simulated the population dynamics of carp populations over 200 years using biological parameters previously estimated for two Victorian populations within the Murray–Darling basin. Carp management scenarios simulated included the effects of fishing the spawning stock; of fishing the whole stock; of spawning or recruitment sabotage; and of driving the population sex ratio towards male dominance. Model predictions suggests that faster growing, shorter-lived populations may be better controlled by molecular methods inducing male-dominance, or spawning sabotage type methods whereas slower growing, long-lived populations may respond best to removal type approaches. Unselective removal, such as poisoning or trapping all age-classes is more likely to cause pseudo-extinction at levels of instantaneous fishing mortality (F) >0.7; while size-selective removal at similar F levels may only be useful to reduce the biomass below 60% of virgin biomass. CARPSIM simulations show that the probability is small for any removal-based method achieving <10% of virgin biomass when F <1.4.

12.2 Introduction

Carp (*Cyprinus carpio* L.) in Australasia and North America are an introduced species widely regarded as a pest and a threat to endemic ecology (McCrimmon, 1968; Brumley, 1996; Koehn et al., 2000). In the present study, stochastic simulation is used to combine comparative analysis of different management strategies, with assessment of extinction risk, applying it to two carp populations in the Murray–Darling basin, southeastern Australia.

The carp management objectives in this case are population control or extinction. Several methods of carp management have been discussed for Australian populations (Roberts and Tilzey, 1996; Koehn et al., 2000) and most of them are variations on the themes of physical removal or biological control.

Fishing, or removal and culling by some-means, was discussed as a method of carp management by Thresher (Thresher, 1997) who suggested that environmental variability may increase the likelihood of its success as a carp control method.

Early attempts in the USA to use water-level manipulation as a carp control option reduced recruitment success for a few year-classes by causing mass egg mortality (Shields, 1958). In Australia, a strategy of maintaining low water levels in Lakes Sorell and Crescent, to keep spawning habitat dry in marginal marshes, has been part of a suite of management measures that have successfully contained and reduced a feral carp population significantly over a 7-year period (Koehn et al., 2000).

Prevention of adult access to spawning grounds combined with trapping and culling juveniles emigrating from wetland spawning grounds has also been suggested as having potential for ‘point-source’ control of carp (Stuart et al., 2001).

For broad-scale application, biological control methods for carp have received some attention. Importation of a potential viral agent (*Rhabdovirus carpio*) was considered somewhat paradoxically, to be too high a risk to native fauna and yet not virulent enough to significantly control carp (Hume et al., 1983). Carp genetics and the mechanisms of sterility were first investigated in the 1980s for the potential to control carp populations by producing and stocking sterile-males (Brown, 1980). Although the sterile-male approach was rejected as impractical, genetic control of reproduction has recently been revisited with the concept of transgenic gender manipulation for carp and a range of other pest organisms (Grewe, 1996; Grewe, 1997a; Thresher et al., 2001). The most promising theoretical effect of this so-called ‘daughterless carp’ technology is to cause male-dominance over several generations to the point of population collapse. Furthermore, modelling trials of the introgression of such a transgene into wild populations has suggested that variability in reproductive success within the wild population has a direct bearing on the speed of transgene introgression (Davis et al., 1999b).

Recent studies have described carp population parameters in detail for two stocks within the Murray–Darling Basin (Appendices 3–5). The current study uses these parameters and considers population viability and abundance under the impacts of three types of management scenario; removal, spawning sabotage and male-dominance and examines how environmental stochasticity affects the outcomes.

12.3 Methodology

12.3.1 Biological Systems

Each modelled carp population can be considered as a sub-population of a larger reproductively isolated stock existing across the Murray–Darling basin, that is dominated by a single genetic strain, although two other strains are present elsewhere in the basin (Davis et al., 1999a). The population of carp inhabiting the Barmah–Millewa forest wetlands (ie. Barmah stock) and the mid reaches of the Murray River (145^0 00' E, 36^0 00' S) is considered and compared with the carp population of the Campaspe irrigation system (ie. Campaspe stock) in central Victoria (144^0 70' E, 36^0 36' S). Both populations are open to immigration and emigration and as such may be managed, although not effectively controlled, in isolation. However, both populations will serve as realistic examples of Murray–Darling basin carp for the purpose of simulating the effects of management scenarios that may be applied to similar, closed populations.

Biological characteristics of these populations used as inputs to the model have largely come from Appendices 3–5, unless otherwise stated. Broadly speaking the Campaspe stock are faster-growing better conditioned carp that mature earlier, are shorter-lived and have higher natural mortality rates than the Barmah stock. This description is reflected in the input parameters to the model listed in Table 22. Despite these differences, both stocks are reasonably typical of carp in much of southern Australia and show similar growth rates to other stocks worldwide (Figure 50).

Table 22 The subset of carp population specific parameters, from (Appendices 4 and 5) used as inputs to the CARPSIM models

Description	Parameter (units)	Campaspe		Barmah	
		males	females	males	females
Growth	L_∞ (mm)	495	538	489	594
	t_0 (year)	-0.291	-0.391	-0.519	-0.609
	K ($year^{-1}$)	0.475	0.380	0.249	0.177
	a ($n \times 10^5$)	3.726	4.109	1.739	1.669
	B	2.902	2.902	3.000	3.000
Maturity	Lm_{50} (mm)	287	273	307	328
	Lm_{95} (mm)	344	310	379	392
Mortality	M ($year^{-1}$)	0.326	0.326	0.262	0.199
Mature sex ratio	% female		50		50[9]

[9] mature sex-ratio was not significantly different to 50% female

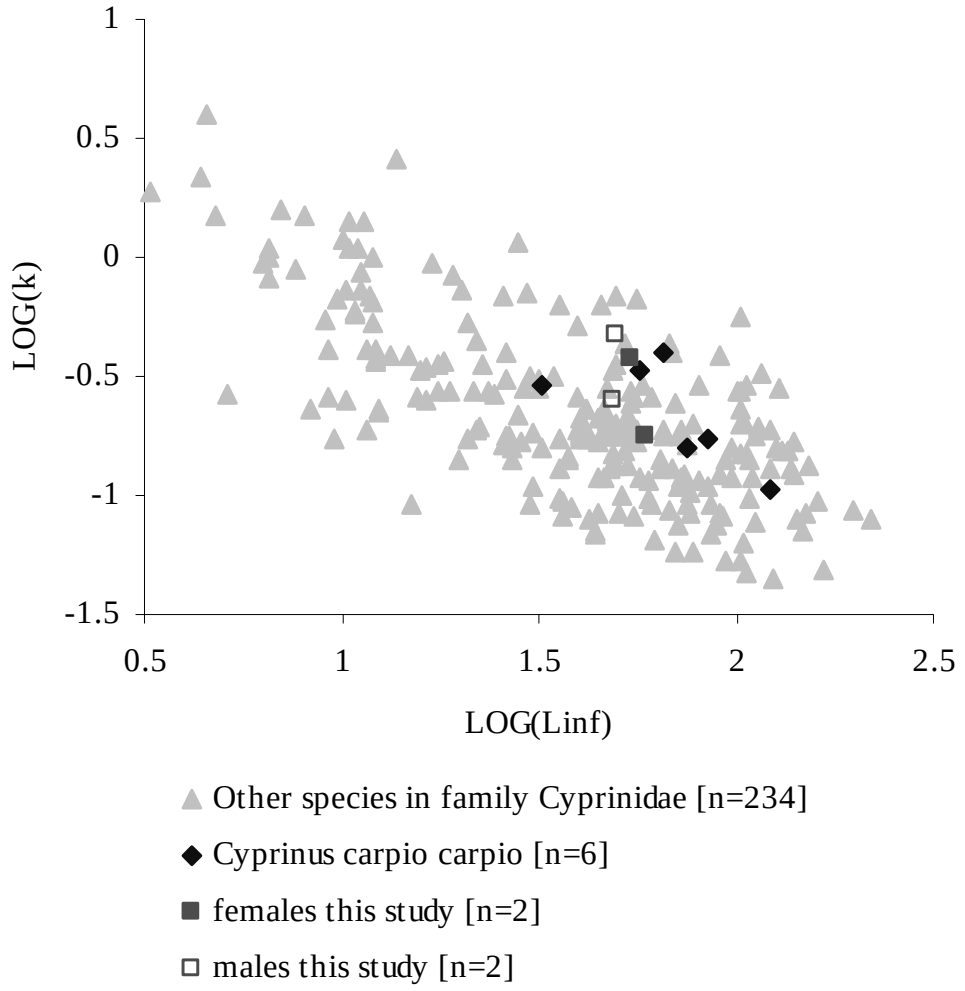

Figure 50 Auximetric plot of growth parameters including data from (Froese and Pauly, 1999) for Cyprinidae in general (triangles); carp, *Cyprinus carpio carpio*[10] (diamonds) and carp *C. carpio* males (open squares) and females (solid squares) in present study.

12.3.2 Deterministic model description

The model consists of a series of difference equations that operate over annual time-steps to increment the numbers and biomass of carp populations composed of up to 30 annual age-classes. The model considers 1970 as year-zero and simulates a population over a 200-year period.

Growth in length is simulated using von Bertalanffy's (1938) model to predict mean length (*l*)-at-age (*i*) (mm).

$$l = L_{\infty}\left(1 - e^{-k(i-t_0)}\right)$$

[10] Froese and Pauly (1999) consider *C. carpio carpio* and *C. carpio haemopterus* (Amur carp, from the Lake Baikal catchment) as separate subspecies

Parameters (L_∞, k and t_0) were previously estimated for each modelled population by sex (Table 22) where L_∞ is the asymptotic mean length (mm) at age ∞, k is the rate at which L_∞ is reached (year^{-1}) and t_0 is the theoretical age at zero length. Growth in mass (w) is simulated using weight–length equation of the form $w = a\,l^b$, where a and b are constants previously estimated for each stock by ln(w) against ln(l) linear regression. Growth is modelled separately for each gender (g) (ie. males and females). Mortality is simulated with separate instantaneous rates of natural (M) and fishing (F) mortality.

The model is initialised with 50 individual males and 50 individual females of age 0 years, although preliminary trials have shown final outcomes to be relatively insensitive to the initial population configuration. If N is the number of carp with subscripts identifying each gender (g), age-class (i) and year (t) in the model then the model is populated with carp according to:

$$N_{g,i+1,t+1} = N_{g,i,t} \exp^{-(F+M)}$$

where M is an exogenous input to the model, whereas F is calculated from exogenous inputs for catchability (q), selectivity (μ_A) and fishing effort (f_t) so that $F = q\,\mu_A\,f$ Since F has been previously estimated for each stock this is set initially by increasing f from zero until the desired F is attained. For the current simulations q =1, which assumes all fish encountering the gear for one unit of fishing effort are caught and all fish in the stock are available to the gear. For the current simulations a 'trawl-shaped' selectivity ogive is assumed where small fish remain unselected until they reach some threshold size, at which point selectivity increases logistically until it reaches a maximum selectivity threshold. Any increased likelihood of gear-avoidance for larger fish is ignored. Selectivity is a logistic function of length where the probability selection at length l is determined from a random dichotomous variable taking the value 1 with a probability of p for the selection condition and the value of 0 with a probability of 1–p for the unselected condition. Selectivity (μ_i) is expressed as a logistic function

$$\mu_i = \left(1 + e^{Ln(19)\left(\frac{l(i)-\mu 50}{\mu 50-\mu 95}\right)}\right)^{-1}$$

where $l(i) = L_\infty\left(1 - e^{-k(i-t_0)}\right)$ is the mean length-at-age, $\mu 50$ is the length (LCF, mm) at 50% of maximum selectivity and $\mu 95$ is the length at 95% of maximum selectivity. Biomass (B) of carp for each age-class and year in the model is given by:

$$B_{g,i,t} = N_{g,i,t} w_i$$

Age and size at maturity was estimated for each of the simulated carp populations. The model uses parameters for length at 50% maturity (*Lm50*) and 95% maturity (*Lm95*), as these are more easily obtainable than corresponding age-based parameters.

The maturity function is similar to the selectivity function. The probability of a carp being mature at length *l* is determined from a random dichotomous variable taking the value 1 with a probability of *p* for the mature condition and the value of 0 with a probability of 1-*p* for the immature condition. The proportion of animals mature in each age-class (ρ_i) is expressed as a logistic function by the equation

$$\rho_i = \left(1 + e^{Ln(19)\left(\frac{l(i)-Lm50}{Lm50-Lm95}\right)}\right)^{-1}$$

where again $l(i) = L_\infty\left(1-e^{-k(i-t_0)}\right)$, Lm50 is the length (LCF, mm) at 50% maturity and Lm95 is the length (LCF, mm) at 95% maturity.
The biomass of mature carp (B^m) in each gender, age-class and year in the model is given by

$$B^m_{g,i,t} = N_{g,i,t} w_i \rho_i$$

where $w_i = a(l(i))^b$ and ρ_i is the proportion mature in each age-class. Similarily the number of mature carp N^m in each gender, age-class and year is given by

$$N^m_{g,i,t} = N_{g,i,t} \rho_i$$

Total numbers ($\sum N$), biomass ($\sum B$), mature-numbers ($\sum N^m$) and mature-biomass ($\sum B^m$) of carp for each year in the model are summed across all 30 age-classes and are plotted as time series over the 200 years of each model run as a diagnostic output. Previous studies have shown extremely high larval and early-juvenile mortality rates (Gehrke et al., 1999; Koehn et al., 2000) and therefore egg production *per se* may be a poor predictor of future adult abundance. The CARPSIM model uses a recently estimated relationship between body mass and annual fecundity (Appendix 3) to calculate annual egg production from $\sum B^m$, although this is only used as a diagnostic indicator of population productivity.
Carp recruitment is assumed to be density-dependant whereby high densities of spawning adults may reduce recruitment though habitat destruction, and competetive inter- and intra-yearclass interaction. Recruitment to successive yearclasses in the model is derived from the Ricker stock-recruitment relationship between density (ha^{-1}) of yearlings (age 0 years) and of mature adults (aged $\geq$ 2 years) estimated for data from Harris and Gehrke (1997) presented in Koehn et al. (2000). As is typical with many stock-recruitment relationships, variability about the fitted curve is high and is attributed to variable reproductive output, to variable survival to recruitment, and to unknown immigration and emigration rates prior to sampling. However, the use of this parameterisation of the Ricker curve in units of fish numbers per hectare effectively allows the development of CARPSIM outputs of carp numbers and biomass to be expressed in the same units (ha^{-1}).

Thus recruits enter the model each year as yearlings at the end of their first year. In the deterministic model, recruits ha^{-1} (R) for year t are calculated from the ricker stock-recruitment equation as

$$R_t = \alpha\left(\sum_{i=0}^{I} N^{m}_{g,i,t}\right)\exp^{-\beta\left(\sum_{i=0}^{I} N^{m}_{g,i,t}\right)}$$

where α and β are the scale and shape parameters respectively (Table 23) and N^m is numbers of mature individuals ha^{-1}. I is maximum age and is defined as I=30 for this present study. This provides a negative feedback loop to the model that allows the modelled population to reach a stable equilibrium. Sensitivity of the model results to the magnitude of α and β was examined for a deterministic model scenario by varying first α then β by 25% up and down.

Table 23 CARPSIM input parameters

Description	Parameter	Value	Source (if external)
Recruitment (Ricker)	α	8.004	from data presented in (Koehn et al., 2000)
	β	0.008	from data presented in (Koehn et al., 2000)
Pseudo-extinction cut-off	Ext (Ha^{-1})	0.01	
Sex ratio change parameter	Sr	0.1	
Spawning sabotage rate	R_{fail}	50, 80 or 99%	
Fishing mortality	F	0.7, 1.4 or 2.1	
Annual fecundity	A ($n \times 10^3$)	3.470	Appendix 3
	B ($n \times 10^8$)	2.100	Appendix 3
	C	0.309	Appendix 3

12.3.3 Environmental Stochasticity

Observations of year-class strength and recruitment success (Gehrke et al., 1995) in carp may be related to variable river flows, but the nature of the relationship is not clear. Lubinski et al. (1986) cited several reports that suggest successful annual carp recruitment in large rivers may not depend solely on high water and proposed that indeed recruitment may suffer under such circumstances. The relationship between inter-annual climatic variability, the operational flow conditions in irrigation channels, and carp recruitment success are unknown. Nevertheless, it is reasonable to assume that the timing and magnitude of quantitative changes in water in the channel systems may influence recruitment success through changes in opportunities to access spawning habitat and through changes in immigration and emigration of larvae to the channel systems. Annual flow conditions in irrigation channels and major rivers in southern Australia alike, may vary as a result of broad cyclical climatic patterns such as El Niño and La Niña (Nicholls and Kariko, 1993). Climatic patterns such as these are characterised by changes in the southern oscillation index (SOI) which has been shown to influence the abundance distribution and survival of other aquatic wildlife in Victoria (Norman and Nicholls, 1991). To reflect the effect of the stochastic environment on carp recruitment in the model two sources of variability are available:

- a component randomly drawn from a distribution of environmental weighting factors derived from the available time series of annual Murray River flows at Barmah for the years 1985–2001.
- a component randomly drawn from a distribution of environmental weighting factors derived from the southern oscillation index (B.O.M., 2002) for the years 1876–2001

Both elements use a set of simple criteria that transforms the environmental time series into one of good-or-bad years. For the hydrological data if the annual flow is greater than 4 000 ML year^{-1} it is assumed a good year, as are annual positive averages of the SOI index. The actual criteria are somewhat arbitrary, and derived from inspection of the relevant environmental time series and observations of known good and bad years of recruitment. However, it is important to realise that it is the variability within the time series that is being used, the switching between good and bad-years. The actual value of the environmental index attributable as a good or bad year is of little relevance in the model. The hydrological series generated a series of 17 weighting factors with a coefficient of variation of 0.72, whereas the SOI series generated a series of 126 weighting factors that was less variable with a coefficient of variation of 0.57.

12.3.4 Risk assessment framework

To allow evaluation of the effectiveness of a range of management scenarios in reducing the modelled carp population to a level of pseudo-extinction, the population density for each modelled year is stored ($\sum N$). The number of years for which $\sum N > ext$ is the time until pseudo extinction, where *ext* is a pre-set cut-off value for population density regarded as the pseudo-extinction level. In this case we held *ext* at 0.01 carp ha^{-1}.

In the following scenarios the model was run for 1000 iterations and the resulting time-to-extinction values tabulated for females and total stock (males and females). By ranking the 1000 results, particular percentiles with levels of ‘risk of successfully

driving to pseudo extinction' are identified. For a given scenario stochastically modelled 1000 times, in the ordered series of results, the 900th result will give the 90% risk level of that scenario succeeding; ie. one can be 90% certain that the scenario will succeed in driving the population to pseudo-extinction with the resulting time. Natural resource managers in Victoria suggested that an 80% chance of success (20% risk of failure) was acceptable for this exercise.

12.3.5 Simulated Management Scenarios

Preliminary deterministic modelling has shown that a stable stock develops by year 30. The following management scenarios are simulated after a 30-year period during which populations are allowed to build with no intervention. Scenarios are run for 170 years over years 31–200 and repeated for 1000 iterations in the stochastic cases.

12.3.6 Fishing, poisoning or removal scenarios

Carp control using commercial fishing or removal methods has a long history (Neess et al., 1957). By setting various levels of F in the model, any extra mortality over-an-above that of natural mortality, can be simulated. If the selectivity parameters are set for little or no selectivity (eg. $\mu 50 = 10$, $\mu 95 = 12$), this effectively simulates the regular annual removal of carp by poisoning, where all sizes are equally vulnerable. In fact this form of management is practiced in many Australian irrigation channels by default when herbicide is applied regularly to control aquatic plants. It has been noted that extensive carp mortality is a side-effect of such channel management (Appendix 4).

Other removal-based management such as commercial fishing using electrofishing, traps or nets has a size-selective element to it. In the absence of known selectivity parameters for any particular carp fishery, $\mu 50 = Lm50$ and $\mu 95 = Lm95$ which effectively simulates annual trapping of the mature spawning fish. Indeed this has been proposed as a potential management method for the Barmah population (Stuart et al., 2001). For each of these selectivity strategies, three levels of F (0.7, 1.4 and 2.1, equivalent to annual survival rates of 50%, 25% and 12%, respectively) are simulated. For each selectivity and F combination, the model was run deterministically, stochastically using the hydrology time-series as input to recruitment variability, and stochastically using the SOI time-series as input to recruitment variability for each population.

12.3.7 Spawning or recruitment sabotage scenarios

Prevention of recruitment, by barring access to spawning substrate, or hydrological manipulation of water levels to cause stranding of eggs has been suggested as a potential management tool to control carp (Shields, 1958; IFC, 1995; IFC, 2001). Such induced recruitment failure or spawning sabotage can rarely be 100% reliable. The occurrence of floods is unpredictable and may be expected to thwart efforts to contain or restrict movement of carp. Scenarios are modelled in which the probability that recruitment is totally prevented is randomly drawn from a uniform distribution in 50%, 80% or 99%of years (R_{fail}=50%, 80% or 99%). Each sabotage scenario is simulated using the stochastic model first with deterministic recruitment and then with both hydrology and SOI as input to recruitment variability for each population.

12.3.8 Male dominance (daughterless carp) scenarios

This scenario is based on genetic molecular manipulation methods currently under development (Grewe, 1996; Grewe, 1997a; Davis et al., 2001; Thresher et al., 2001). The most promising methods rely on a transgene proliferating throughout a carp population that will bias the sex-ratio toward maleness until the population collapses from recruitment failure.

This model does not consider the complication of how this gene is delivered or spread though the population (Davis et al., 2001). The model simply simulates the expression of such a gene in the population using a single parameter (*Sr*) that exponentially drives the sex ratio towards complete maleness. Preliminary modelling of the theoretical behaviour of such a gene suggests that 50 years is a plausible time-scale for this to occur[11]. Therefore the scenario modelled in the present study is *Sr=0.1* that is equivalent to reducing the sex ratio to 1% females over 50 years. Again, the time to pseudo-extinction was simulated for the deterministic model and the stochastic models with both hydrology and SOI as input to recruitment variability for each population.

12.4 Results

When parameterised for the Barmah population, the fully deterministic CARPSIM model predicts population trajectories that develop stable-limit cycles with a period of ~14 years. The cycles are driven by recruitment and given no other inputs or perturbations, progressively damp-down during the first 130 years to simulate a final population equilibrium biomass of 569 kg ha^{-1}. At equilibrium, the population produces 2.5×10^9 eggs ha^{-1} annually with 10 year-olds contributing the most eggs. Thus the parents of most of the offspring are 10 years old for this population—10 years is the average generation time (Figure 51). Perturbations to the population such as recruitment stochasticity, invariably prolong the cyclical behaviour throughout the 200 year modelled period and the original periodicity of 14 years is still strongly discernible through the stochastic ‘noise’(Figure 52).

[11] Drs. Nic Bax, and Peter Grewe at Centre for Research on Introduced Marine Pests, CSIRO. Personal communication, 2001

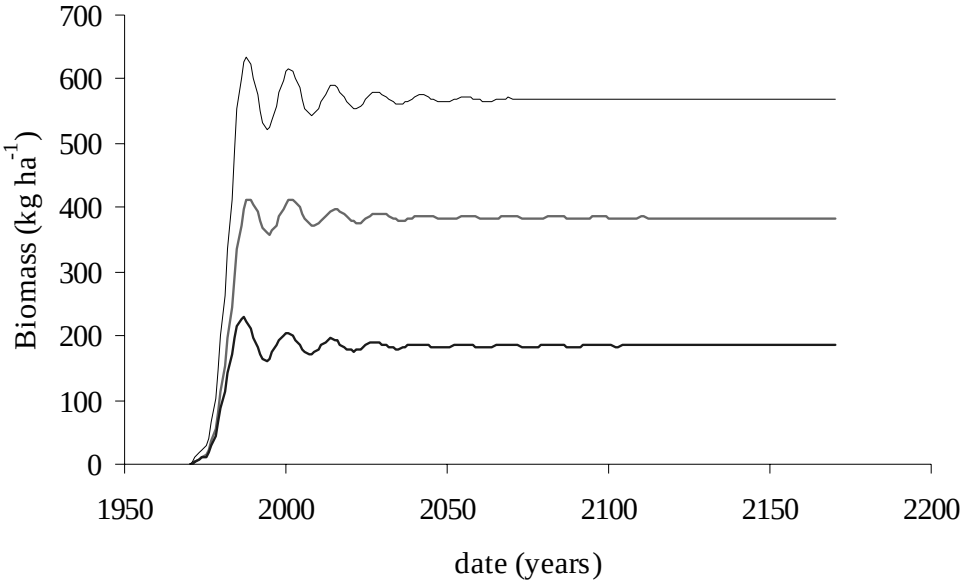

Figure 51 Biomass trajectories from deterministic CARPSIM model parameterised for the Barmah population showing initial stable limit cycles with a period of ~14 years. Upper line = total biomass (kg ha^{-1}), middle line = female biomass (kg ha^{-1}), lower line = male biomass (kg ha^{-1}).

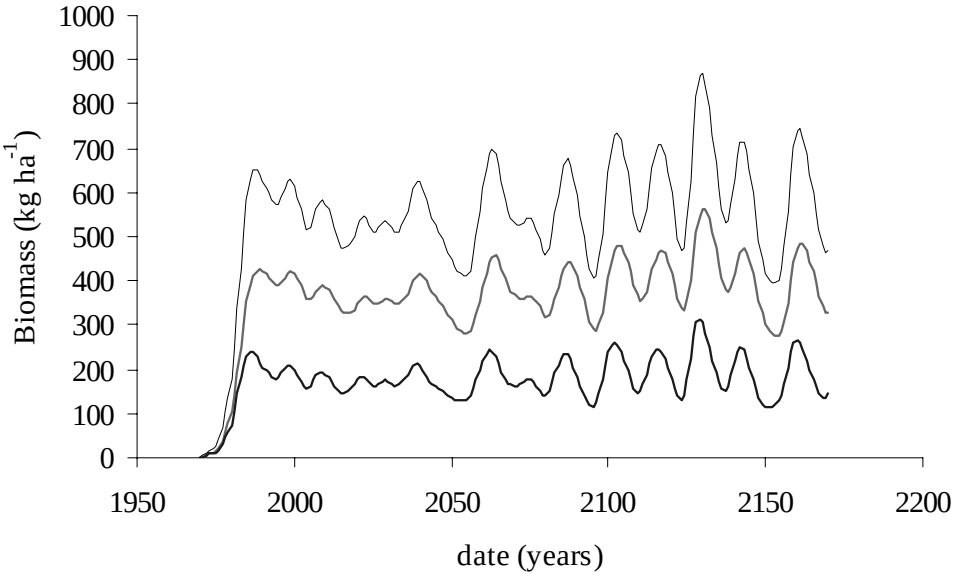

Figure 52 Biomass trajectories from a typical run of the stochastic CARPSIM model using hydrological variability to vary recruitment success and parameterised for the Barmah population. Upper line = total biomass (kg ha^{-1}), middle line = female biomass (kg ha^{-1}), lower line = male biomass (kg ha^{-1}).

When parameterised for the Campaspe irrigation channel population the model again predicts population trajectories that develop stable-limit cycles although now with a shorter period of ~9 years. These cycles in the deterministic model damp-down over a

period of 50 years to simulate a final equilibrium population density of 550 kg ha^{-1} producing 2.4 x 10^9 eggs ha^{-1}. In the Campaspe population, it is 5 year-olds that contribute the most eggs suggesting that the average generation time is around half that of the Barmah stock, at 5 years.

While the amplitude of stable limit cycles is sensitive to the magnitude of the recruitment parameters α and β, the frequency is not. However, manipulation of *Lm50* and *Lm95*, the parameters determining rate of maturation, produces variation in the frequency of stable-limit cycles in recruitment. It seems that variation in age at maturity is the likely cause of the difference between frequency of recruitment cycles in simulations of Campaspe and Barmah stocks.

Two types of results are considered, population viability (PV) and population abundance. The first is measured as time to pseudo-extinction in years after the initial period of 30 years allowed for the population to build-up. Note that the threshold of pseudo-extinction, *ext* <0.01 carp ha^{-1}. The second is considered only for those simulated populations that persist for the remaining 170 years and is measured as the final biomass (B_{170}) as a percentage of the virgin biomass. Virgin biomass is defined as biomass existing at the end of the 30-year period of population build-up (B_{30}). Both types of result are reported for the nine simulated management scenarios for each population in Table 24–Table 27

Table 24 Years to pseudo-extinction results of carp poisoning (or unselective fishing) scenario's modelled with CARPSIM for two populations. $D_{100\%}$ = deterministic model; $S_{80\%}$ Hyd.= stochastic model using hydrological data as source of environmental stochasticity; $S_{80\%}$ SOI = stochastic model using southern oscillation index as source of environmental stochasticity. Scenarios are modelled for 170 years after a 30-year period of stabilisation and stochastic models are run for 1000 iterations. Figures in parenthesis are range of B_{170}/B_{30} (ie.final biomass' as a percentage of original biomass').

Scenario	Selectivity	Barmah			Campaspe		
		$S_{80\%}$ SOI	$S_{80\%}$ Hyd	$D_{100\%}$	$S_{80\%}$ SOI	$S_{80\%}$ Hyd.	$D_{100\%}$
F=0.7	all	78	59	63	170 (2–30%)	170 (2–30%)	170 (13%)
F=1.4	all	16	15	15	52	35	40
F=2.1	all	9	9	9	16	14	15

Table 25 Years to pseudo-extinction results of size selective carp fishing scenario's modelled with CARPSIM for two populations. D = deterministic model; S $_{80\%}$ Hyd.= stochastic model using hydrological data as source of environmental stochasticity; S $_{80\%}$ SOI = stochastic model using southern oscillation index as source of environmental stochasticity. Scenarios are modelled for 170 years after a 30-year period of stabilisation and stochastic models are run for 1000 iterations. Figures in parenthesis are range of B_{170}/B_{30} (ie.final biomass' as a percentage of original biomass').

Scenario	Selectivity	Barmah			Campaspe		
		S $_{80\%}$ SOI	S $_{80\%}$ Hyd	D	S $_{80\%}$ SOI	S $_{80\%}$ Hyd.	D
F=0.7	Mature	170 (9–56%)	170 (10–60%)	170 (29%)	170 (8–57%)	170 (8–58%)	170 (26%)
F=1.4	Mature	170 (2–34%)	170 (1–34%)	170 (12%)	170 (2–30%)	170 (1–31%)	170 (11%)
F=2.1	Mature	170 (0–4%)	159	170 (0.004%)	170 (0.1–16%)	170 ($5x10^{-7}$–7%)	170 (3%)

Table 26 Years to pseudo-extinction results of carp recruitment/spawning sabotage scenario's modelled with CARPSIM for two populations. $D_{80\%}$ = deterministic model with random recruitment variability; $S_{80\%}$ hyd.= stochastic model using hydrological data as source of environmental stochasticity; $S_{80\%}$ SOI = stochastic model using southern oscillation index as source of environmental stochasticity. Scenarios are modelled for 170 years after a 30-year period of stabilisation and stochastic models are run for 1000 iterations. Figures in parenthesis are range of B_{170}/B_{30} (ie.final biomass' as a percentage of virgin biomass').

Scenario	Barmah			Campaspe		
	$S_{80\%}$ SOI	$S_{80\%}$ hyd	$D_{80\%}$	$S_{80\%}$ SOI	$S_{80\%}$ hyd.	$D_{80\%}$
R_{fail}=*50%*	170	170	170	170	170	170
	(12–137%)	(14–167%)	(22–107%)	(7–148%)	(3–191%)	(5–100%)
R_{fail}=*80%*	170	170	170	170	170	170
	(0–122%)	(0–127%)	(0–82%)	(0–145%)	(0–138%)	(0–96%)
R_{fail}=*99%*	41	41	41	39	34	38

Table 27 Years to pseudo-extinction results of carp male-dominance scenario's modelled with CARPSIM for two populations. D = deterministic model; $S_{80\%}$ Hyd.= stochastic model using hydrological data as source of environmental stochasticity; $S_{80\%}$ SOI = stochastic model using southern oscillation index as source of environmental stochasticity. Scenarios are modelled for 170 years after a 30-year period of stabilisation and stochastic models are run for 1000 iterations.

Scenario	Barmah			Campaspe		
	$S_{80\%}$ SOI	$S_{80\%}$ Hyd	D	$S_{80\%}$ SOI	$S_{80\%}$ Hyd.	D
Sr=0.1	97	94	95	77	75	75

Simulating the intensive and unselective removal of carp as a control method suggests that subtle variation in biological parameters typical of the target carp population have a bearing on the likelihood of population persistence. As Thresher (1997) suggested, the most variable stochastic input to the recruitment process produced the least population persistence (Table 24). However, at higher F values this difference became less substantial. Management activities in this category, such as the regular use of a piscicide, trapping all size classes or regular de-watering to strand all size-classes, are more efficient in the simulated Barmah population where pseudo-extinction is simulated for all scenarios. For the simulated Campaspe population, pseudo-extinction was achieved in the high F scenarios (F=1.4 & 2.1) and a fish down to $\leq$ 30% of B_{30} was achieved at F=0.7 (Figure 53). In unselective removal scenarios increasing F reduces egg production but does not alter the modal age for egg production in the population. The age-class producing the most eggs remains as 5 years and 10 years for Campaspe and Barmah simulated populations, respectively.

Simulating the intensive selective removal of carp as they mature is, perhaps not surprisingly, less successful in extinguishing populations than removing all size-classes (Table 25). Trapping spawners as they migrate to spawning grounds, or targeted culling of spawning aggregations is not likely to drive stocks to pseudo-extinction at these levels of F however, significant reductions of population biomass ($\leq$ 60% of B_{30}) were simulated in most cases. Parameterisation of CARPSIM with either Barmah or Campaspe population biological characteristics made little difference to the results. Neither did the type of stochastic variability used for recruitment. Size-selective fishing or removal alters the age-structure of simulated populations such that the modal age-class for egg-production (A_{mode}) is reduced. Deterministic simulations show that at F=0.7 for simulated Campaspe channel populations A_{mode} is reduced from 5 to 3 years; and for simulated Barmah populations from 10 to 5 years. These changes represent a considerable shortening of the average inter-generation time for populations subject to such size-selective fishing.

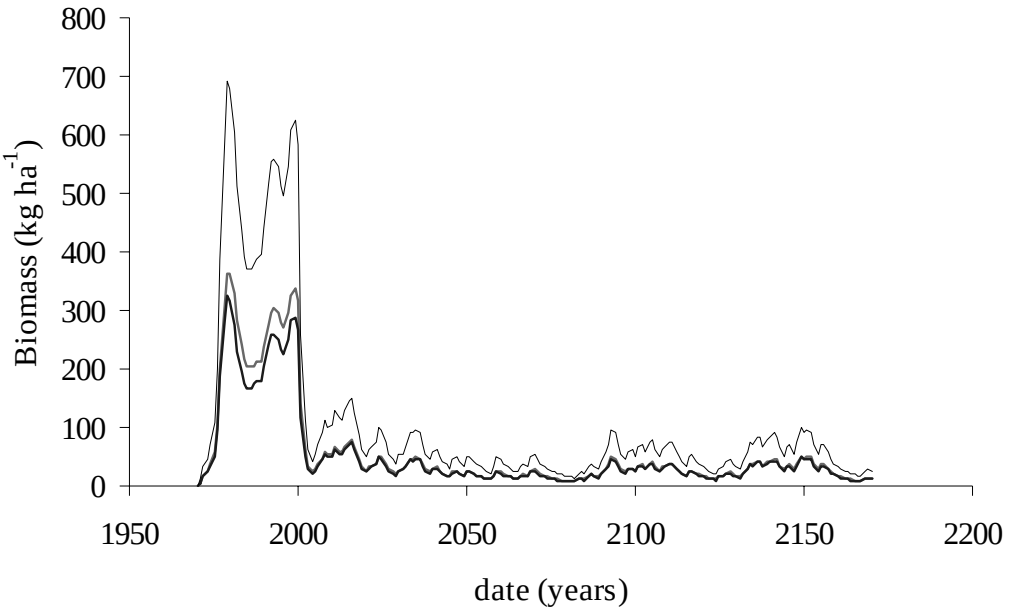

Figure 53 Biomass trajectories from a typical run of the stochastic CARPSIM model simulating fish-down by unselective removal (eg. by piscicide) with F=0.7, parameterised for the Campaspe irrigation channel population. Upper line = total biomass (kg ha^{-1}), middle line = female biomass (kg ha^{-1}), lower line = male biomass (kg ha^{-1}).

Simulations of spawning sabotage or recruitment prevention suggest that when sabotage can only be achieved at low rates (eg. R_{fail} = ≤80%) carp populations will persist although pseudo-extinction was achieved rapidly at extremely high rates of simulated spawning sabotage (eg. 99 years in 100, R_{fail} =99%) (Table 26). Furthermore, low rates of spawning sabotage produced highly variable responses in biomass trajectories. Simulations of final biomass ranged from an effective complete fish-down, to almost double the virgin biomass. Recruitment variability based on either SOI or hydrological variability increase the risk of exceeding virgin biomass beyond that simulated in the deterministic model. By examining the results of each 1000 stochastic model iterations as probability-distributions the probability of B_{170} exceeding virgin biomass with R_{fail} = 50% was estimated as 0.08–0.09 for the Campaspe cases and 0.06–0.08 for the Barmah cases. Note that this result is drawn from the probability distribution for *final-biomass* (B_{170}) and that, due to the fluctuating nature of the biomass trajectory, it follows that the probability of exceeding virgin biomass at some point during the time series would be even higher. These simulations suggest that spawning sabotage alone is an extremely risky strategy for population control if only low rates of spawning sabotage can be attained.

Our simulations of male-dominance suggest that given realistically parameterised populations that are driven to a 1% female sex-ratio over 50 years, we can expect an 80% success rate achieving pseudo-extinction within 75–90 years (Figure 54). Results seem more sensitive to the initial biological parameters, than to the source of stochastic recruitment variability. The simulations parameterised for the Campaspe population are slightly more optimistic than those for the Barmah population.

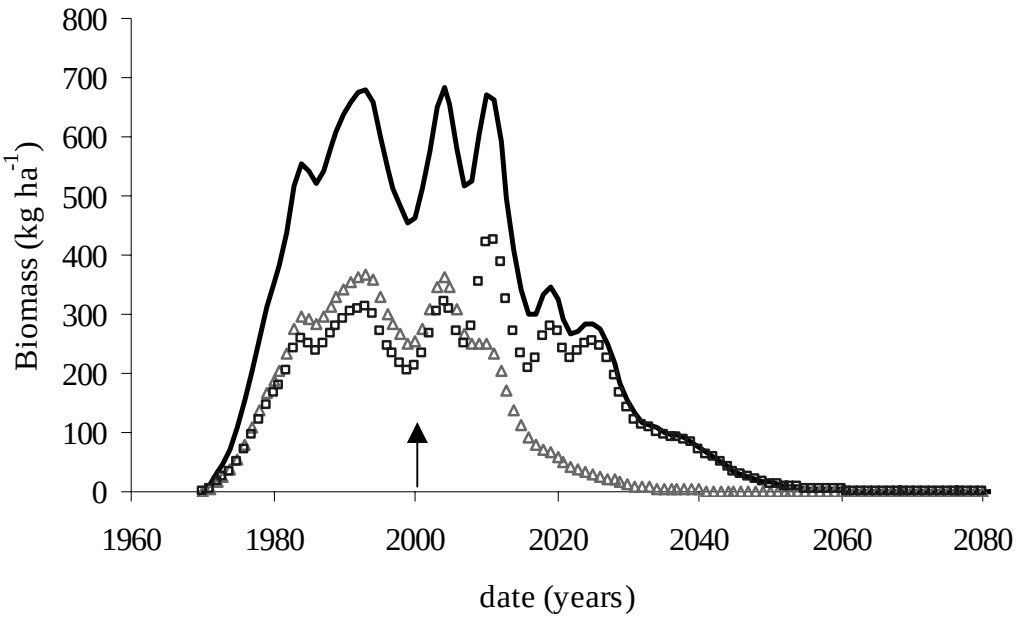

Figure 54 Biomass trajectories from a typical run of the stochastic CARPSIM model simulating male-dominance in 50 years with *sr*=0.1, parameterised for the Campaspe irrigation channel population. Solid line = total biomass (kg ha^{-1}), triangles = female biomass (kg ha^{-1}), squares = male biomass (kg ha^{-1}). Arrow marks year male-dominance scenario is implemented.

The sensitivity of the model to variations in the initial recruitment parameters was tested using the deterministic models' unselective fishing scenarios (μ50 =10, μ95=12) parameterised for the Campaspe channel population. The PV and abundance results for the base-case are shown in Table 24. Under a zero fishing scenario, an equilibrium population is simulated at a density of 550 kg ha^{-1}. Increasing or decreasing the scale parameter α simulates larger or smaller equilibrium population densities to develop respectively as this effectively changes the *carrying capacity* for the population (Table 28). Under fishing-scenarios, a reduced α produces more optimistic management outlooks of smaller final biomass or shorter time to pseudo-extinction. Increased α produce the opposite response in the model, with more pessimistic outlooks as fishing reduces the population less over a given time or allows the population to persist longer. Lowering or raising the *shape* parameter β also increases or decreases the equilibrium biomass when F=0; however, both variations to β result in more pessimistic management outlooks in response to increasing F.

Table 28. Sensitivity testing for the Ricker recruitment parameters α and β in the deterministic model, using the base-case of unselective fishing or variations of ± 25% to each parameter. The deterministic model is parameterised for the Campaspe channel population. Final equilibrium biomass at year 170 (B_{170}) is shown for the base case and each variation of α or β. Results are shown as B_{170} as a percentage of virgin biomass (B_{30}). For those scenarios where the population does not persist, time until pseudo-extinction (t_{ext}) is shown in parenthesis.

	Base case	α - 25%	α +25%	β - 25%	β + 25%
B_{170} (kg ha^{-1})	550	493	595	734	440
B_{170}/B_{30} x 100%					
Scenario F=0.7	13%	8%	16%	26%	26%
Scenario F=1.4	0 (40)	0 (28)	0 (58)	11%	11%
Scenario F=2.1	0 (15)	0 (13)	0 (17)	3%	3%
Management outlook		optimistic	pessimistic	pessimistic	pessimistic

12.5 Discussion

Previous models of carp populations have been used as *eye-openers* (Van Daalen et al., 2002) to raise awareness in the resource management community of the potential of emerging pest-control technology (Grewe, 1996; Davis et al., 1999b; Davis et al., 2001). In addition, those models provided *arguments in dissent* (Van Daalen et al., 2002) of the ineffective nature of alternative management actions for carp (Thresher, 1997). However, in the absence of estimates of local biological population parameters, such models have been generalised using simplified inputs from the literature. Recent investigations of Australian feral carp populations have provided biological parameter estimates with which to add realism to a modelling approach (This study, Appendices 3–5; Koehn, et al. 2000). With the benefit of these investigations, it now seems that previous models have somewhat underestimated carp life spans and used unrealistic rates of maturity and mortality. Even in Australia carp occupy a geographic and climatic range (Kailola et al., 1993) that may confer a variety of biological characteristics at the population scale by varying lengths of growing season and habitat productivity. The actual estimated local biological characteristics used as inputs to CARPSIM, are more likely to simulate the response of real populations to a range of management scenarios. Although typical of stocks found in Victoria, the two populations simulated here probably do not well represent the extremes of carp life-history strategies in Australia. For instance, more extreme growth rates are likely to be found in cold Tasmanian lakes (IFC, 2001) and warm Queensland streams (Gehrke et al., 1999). Further exploration of the effects of such extreme biological inputs on the predicted population viability and abundance is warranted under a range of simulated management scenarios.

The presence of stable-limit cycles in the simulated population trajectories is a consistent phenomenon driven by recruitment and independent of extraneous environmental variability. Previous investigations of cyprinid (*Rutilus rutilus*) population dynamics have determined that cycles in abundance may occur (Townsend et al., 1990). These may sometimes be attributed to competitive interactions between age-classes (Townsend and Perrow, 1989). However, Townsend et al. (1990) also showed that the period of such damped oscillations in *R. rutilus* can be derived from the time to initial maturity. The lack of any long-term time series of abundance indices precludes confirmation of the actual presence of such cycles within Australian feral carp stocks. However if they do occur, such natural variation in abundance over time-scales of 6–9 years would make detecting longer-term trends in abundance due to pest-control strategies more difficult.

Empirical estimates of fishing mortality in the two populations that were simulated are much lower than the values that CARPSIM shows are needed to achieve any level of control. To put the simulated scenario's in context, the lowest *F* scenario (F=0.7) in the present study is more than double the estimate of F for the intensively managed channel population subject to regular herbicide and de-watering treatments. Estimates of *F* for other carp populations are rare. Neess et al. (1957) calculated estimates of *M* during three years of seine-netting carp from Lake Wingra, a 130-ha, shallow (mean depth ~2.1 m) lake in Wisconsin, USA. During 1953–1955 the seine fishery took 18 tonnes of carp from Lake Wingra's estimated virgin biomass (B_o) density of 465 kg ha^{-1}, in doing so carp density was reduced to ~54 kg ha^{-1} (11% of B_o). His concluding comments suggest that as yield approximated losses estimated through natural mortality, fishing mortality (F) was equivalent to their average estimate of *M* at ~0.6 year^{-1}. Carp are still found in Lake Wingra today (UWMCL, 2002).

CARPSIM model predictions of biomass density are higher than those estimated for these populations. The single Barmah population density estimate was approximately one third (Appendix 5) of the equilibrium density predicted by the deterministic CARPSIM simulation. However, the predicted equilibrium density for the Campaspe channel population is within the range of standing stock estimates available for this population from studies during 1999–2000 (Appendix 4). The Barmah density estimate was estimated from the fishery yield as wetlands were drained in 1999 (Appendix 5) under the assumptions of total harvest and no escapement, therefore estimation error may be large.

Clearly, quantitative outcomes from CARPSIM are sensitive to the scale and shape parameters of the stock-recruitment relationship. However, the chosen stock-recruitment relationship (Koehn et al., 2000) is the only published estimate available for carp and uses empirical stock-recruitment data collected recently from New South Wales rivers in southeastern Australia, to estimate the parameters. There is a lack of suitable catch or effort data for most Australian carp stocks to enable any formal *fit* of the model to empirical data. However, given reliable population estimates for more stocks it may be possible to further fine-tune CARPSIM by adjusting stock recruitment parameters until the simulated initial abundance matches empirically estimated abundance. This has not been attempted in the present study due to the paucity of reliable population abundance estimates. Those obtained for the Campaspe channel population reasonably matched simulated abundance using the current stock-recruitment parameters.

Carp management scenarios that are based on size-selective removal, such as gill-netting, seining, trapping mature adults on the spawning grounds, alter the size and age-distribution of the remaining stock. There are indirect advantages in doing this in addition to simple removal of individuals. In many Victorian carp stocks, larger females produce larger eggs (Appendix 3). Larger eggs may confer an early survival advantage in fishes for a range of reasons including increased larval size at hatching (Pitman, 1979; Springate and Bromage, 1985), higher larval and juvenile growth rates (Sehgal and Toor, 1991; Ojanguren et al., 1996)), larger yolk-size and longer survival times under starvation conditions (Vøllestad and Lillehammer, 2000). Therefore carp management efforts that selectively remove large fish are likely to infer a qualitative as well as quantitative disadvantage on the stock recruitment.

Whereas spawning or recruitment sabotage (Shields, 1958) may be successful when high sabotage-probabilities can be maintained for 30–40 years, simulations of low sabotage-success (eg 1 in 2 years) suggest that an unacceptable risk occurs ($p>0.05$) that populations will persist at greater than virgin biomass densities.

Recent models of molecular approaches to carp control (Grewe, 1996; Grewe, 1997b) suggest a period of up to 28 generations is required before complete introgression of a transgene such as the male-dominance *daughterless carp* contruct. In our simulated populations, the median age for initial female maturity is 1.4 years for the Campaspe channel (Appendix 4) population, and 2.7 years for the Barmah population (Appendix 5). At these maturity rates the average duration for 28 generations would be 39–75 years. Our simulations suggest an even lengthier 75–97 years is more likely before we can be 80% certain of driving similar carp stocks to pseudo-extinction. Davis et al. (1999b) suggested that carp control using the introgression of a *killer* transgene will be more efficient in stochastically variable environments. However, the choice of stochastic or deterministic recruitment environment made little difference to our simulation of male-dominance results.

In summary CARPSIM simulations suggests that faster growing, shorter-lived populations may be better controlled by male-dominance, or spawning sabotage type

methods whereas slower growing, long-lived populations may respond best to removal type approaches. Unselective removal, such as poisoning or trapping all age-classes is more likely to cause pseudo-extinction at levels of $F>0.7$; while size-selective removal at similar F levels may only be useful to reduce the biomass below 60% of B_{30}. Thresher (1997) suggested that reductions to <10% of virgin biomass are needed to shift populations to a relatively-stable low growth-rate. CARPSIM simulations show that the probability is small of any removal-based method achieving <10% of virgin biomass when $F<1.4$. While, lesser biomass-reductions such as those simulated here may still be useful in reducing ecological damage (Koehn et al., 2000), the high level of effort necessary to produce this biomass reduction would need to be maintained indefinitely to avoid rapid, exponential population growth.

Hopefully, the CARPSIM model is shown as useful in fulfil van Daalen's (2002) two remaining roles of computer models in environmental policy. As an impartial pest-management planning tool that can be used *to create political consensus*. Although only two carp stocks were simulated in this study, CARPSIM is also flexible enough to be used as *a model for management* of other individual stocks.

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12.7 References cited in Appendix 6

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