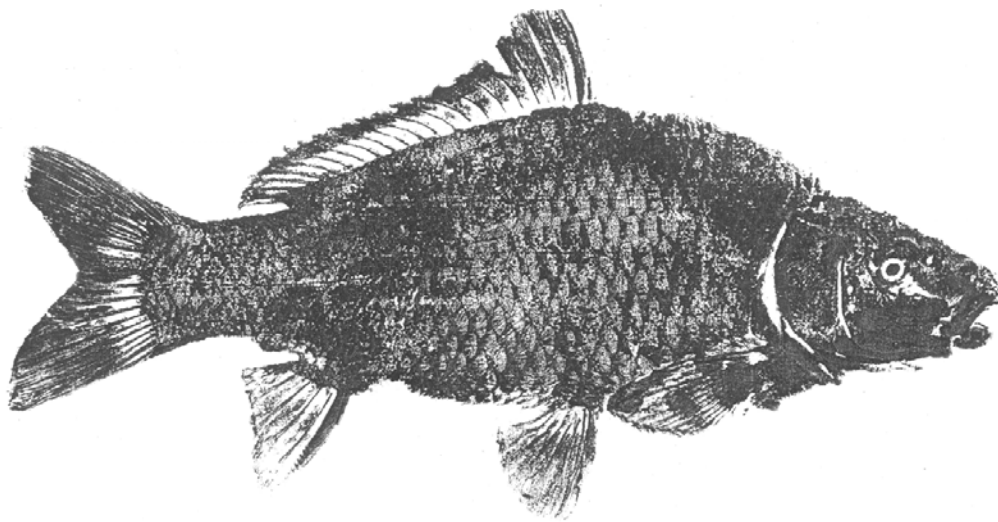


The state of the art: a synopsis of information on common carp (*Cyprinus carpio*) in Australia

Final Technical Report



Benjamin Smith

Senior Research Officer (Carp Ecology)
Pest Animal Control CRC, SARDI Aquatic Sciences
PO Box 120, Henley Beach, South Australia 5022.

- April 2005 -

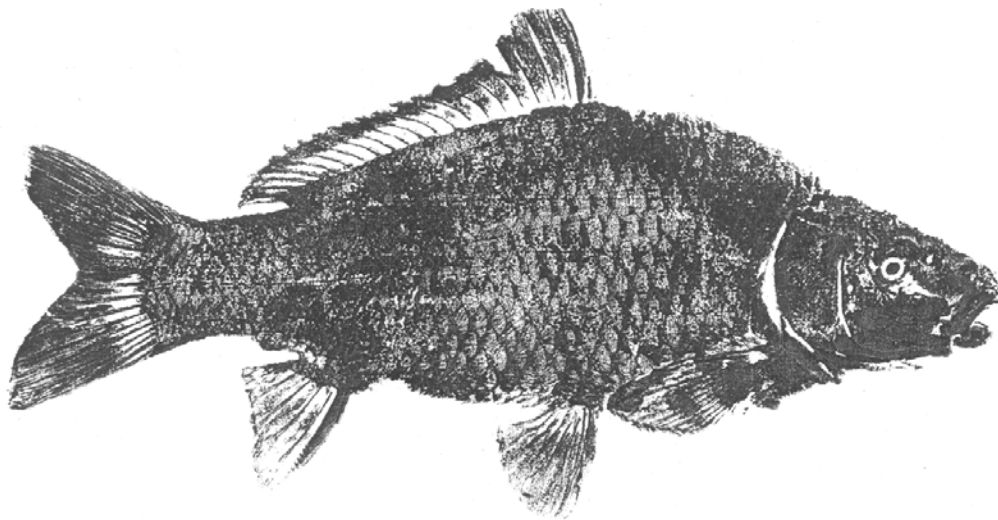


Pest Animal Control CRC



The state of the art: a synopsis of information on
common carp (*Cyprinus carpio*) in Australia

Final Technical Report



Benjamin Smith

Senior Research Officer (Carp Ecology)
Pest Animal Control CRC, SARDI Aquatic Sciences
PO Box 120, Henley Beach, South Australia 5022.

SARDI Aquatic Sciences Publication No. RDO4/0064-2
SARDI Research Report Series No. 77

- April 2005 -

This publication should be cited as:

Smith, B. B. (2005). The state of the art: a synopsis of information on common carp (*Cyprinus carpio*) in Australia. Final Technical Report, SARDI Aquatic Sciences Publication No. RDO4/0064-2; SARDI Research Report Series No. 77, prepared by the South Australian Research and Development Institute (Aquatic Sciences), Adelaide. 68 pp.

South Australian Research and Development Institute

SARDI Aquatic Sciences,
PO Box 120,
HENLEY BEACH, SA 5022.

Telephone: 8207 5400
Facsimile: 8207 5481
<http://www.sardi.sa.gov.au>

DISCLAIMER

The author warrants that he has taken all reasonable care in producing this report. The report has been through the SARDI Aquatic Sciences internal review process, and has been formally approved for release by the Chief Scientist. The recommendations given in this report are based on the best available information at the time of writing. The South Australian Research and Development Institute (SARDI) makes no warranty of any kind, expressed or implied, concerning the use of the information mentioned in this report. To avoid duplication of time and effort, various elements of this review have been paraphrased from Smith (2004).

© 2005 SARDI AQUATIC SCIENCES.

This work is copyright. Except as permitted under the *Copyright Act* 1968, no part of this report may be reproduced by any process, electronic or otherwise, without specific written permission of the author. Neither may information be stored electronically in any form whatsoever without such permission.

SARDI Aquatic Sciences Publication No. RDO4/0064-2
SARDI Research Report Series No. 77
ISBN: 0 7308 5327

Printed in Adelaide April 2005

Author(s): B. B. Smith
Reviewers: J. Carragher & L. McLeay
Approved by: J. Carragher

Signed: 

Date: Friday, 15th April 2005

Distribution: SARDI Aquatic Sciences Library, Pest Animal Control CRC,
CSIRO Marine (Hobart), State Fisheries Departments.

Circulation: Public Domain

“Our window of opportunity to enact a carp control strategy and education program is closing. In a short while, the majority of people won’t be able to remember a river without carp - so where will their vision or desire come from to return the river to a carp-free condition. It is clearly time to focus on what we can do now, and do it”.

(Pierce 1996).

TABLE OF CONTENTS

1. BACKGROUND.....	9
2. AIMS	10
3. SCOPE.....	10
4. INTRODUCTION.....	11
4.1 CARP IN AUSTRALIA	11
4.2 HABITAT USE	12
4.3 EFFECTS ON THE ENVIRONMENT	14
4.4 RESILIENCE TO CONTROL PROGRAMS.....	16
4.5 RESILIENCE TO THE ENVIRONMENT	16
5. AUSTRALIAN INFORMATION.....	18
5.1 AGE AND GROWTH	18
5.1.1 Ageing	18
5.1.2 Validation.....	19
5.1.3 Accuracy, precision and bias in age estimations.....	20
5.1.4 Longevity.....	21
5.1.5 Growth	21
5.1.6 Estimating age from measurements of otolith size and weight.....	28
5.2 REPRODUCTION	30
5.2.1 Overview	30
5.2.2 Previous Australian studies of carp spawning pattern.....	31
5.2.3 Other reproductive information.....	34
5.2.4 Maturation	34
5.2.5 Gonadosomatic index (GSI).....	35
5.2.6 Gonad staging.....	36
5.2.7 Fecundity.....	37
5.2.8 Sex ratio	39
5.3 RECRUITMENT	39

5.4	MOVEMENT (DISPERSAL) PATTERNS	40
5.4.1	<i>Dispersal through fishways</i>	41
5.4.2	<i>Lateral spawning migrations</i>	41
5.4.3	<i>Downstream transport of young carp</i>	42
5.4.4	<i>Diurnal movement patterns</i>	42
5.4.5	<i>Tagging using radio-transmitters, and dart and T-bar tags</i>	43
5.4.6	<i>Exploiting the “jumping instinct” of carp</i>	44
5.4.7	<i>Evaluating potential barriers to movement</i>	44
5.5	DIET AND FEEDING	45
5.6	MORTALITY AND PREDATION	46
5.7	ABUNDANCE.....	47
5.8	MAXIMUM SIZE	48
5.9	DISEASES INTRODUCED TO AUSTRALIA BY CARP	49
5.10	SAMPLING METHODS.....	49
6.	PRIORITIES FOR FUTURE CARP RESEARCH.....	51
6.1	CONFIRM THE ACCURACY OF THE AGEING METHOD.....	51
6.2	THE RECRUITMENT PROBLEM: DEFINING STOCHASTICITY WITHIN CARP POPULATION MODELS	52
6.3	POPULATION STRUCTURE	53
6.4	IDENTIFYING “HOT SPOTS” FOR CARP SPAWNING AND RECRUITMENT	54
6.5	CONTINUED DEVELOPMENT OF NOVEL METHODS TO EXPLOIT INSTINCTUAL SPAWNING AND DISPERSIVE MOVEMENTS.....	55
7.	ACKNOWLEDGEMENTS.....	56
8.	REFERENCES.....	57

1. BACKGROUND

In January 2003, the Murray-Darling Basin Commission, through the Pest Animal Control CRC, and in alignment with the Commission's Native Fish Strategy, initiated their 'Daughterless Carp' (DC) program; a blue-sky project of relatively high risk, aimed at reducing the number of common carp (*Cyprinus carpio*) in the Basin by severely skewing the sex-ratio of wild carp towards males. Although in its early stages, the DC technology offers promise in the long-term because the genetic sequence used to produce daughterless carp is found naturally in the carp itself, and is species-specific and self-liberating.

The genetic DC technology is currently being trialled in the laboratory with Medaka (*Oryzias latipes*) before testing with common carp. Medaka is more apposite for genetic trials because it thrives under laboratory conditions, and has short generation times due to its small size, fast growth and early maturity. Testing on carp is, however, imminent. In the meantime, carp population models are being developed by the Commonwealth Scientific and Industrial Research Organisation (CSIRO Marine, Hobart) and Primary Industries and Resources Victoria (PIRVIC) to establish appropriate release strategies, to indicate the likely spread of the daughterless gene post-release, and to test combinations of complementary control scenarios as part of an Integrated Pest Management program (Haddon 2003).

To ensure that the models are useful, their inputs must be realistic i.e., all aspects of carp ecology, and variations among heterogenous environments must be understood at spatial scales relevant to the Basin-wide control of carp. To this end, an evaluation of existing data for modelling purposes is not available. Accordingly, this review summarises the available information on common carp in Australia.

2. AIMS

This review had three aims:

1. To collate, synthesise and evaluate Australian information on carp population dynamics, to help optimise the CSIRO and PIRVIC models.
2. To dispel obvious myths about carp and provide a comprehensive document to interested parties regarding the ecology of carp in Australia.
3. To establish priorities for future research by identifying knowledge gaps, thus saving time and other resources by avoiding duplication of research.

3. SCOPE

This review included information from peer-reviewed articles in scientific journals, “in-house” fishery and departmental reports, and unpublished manuscripts and honours, masters and PhD theses. Other media including photographs, newspapers, commercial catch records, anecdotes and museum collections were excluded because they provide low to zero ecological information (Ebner and Roberts 1997). In addition, articles focussed on control strategies other than Daughterless Carp (Hume *et al.* 1983a; Harris 1995; Roberts and Tilzey 1996) and prior review articles (Wharton 1979; King 1995; Roberts and Ebner 1997a, b; Koehn *et al.* 2000) were excluded because none specifically consider Australian data, and in this instance, an evaluation from the primary data source was required. Also, significant new information has arisen from large-scale research projects since the last comprehensive review was published (Koehn *et al.* 2000).

With respect to the larger studies of carp ecology, only the final report and associated published papers are reviewed: annual reports and their associated chapters are not. For example, although a pioneering 3-year study of carp ecology in the Goulburn River Basin resulted in three Annual Reports, a bibliography of carp studies, and three separate reviews of carp biology, genetics and environmental impacts, only the Final Report was considered (Hume *et al.* 1983a). Further, research published via the mainstream scientific literature was evaluated in preference to original data contained within unpublished reports or the relevant chapters of PhD theses.

4. INTRODUCTION

4.1 CARP IN AUSTRALIA

The common carp, *Cyprinus carpio* (Linnaeus) (Teleostei: Cypriniformes: Cyprinidae), is the sole member of the genus *Cyprinus* (Artemi). In Australia, carp are the largest alien pest fish species, and there are three distinct varieties, each with a different pattern of scales. The original form of carp, *C. carpio* var. *communis*, has regular rows of scales covering the entire body. The mirror carp, *C. carpio* var. *specularis*, has a few, large, bright scales divided by naked skin. The koi carp is a coloured variant of the scale and mirror varieties and the line carp, another variety of mirror carp, has a prominent line of regular scales along each side of the body. Finally, the leather carp, *C. carpio* var. *nudus*, is devoid of scales except for small, degenerate scales at fin bases and along the dorsal fin (Stead 1929; Alikunhi 1966; Balon 1995b, a). All varieties are present in Australia, although the mirror and particularly the leather varieties are uncommon. For example, in Victoria, mirror carp are widespread but comprise only 1.6% of carp caught (Hume *et al.* 1983a).

In addition to the three varieties, there are also three resident strains of carp in Australia, identified by DNA analysis (Mulley *et al.* 1980; Hume *et al.* 1983a; Davis *et al.* 1999). *Yanco*, a Singaporean strain of koi, was released into the Murrumbidgee Irrigation Area (Griffith) in 1876. The ornamental *Prospect* strain was introduced to Prospect Reservoir (Sydney) in 1907 (Stead 1929) and perhaps also during the 1850s (Brumley 1996). Both strains were non-invasive, and remained near the sites of release (Weatherly and Lake 1967; Shearer and Mulley 1978; Wharton 1979; Davis *et al.* 1999). In 1960, however, the wild *Boolarra* strain was imported illegally from Germany (Shearer and Mulley 1978; Hume *et al.* 1983a). In defiance of Victorian authorities, Boolarra carp were liberated to farm dams throughout Gippsland. In 1962, the State Government legislated to ban sales and eradicate carp, but individuals were later discovered in Serpentine Creek and the Yallourn Storage Dam in the Latrobe Valley (Olsen 1995).

In 1968, the Boolarra carp gained entry into the Murray River via Lake Hawthorne near Mildura (Wharton 1979; Brown 1996). They dispersed widely during floods in 1974-75, and subsequently interbred with koi (Yanco) carp in the Murrumbidgee River to produce a stock with a broad genetic makeup (Brumley 1996). Today, carp are ubiquitous in the Murray-Darling Basin (MDB). They have also spread to all Australian states and territories, except for the Northern Territory (McKay 1989).

Intraspecific hybridisation between the Yanco and Boolarra strains of carp and interspecific hybridisation between carp and goldfish (*Carassius auratus*) are commonplace (Trautman 1957; Mulley *et al.* 1980; Hume *et al.* 1983a). The meristic characters of carp × goldfish hybrids are often intermediate between those of the parents. Thus, while carp have two pairs of mouth barbels, goldfish have none and their hybrids have either two reduced pairs or merely a single pair (Hume *et al.* 1983b). In addition, carp and goldfish are distinguished by counts of lateral line scales, by the number and arrangement of pharyngeal teeth and by the position of the dorsal fin in relation to the ventral fins (Verma 1970; Koehn *et al.* 2000). Taxonomic diagnoses of each species are provided by Trautman (1957), Cadwallader and Backhouse (1983) and McDowall (1996). Characters for distinguishing the larvae of carp and goldfish are provided by Gerlach (1983).

4.2 HABITAT USE

Carp are habitat generalists and have spread to all Australian states and territories, except for the Northern Territory. Their major affiliation is with degraded habitats that reflect sustained human impact (review of impacts by Cadwallader 1978). Amongst the highly regulated lowland rivers of the Murray and Murrumbidgee catchments, carp dominate the catch in numbers and biomass, and species diversity is low (Gehrke *et al.* 1995b; Gehrke and Harris 2000; Gehrke and Harris 2001). Where semi-natural flow patterns and diverse plant and animal communities are maintained, however, carp are absent or present in only minor numbers (Hume *et al.* 1983a; Gehrke *et al.* 1995b). The effect of human impact on riverine fish fauna has been highlighted in four catchments of the MDB, by associating species diversity (Shannon's H) and the annual proportional flow deviation (APFD) (Figure 1) (Gehrke *et al.* 1995b):

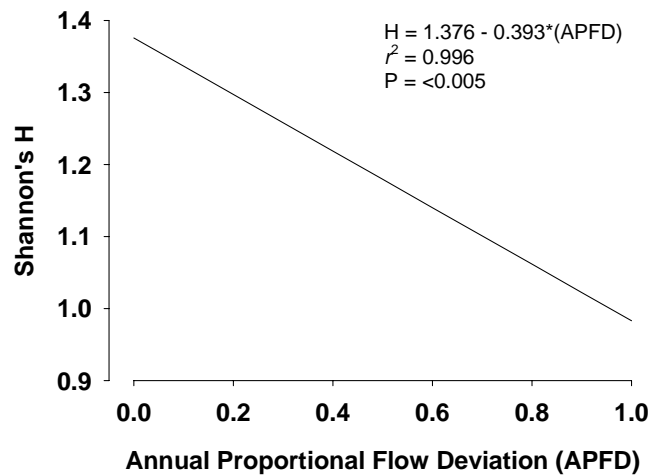


Figure 1. Regression relating species diversity (Shannon's H) and the annual proportional flow deviation (APFD). Regression from Gehrke *et al.* (1995b).

Carp may be found amongst all the major and minor aquatic habitat types including the main channel, floodplain lakes, anabranches, swamps, billabongs, irrigation channels, macrophytes, open water, overhanging riparian vegetation, undercut banks and woody debris (Stuart and Jones 2002; Nicol *et al.* 2004). They prefer sites with diverse habitat (Merideth 1996), and although carp are rarely found in montane sites at altitudes > 500 m above sea level (ASL), a marginal relationship indicates that the size of carp increases with altitude (Driver *et al.* 1997). This is probably a reflection of the higher abundance of sub-adult carp in lowland rivers, where carp recruitment is greatest (Gehrke and Harris 2000).

The daily and seasonal habitat use of carp is dynamic. Major habitat shifts occur with the change in season and the variation that this brings to light, temperature, stream-flow and other environmental conditions. During low flows in winter (all seasons are austral; winter is June, July, August), carp form aggregations in deep river water. Prior to the onset of high river flows in spring, carp have been found to congregate around key access points to off-stream spawning habitat (Stuart and Jones 2002). Subsequently, they are the first large species to colonise the wetlands and are often the last to leave. Consequently, many become trapped and die (Stuart and Jones 2002). Young-of-the-year (YOY) carp are strongly affiliated with submerged macrophytes (Hume *et al.* 1983a; Vilizzi and Walker 1999b; Smith and Walker 2003a, b; Smith 2004).

4.3 EFFECTS ON THE ENVIRONMENT

Many of the assertions regarding the effects of carp on the environment are speculative and based on uncritical extrapolations from observations of captive fish (i.e., Khan *et al.* 2003). Yet, debate about whether carp are a cause or symptom of declining river health is unremitting. In that regard, carp are claimed to increase turbidity, disturb and re-distribute benthic seeds and invertebrates, undermine aquatic plants, prevent the establishment of seedlings and compete with small native fishes for food and space. Indirectly, they are also implicated in the development of toxic algal blooms and in reducing the growth of algal biofilms and aquatic plants. These concerns primarily relate to the benthic feeding of carp, whereby mouthfuls of bottom sediment are sucked into the mouth and separated from food in the pharyngeal slits (Sibbing *et al.* 1986). Food items are retained, finer particles are expelled behind the opercula and large particles are forcibly egested (Lammens and Hoogenboezem 1991).

Two factors make it difficult to assess the effects of carp in natural systems. First, carp have been established in most parts of the MDB for several decades and documented information on the condition of river and wetland environments before their introduction is virtually non-existent (Robertson *et al.* 1997). Thus, true “before and after” comparisons are unworkable. Second, the establishment of carp in Australia was preceded, and assisted, by co-occurring anthropogenic influences. Accordingly, it is virtually impossible to discriminate the short-term effects of carp from the long-term, cumulative effects of human disturbance. These stem from river regulation, catchment clearance and destruction of riparian vegetation, overgrazing, bank erosion, siltation, ‘river improvement’ schemes, pesticide use and overfishing (Cadwallader 1978; Walker 1983). In essence, carp thrive in degraded environments supporting plant and animal communities with little resistance to invasive species (Driver *et al.* 1997). This, together with the species conspicuous behaviour has encouraged a belief that carp are the primary cause, rather than a contributor or symptom of degradation (Roberts 1996).

Previous attempts to investigate the environmental effects of carp in Australia have been inconclusive and contradictory. Analyses have been hindered by low statistical power owing to interaction of main effects, a lack of experimental controls and few replicates, and the inability to maintain and monitor desired levels of carp abundance, or by failing to consider temporal changes in carp behaviour. Indeed, in many cases, the experiments were obscured by the variability inherent in large-scale systems (e.g. Wharton 1979; Hume *et al.* 1983a; Fletcher *et al.* 1985; Gehrke and Harris 1994; Recknagel *et al.* 1995; Roberts *et al.* 1995; King *et al.* 1997; Robertson *et al.* 1997; Loughheed *et al.* 1998).

Despite the limitations noted above, the mere presence of carp and their sheer biomass in many of Australia's lowland rivers (Gehrke *et al.* 1995b; Gehrke and Harris 2000) must contribute to river degradation. Effects are likely to be greatest in small, shallow (drying) lakes with high densities of carp and limited food resources (Fletcher *et al.* 1985). In these instances the effects that carp are accused are probably realistic. There is no evidence, however, to suggest that carp:

1. Uproot vegetation that they spawn over.
2. Undermine emergent, robust plants (i.e., *Juncus*, *Typha*, *Phragmites* spp.), or species that form dense masses and thick growth (*Myriophyllum*, *Ludwigia* spp.). Only submerged, shallow-rooted aquatics with soft-leaves are vulnerable (i.e., *Potamogeton*, *Chara* and *Vallisneria* spp.).
3. Undermine river-banks or contribute to bank slumping.
4. Reduce plant growth via sustained shading caused by temporary increases in turbidity.

4.4 RESILIENCE TO CONTROL PROGRAMS

The resilience of carp to control (physical removal) programs is exemplified by their continued occupation of Lakes Crescent (2365 ha) and Sorrel (4770 ha), Tasmania, despite 10 years of sustained fishing effort. In January 1995, when carp were first discovered, the lakes were immediately closed to fishing, and a weir with a series of mesh screens was installed at the outlet of Lake Crescent; the downstream lake. An intensive eradication program using fyke nets, seine nets, gill nets, traps, and backpack and boat-electrofishing was initiated. Water level manipulations and fencing have also been used to limit and prevent carp access to preferred spawning habitat (marshy areas). Further, in 1997, radio-tagged male 'Judas' fish were used to identify spawning/overwintering aggregations, and to help understand carp movements and habitat preferences; nonetheless, intermittent spawning has occurred in both lakes (Walker and Freeman 2003; Diggle *et al.* 2004).

Whilst the program has proven successful in reducing the population from *c.* 8,000 to 30 fish in Lake Crescent, the last fish are proving difficult to remove (an optimistic estimate suggests another 140 fishing days will be required to remove the last fish; a conservative estimate is 213-435 days - Diggle *et al.* 2004), and a strong reproductive population still exists in Lake Sorrell. Consequently, whilst eradication is still the long-term goal of the Inland Fisheries Service, in the short-term, they hope to remove the last female fish because female fish are highly fecund and this intermediate goal is thought to be more achievable (Donkers 2003; Day *et al.* 2004).

In the Campaspe irrigation supply channels, chemical treatments have also proven ineffective. In almost 12 km of channel, immigration and rapid recruitment has allowed carp to re-establish strong populations, despite up to three virtually complete fish kills by acrolein treatment in the past 8 years (Brown *et al.* 2003).

4.5 RESILIENCE TO THE ENVIRONMENT

The ability of carp to disperse widely and displace native fish is linked to intrinsic attributes that predispose them for survival in diverse habitats and equip them as invaders (Koehn 2004). Among freshwater fish, carp are particularly remarkable for their physiological tolerances. This is reflected in their wide distribution and generalist choice of forage and habitat. Reports

from Northern Hemisphere countries confirm their extreme adaptability. One notable article suggests that carp have survived being frozen in ice, are capable of burrowing into the bottom mud to a depth of 20-30 cm to escape fishing gear, and can withstand a layer of silt up to 50 cm in depth (Alikunhi 1966).

In Australia, only the tolerances of carp to salinity and blue-green algae have been investigated, and observations of larval tolerance to toxic polyphenols and hypoxia have been noted (Gehrke 1991, 1992). With respect to the salinity tolerance of carp, mature fish from Lakes Alexandrina and Albert survived direct transfer to salinities of 12.5 ppt at 16-21°C and with acclimation over 38 days, there was 50% survival at 15 ppt (c. 43% sea-water) (Geddes 1979). The tolerance of juvenile carp from the lower Murray is similar (direct transfer $LC_{50} = 11.7$ ppt; slow-acclimation $LC_{50} = 13.1$ ppt) but sperm viability may be reduced in salinities above a critical threshold of 8.3 ppt (Whiterod 2001). Although carp tolerate high salinities, they apparently avoid conditions above 3.4 ppt (Shane Warrick, commercial fisherman, pers. comm., cited in Whiterod 2001). Thus, salinities in many inland Australian rivers will not restrict the distribution of carp (nor will climatic conditions; see Koehn 2004) but many wetlands in the MDB are considerably more saline and carp populations there may be affected by reduced recruitment and survival, and alteration of physiological systems and behavioural patterns (Geddes 1979; Whiterod 2001).

Blue-green algae are common in regulated, freshwater environments enriched with dissolved nitrogen and phosphorous. They proliferate during spring and summer, and algal 'blooms' can form a visible scum on surface waters during warm, calm weather. These blooms are largely comprised of cyanobacteria such as *Microcystis aeruginosa*; the cells of which contain toxic microcystins. After intestinal absorption, microcystins accumulate in the liver where they cause liver failure in mammals, birds and some fish. However, carp are agastric (they have no stomach either) and their entire digestive tract is neutral or basic (Carbis *et al.* 1997; Billard 1999); this limits the absorption of microcystins, which requires an acidic environment. Thus, although carp at lake Mokoan, Victoria, were exposed to a blue-green algal bloom over 4 months, and ingested *M. aeruginosa*, no mortalities or clinical indications were reported (Carbis *et al.* 1997).

5. AUSTRALIAN INFORMATION

5.1 AGE AND GROWTH

5.1.1 Ageing

Interpretations of annulus patterns in carp scales, opercular bones and otoliths are not easy, and instruction and experience are required for precise assessments.

(Vilizzi *et al.* 1998, p. 125)

Age data are critical in fisheries management. They indicate age at maturity and other growth transitions, spawning, hatch and settlement dates, rates of growth, mortality and recruitment and morphometric relationships. Age is estimated via enumeration of growth increments in otoliths, scales, opercles, fin rays and vertebrae. Under a light microscope, these appear as paired concentric, translucent (light) and opaque (dark) bands, typically representing one year's growth for mature fish or one day for young-of-the-year (YOY) fish aged 0+ (fish in their first growing season).

Mature fish

Early comparative studies of potential ageing structures in carp suggested that scales were most appropriate to read, collect and handle (Jones 1974; Hume *et al.* 1983a). Notably, they are also desirable as a non-destructive sampling method. However, this judgment appears to have been based on the convenience of collecting scales and the diminutive effort required to process them, rather than on a rigorous evaluation of growth patterns. In both cases, only a cursory examination of otoliths (pair not named), opercles and dorsal fin rays was made from a few individuals. This conclusion is reinforced by a statement from Hume *et al.* (1983a) - "otoliths were found to be too small and difficult to extract, fin spines required much preparation and sectioning, and opercular bones were bulky to store and required cleaning and drying after collection" (p. 72).

Otoliths are most often used in ageing studies because scales have been found to underestimate the age of old fish. Scales also have a tendency to be resorbed or eroded at the margins and their annual growth checks are comparatively hard to decipher from other marks. Each of these problems were evident in studies by Hume *et al.* (1983a), where scales were only judged to be useful in ageing fish < 3+ years. Indeed, otoliths, specifically the asterisci,

show the greatest utility for ageing carp: the lapilli have been found to be useful only when 2-3 annuli are present, and the sagittae show no recognizable pattern (Vilizzi and Walker 1995). Sectioned asterisci are recommended for ageing carp by Day *et al.* (2004), Diggle *et al.* (2004) and Brown *et al.* (2004), and whole asterisci by Vilizzi and Walker (1999a). Although sectioning is usually found to improve the clarity of otolith increments, the latter authors found that sectioning obscured increments near the otolith edge. Vilizzi and Walker (1999a) also advocate the use of opercular bones to age fish > 10+ years to resolve difficulties in the detection of later annuli.

Larvae and Juveniles

Whereas a range of bony structures is potentially useful in ageing mature carp, only otoliths are suitable for ageing YOY fish. In carp, as in other teleosts, other structures are not formed until near the time of the larva-juvenile transition (Vilizzi 1998; Vilizzi and Walker 1999b). Of the three pairs of otoliths, only the lapilli show obvious daily increments (Vilizzi 1998). These increments are most easily enumerated in young fish up to *c.* 3 months of age (Vilizzi 1998; Smith and Walker 2003b; Smith 2004; Smith and Walker 2004a). Whilst Vilizzi (1998) suggested that it was not necessary to grind otoliths (sagittal sectioning of lapilli) for carp with < 20-30 micro-increments, Smith and Walker (2003b) recommend that all otoliths be ground to achieve the highest clarity of otolith increments. Further, age estimates should be reduced by 1 to allow for there being, on average, one increment present at the time of hatching (Smith and Walker 2003b).

5.1.2 Validation

Mature Fish

Validation is an essential criterion of age-based studies, and is required to ensure that age estimates reflect true ages. In that regard, Campana (2001) provides an excellent review of methods, and advocates the use of known-age fish when possible. However, only Marginal Increment Ratio Analysis (MIRA), Edge Type Analysis (ETA) and capture-mark-release-recapture methods have been used in South Australia and Victoria with fish aged up to 14+ years (Vilizzi and Walker 1999a; Brown *et al.* 2004). In South Australia, the time at annulus formation was estimated at Nov/Dec for otoliths and Oct/Nov for scales and

opercular bones (Vilizzi and Walker 1999a). To establish the age at first annulus formation, Brown *et al.* (2004) repeatedly sampled a discrete YOY cohort over 1 year.

Larvae and juveniles

Vilizzi (1998) was the first to validate the daily deposition of otolith increments to *c.* 50 days in YOY carp using tetracycline-marked, laboratory-reared fish. Subsequently, Smith and Walker (2003b) used known-age, laboratory-reared carp to determine the number of increments present at hatching (1, range 0-2). They also confirmed that light microscopy alone (as opposed to a combination of light- and scanning-electron microscopy) is sufficient for ageing YOY carp to *c.* 45 mm SL or 3 months of age.

5.1.3 Accuracy, precision and bias in age estimations

The definitions of accuracy and precision in teleost age estimation are most easily expressed via an analogy with throwing darts at a dart-board (Campana 2001). Accurate throwers hit the bulls' eye every time. Precise throwers may never do this, but they might consistently hit another number. The goal of ageing studies is to hit the bulls' eye (determine the true age of the fish) on every throw (every time an age estimate is made). Accuracy may be confirmed or strengthened via validation, whilst precision (the consistency of age interpretations between or within-readers) is usually articulated as the coefficient of variation (CV) or the index of average percent error (IAPE). Between-reader bias is evaluated via an age-bias plot.

Mature fish

The between-reader precision of age estimates made from whole and sectioned carp otoliths rarely exceeds the 95% target suggested by Campana (2001). This implies that annuli are hard to distinguish and therefore, that carp are a difficult species to age. Estimates of precision are also spatially variable, meaning that there may be (a) basin-wide variation in the clarity of otolith increments, (b) differences in laboratory protocols used in otolith processing, or (c) differences in the experience of interpreters and their familiarity with the structures in question (Vilizzi and Walker 1999a; Brown *et al.* 2004; Diggle *et al.* 2004).

In South Australia, estimates of IAPE and CV for annulus counts made from whole otoliths ranged from 6.2-12.7% and 8.8-18%, respectively (Vilizzi *et al.* 1998; Vilizzi and Walker 1999a). In Victoria and Tasmania, estimates for CV are typically less than 8% and 5% respectively (Brown *et al.* 2004; Diggle *et al.* 2004). In each of these studies, between-reader bias was not considered to be a problem. No estimate for the accuracy or precision of scale readings is available (Jones 1974; Hume *et al.* 1983a).

Larvae and juveniles

In comparison with mature fishes, the ageing of YOY carp is an easy and relatively straight-forward process. This is indicated by the high precision (IAPE and CV < 3 %) and estimated accuracy (100% within 3 days) of the ageing method (Smith and Walker 2003b).

5.1.4 Longevity

The maximum age recorded for carp in Australia is 32 years, although most carp are in the range 3-11 years (Brown *et al.* 2003).

5.1.5 Growth

Mature fish

The pattern of growth for fish is analogous to the growth pattern of humans. That is, until soon after maturation, fish grow rapidly in length. Subsequently, growth in length declines to an asymptote, the fish stop growing in length and begin growing in girth (weight). Fish growth in length and weight are best described by the standard- and weight-adjusted Von-Bertalanffy growth functions (VBGF), respectively (Equations 1-2):

Standard VBGF:
$$L_t = L_\infty \left(1 - e^{-K(t-t_0)}\right) \dots \dots \dots \text{Equation 1.}$$

Where L_t is the mean total length at age t ; L_∞ is the asymptotic mean length predicted by the equation; K is a curvature parameter describing how rapidly this length is achieved, and; t_0 is the hypothetical age (years) at which length would be zero, if growth followed that predicted by the equation. The weight-adjusted VBGF is similar, although it incorporates another constant, b (Equation 2).

Weight-adjusted VBGF: $W_t = W_\infty \left(1 - e^{-K(t-t_0)}\right)^b$ Equation 2.

The weight-length relationship is described by a two-parameter power function (Equation 3):

$$Weight = a.Length^b \quad \text{.....Equation 3.}$$

In Australia, mature carp are sexually dimorphic and their growth is spatially and temporally variable, and different from northern hemisphere countries (Jones 1974; Hume *et al.* 1983a). Females grow at a faster rate than males (Vilizzi and Walker 1999a; Brown *et al.* 2003) and attain larger body sizes (Stuart and Jones 2002). Whilst some studies have also found gender differences in the length-weight relationship (Brown *et al.* 2003), others have not (Vilizzi and Walker 1999a). Growth is fastest immediately after a flood and in spring when water temperatures are warm and food is relatively abundant (i.e., in 1981, Hume *et al.* 1983). It is low during winter and during periods of drought or low flows (Hume *et al.* 1983).

Tables 1-3 and Figures 2-4 illustrate the gender, spatial and temporal variation in carp growth, and the effect that this has on length-at-age, weight-at-age and weight-length relationships.

Table 1. Von-Bertalanffy growth equation parameters (see Equation 1) describing the length-at-age relationships for carp in the Campaspe irrigation supply channels, Barmah-Millewa forest and the South Australian Murray.

Study	Location	Sex	L _{max}	L _{infinity}	K	t ₀	r ²
Brown <i>et al.</i> (2003)	Campaspe irrigation supply channels	M	570	495	0.48	-0.29	n/a
		F	680	538	0.38	-0.39	n/a
	BarmahMillewa forest and surrounds	M	570	489	0.25	-0.52	n/a
		F	623	594	0.18	-0.61	n/a
Vilizzi and Walker (1999)	South Australian Murray	M		600.3	0.35	0.17	0.32
		F	700	639.2	0.35	0.17	0.35

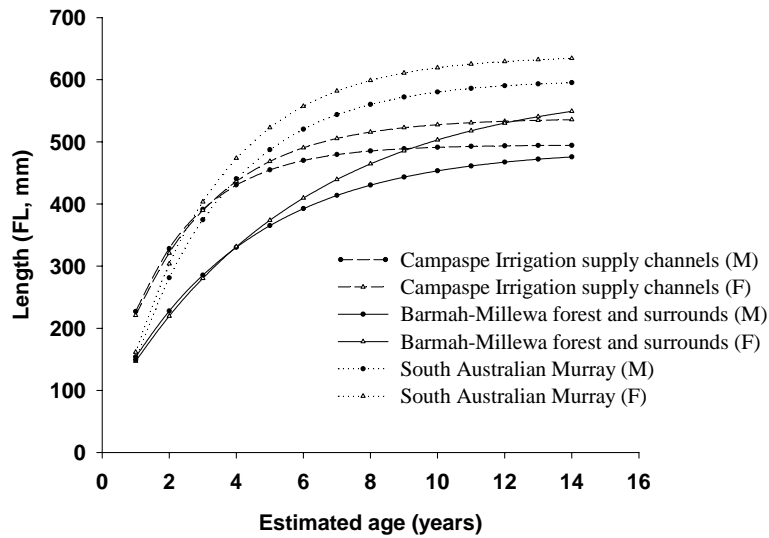


Figure 2. Von-Bertalanffy growth curves illustrating the gender, spatial and temporal variation in growth (length-at-age relationships, parameters in Table 1) for carp in the Campaspe irrigation supply channels, Barmah-Millewa forest and the South Australian Murray.

Table 2. Weight-adjusted von-Bertalanffy growth equation parameters (Equation 2) describing the weight-at-age relationship for male and female carp in the South Australian Murray.

Study	Location	Sex	w_{max}	$w_{infinity}$	K	t_0	b	r^2
Vilizzi and Walker (1999)	South Australian Murray	M	4.749	0.279	-0.242	2.848	0.35	
		F	5.123	0.314	-0.242	2.857	0.318	

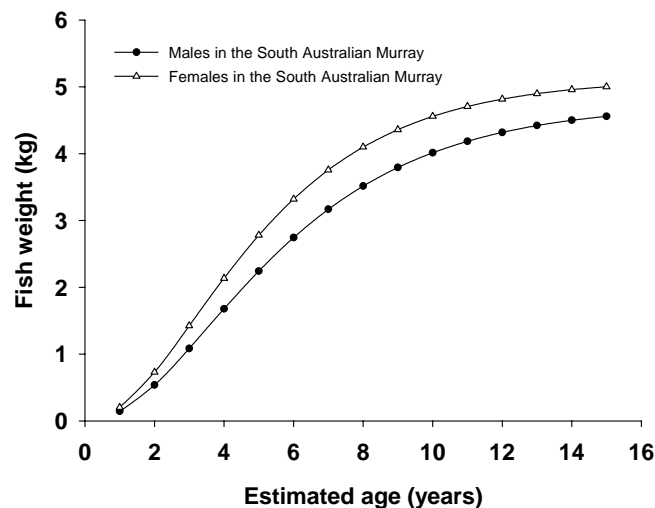


Figure 3. Weight-adjusted von-Bertalanffy growth curves illustrating the variation in growth (weight-at-age relationships, parameters in Table 2) for male and female carp in the South Australian Murray.

Table 3. Parameters for the power function (Equation 3) describing the relationship between fish weight (g) and length (FL, mm) for carp in Lakes Crescent and Sorrell (Tasmania), the South Australian Murray, the Campaspe irrigation supply channels, Barmah-Millewa forest and the Glenelg River/Rocklands Reserve.

Study	Location	Sex	a	b	r ²	n
Vilizzi (1998)	Lakes Crescent and Sorrell, Tasmania	M + F	4.60E-05	2.8560	0.963	332
Vilizzi and Walker (1999)	South Australian Murray	M + F	3.50E-05	2.9430	0.9	484
	Campaspe irrigation supply channels*	M	3.73E-05	2.9019	n/a	n/a
		F	4.11E-05	2.9019	n/a	n/a
Brown et al. (2003)	Barmah Millewa forest and surrounds*	M	1.74E-05	2.9999	n/a	n/a
		F	1.67E-05	2.9999	n/a	n/a
	Glenelg River / Rocklands Reserve	M + F	5.50E-06	3.2397	n/a	n/a

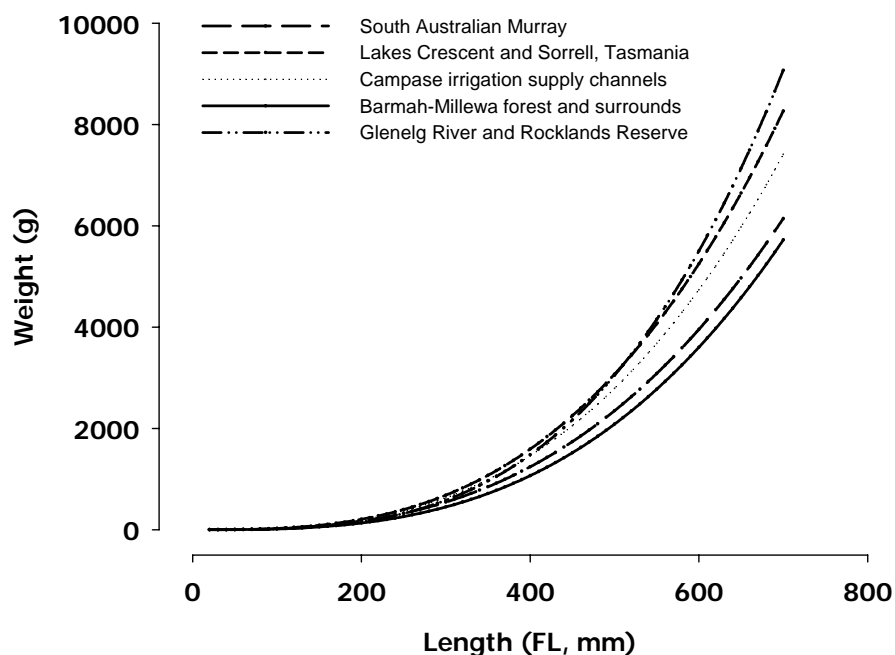


Figure 4. Growth curves illustrating the spatial variation in weight-at-length for carp in the South Australian Murray, Lakes Crescent Tasmania, Campaspe irrigation supply channels, Barmah-Millewa forest and the Glenelg River/Rocklands Reserve (parameters in Table 3). NOTE: although the weight-length relationships were determined to be statistically different at some locations, the biological differences are not visually obvious. Thus, for these sites and for clarity of comparison, only the female data is presented.

Larvae and juveniles

In studies of the age and growth of larval and juvenile fish, there are three caveats that must be considered. The first relates to the shrinkage of YOY fish that occurs upon fixation or preservation. In that regard, collections of larval and juvenile fish often are not processed in the field or within hours (or even weeks) of collection (unlike most mature fishes), and must be preserved to minimise post mortem degeneration. Preservation causes body shrinkage, however, and pre-preservation measurements of body size must be calculated from

measurements made after preservation. With respect to YOY carp (10-45 mm SL) regression equations are available for specimens preserved in 70% and 95% ethanol (Smith and Walker 2003a). These are important since length shrinkage peaks at about 14% and weight shrinkage peaks at about 75% for the smallest individuals (Smith and Walker 2003a). The second and third caveats relate to adjustments that must be made to calculations of estimated age- and growth rates. Thus, all age estimates for larval and early-juvenile carp (10-45 mm SL) should be reduced by one day, to account for the occurrence of one visible increment at the time of hatching (Smith and Walker 2003b). In addition, calculations of growth rates should only consider post-hatch lengths, because typically only post-hatch ages are calculated (Equation 4). If this is ignored, growth rate estimates are exaggerated, particularly with respect to very small/young fish.

$$\text{Growth Rate (mm.d}^{-1}\text{)} = \frac{\text{shrinkage corrected length at capture} - \text{mean length at hatch}}{\text{daily increment count (adjusted for the mean number of increments at hatching)}} \dots\dots\dots \text{Equation 4.}$$

To date, three Australian studies have used daily increment counts to study the age and growth of YOY carp (Vilizzi 1998; Smith and Walker 2004a, b) and of these, only two considered the aforementioned caveats (Smith and Walker 2004a, b). Thus, only data from Smith and Walker (2004a, b) is considered here.

Analyses of length-at-age and weight-at-age relationships indicate that larval and early-juvenile (10-45 mm SL) growth is highly variable between locations and years, but there is no difference in the weight-length relationship. Mean growth rates depend on the average size and age of fish examined but are typically in the range 0.3-0.7 mm.d⁻¹, (Smith and Walker 2004a). Fish that are spawned late in the season (Feb 11 - April 10) grow faster than those spawned early (onset - Dec 10), or in the middle (Dec 10 - Feb 10) of the season. While early spawned fish grow relatively slowly, they benefit from a long growing season and may achieve a greater size by the onset of winter than late-spawned, faster growing fish.

Tables 4-6 and Figures 5-7 below illustrate the spatial and temporal variation in the growth of larval and early-juvenile carp, and the effect that this has on age-at-length, age-at-weight and weight-length relationships.

Table 4. Regression equation parameters describing the age-at-length relationships for larval and juvenile carp in the lower River Murray at Walker Flat (“Walker Flat South”, WFS), Punyelroo (PUN) and Gurra Lakes. The equations for Walker Flat and Punyelroo are in the form of a 3-parameter power function, whilst for Gurra Lakes, it is a linear regression split for larvae and juveniles.

Study	Location	Age = $Y_0 + a \cdot \text{length}^b$				n
		Y_0	a	b	r^2	
Smith and Walker (2004c)	Punyelroo (PUN) 2001-2002	0.836	1.171	1.113	0.74	161
	PUN 2002-2003	2.068	0.792	1.117	0.64	141
	Walker Flat South (WFS) 2001-2002	-2.635	1.383	1.111	0.74	237
	WFS 2002-2003	-2.578	1.373	1.050	0.85	118
Vilizzi (1998)	Gurra Lakes, near Berri, SA area	Piecewise linear regression				
		larvae: $\text{length}_t = 5.651 + 0.336t$ ($r^2 = 0.75$, $n = 228$)				
		Juveniles: $\text{length}_t = -7.386 + 1.181t$ ($r^2 = 0.69$, $n = 81$)				

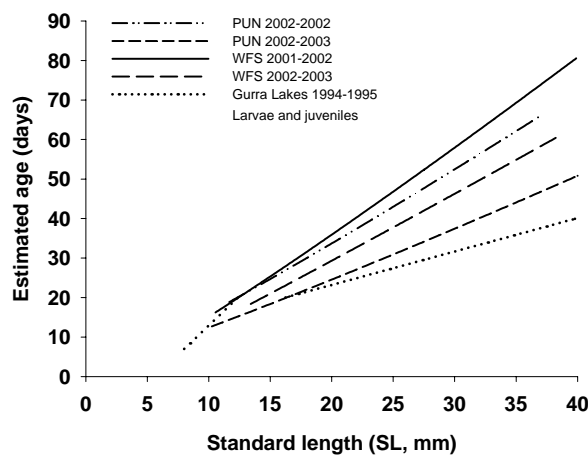


Figure 5. Regressions illustrating the spatial and temporal variation in the age-length relationship (parameters in Table 4) for larval and juvenile carp in the lower River Murray at Walker Flat (WFS), Punyelroo (PUN) and Gurra Lakes.

Table 5. Regression equation parameters describing the age-at-weight relationships for larval and juvenile carp in the lower River Murray at Walker Flat, Punyelroo and Gurra Lakes. The equations for Walker Flat and Punyelroo are in the form of a 3-parameter power function, whilst for Gurra Lakes, it is a non-linear regression split for larvae and juveniles.

Study	Location	Age = $Y_0 + a \cdot \text{weight}^b$				n
		Y_0	a	b	r^2	
Smith and Walker (2004c)	Punyelroo (PUN) 2001-2002	-0.971	57.210	0.322	0.7	161
	PUN 2002-2003	7.955	32.990	0.455	0.68	141
	Walker Flat South (WFS) 2001-2002	-5.228	67.720	-0.321	0.73	237
	WFS 2002-2003	-10.660	60.270	0.257	0.82	118
Vilizzi (1998)	Gurra Lakes, near Berri, SA area	Piecewise non-linear regression				
		larvae: $\text{weight}_t = 76.3 / (1 + \exp(-0.215(t - 23.034)))$ ($r^2 = 0.68$, $n = 228$)				
		Juveniles: $\text{weight}_t = 36.6 / (1 + \exp(-0.079(t - 81.034)))$ ($r^2 = 0.76$, $n = 81$)				

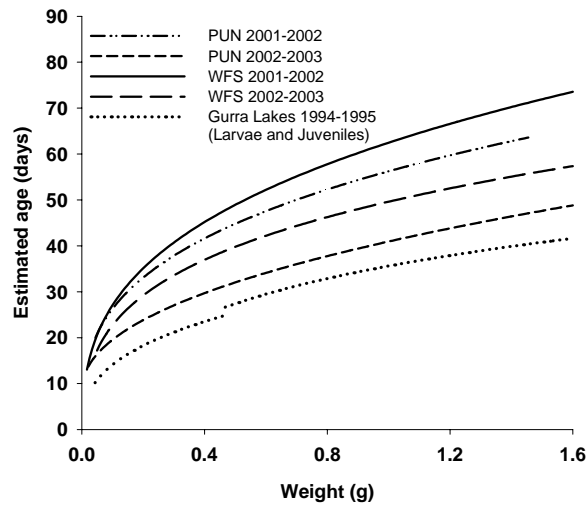


Figure 6. Regressions illustrating the spatial and temporal variation in the age-weight relationship (parameters in Table 5) for larval and juvenile carp in the lower River Murray at Walker Flat, Punyelroo and Gurra Lakes.

Table 6. Regression parameters describing the relationship between fish weight (g) and length (SL, mm) for larval and juvenile carp in two backwaters at Walker Flat (WFS) and Punyelroo (PUN).

Study	Location	Weight = $Y_0 + a \cdot \text{length}^b$				r^2	n
		Y_0	a	b			
	Punyelroo (PUN) 2001-2002	-0.00347	0.00001726	3.154	0.99	161	
Smith and Walker (2004c)	PUN 2002-2003	-0.01905	0.00002311	3.082	0.99	141	
	Walker Flat South (WFS) 2001-2002	0.03452	0.00003613	2.958	0.98	237	

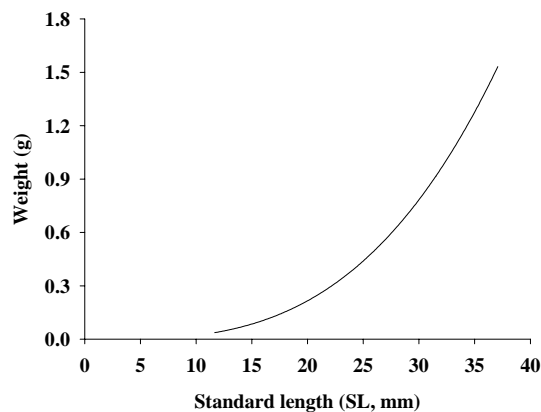


Figure 7. Growth curve illustrating the weight-length relationship for larval and juvenile carp (10-45 mm SL) in the lower River Murray (Parameters in Table 6). NOTE: there is no statistically significant difference in this relationship between locations (WFS + PUN) and years (2001-02 + 2002-03).

5.1.6 Estimating age from measurements of otolith size and weight

Estimating the ages of a large number of fish, via enumeration of otolith increments, is a relatively complex and time-consuming process. An alternative and faster method is to estimate age from measurements of otolith size. To do this, relationships between age and otolith size and weight are first described for a small sub-sample of fish via non-linear statistics. If the amount of variation in age that is explained by its relationship with otolith size is high, then the relationships may be useful in predicting the ages of remaining fish; and *vice versa* if the explained variation is low. The potential for ageing carp from morphometric relationships between age and otolith size are examined below.

Mature fish

For mature carp, otolith weight (followed by otolith width and otolith length) explains the greatest amount of the variation in age, but the explained variation is too low ($r^2 = <0.64$) to warrant the computation of a predictive relationship. This remains true even after inclusion of the addition of all morphometric variables in a step-wise multiple linear regression (Vilizzi and Walker 1999a). A relationship that explains little of the variation in age may be indicative of extreme variability in growth, or otolith increments that are difficult to interpret.

Larvae and juveniles

For larvae and juveniles, regressions are better and typically, more than 85% of the variation in age between locations and years is explained by its relationship with otolith size (Table 7, Figure 8, Smith and Walker 2004a).

Table 7. Growth equation parameters describing the temporal and spatial variation in the relationship between age (days) and otolith length (mm) for larval and juvenile carp at Walker Flat (WFS) and Punyelroo (PUN) in the South Australian Murray.

Study	Location	Y_0	Age = $Y_0 + a \cdot e^{-bx}$			n
			a	b	r^2	
Smith and Walker (2004c)	Punyelroo (PUN) 2001-2002	-55.690	61.430	-0.840	0.83	184
	PUN 2002-2003	-28.630	34.130	-1.060	0.91	141
	Walker Flat South (WFS) 2001-2002	-150.400	148.000	-0.489	0.78	237
	WFS 2002-2003	-128.000	131.100	-0.423	0.93	118

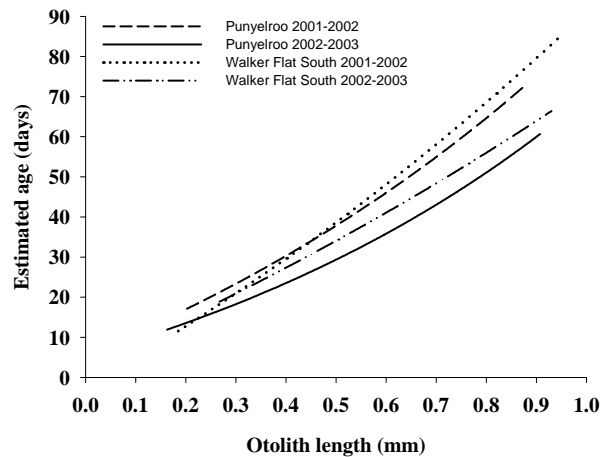


Figure 8. Regressions illustrating the spatial and temporal variation in the age-otolith length relationship (parameters in Table 7) for carp in the lower River Murray at Walker Flat and Punyelroo.

Table 8. Growth equation parameters describing the temporal and spatial variation in the relationship between age (days) and otolith width (mm) for carp at Walker Flat (WFS) and Punyelroo (PUN) in the South Australian Murray.

Study	Location	Y_0	Age = $Y_0 + a \cdot e^{-bx}$			r^2	n
			a	b			
Smith and Walker (2004c)	Punyelroo (PUN) 2001-2002	-154.300	151.900	0.676	0.87	184	
	PUN 2002-2003	-31.360	34.440	1.632	0.87	141	
	Walker Flat South (WFS) 2001-2002	-25.620	32.020	1.974	0.76	237	
	WFS 2002-2003	-157.800	156.500	0.591	0.93	118	

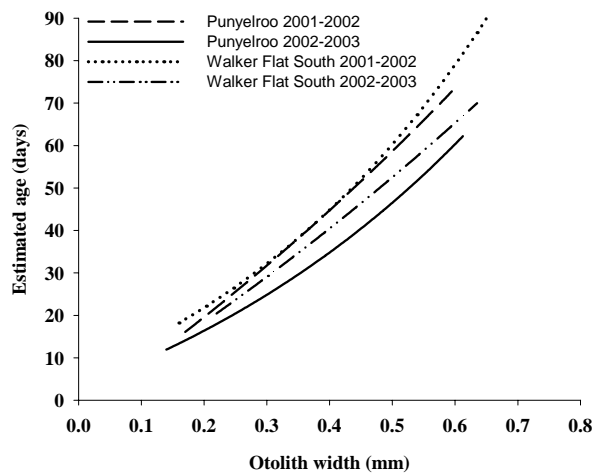


Figure 9. Regressions illustrating the spatial and temporal variation in the age-otolith width relationship (parameters in Table 8) for carp in the lower River Murray at Walker Flat and Punyelroo.

The above-mentioned predictive relationships need to be re-calibrated annually, and also for new populations, to accommodate inherent spatial and temporal variations in growth patterns.

5.2 REPRODUCTION

5.2.1 Overview

Carp are asynchronous, multiple-batch spawners with indeterminate breeding season fecundity (Sivakumaran *et al.* 2003; Smith and Walker 2004c). Egg maturation is complete by the end of winter and reproduction begins in early spring. Spawning occurs during daylight hours and is most intense before 13:00-15:30 pm (Hume *et al.* 1983; BBS, pers. obs.). Not all females spawn at once, and the gonads of individuals include a range of developmental stages (Sivakumaran *et al.* 2003; Smith and Walker 2004c). All oocytes of a matured batch generally are spawned at once, but up to 20% may be retained for repeat spawning (Smith and Walker 2004c). After spawning and absorption of residual oocytes, re-maturation of the ovaries takes at least 3-4 months, or *c.* 1200 degree days (i.e. 60 days at 20°C, Billard 1999).

Carp spawning may occur whenever the mean water temperature and photoperiod exceed 15-16°C and 10h light, respectively, and where there is access to submerged vegetation in shallow, lentic habitat (Hume *et al.* 1983a; Smith and Walker 2003a, b). In South Australia, the temperature and light thresholds are breached annually from about mid-September to March/April (6-7 months), and these dates describe the known spawning period (Smith 2004; Smith and Walker 2004c; Smith and Walker 2004b). In the Barmah-Millewa forest, Victoria, climatic conditions are similar to those in South Australia and carp also spawn from mid-September to April (Sivakumaran *et al.* 2003). Thus, in these locations, individual females probably spawn 2-3 batches of eggs per annum; once at onset and another 3-4 months later when their gonads have re-matured. Even in Lakes Crescent and Sorrel, Tasmania, female carp may spawn up to 2 batches of eggs per annum, as the temperature and light thresholds are breached from November to March (over 5 months) (Donkers 2003; Day *et al.* 2004).

Suitable spawning habitat is scarce in the main channel of most rivers, and consequently, off-stream water-bodies such as Barmah-Milewa forest have been implicated as major point-sources for carp recruitment (Stuart and Jones 2001, 2002).

5.2.2 Previous Australian studies of carp spawning pattern

The results of Australian studies of carp reproduction are contradictory and can largely be categorised as pre- and post-2003. Pre-2003, carp in the southern MDB were thought to spawn once annually over 1-4 months (October to January) and most intensely at the onset of reproduction in spring (Hume *et al.* 1983a; Vilizzi 1998; Smith 1999; Humphries and Lake 2000; Humphries *et al.* 2002; Stuart and Jones 2002; but see Jones 1974). Post-2003, carp were found to spawn over 6-9 months, with two peaks in reproductive activity around spring and autumn (Sivakumaran *et al.* 2003; Smith and Walker 2004a, b, c). These latter reports are consistent with observations by commercial fishers on the Murray, who believe that carp spawn throughout most of the year (S. Warrick, pers. comm.). Ecological/meteorological data from the global literature confirms the likelihood of this scenario, largely because mean water temperatures in the region exceed the spawning requirement for 6-7 months, but also because of flow regulation, and the abundance of spawning habitat in shallow off-stream water bodies. The results of each study are described below:

Pre-2003

In 1979, the Victorian Fisheries and Wildlife Division initiated an inaugural three-year Australian study of the ecology and impact of carp in the Goulbourn River catchment near Shepparton (Hume *et al.* 1983b). With regards to carp reproductive strategy, information on the size- and age-at-maturity, fecundity, gonadosomatic index (GSI), pre-spawning migrations, and spawning pattern was provided. Carp spawning pattern (timing, frequency, duration) during 1980-82 was inferred by monitoring the ovarian condition of mature fish via the GSI and macroscopic staging, and from the monthly capture of YOY carp. Spawning timing and hatch dates were subjectively back-calculated from age-length regressions, and water temperatures corresponding to these 'spawning dates' were predicted from bi-weekly temperature readings. It was concluded that carp spawn only once per year over 1-4 months, from mid-September to December, at water temperatures of 17-25°C.

Two problems regarding YOY sampling and data analysis are evident from this study. Firstly, active seine netting amongst submerged vegetation in shallow, off-stream habitat is most effective at capturing YOY carp. Where littoral vegetation is absent, or made inaccessible by falling water levels, YOY carp are forced into deeper, open water where they may escape capture (Hume *et al.* 1983b; Smith and Walker 2003a, 2004b). Regular seine

samples were obtained only from one lake (Lake Cooper), however, where there was 'very sparse aquatic vegetation' (Hume *et al.* 1983a, p. 10). Second, beginning three months after the completion of the expressed spawning period is another apparently overlooked period of spawning during autumn. Figures 3.6 and 4.1 support this claim. Figure 3.6 illustrates that approximately 40 % of carp captured during March 1980 and March 1981, were either spent or ripe. This means that they had either recently spawned (spent) or spawning was imminent (ripe). Figure 4.1 indicates that 142 juveniles were captured in mid-December 1979 with a mean length of 70 mm FL. Since carp reach approximately 160 mm FL in one year (McDowall 1996) or 70 mm FL in 5 - 6 months (Hume *et al.* 1983a, p. 73; see also Vilizzi 1998; Smith and Walker 2003b, 2004b), it is reasonable to believe that these fish hatched in late summer or early autumn, given that growth ceases during winter. Put another way, it is unrealistic to assume that these fish were spawned in October, or September at the earliest, and grew so rapidly as to achieve a size of 70 mm FL (*c.* 95 mm TL) by mid-December.

In South Australia, Vilizzi (1998) and Smith (1999) examined the spawning pattern of carp via hatch-dates estimated from the ages of YOY samples. In both cases however, sampling was conducted over a single spring/summer period and was limited to the period during October to February. Neither study investigated spawning at other times of the year. Vilizzi (1998) did sample during April to September but admits that juveniles caught during this 'occasional' sampling were a by-product of sampling for older carp using monofilament gill nets of 20-150 mm stretched mesh. This sampling method, together with the mesh size used, the number of sampling occasions ($n = 3$) and the number of juveniles sampled ($n = 22$) indicate that this sampling strategy was not appropriate for larval/juvenile sampling and would have failed to identify a subsequent spawning event if it had occurred. Both studies, however, identified two peaks in carp spawning timing. The first and most pronounced peak occurred in mid-October. Secondary, less intense events occurred from early-November to mid-December. Finally, a few individuals were estimated to have hatched as late as early February.

Smith (1999) also attempted to relate the timing of spawning to various proximal and distal in-stream and meteorological parameters. Although no statistics were employed, it was concluded that increasing day length and rising water temperatures in spring most likely promoted the maturation of gonads to a state of readiness. Subsequently, short-term proximal cues, including periods of fine, warm, sunny weather and gradually rising water levels that

inundated terrestrial vegetation, appeared to be important spawning triggers. This study was limited by the number of sampling occasions ($n = 2$), the number of fish aged ($n = < 120$) and inadequate analysis.

The effects of river regulation on fish assemblages were investigated in the Campaspe and Broken Rivers, near Shepparton (Humphries and Lake 2000; Humphries *et al.* 2002). The timing and duration of carp spawning, indicated by the occurrence of larvae, was spatially and temporally variable. It was found to last between 1-4 months in the Campaspe river (Sep-Feb) and 2-4 months in the Broken River (Sept-Jan) despite the fact that the mean temperatures in the region exceeded 15-16°C from October to April each year (7 months). Again, these results may have been prejudiced by using fishing methods (light traps, drift nets and plankton tow nets) that may only be effective when YOY carp are abundant (Smith and Walker 2004c) and by concentrating most fishing effort in lotic environments, where carp spawning is minimal (Stuart and Jones 2002; Keith Bell, K & C Fisheries, Sale, Victoria, pers. comm.).

Stuart and Jones (2002) captured several cohorts of YOY carp in the Barmah-Millewa forest. Spawning began in mid-September when the water temperature reached 15°C and lasted until at least January, when sampling ended. The authors commented that spawning probably extended into autumn but no formal estimation of the total duration was provided.

Post 2003 (and 1974)

Jones (1974) studied the age and growth of four fish species, including carp, in the South Australian Murray. Although this study was not designed to investigate the dynamics of fish reproduction, it was the first to acknowledge the potential for protracted spawning by carp in Australia. The only valid observation to support this claim was that of mature and running ripe female carp being captured in all months of the year.

Three recent studies confirm the observations of Jones (1974). Sivakumaran *et al.* (2003) and Smith and Walker (2004c) examined seasonal trends in gonadosomatic indices, together with changes in the macroscopic and microscopic condition of ovaries, to investigate carp spawning pattern in Victoria and South Australia, respectively. In both locations, spawning was protracted over 7-9 months (Victoria, Sept-Mar; South Australia, Oct-Apr), and reproductive activity was greatest at onset when GSI peaks and spawning is most intense.

Smith and Walker (2004b) used a complementary approach to investigate the spawning dynamics of carp in South Australia, which incorporated YOY sampling and gonad staging. Hatch-dates estimated from otolith analyses revealed that in each year, spawning is continuous from onset until completion, and that there are two peaks in YOY production between mid-October and December and mid-January and mid-March. Over the period of study, from August 2001 to December 2002, there were at least 29 discrete spawning events at two locations about 30 river-km apart, most of them synchronous. There was also evidence of successful spawning by adults but unsuccessful YOY survivorship during May and September 2002. In those months, the microscopic inspection of ovaries indicated spawning activity (abundant post-ovulatory follicles) but no YOY carp were estimated to have hatched then.

5.2.3 Other reproductive information

5.2.4 Maturation

Maturity in female carp is indicated by ovaries with a majority of resting vitellogenic oocytes, and in males by an accumulation of sperm within the testicular matrix (Smith and Walker 2004c). The size at maturity is inversely related to growth rate and thereby is influenced by water temperature. Males mature earlier than females (Hume *et al.* 1983a; Sivakumaran *et al.* 2003; also see Table 9 from Brown *et al.* 2003), as in most teleosts (Harris 1986; Gooley *et al.* 1995). In the southern MDB, the youngest mature carp are <1 year of age, and minimal lengths at maturity are reported as 150 and 250 mm TL for males and females, respectively (Hume *et al.* 1983a). The majority (>95%) of all carp are mature by 350 mm TL (Jones 1974; Sivakumaran *et al.* 2003; Smith and Walker 2004c).

Table 9. Summary table describing the length- (FL, mm), weight- (g) and estimated age-at-maturity (years) for males and females in the Campaspe irrigation supply channels and the Barmah-Millewa forest. Data from Brown *et al.* (2003).

Description	Parameter	Campaspe		Barmah	
		males	females	males	females
Initial length at maturity	L_{mi}	280	240	230	280
Length at which 50% are mature	L_{m50} (mm)	287	273	307	328
Length at which 95% are mature	L_{m95}	344	310	379	392
Initial weight at maturity	W_{mi}	400	200	400	400
Weight at which 50% are mature	W_{m50} (grams)	556	490	584	688
Weight at which 95% are mature	W_{m95}	872	825	932	1032
Age at initial maturity	A_{mi}	0+	0+	0+	0+
Age at which 50% are mature	A_{m50} (years)	1.3	1.4	1.1	2.7
Age at which 95% are mature	A_{m95}	2.4	2.6	1.2	4.7

5.2.5 Gonadosomatic index (GSI)

Mature gonads undergo cyclical changes in development. These changes can be tracked via observations of gonadosomatic index (GSI). GSI expresses gonad mass (Mg) as a percentage of somatic mass (Ms), where $GSI = Mg / Ms \times 100\%$. Somatic mass is the sum of the total fish mass (M) minus Mg (Wootten 1998). Some studies only use total fish mass when calculating GSI. This index is known as the pseudo-gonadosomatic index (PGSI) (Szabo *et al.* 2000). The following figure provides regression equations to estimate PGSI from GSI, and *vice versa* for PGSI.

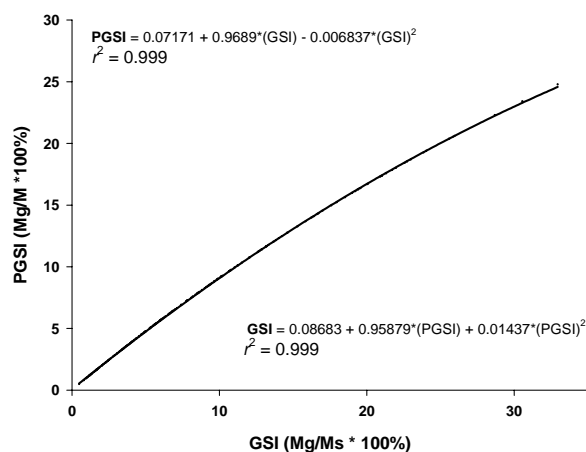


Figure 10. Regression equation describing the relationship between PGSI and GSI, and *vice versa*. BBS, Unpub. Data.

GSI can provide information about a species reproductive cycle, an individual's reproductive status or to estimate sizes and ages at maturity. Fluctuations in GSI reflect the accumulation, development and release of eggs or sperm: peaks occur prior to spawning and spawning is evidenced by sharp declines in GSI. GSI covaries between males and females, although it is always greatest in female carp, since the eggs must accumulate yolk to sustain the embryos until hatching (Hume *et al.* 1983b; Sivakumaran *et al.* 2003; Smith and Walker 2004c).

In Victoria and South Australia, data has been recorded as PGSI, although blushing, Smith and Walker (2004c) indicate that they calculated GSI, when this is not true. In Victoria, maximum-recorded PGSI values are 14% for males and 35% for females (Hume *et al.* 1983a; Sivakumaran *et al.* 2003). In South Australia, the PGSI estimates are lower at 12 and 25% for males and females, respectively (Smith and Walker 2004c). In both states, there are usually two peaks in PGSI. The major peak occurs before the onset of spawning in spring. A secondary, minor peak occurs about 3-4 months later during autumn after the gonads have re-matured. This suggests that the number of eggs per batch is reduced in subsequent spawnings.

5.2.6 Gonad staging

Whilst GSI provides a broad indication of teleost reproductive stage, closer examination of the gonads (ovaries and testis) can indicate their mode of development i.e, immature, developing, mature, ripe, spent or regressing. This can be achieved via macroscopic or microscopic (histological) methods. Macroscopic classification is cheap and fast but may be prejudiced by inexperienced observers or the difficulties of working with small ovaries and oocytes. Histological methods are accurate, but costly in time and money. Clearly, the study objectives will govern the methods used but two recent papers recommend histological examination for staging carp gonads (Sivakumaran *et al.* 2003; Smith and Walker 2004c). These studies also provide photographs and descriptions of each stage to assist unfamiliar users. Histological inspection is particularly useful in staging female fish, and in distinguishing between immature, spent and regressing ovaries (Smith and Walker 2004c).

5.2.7 Fecundity

Fecundity describes the average number of mature eggs produced per individual, per annum. Depending on the mode of ovarian development, a distinction is required between batch fecundity and breeding season fecundity (Wootten 1998). For total spawners that mature one batch of eggs per year and release them totally in one spawning event, then breeding season fecundity and batch fecundity are the same. For fractional spawners that release batches of mature ova periodically throughout the reproductive season (Taylor and Miller 1990), fecundity may be determinate or indeterminate. In fractional spawners with determinate breeding season fecundity, each spawning event simply draws on portions of a finite number of eggs that are present from the onset of spawning (Brown *et al.* 2003). In fractional spawners with indeterminate breeding season fecundity, the number of eggs that are available to spawn during the breeding season is not fixed. Egg production is continuous and oocytes usually co-occur in all developmental stages (Wootten 1998; Fowler *et al.* 1999). True multiple spawners develop several discrete batches of eggs during a single breeding season (Mills 1991; McDowall 1996).

Carp are fractional spawners with indeterminate breeding season fecundity (Smith and Walker 2004c). Thus, it is not possible to estimate their annual fecundity without knowledge of the duration of the breeding season, the mean number of discrete batches of eggs spawned per individual, per year, and the mean number of eggs produced per batch. Whilst no estimate of annual fecundity is available for Australian populations, it is a relatively straightforward calculation (Equation 5):

$$Af = N_s * B_f, \text{ where } \dots \dots \dots \text{ Equation 5.}$$

Af = Annual fecundity

N_s = Number of batches of eggs spawned per annum

B_f = Batch (or instantaneous) fecundity, which is the mean number of eggs produced per batch

To date, only two studies have provided estimates of ‘fecundity’, but these are actually estimates of batch (or instantaneous) fecundity, and are based on the mean numbers of vitellogenic oocytes at the time of sampling. In that regard, batch fecundity is high and variable, and mean estimates for Victoria range from 0.12-1.54 million vitellogenic oocytes per fish. This equates to a mean relative batch fecundity of 163,000 eggs.kg⁻¹ (range 75,000-262,000 eggs.kg⁻¹) (Hume *et al.* 1983a; Sivakumaran *et al.* 2003). In the Campaspe irrigation channels, mean relative batch fecundity is 220,000 eggs.kg⁻¹. In the mid-Murray and Barmah-Millewa forest, it is significantly lower at 110,000 eggs.kg⁻¹ (Brown *et al.* 2003).

Batch- or instantaneous fecundity is positively related to fish length and weight but not age, and egg size is related to maternal size but not age (Figure 11, Sivakumaran *et al.* 2003). Thus, rather than the biomass of the spawning stock, it is a combination of the duration of spawning, the number of batches of eggs spawned, and the number and size of mature females that determines egg production in wild populations.

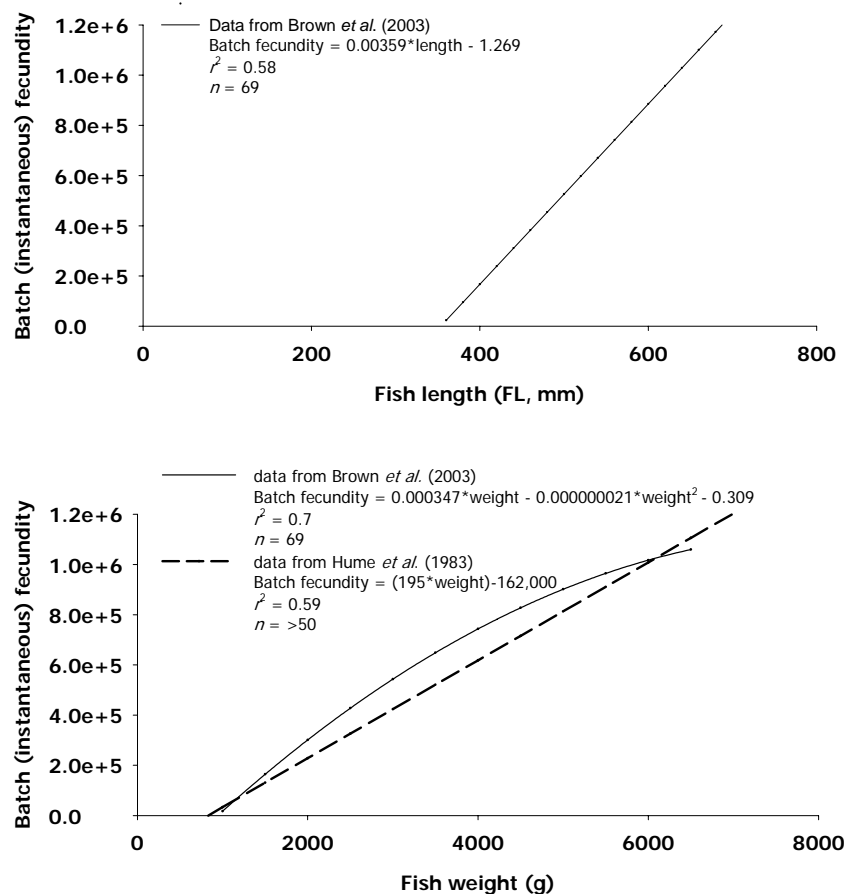


Figure 11. Regressions describing the relationship between batch (instantaneous) fecundity and carp length (FL, mm) and weight (g).

5.2.8 Sex ratio

Sex ratios for wild carp in Australia have been little studied, but recent results indicate that they are spatially and temporally variable, and that they may become increasingly disproportionate with age. For example, whilst there is no difference in the sex ratio of 0+ carp within Barmah Millewa Forest, mature females become increasingly scarce with age (at age 12+, M:F = 1.4:1, Brown *et al.* 2003). In other locations, M:F estimates range from 1:1 in the Campaspe irrigation supply channels (Brown *et al.* 2003), to being female-biased in the lower Murray (1:1.7, Smith 1999) and male biased at sites around Barmah-Millewa forest and Deep Creek billabong (2:1 - 7:1, Stuart and Jones 2002). Interestingly, at Barmah, sex ratios favoured males at riverine sites distant from key access points to the floodplain, whilst slightly more females were found at sites close to key access points (Stuart and Jones 2002).

5.3 RECRUITMENT

“Without a sound understanding of the degree of natural variation in recruitment, there is a serious risk that people will develop unrealistic expectations for the success of management actions and misinterpret natural variability as failure of management. The consequences of wrongly rejecting a sound management strategy are twofold. Firstly, the costs of establishing the strategy are lost. Second, in view of the perceived failure, it may be much more difficult to generate support to develop a successful alternative strategy”

(Gehrke et al. 1995b, p. 14).

For the majority of fish species, there is variability in the relative strength of annual year-classes. This variability reflects the number of fish that survive (are recruited) to the fishery, or to the sexually mature population. Traditional marine models attribute recruitment variability to changes in the biomass of mature adults, whereby recruitment increases with adult biomass until YOY survivorship is moderated by density-dependent effects. Meta-analysis confirms this relationship, but only where the range in biomass of spawners is large. For individual stocks, however, recruitment is unpredictable, particularly at low-medium spawner biomass. In fact, due to the high variability of fishery data, the shape of the stock-recruitment (S/R) relationship cannot be discerned with confidence for a majority of species.

The variability of the S/R relationship may be a consequence of sampling error in large and dynamic systems, or, according to more recent studies, it may reflect the variable production of offspring, caused by density-independent climatic and hydrological events that either interrupt cues for spawning or that impose high and variable mortality on the early life-stages (Harris 1992; Humphries and Lake 2000). Indeed, recruitment is likely to be set during early life, particularly during the first 1-2 months post-fertilisation, because this is when YOY growth and survival is most variable (Houde 1997). Due to high fecundities, even small variations in egg, larval and juvenile mortality result in substantial changes in recruitment (Koslow 1992).

Carp recruitment is variable and is governed more by stochastic abiotic environmental parameters than the biomass of the parental stock (Hume *et al.* 1983a; Schiller *et al.* 1995; Brown *et al.* 2003; Smith and Walker 2004a; pers. comms: Keith Bell, K & C Fisheries; Henry Jones, Clayton). Arguably, this is a consequence of the extreme temporal flow variability of Australian rivers, and the intrinsic species attributes of carp that characterise their opportunistic disposition. At least some recruitment occurs annually (Humphries *et al.* 2002; Stuart and Jones 2002), although strong recruitment is favoured by the more stable conditions of highly regulated rivers (Gehrke *et al.* 1995a; Schiller *et al.* 1995; Gehrke and Harris 2000; Humphries *et al.* 2002; Smith 2004). Strong recruitment may also be assisted by years with greater-than-average flooding, as higher water levels increase the amount of available spawning and nursery habitat (Brown *et al.* 2003).

5.4 MOVEMENT (DISPERSAL) PATTERNS

An early tagging study concluded that carp are essentially non-migratory, making only short, random movements (Reynolds 1983). Subsequent studies have dispelled this theory, with convincing data that identifies three types of movement. These are large-scale upstream dispersive movements through fishways (Mallen-Cooper *et al.* 1995; Stuart and Jones 2002), lateral movements from the main river-channel to shallow, lentic habitats for spawning (Merideth 1996; Stuart and Jones 2001, 2002), and the downstream transport of carp larvae and juveniles from wetland habitats after high flow events (Gilligan and Schiller 2003). Considering the rapid rate of dispersal and establishment of carp in Australia since the late 1960's, this conclusion is perhaps unsurprising. In addition, their spread is still being assisted

by illegal aquarium releases, and introductions by naïve and/or fanatical coarse fishers (Hume *et al.* 1983a; Harris 1995; Pierce 1996); new sites of establishment are recorded each year (Graham Creed, National Carp Task Force, pers. comm.).

5.4.1 Dispersal through fishways

The study by Mallen-Cooper *et al.* (1995) showed that most carp preferred to ascend the Torrumbarry fishway when water temperatures were $> 20^{\circ}\text{C}$ and rising, and when flows were low and stable. This is in stark contrast to Australia's larger native species, whose movements are dissuaded by regulated flows. Only carp >220 mm TL could ascend the fishway, and the majority moved from October to January. Although only relatively large carp are able to pass this fishway, other fishways are known to pass smaller individuals at standard operating velocities (1.79 ms^{-1}). For example, in an experiment to determine the swimming ability of carp at Rice's Weir fishway, 30% of juveniles with a mean length of 76 mm FL successfully negotiated the slots (Stuart and Jones 2002).

5.4.2 Lateral spawning migrations

At Barmah-Millewa forest and in NSW irrigation canals, large-scale lateral spawning migrations have been found to occur after winter, when aggregations of carp in deep water (Diggle *et al.* 2004) move to shallow floodplain habitat for spawning (Hume *et al.* 1983a; Merideth 1996; Stuart and Jones 2001, 2002; Brown *et al.* 2003). In the studies by Stuart and Jones (2001, 2002), lateral spawning migrations were demonstrated by radio-tracking 39 adult carp over 18 months, T-bar tagging 3000 carp and by trapping carp at key access points to the floodplain. Other key findings of that study were that (1) most carp show a strong degree of site fidelity and occupy one or two home areas, both in the river and on the floodplain, (2) these home areas include snags in the main-river and patches of spike rush or some other cover within semi-permanent lakes, (3) carp leave the main-channel to enter newly flooded habitat at the onset of heightened river flows in spring, (4) when water levels recede, carp are often the last to leave the floodplain, (5) male carp arrive at the spawning grounds before females, and await their arrival near key entry points, (6) translocated carp are capable of homing behaviour, and (7) movement of adult fish, or straying, between catchments and adjacent populations was uncommon. The general dispersal of small carp (mean length 326 mm TL) from spawning habitat, the occupation of restricted home ranges,

and homing behaviour by translocated carp are also described in Reynolds (1983) and Crook (2004b).

The monitoring of sub-adult carp using radio-transmitters suggests that small carp, in comparison with mature fish, occupy a smaller home range, show a strong preference for off-stream habitat and are not cued to move by changes in water temperature or river flow. However, some small males (*c.* <20 cm TL) may move further than their mature counterparts (Stuart and Jones 2002).

5.4.3 Downstream transport of young carp

Young carp are a common component of ichthyoplankton fauna in drift samples taken from lotic riverine environments, and their capture is primarily allied to the receding tails of flow peaks (Humphries *et al.* 1999; Gilligan and Schiller 2003). Conversely, in lentic wetland environments (and weir pools etc.), young carp prefer to reside in well-vegetated riparian nursery habitats, and are rarely caught in the pelagic zone (Gilligan and Schiller 2003; BBS, unpublished data). In a recent study, *c.* 24,000 young carp were sampled during 1997-2000 from a 450km reach of the Murray between Yarrowonga Weir and Barham (Gilligan and Schiller 2003). Most carp larvae appeared at the onset of the spawning season in mid-October, but carp larvae appeared in some samples until February. The mean density, length and age of sampled carp were $50.97 \pm 23.68 \text{ ML}^{-1}$, $18.6 \pm 0.19 \text{ mm TL}$ and 32 ± 2 days, respectively. Thus, during high flow events, young carp of varying sizes and ages are entrained from off-stream spawning habitats to the main river channel. This downstream transport occurs over the duration of spawning (4-9 months), and is likely to have contributed to the rapid dispersal and establishment of carp throughout Australia's Murray Darling Basin.

5.4.4 Diurnal movement patterns

With respect to the diurnal movements of carp, there is a disparity between dispersing and non-dispersing carp. That is, carp dispersing through fishways have been found to largely move during daylight hours (*i.e.*, Torrumbarry fishway, Stuart and Jones 2002). In contrast, trials using an echo sounder in a small (0.4ha) pond near Willunga, South Australia, indicated that non-dispersing carp are active at night, especially around dawn and during the period

from dusk until midnight (Pierce 1986). Crook (2001) also noted heightened activity during the night, after radio-tracking seven carp in the Broken River. Indeed, carp were found to move from their daytime residence in deeper water in areas with overhead cover (as opposed to snags and macrophytes) to open, shallow and lentic habitats during the night. These behaviour patterns suggest that most feeding occurs during the night, including the period around dawn and dusk.

5.4.5 Tagging using radio-transmitters, and dart and T-bar tags

Stuart and Jones (2002) estimate tag-shedding rates. With respect to dart tags and small or medium T-bars, only 34/427 (7.9 %) double-tagged mature carp were re-captured. Of these, 25% had lost one of the tags, and tag loss was significantly higher for the medium T-bars. Within one year, 25% of all carp had lost at least one tag, which equals an estimated instantaneous tag shedding rate of $0.29.d^{-1}$. Fewer tagged sub-adult carp were recaptured and these fish may be subject to greater tag loss or post tagging mortality.

Other studies show similar tag shedding rates. Brown *et al.* (2003) estimated tag retention rates at only 42%. Day *et al.* (2004) distinguish between shedding rates of small and large tags, and conclude that small tags are shed more easily than large tags: their maximum likelihood estimates of annual tag shedding rates were 0.48 for small tags and 0.081 for large tags. Accordingly, it is recommended that population estimates be adjusted for known tag shedding rates. Clipping the anal fin and double tagging all carp may also prove useful in identifying tagged carp (Donkers 2003; Day *et al.* 2004).

Radio-transmitters show a similar rejection rate as conventional dart- and T-bar tags. Of 46 mature carp implanted with radio-transmitters, 37% rejected their transmitter after an average of 195 d (Stuart and Jones 2002).

A new method for attaching radio-transmitters to carp and other fish, which reduces the contact between the transmitter and the fish, is provided by Crook (2004a). Accordingly, this new method reduces the potential for dermal irritation and transmitter rejection rates.

5.4.6 Exploiting the “jumping instinct” of carp

Sub-adult and adult carp are known to jump when they are confronted by a fixed barrier: one observation reports a 35 cm carp jumping *c.* 1.2 metres above the water surface to scale a small sill within the irrigation supply channels of the Mirrool catchment (Merideth 1996). This jumping behaviour has been successfully exploited using a specially designed separation cage that can be retrofitted to existing fishways (see further, Stuart *et al.* 2003). Field trials have proven particularly promising as native fish do not, or are reluctant to jump, and almost all carp are separated at a barrier operating height of 15-20 cm above the water surface (Stuart *et al.* 2003). Importantly, the cages are a comparatively cheap harvesting method at less than \$5000 each. However, there is a need to trial the cages with sub-adult carp and during large-scale movements, and investigate the potential for remote operation of the gates to release trapped natives. Other recommendations have been to trial a contoured floor for native fish to follow and to use stronger attraction flows (Stuart *et al.* 2003).

5.4.7 Evaluating potential barriers to movement

Light, sound, a bubble curtain and a half barrier were all trialled in a laboratory flume, as alternates to ‘carp gates’ for excluding carp from wetlands (Champion *et al.* 2002). Whilst each system acted as a deterrent to carp moving to their preferred side of the laboratory flume, only the half barrier completely stopped them; the half barrier was a solid metal screen that extended approximately one-third of the way from the substrate to the water surface (total depth = 600 mm). Further, where carp were unable- or showed little desire to pass a deterrent, they showed a strong tendency to try to force their way underneath the different systems. Thus, any device to exclude carp must be buried into the substrate, and there may be scope to exploit this forceful digging behaviour in a manner similar to the carp separation cages.

5.5 DIET AND FEEDING

Carp are opportunistic feeders on living and non-living organic material. As larvae they are vision-oriented particulate feeders that utilise zooplankton, mostly rotifers, cyclopoid copepods and cladocerans (Hall 1981; Vilizzi and Walker 1999b). Benthic feeding begins at approximately 20-25 mm SL (the 'larva-juvenile transition'), and is indicated by the presence of sand in the gut (Vilizzi and Walker 1999b). Carp are adapted for benthic feeding with a protrusible mouth, large sensory lips, barbels with chemosensory cells, toothless jaw, toothless palate, specialised pharyngeal teeth and a cornified chewing pad (Sibbing *et al.* 1986). The diet of small carp (<30 cm) includes chironomids (preferred prey item), benthic insects (Hume *et al.* 1983a) and microcrustacea (khan 2003). The adults are omnivores, and their diet includes molluscs, epibenthic cladocerans, copepods, amphipods, chironomids, aquatic and terrestrial insects, detritus, seeds, fragments of dead aquatic plants and filamentous algae (Hall 1981). Thus larger carp eat larger prey, and this is likely a reflection of the positive relationship between fish length and the inter gill-raker distance (Hall 1981, Figure 12).

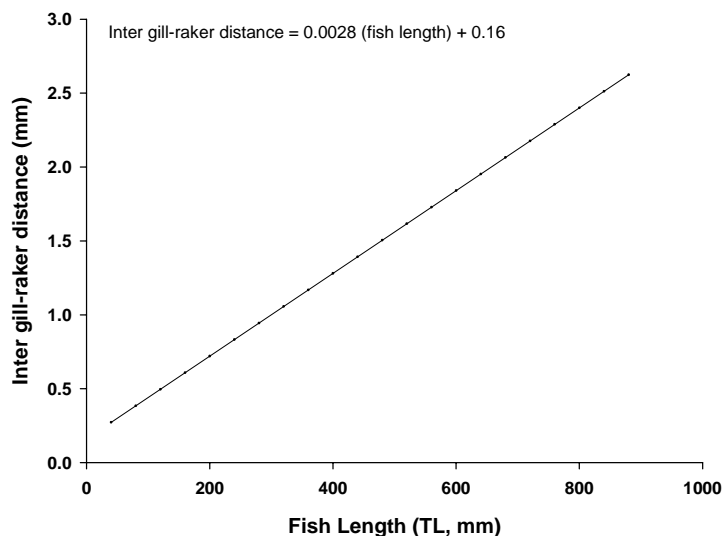


Figure 12. Regression describing the relationship between the inter gill-raker distance and the length (FL, mm) of carp in Lakes Alexandrina and Albert. Data from Hall (1981).

Hume *et al.* (1983) suggested that the diet of medium- and large-sized carp may overlap with western carp gudgeons (*Hypseleotris klunzingeri*), Australian smelt (*Retropinna semoni*) and flathead gudgeon (*Philypnodon grandiceps*), but no competition effects were considered.

Contrary to popular opinion, live plant matter contributes little to the overall diet of carp, and may be eaten only when other prey items are unavailable (Hume *et al.* 1983a). Further, mobile organisms like shrimps, corixids and small fishes are rarely eaten as they are able to avoid capture (Hall 1981), and there is no evidence of carp preying on small native fish or native fish eggs (Hume *et al.* 1983a). However, there is some evidence of cannibalism of larvae by larger carp (Hume *et al.* 1983a).

Carp can switch feeding modes according to local, seasonal and diurnal peaks in prey abundance, and the availability of prey is reflected in the food items eaten (Hall 1981; Hume *et al.* 1983). The modes include benthic feeding, pump-filter feeding and gulping (Lammens and Hoogenboezem 1991). Pump-filter feeding and gulping enable pelagic feeding and, together with benthivory, are effective at night or in turbid water where vision is impaired (Lammens and Hoogenboezem 1991). Thus, carp are not restricted to clear waters (Roberts and Ebner 1997a, b).

5.6 MORTALITY AND PREDATION

“Holding cages with fish were placed within 2 m of a charge of three sticks of gelignite. No carp or goldfish were killed outright. One rainbowfish was found dead. Some fish were dissected to check for internal injuries. There were no injuries. The remaining fish were kept alive in aquaria to check for delayed reactions. Again, there were no injuries or mortalities as the fish lived for several months”.

Hume *et al.* (1983, p. 206)

In Australia, there is no quantitative data regarding the mortality/survivorship of carp eggs and larvae in natural systems. However, a high proportion of eggs (>60-80%) may be lost to fungal infection, and egg predation by birds (especially ducks) is commonplace (BBS, pers. obs.). With respect to juvenile carp, pelicans (*Pelecanus conspicillatus*) prey on carp weighing <2 kg or <300 mm TL, and darters (*Anhinga melanogaster*) and pied cormorants (*Phalacrocorax varius*) may also prey on carp <150 mm TL (Hume *et al.* 1983; S Warrick, commercial fisher, pers. comm.). Small carp are also potential prey for large piscivorous native fish, including callop (*Macquaria ambigua*) and Murray cod (*Maccullochella peelii peelii*), although the abundance of both species has declined significantly in recent years (McDowall 1996; Koehn *et al.* 2000). Further, neither species are free-ranging, aggressive predators and are considered unlikely to control carp numbers (Wharton 1979).

Carp >300 mm TL (age 2+ years, Billard 1999; Vilizzi and Walker 1999a; Brown *et al.* 2004) are virtually free of animal predators, other than commercial and recreational human fishers (Crivelli 1981; Koehn *et al.* 2000; Diggle *et al.* 2004). Nevertheless, the proportion of carp biomass removed by fishing is insignificant. Despite attempts to market carp as a palatable fish in Australia (Easton and Elder 1997), their unsavoury reputation precedes them (Koehn 1992): commercial fishers provide enough carp to supply very limited local markets (S. Warrick, pers. comm; Koehn 1992). Thus, whilst young carp are vulnerable to size-limited bird and fish piscivores, they quickly grow to an unpalatable size where fishing and other pressures are negligible.

Brown *et al.* (2003), provide tabulated estimates of total, natural and fishing mortality for carp in the Campaspe irrigation supply canals and the Barmah-Millewa forest (Table 10).

Table 10. Parameter estimates for total, natural and fishing mortality for carp in the Campaspe irrigation supply channels and the Barmah-Millewa forest. † based on Z from age-at-full-recruitment = 2 years. ‡ based on Z from age-at-full-recruitment = 7 years for males and 9 years for females.

Description	Parameter	Campaspe				Barmah	
		Males	Females	East Channels	West Channels	Males	Females
Total mortality rate	Z (yr ⁻¹)	0.54	0.47	0.63	0.33	0.27	0.43
Natural mortality rate	M	0.40	0.34	0.40	0.33	0.26	0.20
Fishing mortality rate	F	0.14 [†]	0.13 [†]	n/a	n/a	0.01 [‡]	0.23 [‡]

5.7 ABUNDANCE

Estimating carp abundance in natural systems is difficult. Historically, four approaches have been used:

- (1) **Estimating the relative abundance (biomass) of carp compared with other species:** Estimates of relative abundance over 2-years indicated that carp formed up to 86% of the biomass in the Murray River and floodplains of the Barmah-Millewa forest (Stuart and Jones 2002). In the Campaspe irrigation canals, biomass densities ranged from 0-100 kg.ha⁻¹ (Brown *et al.* 2003).

(2) **Water drawdown followed by the complete removal of stranded fish:** De-watering a known area in Moira Lake, combined with the trapping of all stranded carp, revealed up to 87kg of juvenile carp for every 1 tonne of adult carp (Stuart and Jones 2002; Brown *et al.* 2003). In that lake, the biomass density of adult carp was estimated at 190 kg.ha⁻¹ (Brown *et al.* 2003).

(3) **Capture-mark-release-recapture:** Population estimates using the modified Schnabel method (Equation 6) were made at Lake Cooper, Loch Garry and Pogues Billabong. Results varied from 150 kg.ha⁻¹ (range, 140-250) to 690 kg.ha⁻¹ (range 360-1500) at Lake Cooper and Pogues Billabong, respectively (Hume *et al.* 1983).

$$N = (C_t \times M_t) / (R_t + 1) \quad \dots\dots\dots \text{Equation 6.}$$

where: N = number in population

C_t = total catch taken on day *t*

M_t = total number of marked fish in the water at the start of day *t*

R_t = number of recaptures on day *t*

(4) **Depletion experiments:** From depletion surveys at 7 sites across NSW, the NSW Rivers Survey concluded that only an order-of-magnitude estimate of carp abundance is possible from routine boat-electrofishing. Carp abundance in the Bogan River was estimated at 609kg.ha⁻¹, or one carp for every square metre of river surface area. No estimate could be made for small carp (Reid and Harris 1997). Using the sampling efficiency derived from the depletion experiments, Brown *et al.* (2003) estimated that the standing stock of carp in the Campaspe irrigation supply channels ranged from 0-619kg.ha⁻¹ with a mean of 144kg.ha⁻¹.

5.8 MAXIMUM SIZE

The maximum size for carp in Australia, as recorded in the fisheries literature, is 760 mm FL and 8.5 kg (Stuart and Jones 2002, Table 11), although fish of 1-3 kg are more common.

Table 11. Summary table describing the maximum length, weight and age of carp sampled from several large studies of carp ecology in the Murray-Darling Basin.

Reference	Location	n	Maximum		
			Length (FL, mm)	Weight (kg)	Age (yrs)
Vilizzi and Walker (1999)	River Murray, near Berri	856	700	7	12+ (males)
					15+ (females)
Stuart and Jones (2002)	Barmah	4117	760	8.5	n/a
Brown et al (2003)	Campaspe irrigation channels	1114	570 (male)	3.2	17+ years
			680 (female)	4.1	
	Barmah	7357	570 (male)	3.2	23+ (male)
			623 (female)	4.1	28+ (female)
Sivakumaran et al (2004)	Victoria	6800	770	n/a	n/a
Smith and Walker (2004a)	River Murray, near Swan Reach	240	755 (TL, females)	6.7	n/a
			705 (TL, males)		

5.9 DISEASES INTRODUCED TO AUSTRALIA BY CARP

There is no evidence to implicate carp, as the sole perpetrator, in the introduction of any fisheries-related disease into Australia. However, carp are one of five exotic species that may have introduced the Asian Fish Tapeworm (*Bothriocephalus acheilognathi*). Young fish are particularly susceptible to infection by this worm and mortality is high (98%). At Ginninderra Falls, NSW (near the ACT border), approximately 35% of all juvenile carp (mean TL = 5 cm) were infected, and the worm has the potential to infect Australia's important commercial fishes including golden perch, silver perch (*Bidyanus bidyanus*) and Murray cod (Dove *et al.* 1997).

5.10 SAMPLING METHODS

Sampling methods for freshwater fish generally include gill, drift, fyke, drum and seine nets, light traps, and boat- and backpack electrofishers. The usefulness of each method will vary amongst species and life-stages according to behavioural and habitat preferences. For mature carp, boat-electrofishing is most efficient and effective at catching high numbers of fish (size-range 105-693 mm FL, mean 440 mm) within a comparatively short time frame (Stuart and Jones 2002). It is also effective as a non-destructive sampling tool that, in most instances, allows threatened or high-value native fish to be returned to the water live (Hume *et al.* 1983; Brown *et al.* 2003). Further, results from the NSW Fish Survey demonstrate that electrofishing is the most cost-effective approach to sampling (Faragher and Rodgers 1997).

For example using boat-electrofishing gear in 1997, the average cost for a site was greatly reduced because, although three people were needed, two sites were sampled in one day, without overtime. The estimated cost per site for electrofishing was about \$400, compared to around \$800 for using passive sampling gear such as gill and fyke nets (Faragher and Rodgers 1997).

Boat-electrofishing is most effective in waters of low turbidity, low conductivity and depths of 1-2 m (Faragher and Rodgers 1997). However, the efficiency of individual electrofishing boats is variable and depends on the power of the generator, the number and arrangement of anodes and cathodes, and the settings applied by the operator. Temporal and spatial variations in efficiency are also caused by site-specific variations in temperature, salinity, depth, substrate and water flow. Thus, an evaluation of the efficiency of each boat is recommended, to allow useful comparisons between catches (Hume *et al.* 1983). Further, although boat-electrofishers catch more fish of a wider size-range than other methods, recent estimates suggest that a single pass of the electrofisher will only capture between 6-13% of carp from a given location (Brown *et al.* 2003).

With respect to YOY carp (< 100mm FL) in off-stream (nursery) habitat, the usefulness of boat-electrofishing is often limited by high salinities and shallow depths (access restrictions), and active sampling amongst submerged vegetation is recommended. In that regard, seine nets (Hume *et al.* 1983a; Smith and Walker 2003a; Smith and Walker 2004c; Smith and Walker 2004b) are most useful, although in waters of low salinity, sweep-net electrofishers should be considered (King and Crook 2002). In muddy or 'snaggy' sites that are difficult to sample with a seine net, fyke nets may be used but their catch rates are usually lower (Brown *et al.* 2003; BBS unpub. data.).

6. PRIORITIES FOR FUTURE CARP RESEARCH

Past efforts to control carp have been unsuccessful in the main part because there was an emphasis on killing, rather than collecting the key biological information needed to formulate a strategic plan.

(Stuart and Jones 2002, p. vi).

6.1 CONFIRM THE ACCURACY OF THE AGEING METHOD

Clearly, accurate age estimates are paramount for precise assessments of carp recruitment (year-class strength) and any biological/ecological measure that is derived from them (i.e., age-length relationships, growth rates, longevity, age-at-maturity and age-specific fecundity schedules). Thus, accurate age estimates are also paramount to the carp population models and scenario testing of the Daughterless Carp technology.

Carp are a difficult species to age, however, and methods used to validate the formation of annuli (otolith marking, edge-type analysis and marginal increment ratio analysis) have only confirmed their regular formation during the years of study (Vilizzi and Walker 1998). The difficulties of ageing mature carp are highlighted by the fact that predicted age-based growth trajectories do not match observed growth trends (Diggle *et al.* 2004), and that otoliths have been rejected as a possible ageing structure in some studies (Jones 1974; Hume *et al.* 1983; Gehrke *et al.* 1995) and only used with caution (Day *et al.* 2004) or after extensive observation (and with cautionary notes about the difficulty of interpretation) in others (Vilizzi *et al.* 1998). Only one study has reported few, if any, problems in distinguishing otolith increments (Brown *et al.* 2004). Additionally, the consequence of protracted spawning on the timing of the formation of the first annuli has not been considered. In this regard, Jones (1974) notes that conventional age analyses are based on the assumption that fish with the same number of annuli are approximately (within 1-2 months) the same age. Therefore, the implications for adjusting age estimates around a common birth-date for carp require significant consideration. Second, regardless of their date-of-birth, it is unknown whether all YOY carp deposit an annual increment in their first year i.e., if a carp is hatched in autumn, will their first annulus be formed in the spring/summer of that same year, or will it be delayed until the following year?

Although the results of some studies of carp age and growth specify tolerable *precision*, this may be a reflection of the methods used, rather than of the interpretability of carp otoliths: arguably, the otoliths are difficult to read and the *accuracy* of the age estimates remains uncertain. In that regard, confirming annual increment formation over a much longer time frame is desirable and this should be achieved via examination of known-age fish or marked fish (Brown *et al.* 2004) that have been at liberty for many years. Indeed, assessments from known-age fish are desirable for all validation studies, and this should be a key objective for the Daughterless Carp program.

6.2 THE RECRUITMENT PROBLEM: DEFINING STOCHASTICITY WITHIN CARP POPULATION MODELS

The output of current carp population models for the Murray-Darling Basin (CSIRO marine and PIRVIC) is driven largely by the Ricker Stock-Recruitment (S/R) relationship that is explicitly defined in each of the models (Haddon 2003): even though some elements of environmental stochasticity are considered (Brown *et al.* 2001). Stock-Recruitment relationships have never been proven for any freshwater fish, however, and have been specifically disproven for carp (see Mraz and Cooper 1957). Indeed, carp recruitment varies from year-to-year and appears to depend on the duration of the spawning season and the environmental conditions to which the early life stages are exposed (Harris 1992; Smith and Walker 2004a). Although the ‘Environment-Recruitment’ (E/R) relationship is little understood for carp, the model outputs must better reflect the effect of stochastic environmental variability on carp recruitment, rather than abide by the density-dependent assumptions of the Ricker S/R relationship.

Adding stochasticity to fisheries-based models has been achieved elsewhere and it may be useful to seek advice from others with experience in the field. Nominees might include C. Todd (Arthur Rylah Institute) and S. A. Davis (from Davis *et al.* 1999). Todd has derived the Leslie Matrix model, which follows the survivorship of age-classes through time along with the recruitment/fecundity derived from each age-class. It also uses a fundamentally different approach for including stochasticity into the model (Haddon 2003). Davis *et al.* (1999) added stochasticity and age/size specific fecundity/survival/recruitment relationships to their model and state that “it is shown that the speed of introgression may be underestimated if models do not allow for year-to-year variability in natural processes, such

as the number of young arising from natural breeding or the number of adults surviving to breed” (p. 267).

Current knowledge of carp recruitment processes is minimal. Priority areas for future research include:

- a) Evaluating the temporal and spatial variability in carp recruitment i.e., Does recruitment occur uniformly throughout a river or only in restricted reaches? What characters describe a good reach for carp recruitment?
- b) Describing the S/R relationship for geographically distinct populations of carp.
- c) Describing the ‘Environment-Recruitment’ (E/R) relationship i.e., what environmental factors are the key drivers of recruitment variability?

6.3 POPULATION STRUCTURE

Essential to the Daughterless Carp (DC) program will be an ability to monitor the success of the Daughterless Gene (DG), post-release. That is, to be able to answer such simple questions as:

- a) How far and how fast has the DG spread, and is the rate of spread increasing over time?
- b) To what extent has the DC technology reduced carp abundance or altered population sex ratios?
- c) What percentage of new recruits are females, and has this changed from the pre-release condition?

To answer the first question, a genetic marker may be required to identify DC under field conditions. For the remaining questions, an evaluation of the success of the DC technology will require comparative data to examine current carp population structures (including temporal and spatial variability) at key experimental and control sites pre- and post-release. This might include monitoring for abundance, sex ratios, and numbers at age, size and maturity.

Ecosystem responses pre- and post-release should also be considered. For example, carp are thought to increase turbidity, destroy delicate aquatic macrophytes, prevent seedling establishment and compete with small native fishes for food and habitat. If DC performs as expected and carp numbers are considerably reduced, improvements in the diversity and abundance of other native flora and fauna might be expected. Conversely, severe reductions in the biomass and numbers of carp might disrupt existing ecosystem processes or pave the way for another pest species to establish. Understanding and documenting ecosystem responses is important from a scientific perspective, and also from management and community perspectives.

6.4 IDENTIFYING “HOT SPOTS” FOR CARP SPAWNING AND RECRUITMENT

A ‘Hot Spot’ describes any location where adult carp congregate in unusually large numbers prior to- and for the purpose of spawning. Consequently, hot spots are thought to be key source areas from which young carp disperse and recruit to adult populations (Barmah-Milewa Forest in New South Wales and Walker Flat in South Australia are suspected examples). Unlike over-wintering congregations in deep river water, carp at hot spots are biologically and reproductively active. Consequently if hot spots do exist, and it appears that they do, they represent exciting areas for furthering our knowledge of carp ecology. In particular:

- a) Investigations of carp reproduction, sex ratios, abundance, habitat preferences, behaviour, genetic diversity, impacts, spawning migrations, YOY dispersal and other life history traits would receive the best cost-benefit ratio at these sites i.e., more fish could be analysed per sampling dollar.
- b) They would be pursued as targeted release sites for DC as they would promote the transmission and liberation of the daughterless gene, and over 20+ years, may begin to reduce carp numbers at source populations to very low levels.

So what defines a hot spot? Can we identify them from their physical structure i.e., number of floodplain access points, surface area, depth, substrate type or the abundance of riparian vegetation (spawning and nursery habitat)? What constitutes an unusually large spawning congregation (i.e., 300, 500, 1000 or 3000 kg of carp.ha⁻¹)? Answering these questions will

rely on intensive field sampling, similar to the work required above, to assess spatial and temporal variation in the relative abundance of carp at suspected hot and ‘cold’ spots. To date, there has been no real comparison of relative carp abundance estimates amongst disparate spawning locales, so even the *idea* of hot spots remains speculative and must be confirmed.

6.5 CONTINUED DEVELOPMENT OF NOVEL METHODS TO EXPLOIT INSTINCTUAL SPAWNING AND DISPERSIVE MOVEMENTS

Trials of the efficacy of carp separation cages in existing fishways have proven their usefulness in exploiting a behavioural, instinctive trait of dispersing carp. These cages, however, require regular inspections, and captured carp and native fish are costly to remove and dispose of. Thus, improvements to the existing design need to be evaluated, and Stuart and Jones (2003) recommend various avenues for investigation. They also advocate trialling the cages at key floodplain access points, given the extraordinary mass-migration of spawning carp from the main channel to floodplain habitats after winter. Further, although there are preliminary data on carp movements, they suggest that it is important to collect additional information about the season, sex, diel-patterns, size and age of dispersing carp, and the timing and triggers of mass movements to better target the use of the technology (Stuart *et al.* 2003).

Another behaviour that shows promise in separating carp from natives is their burrowing behaviour (Champion *et al.* 2002). In that regard, carp have a strong tendency to try to force their way underneath fixed barriers in an attempt to reach preferred habitat, and there may be scope to exploit this forceful digging behaviour in a manner similar to the carp separation cages.

Pheromone attractants are also being investigated as a control strategy to complement the Daughterless Carp technology and increase the efficiency of commercial harvesting operations. They may also be useful in further exploiting the instinctual movements of carp. Pheromone attractants are little used in fisheries management but they have proven to be a successful control option. For example, in their only application to pest fish control, the US Fisheries and Wildlife Service has used pheromone attractants, amongst a suite of measures, to reduce populations of the parasitic sea lamprey in the Great Lakes by 90% over the past 20

yrs. Thus, continued development of this technology, with application to pest fish control (for a range of species, including carp), is recommended.

7. ACKNOWLEDGEMENTS

Thanks to Dr Qifeng Ye, Dr John Carragher, Lachie McLeay, Brenton Zampatti (all SARDI Aquatic Sciences) and Paul Brown (Primary Industries and Resources, Victoria), for providing constructive comments on an earlier version of this manuscript. This work was funded by the Pest Animal Control Cooperative Research Centre.

8. REFERENCES

- Alikunhi, K. H. (1966) 'Synopsis of Biological Data on common carp *Cyprinus carpio* Linnaeus, 1758 (Asia and the Far East)'. (Food and Agriculture Organisation of the United Nations. FAO Department of Fisheries: Rome). 114 pp.
- Balon, E. K. (1995a) The common carp, *Cyprinus carpio*: its wild origin, domestication in aquaculture, and selection as coloured nishikigoi. *Guelph Ichthyology Reviews* **3**: 1-55.
- Balon, E. K. (1995b) Origin and domestication of the wild carp, *Cyprinus carpio*: from Roman gourmets to the swimming flowers. *Aquaculture* **129**: 3-48.
- Billard, R. (1999). 'Carp biology and culture'. Springer-Praxis Series in Aquaculture and Fisheries (L Laird and S Stead Eds.). Springer-Praxis: Chichester, UK. 342 pp.
- Brown, P. (1996) Carp in Australia. *Fishfacts*. **4**, 1-4.
- Brown, P., Green, C., Sivikumar, K. P., Stoessel, D. and Giles, A. (2004) Validating otolith annuli for annual age determination in common carp. *Transactions of the American Fisheries Society* **133**: 190-196.
- Brown, P., Sivakumar, K. P., Stoessel, D., Giles, A., Green, C. and Walker, T. (2003) 'Carp population biology in Victoria.' Marine and Freshwater Resources Institute, Department of Primary Industries, 56, Snobs Creek. 202 pp.
- Brown, R. S., Power, G. and Beltaos, S. (2001) Winter movements and habitat use of riverine brown trout, white sucker and common carp in relation to flooding and ice break-up. *Journal of Fish Biology* **59**: 1126-1141.
- Brumley, A. R. (1996). Family Cyprinidae: carps, minnows, etc. In 'Freshwater fishes of south-eastern Australia.' (Ed. R McDowall) p. 246. (Reed Books: Sydney).
- Cadwallader, P. L. (1978) Some causes of the decline in range and abundance of native fish in the Murray-Darling river system. *Proc. Roy. Soc. Vic.* **90 (1)**: 211-224.
- Cadwallader, P. L. and Backhouse, G. N. (1983) 'A guide to the freshwater fish of Victoria.' Victorian Government Printing Office. 160-171. pp.

-
- Campana, S. E. (2001) Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology* **59**: 197-242.
- Carbis, C. R., Rawlin, G. T., Grant, P., Mitchell, G. F., Anderson, J. W. and McCauley, I. (1997) A study of feral carp, *Cyprinus carpio* L., exposed to *Microcystis aeruginosa* at Lake Mokoan, Australia, and possible implications for fish health. *Journal of Fish Diseases* **20**: 81-91.
- Champion, T., Cox, J., Ide, A. and Kelly, N. (2002) 'Species-specific barriers: the response of carp (*Cyprinus carpio*) to behavioural deterrents.' Unpublished manuscript. The University of Adelaide. 22 pp.
- Crivelli, A. J. (1981) The biology of the common carp, *Cyprinus carpio* L. in the Carmargue, southern France. *Journal of Fish Biology* **18**: 271-290.
- Crook, D. A. (2001) The influence of spatial scale and habitat arrangement on diel patterns of habitat use by two lowland river fishes. *Oecologia* **129**: 525-533.
- Crook, D. A. (2004a) Brief communication: a method for externally attaching radio transmitters to minimise dermal irritation. *Journal of Fish Biology* (in press).
- Crook, D. A. (2004b) Is the home range concept compatible with the movements of two species of lowland river fish? *Journal of Animal Ecology* **73**: (in press).
- Davis, K. M., Dixon, P. I. and Harris, J. H. (1999) Allozyme and mitochondrial DNA analysis of carp, *Cyprinus carpio* L., from south-eastern Australia. *Marine and Freshwater Research* **50**: 253-260.
- Day, J. M., Farrell, T., Diggle, J., Donkers, P., Emmerson, L. and Bax, N. (2004) Stock assessment, mortality and tag shedding estimates in a declining, closed introduced fish population. **(in review)**.
- Diggle, J., Day, J. and Bax, N. (2004) 'Eradicating European carp from Tasmania and implications for national European carp eradication.' Inland Fisheries Service, Hobart, Tasmania. 66 pp.

-
- Donkers, P. (2003) 'An investigation into the abundance of European carp (*Cyprinus carpio*) in lakes Crescent and Sorrel by the Inland Fisheries Service Carp Management Program.' Technical Report Inland Fisheries Service, Moonah, Tasmania. 16 pp.
- Dove, A. D. M., Cribb, T. H., Mockler, S. P. and Lintermans, M. (1997) The Asian fish tapeworm, *Bothriocephalus acheilognathi*, in Australian freshwater fishes. *Marine and Freshwater Research* **48**: 181-183.
- Driver, P. D., Harris, J. H., Norris, N. H. and Closs, J. P. (1997). The role of the natural environment and human impacts in determining biomass densities of common carp in New South Wales rivers. In 'Fish and Rivers in Stress - The NSW Rivers Survey'. (Eds JH Harris and PC Gehrke) pp. 225-251. (NSW Fisheries: Narrandera).
- Easton, C. and Elder, J. (1997) 'A mouthful of ideas for better rivers. The carp cook book.' (Department of Land and Water Conservation: Tamworth, NSW). 42 pages.
- Ebner, B. and Roberts, J. (1997) 'Historical information on carp in Australia: an evaluation for scientific purposes.' CSIRO Division of water Resources, Griffith Laboratory. 28 pp.
- Faragher, R. A. and Rodgers, M. (1997). Performance of sampling-gear types in the NSW Rivers Survey. In 'Fish and Rivers in Stress - The NSW Rivers Survey'. (Eds JH Harris and PC Gehrke) pp. 251-268. (NSW Fisheries: Narrandera).
- Fletcher, A. R., Morison, A. K. and Hume, D. J. (1985) Effects of carp, *Cyprinus carpio* L., on communities of aquatic vegetation and turbidity of waterbodies in the lower Goulbourn River Basin. *Australian Journal of Marine and Freshwater Research* **36**: (311-27).
- Fowler, A. J., McLeay, L. and Short, D. A. (1999) Reproductive mode and spawning information based on gonad analysis for the King George whiting (Percoidei: Sillaginidae) from South Australia. *Marine and Freshwater Research* **50**: 1-14.
- Geddes, M. C. (1979) Salinity tolerance and osmotic behaviour of European carp (*Cyprinus carpio* L.) from the River Murray, Australia. *Transactions of the Royal Society of South Australia* **103** (7): 185-189.

-
- Gehrke, P. C. (1991) Avoidance of inundated floodplain habitat by larvae of golden perch (*Macquaria ambigua* Richardson): influence of water quality or food distribution? *Australian Journal of Marine and Freshwater Research* **42**: 707-719.
- Gehrke, P. C. (1992) Diel abundance, migration and feeding of fish larvae (Eleotridae) in a floodplain billabong. *Journal of Fish Biology* **40**: 695-707.
- Gehrke, P. C., Brown, P. and Schiller, C. (1995a) Recruitment ecology of native fish larvae and juveniles. In 'Proceedings of the 1995 Riverine Environment Research Forum'. Attwood, Victoria. (Eds RJ Banens and R Lehane) pp. 9-16. (Murray-Darling Basin Commission)
- Gehrke, P. C., Brown, P., Schiller, C. B., Moffatt, D. B. and Bruce, A. M. (1995b) River regulation and fish communities in the Murray-Darling river system, Australia. *Regulated Rivers: Research and Management* **11**: 363-375.
- Gehrke, P. C. and Harris, J. H. (1994) The role of fish in cyanobacterial blooms in Australia. *Australian Journal of Marine and Freshwater Research* **45** (5): 905-915.
- Gehrke, P. C. and Harris, J. H. (2000) Large-scale patterns in species richness and composition of temperate riverine fish communities, south-eastern Australia. *Marine and Freshwater Research* **51**: 165-182.
- Gehrke, P. C. and Harris, J. H. (2001) Regional-scale effects of flow regulation on lowland riverine fish communities in New South Wales, Australia. *Regulated Rivers: Research and Management* **17**: 369-391.
- Gerlach, J. M. (1983) Characters for distinguishing the larvae of carp, *Cyprinus carpio*, and goldfish, *Carrasius auratus*. *Copeia* **1**: 116-121.
- Gilligan, D. and Schiller, C. (2003) 'Downstream transport of larval and juvenile fish in the Murray River.' NSW Fisheries, NMRS project No. R7019, Naranderra. 66 pp.
- Gooley, G. J., Anderson, T. A. and Appleford, P. (1995) Aspects of the reproductive cycle and gonadal development of Murray Cod, *Maccullochella peelii peelii*, (Mitchell) (Percichthyidae), in Lake Charlegrark and adjacent farm ponds, Victoria, Australia. *Marine and Freshwater Research* **46**: 723-728.

-
- Haddon, M. (2003) 'Review of carp models for the Murray-Darling Basin.' Marine Research Laboratory, Tasmania Aquaculture and Fisheries Institute, University of Tasmania, Taroona. 18 pp.
- Hall, D. (1981). The feeding ecology of the European carp (*Cyprinus carpio* L.) in Lake Alexandrina and the lower River Murray, South Australia. Hons thesis, Department of Zoology, University of Adelaide. 57 pp.
- Harris, J. H. (1986) Reproduction of the Australian Bass, *Macquaria novemaculeata* (Perciformes: Percichthyidae) in the Sydney Basin. *Australian Journal of Marine and Freshwater Research* **37**: 209-235.
- Harris, J. H. (1992). Stock/recruitment versus abiotic models in Australian freshwater fisheries. In 'Recruitment Processes. Australian Society for Fish Biology Workshop.' (Ed. DA Hancock) pp. 124-125. (Bureau of Rural Resource Proceedings No. 16., Canberra).
- Harris, J. H. (1995) Carp: the prospects for control? *Water* **May/June**, 25-28.
- Houde, E. D. (1997). Patterns and consequences of selective processes in teleost early life histories. In 'Early life history and recruitment in fish populations.' (Eds RC Chambers and EA Trippel) pp. 173-196. (Chapman & Hall: London).
- Hume, D. J., Fletcher, A. R. and Morison, A. K. (1983a) 'Carp Program. Final Report.' Arthur Rylah Institute for Environmental Research, Fisheries and Wildlife Division, Ministry for Conservation, Victoria, Australia, 10. 214 pp.
- Hume, D. J., Fletcher, A. R. and Morison, A. K. (1983b) Interspecific hybridisation between carp (*Cyprinus carpio* L.) and goldfish (*Carassius auratus* L.) from Victorian waters. *Australian Journal of Marine and Freshwater Research* **34**: 915-919.
- Humphries, P., King, A. J., Koehn, J. D. and O'Connor, W. G. (1999) Fish, flows and floodplains: links between freshwater fishes and their environment in the Murray-Darling river system, Australia. *Environmental Biology of Fishes* **56**: 129-151.
- Humphries, P. and Lake, P. S. (2000) Fish larvae and the management of regulated rivers. *Regulated Rivers: Research and Management* **16**: 421-432.

-
- Humphries, P., Serafini, L. G. and King, A. J. (2002) River regulation and fish larvae: variation through space and time. *Freshwater Biology* **47**: 1307-1331.
- Jones, W. (1974). Age determination and growth studies of four fish from the River Murray. Unpub. Honours thesis, Department of Zoology, The University of Adelaide. 113 pp.
- khan, T. A. (2003) Dietary studies on exotic carp (*Cyprinus carpio* L.) from two lakes of western Victoria, Australia. *Aquatic Sciences* **65 (3)**: 272-286.
- khan, T. A., Wilson, M. E. and Khan, M. T. (2003) Evidence for invasive carp mediated trophic cascade in shallow lakes of western Victoria, Australia. *Hydrobiologia* **506-509**: 465-472.
- King, A. (1995) 'The effects of carp on aquatic ecosystems - A literature review.' School of Science and Technology, Charles Sturt University, Wagga Wagga, NSW. 24. pp.
- King, A. J., Robertson, A. I. and Healy, M. R. (1997) Experimental manipulations on the biomass of introduced carp (*Cyprinus carpio*) in billabongs. I. Impacts on water-column properties. *Marine and Freshwater Research* **48**: 435-443.
- Koehn, J. (1992). Habitat: the essential component of fisheries management. In 'Freshwater fisheries in Victoria - today and tomorrow. Proceedings of a symposium held at the Radisson Presidential Hotel.' (Ed. PL Cadwallader) pp. 5-20.: Melbourne, Australia).
- Koehn, J., Brumley, A. and Gehrke, P. (2000) 'Managing the Impacts of Carp.' (Bureau of Rural Sciences: Canberra). 250 pp.
- Koehn, J. D. (2004) Carp (*Cyprinus carpio*) as a powerful invader in Australian waterways. *Freshwater Biology* **49**: 882-894.
- Koslow, A. J. (1992) Fecundity and the stock-recruitment relationship. *Canadian Journal of Fisheries and Aquatic Sciences* **49**: 210-217.
- Lammens, E. H. R. R. and Hoogenboezem, W. (1991). Diets and feeding behaviour. In 'Cyprinid fishes: systematics, biology and exploitation.' (Eds IJ Winfield and JS Nelson) pp. 353-376. (Chapman and Hall: London).

-
- Lougheed, V. L., Crosbie, B. and Chow-Fraser, P. (1998) Predictions on the effect of common carp (*Cyprinus carpio*) exclusion on water quality, zooplankton, and submergent macrophytes in a Great Lakes wetland. *Canadian Journal of Fisheries and Aquatic Sciences* **55**: 1189-1197.
- Mallen-Cooper, M., Stuart, I., Hides-Pearson, F. and Harris, J. (1995) 'Fish migration in the Murray River and assessment of the Torrumbarry fishway. Final report for Natural Resources Management Strategy Project N002.' NSW Fisheries Research Institute and the Cooperative Research Centre for Freshwater Ecology. 149 pp.
- McDowall, R. (1996). 'Freshwater Fishes of South-Eastern Australia.' Reed Books: Sydney. 246 pp.
- McKay, R. J. (1989). Exotic and translocated freshwater fishes in Australia. In 'Exotic aquatic organisms in Asia. Proceedings of the Workshop on Introduction of Aquatic Organisms in Asia.' (Ed. S DeSilva) 3 pp. 21-34. (Asian Fisheries Society Special Publication: Asian Fisheries Society, Manila, Philippines).
- Merideth, S. (1996). Sediment and phosphorous bioturbation by carp (*Cyprinus carpio* L.) in irrigation drains near Griffith, New South Wales. Masters thesis, Department of Zoology, The University of Adelaide and CSIRO Division of Water Resources. 136 pp.
- Mills, C. A. (1991). Reproduction and life history. In 'Cyprinid fishes: Systematics, Biology and Exploitation.' (Eds IJ Winfield and JS Nelson) pp. 483-509. (Chapman and Hall: London).
- Mraz, D. and Cooper, E. L. (1957) Natural reproduction and survival of carp in small ponds. *Journal of Wildlife Management* **21** (1): 66-69.
- Mulley, J. C., Shearer, K. D. and Mulley, J. C. (1980) Identification of natural "Yanco" x "Boolara" hybrids of the carp, *Cyprinus carpio* Linnaeus. *Australian Journal of Marine and Freshwater Research* **31**: 409-411.
- Nicol, S. J., Leischke, J. A., Lyon, J. P. and Koehn, J. D. (2004) Observations on the distribution and abundance of carp and native fish, and their responses to a habitat

-
- restoration trial in the Murray River, Australia. *New Zealand Journal of Marine and Freshwater Research* **38**: 541-551.
- Olsen, M. (1995) History of European carp in Australia. In 'Proceedings of the National Carp Summit: 6-7 October.' Renmark, South Australia. p. 9. (Murray Darling Association Inc.)
- Pierce, B. E. (1986) Pond rehabilitation: removing carp to restock native fish. *Safish* **10 (3)**: 10-13.
- Pierce, B. E. (1996) River Rabbits. *Southern Fisheries* **4 (2)**: 28-33.
- Recknagel, F., Marsh, F., Matthews, S. and Schiller, N. (1995). Common carp in natural wetlands: impacts and management. In 'Weeds and Feral Animals.' pp. 259-266. (University of Adelaide: Adelaide).
- Reid, D. D. and Harris, J. H. (1997). Estimation of total abundance: the calibration experiments. In 'Fish and Rivers in Stress - the NSW Rivers Survey'. (Eds JH Harris and PC Gehrke) pp. 63-70. (NSW Fisheries: Narrandera).
- Reynolds, L. F. (1983) Migration patterns of five fish species in the Murray-Darling river system. *Australian Journal of Marine and Freshwater Research* **34**: 857-871.
- Roberts, J. (1996) Carp: sifting through the issues. *Weeds and Feral Animals*, 253-257.
- Roberts, J., Chick, A., Oswald, L. and Thompson, P. (1995) Effect of carp, *Cyprinus carpio* L., an exotic benthivorous fish, on aquatic plants and water quality in experimental ponds. *Marine and Freshwater Research* **46**: 1171-1180.
- Roberts, J. and Ebner, B. (1997a) 'An overview of carp *Cyprinus carpio* L. in Australia. Part 1 of 2.' CSIRO Land and Water, Griffith. 72 pp.
- Roberts, J. and Ebner, B. (1997b) 'An overview of carp *Cyprinus carpio* L. in Australia. Part 2 of 2.' CSIRO Land and Water, Griffith, New South Wales. 151 pp.
- Roberts, J. and Tilzey, R. (1996) 'Controlling carp: exploring the options for Australia.' (CSIRO Land and Water: Griffith, NSW, Australia). 132 pp.

-
- Robertson, A. I., Healey, M. R. and King, A. J. (1997) Experimental manipulations of the biomass of introduced carp (*Cyprinus carpio*) in billabongs. II. Impacts on benthic properties and processes. *Marine and Freshwater Research* **48**: 445-454.
- Schiller, C., Gehrke, P. C. and Brown, P. (1995) 'Population analysis for four fish species in the Murray-Darling river system.' 5. pp.
- Shearer, K. D. and Mulley, J. C. (1978) The introduction and distribution of the carp, *Cyprinus carpio* Linnaeus, in Australia. *Australian Journal of Marine and Freshwater Research* **29**: 551-563.
- Sibbing, F. A., Osse, J. W. M. and Terlouw, A. (1986) Food handling in the carp (*Cyprinus carpio*): Its movement patterns, mechanisms and limitations. *Journal of the Zoological Society of London* **210**: 161-203.
- Sivakumaran, K. P., Brown, P., Stoessel, D. and Giles, A. (2003) Maturation and reproductive biology of female wild carp, *Cyprinus carpio*, in Victoria, Australia. *Environmental Biology of Fishes* **68**: 321-332.
- Smith, B. B. (1999). Observations on the early life history of carp, *Cyprinus carpio*: fecundity, spawning and tolerance of eggs to dehydration and salinity. Unpublished BSc (Hons) thesis, Department of Environmental Biology, University of Adelaide. 32 pp.
- Smith, B. B. (2004). Carp (*Cyprinus carpio* L.) spawning dynamics and early growth in the lower River Murray, South Australia. A 'PhD by Publication' thesis, Department of Environmental Biology, The University of Adelaide. 108 pp.
- Smith, B. B. and Walker, K. F. (2003a) Shrinkage of 0+ carp (*Cyprinus carpio* L.) after preservation in ethanol. *Marine and Freshwater Research* **54 (2)**: 113-116.
- Smith, B. B. and Walker, K. F. (2003b) Validation of the aging of 0+ carp (*Cyprinus carpio* L.). *Marine and Freshwater Research* **54 (8)**: 1005-1008.
- Smith, B. B. and Walker, K. F. (2004a) Recruitment, age and growth of young-of-the-year carp in South Australia. (in prep).

-
- Smith, B. B. and Walker, K. F. (2004b) Reproduction of common carp in South Australia, shown by young-of-the-year samples, gonadosomatic index and the histological staging of ovaries. *Transactions of the Royal Society of South Australia*. **128** (2): 249-257.
- Smith, B. B. and Walker, K. F. (2004c) Spawning dynamics of common carp in the River Murray, South Australia, shown by macroscopic and histological staging of gonads. *Journal of Fish Biology* **64**: 336-354.
- Stead, D. G. (1929) Introduction of the great carp *Cyprinus carpio* into waters of New South Wales. *Australian Zoologist*: 100-102.
- Stuart, I. and Jones, M. (2001) Freshwater fishing conservation: getting to know the enemy. *Freshwater Fishing Australia*, 50-52.
- Stuart, I. and Jones, M. (2002) 'Ecology and management of common carp in the Barmah-Millewa forest. Final report of the point source management of carp project to Agriculture Fisheries and Forestry Australia.' Arthur Rylah Institute for Environmental Research, Heidelberg, Victoria. 214 pp.
- Stuart, I., McKenzie, J., Williams, A. and Holt, T. (2003) 'A report on preliminary tests of the 'William's Carp Separation Cage' to the Murray-Darling Basin Commission.' Arthur Rylah Institute for Environmental Research, Heidelberg, Victoria. 32 pp.
- Szabo, T., Szabo, R., Urbanyi, B. and Horvath, L. (2000) Review of the results of common carp (*Cyprinus carpio*) breeding at a large-scale hatchery. *Reproduction in Domesticated Animals* **35**: 89-94.
- Taylor, C. M. and Miller, R. J. (1990) Reproductive ecology and population structure of the plains minnow, *Hybognathus placitus* (Pisces: Cyprinidae), in central Oklahoma. *American Midland Naturalist* **123**: 32-39.
- Trautman, M. B. (1957) 'The fishes of Ohio with illustrated keys.' (The Ohio State University Press: Ohio). 283-288.
- Verma, P. (1970) Normal stages in the development of *Cyprinus carpio* var. *communis* L. *Acta Biologica. Academiae Scientiarum Hungaricae*. **21** (2): 207-218.

-
- Vilizzi, L. (1998) Age, growth and cohort composition of 0+ carp in the River Murray, Australia. *Journal of Fish Biology* **52**: 997-1013.
- Vilizzi, L. and Walker, K. F. (1995) Otoliths as potential indicators of age in common carp, *Cyprinus carpio* L. (Cyprinidae: Teleostie). *Transactions of the Royal Society of South Australia* **119** (2): 97-98.
- Vilizzi, L. and Walker, K. F. (1998) Age profile of carp (*Cyprinus carpio* L.) in Lake Crescent, Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* **132**: 1-7.
- Vilizzi, L. and Walker, K. F. (1999a) Age and growth of the common carp *Cyprinus carpio*, in the River Murray, Australia: Validation, consistency of age interpretation, and growth models. *Environmental Biology of Fishes* **54**: 77-106.
- Vilizzi, L. and Walker, K. F. (1999b) The onset of the juvenile period in carp, *Cyprinus carpio*: a literature survey. *Environmental Biology of Fishes* **56**: 93-102.
- Vilizzi, L., Walker, K. F., Jain, T., McGlennon, D. and Tsybmal, V. (1998) Interpretability and precision of annulus counts for calcified structures in carp, *Cyprinus carpio* L. *Arch. Hydrobiol.* **143** (1): 121-127.
- Walker, K. F. (1983). Impact of Murray-Darling basin development on fish and fisheries. In 'FAO Fisheries Reports.' 288 pp. 139-149.
- Walker, R. and Freeman, R. (2003). Lakes Sorell and Crescent Fisheries Management: Integrated and multi-disciplinary approach to the rehabilitation of Lakes Sorell and Crescent. Inland Fisheries Service, Tasmania. 14 pp.
- Weatherly, A. H. and Lake, J. S. (1967). Introduced fish species in Australian waters. In 'Australian inland waters and their fauna. Eleven Studies'. (Ed. AH Weatherly) pp. 217-239. (Australian National University Press: Canberra).
- Wharton, J. C. F. (1979) 'Impact of exotic animals, especially European carp, *Cyprinus carpio*, on native fauna.' pp. 1-13.

-
- Whiterod, N. (2001). Ecological consequences of rising salinity for common carp (*Cyprinus carpio*) populations in the Murray-Darling Basin. Unpub. Honours thesis, Department of Environmental Biology, The University of Adelaide. 54 pp.
- Wootton, R. J. (1998). Reproduction. In 'Ecology of teleost fishes: second edition.' (Ed. RJ Wootton) pp. 141-173. (Kluwer Academic Publishers: New York).