



Carp (*Cyprinus carpio* L.) spawning dynamics and early growth in the lower River Murray, South Australia

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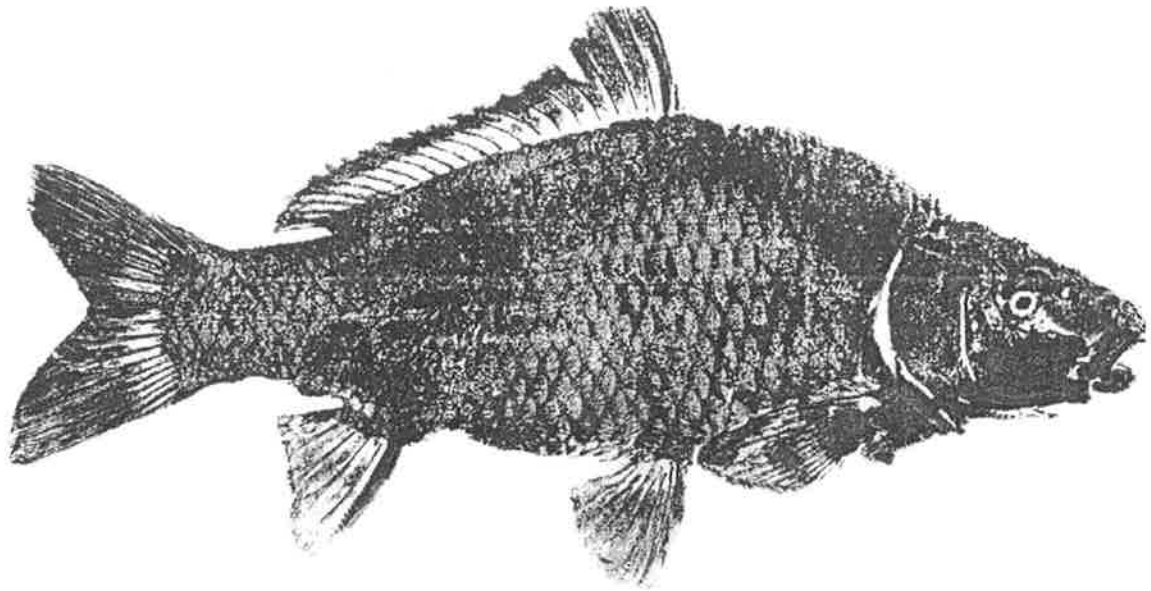
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Common carp (*Cyprinus carpio* L.)

Gyotaku (gyo = fish, taku = rubbing; ghee-yo-tah-koo): *'is the ancient Japanese folk art of printing trophy fish. The concept stemmed from fishermen wanting to prove and preserve the bragging rights of their trophy catch. An original fish print never lies...'*

(DeRyan 2004).

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SYNOPSIS

This thesis extends and summarises Australian data on carp (*Cyprinus carpio* L.) reproductive biology and early growth. Specifically, it (1) validates the aging of larval and early-juveniles via daily otolith increment counts, (2) provides regression equations to account for shrinkage that occurs upon preservation of young-of-the-year (YOY) carp in 70 and 95% ethanol, (3-4) investigates the timing, frequency and duration of spawning via gonad staging *and* via a combination of gonad staging and YOY sampling, and (5) investigates relationships between YOY recruitment and nine hydro-climatic parameters, and examines spatial and temporal variation in YOY growth. Each of the first four topics constitutes a chapter in this thesis (Chapters 4-7) and each chapter represents a paper that has been published in a refereed, scientific journal. Accordingly, this thesis has been submitted as a PhD 'Thesis by Publication', as outlined in Section 9.3 of the 2004 University of Adelaide 'PhD Rules and Specifications for Thesis'. The fifth topic (Appendix 1) represents additional work that was also completed during candidature.

Chapters 1-2 detail the Introduction and Literature Review. Chapter 3 explains the linkages between research topics in Chapters 4-7 and Appendix 1: the key findings are outlined below. Finally, in Chapter 8, there is a general discussion outlining the overall significance of the work, problems encountered and prospectus for future carp research.

KEY FINDINGS

CHAPTER 4: VALIDATION OF THE AGING OF 0+ CARP. Forty carp larvae were reared from eggs spawned in the Torrens River, Adelaide, South Australia, and their otoliths were examined at hatch or at 6, 10, 15 or 20 days after hatching (post-hatch). Using light- and scanning electron microscopy (SEM), otolith increments were counted and compared with known post-hatch ages. Typically, the counts were one day (range 0-2 days) more than the known post-hatch age, but increment formation was daily to at least age 20 days. Thus, age estimates derived from otolith increment counts of wild-caught 0+ carp should be reduced by one day. Comparison with SEM data showed that light microscopy alone offers sufficient resolution for aging 0+ carp.

CHAPTER 5: SHRINKAGE OF 0+ CARP AFTER PRESERVATION IN ETHANOL:

Changes in the length and weight of 240 larval and juvenile carp (10-45 mm SL) were monitored over 180 days after preservation in 70% and 95% ethanol. Shrinkage varied with initial (pre-preservation) size and ethanol concentration, but was stable after 1 day. Absolute shrinkage was directly proportional to initial body size, but per cent shrinkage was inversely proportional to initial size. Length shrinkage peaked at about 14% and weight shrinkage peaked at about 75%. Weight loss in 95% ethanol was almost twice that in 70% ethanol. Regression equations are provided to calculate initial (pre-preservation) measurements of body size (length/weight) from measurements made after preservation.

CHAPTER 6: SPAWNING DYNAMICS OF COMMON CARP IN THE RIVER MURRAY, SOUTH AUSTRALIA, SHOWN BY MACROSCOPIC AND HISTOLOGICAL STAGING OF GONADS. Gonadosomatic indices and macroscopic and histological changes to gonads were monitored in an aggregate sample of 231 male and female carp (359-755 mm total length TL) from the River Murray in South Australia between November 2001 and October 2002. Histological inspection was most accurate and macroscopic inspection was not possible for males, as discrete reproductive stages could not be distinguished. Histological photographs and descriptions are provided for each stage of ovary, testis and oocyte development. Only one (female) fish >350 mm TL was classified as immature. Spawning occurred initially over at least 7 months, from mid-November 2001 to mid-May 2002, and it began again in mid-September 2002. Spawning was asynchronous within the population and each female may have spawned up to three discrete batches of eggs. These data have implications for the control of carp populations and environmental flow management in the region.

CHAPTER 7: REPRODUCTION OF COMMON CARP IN SOUTH AUSTRALIA, SHOWN BY YOUNG-OF-THE-YEAR SAMPLES, GONADSOMATIC INDEX AND THE HISTOLOGICAL STAGING OF OVARIES. Young-of-the-year (YOY) samples, gonadosomatic index (GSI) and the histological staging of ovaries were used to monitor the reproduction of carp in the lower River Murray, from August 2001 to December 2002. Spawning occurred initially over 9 months from late September 2001 to May 2002, the longest period recorded in Australia. It recommenced in September 2002 and continued until at least December, when sampling ended. Contrary to previous reports, hatch-dates estimated from otolith analyses revealed that in each year, spawning was continuous from onset until completion, and that there were two peaks in YOY production between mid-October and December 2001 and mid-January and mid-March 2002. Over the entire period, there were at

least 29 discrete spawning events at two locations about 30 river-km apart, most of them synchronous. GSI and histological evidence indicated spawning over seven months, including two months where the hatch-date data failed to identify any reproductive activity. Thus, the benefits of combining analyses of YOY and ovary samples are apparent here, where reproduction is protracted and there is potentially low YOY survivorship in some months, and where the local ecology of the target species is not well-understood.

APPENDIX 1. RECRUITMENT, AGE AND GROWTH OF YOUNG-OF-THE-YEAR CARP IN SOUTH AUSTRALIA. Young-of-the-year (YOY) carp were monitored in two backwaters of the River Murray, South Australia, during August 2001-2003. The post-hatch age was estimated from daily increments in thin-sectioned otoliths (lapilli). Otolith length and width proved to be better predictors of age ($r^2 = 0.76 - 0.93$) than body length or body weight ($r^2 = 0.64 - 0.85$). Growth rates varied between sites and years, and in 2001-2002, accelerated as the spawning season progressed. Spawning was continuous from onset to completion each year, but the estimated production of YOY carp varied daily. YOY carp were most abundant when there were stable flows and stable atmospheric conditions during the periods of spawning, egg-incubation and larval development. Complex interactions between environmental variables, however, precluded development of a simple model to predict the timing of spawning

DECLARATION

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

I give consent to this copy of my thesis, when deposited in the University Library, being available for loan and photocopying.

Signed: _____.

Date: 20.12.04.

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Marilyn Saxon speedily handled all things 'administrative' and was a prankster's dream. Thanks for all the laughs M.

1. INTRODUCTION

‘What has become the generic name of carp is from Greek - kyprinos or kyprianos [...]. This name was probably derived from ‘Kypris’ (Lat. *Cypria*), a secondary name of the goddess of love, Aphrodite - perhaps because the high fertility of carp and noisy mass spawning in shallows was known even then.’

E. K. Balon (1995b, p. 13).

1.1. ORIGINS AND VARIETIES OF CARP

The common carp *Cyprinus carpio* (Linnaeus) (Teleostei: Cypriniformes: Cyprinidae) is the sole member of the genus *Cyprinus* (Artedi). In 2000 years of domestication (Balon 1995b, 1995a) it has become one of the most widely distributed freshwater fish species. Indeed, it is virtually cosmopolitan, with populations on every continent except Antarctica (Berra 1981; Merrick and Schmida 1984).

Modern carp evolved from an ancestor native to the Black, Caspian and Aral Sea drainages of western Asia (Berg 1964, cited in Balon 1995b). During the Pleistocene-Holocene transition they dispersed eastward to Siberia and China and westward to Europe. In the first and second centuries AD the Romans reared carp in saline reservoirs (*piscinae*) (Balon 1995b; Hoffman 1995), and Christian monasteries later maintained them in ponds (Balon 1995b), a precursor for aquaculture industries that are now commonplace throughout Europe, Asia and the Middle East. Today, in England and other countries, anglers participate in catch-and-release carp fishing competitions (Roberts and Ebner 1997a). In Asia, coloured carp (‘nishikigoi’ or ‘koi’) are striking ornaments for temple ponds and public water-bodies (Balon 1995a).

Domestication and selective breeding has transformed the wild ancestor into three distinct varieties (Stead 1929; Alikunhi 1966; Balon 1995b, 1995a), 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 (Balon 1995b) 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 (Alikunhi 1966). 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).

1.2. CARP IN AUSTRALIA

The establishment of carp in the Murray-Darling Basin of SE Australia is a classic case history of invasion by an exotic species. There are now three resident strains, 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 (Blaylock and Griffith 1971) 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, wild carp were imported illegally from Germany by Boolarra Fish Farms in Victoria (Shearer and Mulley 1978; Hume *et al.* 1983a). In defiance of Victorian authorities, the *Boolarra* strain of carp was 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 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. 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 \times 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.* 1983c). 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).

1.3. ENVIRONMENTAL IMPACT

In eastern and central Europe and Asia, particularly Indonesia, the carp is highly regarded as a table fish (Costa-Pierce *et al.* 1993). In England, it is a popular coarse angling species (non salmonid, Wharton 1979; Garner 1996). In North America, Canada, Western Europe and Australia, however, carp is considered a pest species.

In Australia, many of the assertions regarding the environmental effects of carp are speculative and based on uncritical extrapolations from observations of captive fish. Yet, debate about whether carp are a cause or symptom of declining river health is unrelenting. 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 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 Murray-Darling Basin (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. 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 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; Raecknagel *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.

1.4. CARP MANAGEMENT

Clear evidence of degradation by carp is lacking, hence the environmental, recreational and economic costs are poorly defined. The antithesis of which is that the benefits of carp removal are also not known. Nevertheless, there is widespread demand for the control or eradication of carp where possible (Koehn *et al.* 2000).

Traditional methods of control used direct harvesting and piscicides (rotenone) in small water bodies (Roberts and Ebner 1997a, 1997b). Neither method was effective and populations re-established from surviving individuals (Rehder 1959; Olsen 1995). Current control methods are not effective either and are limited to the prevention of further spread (Carp Control Coordinating Group 2000b), the installation of fish 'carp' gates on wetland inlets (Raacknagel *et al.* 1995), population harvesting and community education into the potential effects of carp in new and existing habitat (Koehn *et al.* 2000). These efforts are thwarted however, by illegal introductions by ignorant and fanatical coarse fishers (Graham Creed, National Carp Task Force, pers. comm.). New sites of establishment are recorded each year.

Future control options are promising. They include biological and viral agents and genetic manipulation, particularly immuno-contraceptives, fertility suppressants, inducible fatality genes and daughterless technologies (reviews Roberts and Tilzey 1996; Thresher 2001). These methods, however, require significant development and a comprehensive understanding of carp population dynamics (Roberts and Tilzey 1996). Unfortunately, current information is fragmentary and in very short supply.

The knowledge problem was recently highlighted by the now defunct Carp Control Coordinating Group (Carp Control Coordinating Group 2000a) and in a general text (Koehn *et al.* 2000). In regards to the former, information gaps were categorised into 9 key areas, including *Biology and Ecology*. This category emphasises the need for 'identifying critical times and conditions for the recruitment of juveniles into the breeding population' and determining 'the influence of density dependent [...and density independent] factors on carp growth, survival and recruitment' (Carp Control Coordinating Group 2000a, p.7). An earlier report suggested a similar approach, indicating that 'a concerted effort is needed on the recruitment phase of carp, from egg to one year-olds and this should be the target for control' (Roberts and Ebner 1997a, p.104).

Recruitment processes are complex and not well understood for many fish species, including carp. Detailed information on carp recruitment is critical however, because the species reproductive strategy, amongst other things, is fundamental to their success as an invader of Australia's freshwaters. For this reason, it may be one of the most effective targets for control.

1.5. PROFILE OF AN INVADER

The ability of carp to disperse widely and displace native fish is linked to intrinsic attributes that predispose them for survival in diverse habitats (Horvath 1985) and equip them as invaders (Koehn 2004). Each attribute is no less important in explaining the success of carp and include feeding behaviour, predators, acoustic abilities, environmental tolerances and reproduction and early life history.

1.5.1. *Feeding behaviour*

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). 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.* 1983a). 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, 1997b).

The diet of small carp includes chironomids (preferred prey item) and benthic insects (Hume *et al.* 1983a). 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).

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).

Hume *et al.* (1983a) 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.

1.5.2. Predators

Fish, birds, fungi and macro-invertebrates, particularly insect larvae are major predators of carp eggs (Alikunhi 1966). Siltation may also be important as in the survival of naturally-spawned dace eggs (Mills 1981). Key predators of carp larvae are frogs, toads, and the 'water bugs' *Nepa rubra*, *Ranatra linearis* and *Notonecta glauca* (Alikunhi 1966). As the larvae grow however, they become progressively faster and stronger and by 20-25 mm TL are able to escape these predators (Rothbard 1981).

Predators of larger carp include birds, fish and humans. In Asia and the Far East, piscivorous birds prey on carp weighing <1.5 kg (Alikunhi 1966). In Australia, pelicans (*Pelecanus conspicillatus*) prey on carp weighing <2 kg or <300 mm TL (Total Length). Darters (*Anhinga melanogaster*) and pied cormorants (*Phalacrocorax varius*) may also prey on carp <150 mm TL (S Warrick, commercial fisher, pers. comm.). Small carp are 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 is a free-ranging, aggressive predator and they are considered unlikely to control carp numbers (Wharton 1979). In the French Camargue, carp are abundant despite the presence of piscivorous pikeperch (*Stizostedion lucioperca*) and pike (*Esox lucius*); in that locale, only grey herons (*Ardea cinerea*) prey on carp 120-260 mm FL (fork length, Crivelli 1981).

Carp >300 mm TL are virtually free of animal predators, other than commercial and recreational human fishers (Crivelli 1981; Koehn *et al.* 2000; AFFA 2003). Nevertheless, the proportion of carp biomass removed by fishing is probably trivial. Shields (1957) stated that 'in large water areas, heavy landings of carp often have been referred to as control, though more correct terminology would be cropping or harvest of surplus' (p. 23). Despite attempts to market carp as a palatable fish in Australia (Easton and Elder 1997), their unsavoury reputation precedes them (Koehn 1992). Commercial fishers only 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 (Tonn and Paszkowski 1992; Mooij *et al.* 1996), they quickly grow to an unpalatable size (Sigler 1958; Vilizzi and Walker 1999a, 1999b) where fishing and other pressures are negligible.

1.5.3. Acoustic ability

The hearing apparatus of Cyprinid fishes is well developed (Chardon and Vandewalle 1991) and includes three pairs of otoliths (primary sound receptors in fish) (Hawkins 1986) and their accessory structures, the Weberian ossicles and swim bladder. The utricular (lapilli), saccular (sagittae) and lagenar (asterisci) otoliths, with excitable mechano-receptive hair cells, perform several functions common to all teleost fishes. First, they serve as gravity receptors, contributing to processes that maintain balance (Chardon and Vandewalle 1991). Second, they register the speed and direction of movement (Hawkins 1986). Third, they register sound pressure waves which enable the fish to locate sounds, separate tones and discriminate frequencies (Hawkins 1986). The Weberian ossicles are unique to cyprinid fishes however, and indicate their ostariophysan affinities (Berra 1981). The ossicles are a chain of moveable bones connecting the anterior chamber of the swim bladder and the paired inner ears, particularly the saccular otoliths. They enable cyprinid fishes to be highly tuned to most biological noises (Hawkins 1986); their sensitivity assists in prey

detection and predator avoidance, and is especially useful in turbid water where vision is impaired. In other fishes, like the Atlantic cod (*Gadus morhua*), the ossicles are absent, there is no close association between the swim bladder and inner ears (Chapman and Hawkins 1973) and the quality and quantity of sound transfer are much restricted.

1.5.4. Environmental tolerances

Most large freshwater fish species, including carp, are potentially highly mobile (Reynolds 1983). In comparison with marine fish however, they are confined in space and the actual distance they can move is restricted. Short lateral movements between the river channel and backwater habitats are possible, but lengthy longitudinal movements, either upstream or downstream, are prevented by dams and weirs that regulate water flow (Cadwallader 1978). With limited ability to avoid environmental change, freshwater fishes must be tolerant to change in order to survive and reproduce (Koehn 1992). The level of tolerance varies between species (Schlosser 1985). In most instances, environmental change alters community composition and incurs a decrease in species diversity and abundance (eg. Crivelli 1981; Fida *et al.* 1988; Jurajda 1999). Thus, several native fish species in the Murray-Darling Basin are now classified as 'threatened' or 'endangered' (McDowall 1996; Humphries and Lake 2000; Koehn *et al.* 2000).

Among freshwater fish, carp are particularly remarkable for their physiological tolerances (Crivelli 1981; Harris and Gehrke 1997). For example, they endure temperatures of 2-40°C, although the optimal range is 12-32°C (Elliot 1980, cited in Hellawell 1986; Opuszynski *et al.* 1989). They tolerate pH values of 5-10.5 (Hellawell 1986). Given acclimation, adults tolerate salinities of 12-15 ‰ (Geddes 1979; Crivelli 1981), although the tolerance of larvae (<25 mm TL) and early-juveniles is less (6-14 ‰, depending on length and temperature: Kasim 1983; Barraclough and Robinson 1971). Carp also tolerate hypoxia (1-2 mg/L, Alikunhi 1966), high turbidity (Bowerman 1975), toxic polyphenols (Gehrke 1991, 1992), ammonia and other nitrogenous wastes (Sigler 1958; Hellawell 1986). For this reason, they are cultivated in sewage ponds (Alikunhi 1966) and stagnant waters from which other fish are excluded (Bowerman 1975; Brumley 1996). Dubious reports also suggest that carp have survived being bodily frozen in ice, that they are capable of burrowing into the bottom mud to a depth of 20-30 cm to escape fishing gear, and that they can withstand a layer of silt up to 50 cm in depth (Alikunhi 1966).

1.5.5. *Reproduction*

Carp are heterosexual, non-guarding, open-substratum, obligatory plant-spawners (*phytophils*) (Alikunhi 1966; Balon 1985a). Preferred spawning sites are lentic habitats with abundant food, warm water and protection from predators (Mills 1991; Garner 1996). Spawning involves polygamous groups of one female and several males and is apparently triggered, at certain times of the year, by rising water that inundates terrestrial vegetation and periods of fine, warm weather (Shields 1957; Swee and McCrimmon 1966; Vilizzi 1998; Smith 1999). The spawning act occurs in shoreline areas (water <1 m deep) and at temperatures >15-16 °C (Crivelli 1981; Santos *et al.* 1997). In Victoria, males and females mature at 1 and 2 years of age respectively (Hume *et al.* 1983a) and estimates of longevity range between 15-40 years (Alikunhi 1966; Vilizzi and Walker 1999a; Brown *et al.* 2004). The females are highly fecund and depending on body size, produce between 500,000 and 3 million eggs per spawning (Alikunhi 1966; Horvath 1985). Thus, the reproductive potential of carp is exceptional as they mature early, are highly fecund, increase their reproductive effort with age over a long life span and reproduce at least once each year when conditions are appropriate for the survival of larvae.

1.5.6. *Early life history*

Young carp are advantaged by being hatched into a warm, sheltered, shallow, lentic habitat. First, with a limited ability to resist current, carp larvae would otherwise be flushed downstream. In strong flow, it is difficult for small fish to maintain orientation and position and if insufficient refuge is available, many die from starvation (Mills 1991). Second, metabolic rate co-varies with temperature and growth is fastest in warm water (Mills 1991; Poizat and Crivelli 1997; Hurst and Conover 1998; Hall and Rudstam 1999). Third, there is little competition for food or other resources: large species that utilise backwaters as spawning grounds or as a residence include bony bream (*Nematalosa erebi*) and the introduced redfin (*Perca fluviatilis*). Small species include the carp gudgeons (*Hypseleotris* spp.), crimson-spotted rainbowfish (*Melanotaenia fluviatilis*), Australian smelt (*Retropinna semoni*), flathead gudgeons (*Philypnodon* spp.) and the introduced gambusia (*Gambusia holbrooki*). Only redfin and gambusia spawn earlier in the year than carp (McDowall 1996; Humphries *et al.* 1999). Thus, carp larvae are well positioned to utilise available zooplankton. Since vulnerability to predation or starvation is an inverse function of size (Mills

1991), rapid growth via early access to food will improve a young carps' prospect of survival (Donald 1997).

A disadvantage to being spawned in warm, newly flooded lentic habitat is that hypoxic conditions (oxygen saturation <2 mg/L) can develop with the decomposition of inundated organic material (Gehrke 1991). Many native fishes are intolerant of hypoxia but the early life stages of carp are little affected (Gehrke 1991). Carp eggs are adhesive in water and stick to the upper stems and leaves of submerged plants over which they are spawned (Swee and McCrimmon 1966). Subsequently, hatched larvae attach themselves to surface vegetation via cement glands on their head (Balon 1985a; Mills 1991). Thus, both life-stages remain separated from anoxic bottom sediment. In non-stratified hypoxic waters, well-developed respiratory vessels maintain larval oxygen supplies (Hume *et al.* 1983c; Balon 1985b, 1985a; Mills 1991).

In conclusion, the species attributes of carp make them a formidable invader of disturbed habitats. In Australia, they have established widely. In rivers and wetlands where they are highly abundant, fears of degradation are fuelling demands for control, but control via existing methods is not possible. New methods are being developed but progress is hampered by deficiencies in knowledge. They are also long term and unproven propositions. The condition of the Murray-Darling Basin is another matter. Roberts and Ebner (1997b) state that 'there is little benefit in controlling or eradicating carp while the Basin remains in its present disturbed and degraded state, as this means there is a reasonable chance that carp will re-establish or another exotic species establish' (p.103). Broad environmental rehabilitation will benefit all river processes that promote native fishes and disadvantage carp.

The most pressing knowledge gap concerns the processes involved in carp recruitment. This has been emphasised for many years, yet little progress has been made. The following chapter reviews the current state of knowledge of carp recruitment, identifies why this study is valid and highlights the main topics for investigation.

2. LITERATURE REVIEW

- Recruitment Processes -

'The regulatory processes [...in fish recruitment] can be subtle; year-class failures or successes need not result from catastrophic or ideal environmental conditions.'

E. D. Houde (1987, p.17).

2.1. INTRODUCTION

Research investigating carp reproduction began in Europe and Asia in the 1950s, when carp were first produced in indoor hatcheries (Billard *et al.* 1995). The goal was to establish methods to maximise the timely, year-round production of eggs and larvae to supply demanding markets (Horvath 1978; Davies and Hanyu 1986; Davies *et al.* 1986; Drori *et al.* 1994; Szabo *et al.* 2000). Scientific advancements in the administration of hormonal stimulants and techniques of artificial propagation have made this possible. Today, institutions such as the Dinnyes Fish Hatchery and Farm in Hungary are capable of the simultaneous production and rearing of 150 million carp fry (Szabo *et al.* 2000).

This early work provided valuable insights into the pre-requisites of carp spawning and larval survival. Most information, however, relates only to cultured carp. Comparatively little is known of carp in natural systems (Crivelli 1981). Accordingly, this chapter reviews the pertinent literature on fish recruitment, with particular emphasis on carp in natural systems but also draws on information from related members of the Cyprinidae for comparison. To begin, I define the term recruitment as it is used in this thesis: there is much variation in the literature. I then introduce the major themes concerning the recruitment of freshwater fishes and describe why studies of recruitment are important. Subsequently, the review is split into four parts. The first section concerns the spawning of adults and well-illustrates the plastic nature of the spawning strategy of carp in disparate environments. In light of this, understanding that the Murray-Darling Basin consists of heterogenous environments, emphasises the need for detailed investigations of carp recruitment throughout Australia. The second section reviews the factors that influence the survival of naturally spawned eggs, larvae and juveniles to the end of the first winter of life. This section is general by necessity: the survival of the early-life stages remains one of the least understood problems in

fisheries biology. The third section reviews past Australian research on carp recruitment. I suggest that incomplete analyses and inadequate/inappropriate sampling methods have restricted the applicability of the data. Finally, I outline the focus for this investigation.

2.2. RECRUITMENT: SURVIVAL FROM EMBRYO TO SEXUAL MATURITY

In fisheries biology, the term 'recruitment' has no fixed definition. In general, it describes the process of survival from one life-stage to another. Specifically, it has described survival from larvae to juvenile (Humphries and Lake 2000), from embryo to a catchable size by specific fishing gear (Hume *et al.* 1983a; Nilo *et al.* 1997; Gundersen and Gjosaeter 1998; Maceina and Bettoli 1998) or more broadly as survival to 'larger' or 'older' size/age classes (Schlosser 1985; Tonn and Paszkowski 1992; Tonn *et al.* 1994; Copp 1997b; Mann *et al.* 1997; DeVries *et al.* 1998; Johnston and Knight 1999; Grenouillet *et al.* 2001). In ecological terms, recruitment is perhaps best defined as survival from embryo to sexual maturity (Mooij *et al.* 1996; Cambray *et al.* 1997). This definition will be used throughout this thesis, except where indicated.

2.3. KEY ELEMENTS OF FISH RECRUITMENT

Recruitment requires the spawning of adults, the hatching of viable fertilised eggs and the survival of young fish. In freshwater fisheries, no convincing stock-recruitment relationship has ever been established (Harris 1992; Mooij *et al.* 1996; Sommer *et al.* 1997). Instead, the population dynamics of freshwater fishes are believed to be governed 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 (Schlosser 1985; Copp and Penaz 1988; Grenouillet *et al.* 2001). This is evident in population analyses of annual recruitment.

Annual recruitment can be examined retrospectively, by back-calculating the age structure of a population and objectively evaluating the strength of year-classes, measured as the percentage of sampled individuals that were born in each year. Those year-classes containing a comparatively high percentage of sampled individuals (>25% of the catch) are evidence of strong recruitment, and *vice versa* for weak year-classes (<5 % of the catch) (Donald 1997; Maceina and Bettoli 1998). Rates of recruitment that are independent of the abundance of adult fish indicate that in most years,

one, if not all of the processes involved in the recruitment of freshwater fishes are vulnerable to failure. Understanding the causes of recruitment failure is an essential requirement of appropriate fisheries management (Maceina 1997). Investigating the spawning strategy of a species can contribute to this knowledge by providing insights into which processes might be vulnerable and when.

The spawning strategy of a species includes various reproductive traits (Mills 1991). These include size- or age-at-maturity, cues for gonad maturation, migration patterns, spawning triggers and substrates, and the timing, frequency and duration of spawning. Some traits are inflexible and their expression is independent of local habitat conditions. Other traits are flexible and allow adaptation to new environments (Wootten 1998). Thus, spawning strategies can vary, but the ultimate goal is to maximise the lifetime production of offspring. The plastic nature of the reproductive strategy of carp is striking and is summarised below.

2.4. THE SPAWNING OF ADULTS

2.4.1. *Maturation of gonads*

A fish cannot reproduce until the gonads mature. The gonads are the gamete-producing sex organs (Campbell *et al.* 1999). They are the testes in males and the ovaries in females. Mature gonads contain eggs or sperm awaiting their release into the gonad lumen (Crivelli 1981). In most fishes, initial gonad maturation coincides with a levelling-off of the length-age relationship and is indicated by the appearance of secondary sexual characteristics. Levelling-off of the length-age relationship occurs as a species approaches its maximum length but also because resources that were once devoted to growth and survival must also contribute to the cost of reproduction (Sigler 1958; Wootten 1998). Secondary sexual characteristics often appear during the breeding season. For female carp, they include the softening and enlargement of the abdomen and the reddening and protrusion of the cloaca (Tay 1973; Szabo *et al.* 2000). Conversely, the abdomen of male carp does not become obviously distended but may become darker in colour and nuptial tubercles appear on the head and on the pectoral fin rays (Swee and McCrimmon 1966). The male cloaca may also

become deep and 'pit-like' (Alikunhi 1966). At other times of the year, male and female carp are difficult to distinguish unless *in-vivo* gonad examination is made via the cloaca (Szabo *et al.* 2000).

The age at maturity in teleosts is endogenously regulated but inversely related to growth rate (Ruiz and Lorenzo 1992), and thereby is influenced by water temperature (Downing and Plante 1993). In tropical climates, carp mature at age 3-6 months (Alikunhi 1966; Adamek *et al.* 1991). In temperate-mediterranean climates, the age at maturity varies between 1 and 5 years (English 1951; Sigler 1958; Rehder 1959; Bishai *et al.* 1974). On average, males mature one year earlier than females (Billard *et al.* 1995), as in most teleosts (i.e., Harris 1986; Gooley *et al.* 1995). In one study, carp at low densities (2500-5000.ha⁻¹) matured earlier than at high densities (7500.ha⁻¹) (Sehgal and Toor 1995).

2.4.2. Gonadosomatic Index (GSI)

Mature gonads undergo cyclical changes in development (i.e., Fouche *et al.* 1985). These changes can be tracked via observations of gonadosomatic index (GSI). GSI expresses gonad mass (M_g) as a percentage of somatic mass (M_s), where $GSI = M_g / M_s \times 100\%$. Somatic mass is the sum of the total fish mass (M) minus M_g (Wootten 1998). Some studies exchange M_s for M . If this figure is used, the index is known as the pseudo-gonadosomatic index (PGSI) (Szabo *et al.* 2000).

GSI can provide information about a species reproductive cycle, an individual's reproductive status or to estimate sizes and ages at maturity (Snyder 1985). For instance, GSI has been used to describe the timing of reproduction in cyprinids such as the small-mouth yellowfish (*Barbus holubi* Tomasson *et al.* 1984), carp (Crivelli 1981), the rare redfin minnow (*Barbus burchelli*, Cambray and Stuart 1985), the plains minnow (*Hybognathus placitus*, Taylor and Miller 1990), the Kinneret sardine (*Mirogrex terraesanctae*, Landau *et al.* 1988) and the bluenose shiner (*Pteronotropis welaka*, Johnston and Knight 1999). 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. As for most teleosts, GSI is greatest in female carp, since the eggs must accumulate yolk to sustain the embryos until hatching (Snyder 1985; Fernandez-Delgado 1990; Taylor and Miller 1990). Recorded estimates are usually around 10% for males and 20% for females (Hume *et al.* 1983a).

2.4.3. *Development of the gonads*

For male carp, testis development is continuous, although GSI peaks prior to the onset of spawning (Crivelli 1981; Davies and Hanyu 1986; Davies *et al.* 1986). In females, ovary development is also continuous, but is related to temperature and is unaffected by short photoperiods (Davies and Hanyu 1986). Ovulation may occur when water temperatures exceed 15-16°C and a day length of 10-16 hours is required to induce spawning (Swee and McCrimmon 1966; Crivelli 1981; Davies *et al.* 1986; Brzuska and Adamek 1989; Guha and Mukherjee 1991). Re-maturation of the ovaries requires ≥ 3 -4 months (Davies *et al.* 1986; Mills 1991; Davis *et al.* 1999).

2.4.4. *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 batches spawned per individual, per year, and the mean number of eggs produced per batch.

Oocyte development in carp is continuous but spawning timing is asynchronous, as indicated by the capture of females at various stages of development throughout a protracted breeding season (Sivakumaran *et al.* 2003; Smith and Walker 2004c). Not all mature eggs are ovulated at once, and up to 20% may be retained for later spawnings (Alikunhi 1966; Swee and McCrimmon 1966).

Depending on local thermo and photo conditions, each female may spawn one to five batches of eggs per year. In India, carp spawn once (Hume *et al.* 1983a; Fida *et al.* 1988; Humphries and Lake 2000). In southern France, Bangladesh, and west Bengal they may spawn twice (Crivelli 1981; Ahmed *et al.* 1989; Guha and Mukherjee 1991). In tropical climates, carp are perennial spawners and spawn 4-5 times per year (Alikunhi 1966).

Egg production in teleosts is related to the size of the oocytes- and the body cavity in which they are contained. Carp are a medium-large sized fish with comparatively small eggs. Maximum reported lengths range from 85-120 cm TL. Maximum reported weights vary from 37 kg in South Africa (Sigler 1958), to 17 kg in Iowa (English 1951) and 10 kg in Australia and Ontario (Swee and McCrimmon 1966; McDowall 1996). Unfertilised eggs are c. 1-1.7 mm diameter (Verma 1970) and average 1.2-1.4 mm (Bishai *et al.* 1974). Larger fish have larger eggs (Crivelli 1981; Cambray and Stuart 1985; Brzuska 1997) and estimates of instantaneous fecundity increase disproportionately with fish length, weight and age (Swee and McCrimmon 1966; Rahman and Moghraby 1984). Estimates of instantaneous fecundity (the average number of stripped eggs per kilogram of fish) range from 114, 000 to 163, 000.kg⁻¹ (Szabo *et al.* 2000).

2.4.5. Spawning substrates and migration

Cyprinid fishes utilise countless spawning substrates, both in the main-channel and in off-stream habitats. For instance, roach (*Rutilus rutilus*) spawn over willow tree roots and long-leaved vegetation (Mann and Bass 1997; Mann *et al.* 1997). Tench (*Tinca tinca*) and silver bream (*Blicca bjoerkna*) spawn amongst dense beds of submerged macrophytes (Copp 1997a). The dace (*Leuciscus leuciscus*) and little Colorado spinedace (*L. vittate*) spawn in the main river channel over gravel substrata (Copp 1997a; Blinn *et al.* 1998). The hornyhead chub (*Notropis biguttatus*) shares its sand nest with nest-associates including the common shiner (*Notropus cornutus*) and the rosyface shiner (*Notropis rubellis*) (Vives 1990), while the eggs of the Kinneret sardine are attached to rocks, singly (Landau *et al.* 1988). *Hemibarbus barbus* bury their eggs in a mixture of pebbles, gravel and sand (Kutano and Hakoyama 1997).

Carp are obligate phytophils (Balon 1985a) and spawn over submerged vegetation, preferably in lentic warm water < 1 m deep. This habitat is scarce in most river channels, but not in off-stream habitats (Poizat and Crivelli 1997; Stuart and Jones 2001). Thus, annual large-scale movements by carp, from the main-channel to off-stream habitats have been recorded in Australia (Stuart and Jones 2001) and North America (Sigler 1958; Rehder 1959; Johnsen and Hasler 1977; Ruiz and Lorenzo 1992). This annual movement commences prior to the onset of spawning in spring, as river water temperatures rise to 12-14°C (Sigler 1958; Ruiz and Lorenzo 1992)

2.4.6. Timing

The change of season brings variation to light, temperature, stream-flow and other environmental conditions (Hoar 1953; Blinn *et al.* 1998). Conditions fluctuate dramatically over time, so spawning usually occurs when conditions are conducive to the survival of the early life stages. In temperate environments during spring/summer, warm weather and long days induce a peak in primary production, supplying food for young fish. The development of eggs and larvae is also faster, so spawning tends to occur at this time of year. In tropical environments where temperature and photoperiod remain invariant, seasonal floods trigger spawning (Wootten 1998). For example, the Orange River labeo (*Labeo capensis*), the splittail (*Pogonichthys macrolepidotus*), and the moggell (*Labeo umbratus*) require inundation of the floodplain (Tomasson *et al.* 1984; Sommer *et al.* 1997). The little Colorado spinedace require localised flooding events and water temperatures > 16°C to induce spawning (Blinn *et al.* 1998). Large Barbus species, such as the smallmouth yellowfish, the largemouth yellowfish (*B. kimberleyensis*) and the barbel (*B. bynni*) spawn within the main channel during floods in spring or summer when water temperatures exceed 18°C (Rahman and Moghraby 1984; Tomasson *et al.* 1984), while *Hemibarbus barbus* spawns at 14-22°C (Kutano and Hakoyama 1997). Conversely, spawning of *B. burchelli* in South Africa coincides with the drawing-off of the greatest quantities of water for irrigation (Cambray and Stuart 1985).

Carp require 10-16 hrs of daylight and water temperatures >15-16°C for ovulation to occur (Smith 2004). Observations suggest that spawning is triggered by warm, calm, sunny weather and rising water levels that inundate terrestrial vegetation (Shields 1957; Vilizzi 1998; Smith 1999). It occurs during daylight hours and the intensity of spawning is low from 15-18°C, optimum at 18-23°C, and ceases at 28°C (Shields 1957; Swee and McCrimmon 1966; Fernandez-Delgado 1990). Carp spawning is a conspicuous act, involving one female and several males. Fertilisation is external and

occurs as sperm and eggs are released, in an often-violent act, over submerged vegetation. At the conclusion of spawning, carp move from shallow spawning habitats to feed and 'over winter' in the main river channel (Stuart and Jones 2002).

2.5. SURVIVAL OF EGGS, LARVAE AND JUVENILES

2.5.1. *A critical period: considerations for recruitment*

Slight variations in the survivorship of fish eggs, larvae and juveniles have important implications for recruitment and year-class strength (Mann and Bass 1997). Accordingly, the early life of fish is often termed 'a critical period' (Tomasson *et al.* 1984; Houde 1987; Copp and Penaz 1988; Johnston *et al.* 1995; Mooij *et al.* 1996; Maceina 1997; Nilo *et al.* 1997; Anderson *et al.* 1998; Gundersen and Gjosaeter 1998; Grenouillet *et al.* 2001). Survival depends on the habitat to which the early life-stages are exposed. The term habitat includes the water, its quality, velocity and depth, the flow regime, aquatic plants, the bank, bank-side vegetation, shade, substrate, wood debris and other physical structures (Koehn 1992). Of crucial importance is food of appropriate size and type, protective cover in the form of in-stream structure and slow flow conditions (Bass *et al.* 1997). The absence or scarcity of any one of these can generate high mortality. Investigating the causes of early mortality forms the basis for the rest of this review on the factors that influence recruitment in carp and other freshwater fishes.

2.5.2. *Water temperature*

Fish are poikilotherms, and rates of food acquisition, metabolism and growth are all related to water temperature (Houde 1987; Downing and Plante 1993; Hurst and Conover 1998; Hall and Rudstam 1999). Fish nursery areas are commonly shallow, lentic, warm waters (Cambray *et al.* 1997; Copp 1997b, 1997a) that tend to warm up earlier and more uniformly than deep river water (Gregory and Powles 1985). Thus, small fish are advantaged by being hatched into such environments.

Temperature effects on growth and metabolism are apparent from observations of embryo development (e.g., Nilo *et al.* 1997; Hurst and Conover 1998; Hall and Rudstam 1999). In carp, the time between egg-fertilisation and hatching ranges from 60-80 degree days (English 1951; Alikunhi 1966; Verma 1970; Ahmed *et al.* 1989). Degree days are calculated by multiplying the value of the average water temperature by the incubation time. For instance, at 20°C carp eggs hatch after approximately 3.5 days. This is calculated as $20 \times 3.5 = 70$ degree days (Alikunhi 1966).

2.5.3. Feeding, food availability and density-dependent growth and mortality

After hatching, carp larvae attach themselves to surface vegetation via cement glands on their heads (Sigler 1958). They remain attached for 4-5 days while yolk is absorbed from a large yolk-sac (Verma 1970) and they undergo organogenesis and other development (Balon 1985b). Exogenous feeding begins before the exhaustion of yolk and is marked by the taking of air to fill the swim-bladder (Rothbard 1981). This strategy secures a continuous supply of food and enables the larvae to develop their foraging skills before the yolk is depleted (Rothbard 1981; Mann *et al.* 1997).

Gape size is also related to larval length (Miller *et al.* 1988, cited in Nilo *et al.* 1997) and in first feeding carp, it is approximately 300µm (Billard *et al.* 1995; DeVries *et al.* 1998). Carp, therefore, may only consume prey that is smaller than this. They have the potential to exploit the 'alternative' food resource that Humphries *et al.* (1999) describe but this is not known to occur. At the start of exogenous feeding, cyprinid fishes are planktivores on zooplankton, particularly cladocerans, rotifers and copepods (Landau *et al.* 1988; Garner 1996; Bass *et al.* 1997). The use of a common food resource supports the notion that ontogeny recapitulates phylogeny (Garner 1996): morphological and behavioural specialisation occurs only at the onset of the juvenile period when the definitive phenotype is realized. In carp, the onset of the juvenile period marks the beginning of benthic feeding (Vilizzi 1997).

Competition for food and effects on growth and mortality are difficult to quantify, yet Mills (1982) provides substantial evidence that competition-induced starvation and reduced growth occur when dace larvae are stocked at high densities. Other studies have inferred density-dependent effects among cyprinids by comparing mortality rates with abundance estimates of young fish only (Grenouillet *et al.* 2001), of young fish to older age-classes (Tonn *et al.* 1994) or of one year class

to another (Nilo *et al.* 1997). For this reason, stocking densities of carp are minimised under hatchery conditions.

2.5.4. Stage duration and size-dependent mortality

Low water temperature, insufficient food, competition, disease, chronic pollution and other unfavourable conditions reduce larval growth and increase stage durations (Houde 1987; Tonn and Paszkowski 1992). That is, the time required to move from one life-stage to another i.e., from embryo to hatching, hatching to the start of exogenous feeding or hatching to juvenile. Fish affected by slow growth are short for their age and short for a longer period of time than faster growing conspecifics. In comparison with longer larvae, short larvae are less mobile, less effective at capturing prey and more vulnerable to predation, and due to their small gape size, may select from a lesser variety of prey than larger fish (Mills 1982; Tonn and Paszkowski 1992; Mooij *et al.* 1996).

2.5.5. Protective cover

Protective cover includes woody debris, submerged or emergent vegetation and other in-stream structures. Similar to large fish, small fishes benefit from an abundance of protective cover in three ways (following Garner 1996; Nicol *et al.* 2004). First, it slows rates of water flow, providing areas of low water velocity amongst swifter currents (Floyd *et al.* 1984; Copp 1992; Freeman *et al.* 2001). Second, it hides them from prey and blocks ambush strikes from predators (Copp 1990). Third, it provides a large surface area for the growth of algal bio-films (West and King 1996; Crook and Robertson 1999) to which second order and higher trophic groups are attracted. Accordingly, such habitats sustain a higher species diversity and abundance than open waters (West and King 1996; Mann and Bass 1997).

Carp and other Cyprinid larvae colonise warm, shallow habitat with abundant vegetation until they are *c.* 70 mm TL (Shields 1957; Swee and McCrimmon 1966; Paller 1987; Jurajda 1999). At this size, they are strong swimmers and comparatively safe from predation (Sigler 1958; Copp 1992, 1997b, 1997a; Blinn *et al.* 1998). However, low water levels expose much shoreline vegetation (Jurajda 1999). If access to this preferred habitat is denied, recruitment is likely to be affected by increased predation or starvation.

2.5.6. River flow, wind and general bad weather

Off-stream nursery habitats provide a significant buffer against strong river flows (Copp 1997a). They are, however, susceptible to disturbance by water level fluctuations and wave action generated by high winds. Such disturbances impair the foraging of small fishes that are unable to hold-station in the water column (Mann and Bass 1997). Many may die from starvation, particularly during the critical transition from endogenous to exogenous feeding (Donald 1997).

The advantages of warm, lentic habitat and appropriate environmental conditions have been emphasised (Hall and Rudstam 1999). It is not enough, however, to have stable hydrologic conditions and calm weather if there is insufficient food due to low water temperatures. Similarly, unstable flows dilute and flush available food from nursery areas (Maceina *et al.* 1996; Copp 1997a; Maceina and Bettoli 1998). Survival is highest when idyllic conditions encompass the period of spawning, egg incubation and larval development (Sommer *et al.* 1997; Freeman *et al.* 2001). The duration of this period will vary amongst species, but it has been suggested as 15-18 days for largemouth bass (*Micropterus salmoides*, Maceina 1997; Maceina and Bettoli 1998), and 30 days for goldeyes (*Hiodon alosoides*, Donald 1997). Carp probably require ≥ 25 days (Vilizzi and Walker 1999b), otherwise significant mortality may result (e.g. Shields 1957; Rehder 1959; Hume *et al.* 1983a).

2.5.7. The first winter and winter stress syndrome

In winter, fish become inactive and rely on energy reserves accumulated during the previous summer to sustain them for the period of over-wintering. Young fish have few reserves however, and their metabolism is comparatively high. Thus, over-winter mortality tends to be highest in young fish (Tonn and Paszkowski 1992; Houde 1994; Blinn *et al.* 1998; Hurst and Conover 1998), and larvae are thought to benefit from hatching early in the spawning period (i.e., Tonn *et al.* 1994). This knowledge is used to maximise production in carp culture (Brzuska 1989).

Over-winter mortality can be exacerbated if larvae develop Winter Stress Syndrome (WSS). WSS causes energy reserves to be used at a faster rate than usual. It is caused by chemical, environmental or biological stressors that instil high rates of respiration in fish, at a time when they are forced to be inactive by cold temperatures (i.e. below 10°C, Lemley 1996). As such, they are unable to

combat the stressing agent by increasing rates of food acquisition. Young fish are particularly susceptible to developing WSS because they reduce feeding to a greater extent than older age classes, and because they enter the over-wintering period with the least energy reserves (Lemley 1996).

2.6. PREVIOUS AUSTRALIAN STUDIES INVESTIGATING CARP RECRUITMENT

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 have been found to spawn continuously over 6-9 months, with two peaks in reproductive activity around spring and autumn (Brown *et al.* 2003; Sivakumaran *et al.* 2003; Smith and Walker 2004c; Smith and Walker 2004b, 2004a). This section describes the results of the pre-2003 studies; the beliefs about carp spawning pattern in south-eastern Australia that prevailed *before* this PhD project was initiated in March 2001. The remaining studies, except Sivikumaran *et al.* (2003), comprise a majority of this thesis.

2.6.1. Pre-2003

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.

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.* 1983a). This study arose from pressure by hunting and angling groups and from concerns within the Division that little was known of carp population dynamics, environmental impact or control options. The study included investigations into carp age and growth, interactions with other

fish, the effect of carp on biotic and abiotic factors and a review of available control options. With regards to carp reproductive strategy, information on size- and age-at-maturity, fecundity, GSI, pre-spawning migrations, and spawning pattern was provided. It is this last point that warrants further discussion.

Carp spawning pattern (timing, frequency, duration) during 1980-82 was inferred by monitoring the ovarian condition of mature fish via the gonadosomatic index (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 deduced from the usually 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 here. First, of all fishing methods, active seine netting amongst submerged vegetation in shallow, off-stream habitat is most effective at capturing YOY carp (Smith 2004). Where littoral vegetation is absent, or made inaccessible by falling water levels, YOY carp are forced into deeper, open water where they cannot be sampled adequately using a small seine (Smith and Walker 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, there is another apparently overlooked period of spawning during autumn, beginning three months after the completion of the expressed spawning period. 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 m (Hume *et al.* 1983a, p. 73; see also Vilizzi and Walker 1999a), 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- (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 are not specific to carp and may only be effective when YOY carp are abundant (Smith and Walker 2004b) and by concentrating most fishing effort in lotic environments, where carp spawning is minimal (Stuart and Jones 2002).

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 comment that spawning probably extended into autumn but no formal estimation of the total duration was provided.

2.7. OVERVIEW

Recruitment describes the process of survival from embryo to sexual maturity. It is the means by which population replenishment occurs but the processes involved are complex and not well understood. At the onset of this PhD (March 2001, i.e. pre-2003), some information on carp recruitment had been compiled for populations in northern Victoria and north-eastern South Australia but the applicability of the data was restricted by incomplete analyses and inadequate and inappropriate sampling methods. Further, latitude and altitude changes were thought to cause variation in carp spawning strategy. It seemed likely that there was variation in carp spawning pattern throughout the Murray-Darling Basin. This needed to be evaluated, particularly considering the near-constant demands for an effective means of carp control.

In light of the above review, this thesis addresses the spawning dynamics and early growth of carp in the River Murray, South Australia.

3. LINKAGES BETWEEN PUBLICATIONS

Explained here are the linkages between four papers and one manuscript (listed below) that comprise chapters 4-7 and Appendix 1, respectively. All were completed during candidature, and the first four have been published in refereed, scientific journals.

- Chapter 4. Smith, B. B. and Walker, K. F. (2003). Validation of the aging of 0+ carp (*Cyprinus carpio* L.). *Marine and Freshwater Research* **54(8)**: 1002-5.
- Chapter 5. Smith, B. B. and Walker, K. F. (2003). Shrinkage of 0+ carp (*Cyprinus carpio* L.) after preservation in ethanol. *Marine and Freshwater Research* **54(2)**: 113-6.
- Chapter 6. Smith, B. B. and Walker, K. F. (2004c). Spawning dynamics of carp (*Cyprinus carpio* L.) in the River Murray, South Australia, shown by macroscopic and histological staging of gonads. *Journal of Fish Biology* **64(1)**: 1-19.
- Chapter 7. 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)**: 249-57.
- Appendix 1. Smith, B. B. and Walker, K. F. (2004c). Recruitment, age and growth of young-of-the-year carp in South Australia. Unpublished manuscript. School of Earth and Environmental Sciences, The University of Adelaide. 31 p.

Much of the data contained within this thesis relies on accurate age and growth estimates for field-captured young-of-the-year (YOY, or 0+) carp. The age estimates enable the calculation of hatch- and spawning dates and are derived from counts of daily increments within the lapillar otoliths. The accuracy of the age estimates was ensured *a-priori* by confirming the number of increments present at hatching and the ability of light microscopy to resolve the narrowest central increments (Chapter 4). The third pre-requisite for valid aging studies, confirming the daily periodicity of increment deposition, had been achieved earlier (Vilizzi 1998).

Age data, combined with measurements of the body size of YOY carp, enable estimates of growth. However, all sampled carp were preserved before laboratory processing, and preservation causes shrinkage in length and weight. The extent of shrinkage of YOY carp in 70- and 95% ethanol is examined in Chapter 5: regression equations are provided to calculate initial (pre-preservation) measurements from measurements made after preservation.

The reproductive biology and spawning pattern (timing, frequency and duration) of carp in two backwaters (Walker Flat South and Punyelroo) of the South Australian Murray is examined in Chapters 6-7. In Chapter 6, macroscopic and histological staging of gonads alone is used. The shortfalls of this 'uni-lateral' approach to sampling are then highlighted in Chapter 7, which considers a 'bi-lateral' approach, incorporating information from gonad staging and YOY sampling. Appendix 1 attempts to characterize the 'window of opportunity' for spawning, relate the abundance of the early life stages to key environmental conditions, and examine spatial and temporal variation in YOY growth.

4. VALIDATION OF THE AGING OF 0+ CARP

Smith, B. B. and Walker, K. F. (2003). Validation of the aging of 0+ carp (*Cyprinus carpio* L.). *Marine and Freshwater Research* **54(8)**: 1002-5.

Statement of Authorship

- for papers published or accepted for publication during candidature -

Ben Smith (Candidate) completed all field sampling, laboratory processing, data analysis and interpretation, wrote manuscript, and acted as corresponding author.

Signed

Date20-12-04.....

Associate Professor Keith Walker (Supervisor) assisted with statistical analyses and interpretation, evaluated the manuscript and provided helpful editorial comments.

Signed

Date20-12-04.....

Smith, B.B., and Walker, K.F., (2003) Validation of the ageing of 0+ carp (*Cyprinus carpio* L.).

Marine and Freshwater Research, v. 54 (8), pp. 1005-1008.

NOTE:

This publication is included in the print copy
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5. SHRINKAGE OF 0+ CARP AFTER PRESERVATION IN ETHANOL

Smith, B. B. and Walker, K. F. (2003). Shrinkage of 0+ carp (*Cyprinus carpio* L.) after preservation in ethanol. *Marine and Freshwater Research* 54(2): 113-6.

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Marine and Freshwater Research, v. 54 (2), pp. 113-116.

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<http://dx.doi.org/10.1071/MF02089>

6. SPAWNING DYNAMICS OF COMMON CARP IN THE RIVER MURRAY, SOUTH AUSTRALIA, SHOWN BY MACROSCOPIC AND HISTOLOGICAL STAGING OF GONADS

Smith, B. B. and Walker, K. F. (2004c). Spawning dynamics of carp (*Cyprinus carpio* L.) in the River Murray, South Australia, shown by macroscopic and histological staging of gonads. *Journal of Fish Biology* **64(1)**: 1-19.

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Signed

Date 20-12-04

Smith, B.B., and Walker, K.F., (2004) Spawning dynamics of common carp in the River Murray, South Australia, shown by macroscopic and histological staging of gonads.

Journal of Fish Biology, v. 64 (2), pp. 336-354.

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It is also available online to authorised users at:

<http://dx.doi.org/10.1111/j.0022-1112.2004.00293.x>

7. REPRODUCTION OF COMMON CARP IN SOUTH AUSTRALIA, SHOWN BY YOUNG-OF-THE-YEAR SAMPLES, GONADOSOMATIC INDEX AND THE HISTOLOGICAL STAGING OF OVARIES

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): 249-57.

Statement of Authorship

- for papers published or accepted for publication during candidature -

Ben Smith (Candidate) completed all field sampling, laboratory processing, data analysis and interpretation, wrote manuscript, and acted as corresponding author.

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Date ...20-12-04

Smith, B.B., and Walker, K.F., (2004) 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, v. 128 (2), pp. 249-257.

NOTE:

This publication is included in the print copy
of the thesis held in the University of Adelaide Library.

8. GENERAL DISCUSSION

8.1. OVERVIEW

At the beginning of this program there was little information regarding the spawning dynamics and early survivorship of carp in natural systems - most published data concerned fish under intensive culture. From the few field studies, it was clear that spawning patterns differed with regional temperature regimes. In the southern Murray-Darling Basin, carp were reported to spawn once annually, in October, and to continue with diminishing intensity for 1-4 months (Chapter 2). These reports, however, were inconsistent with suggestions by commercial fishers that carp in the Murray spawn 2-3 times annually, over 6-9 months (September to May). This appeared feasible, from a review of literature, and because regional mean air temperatures exceed the spawning requirement for 6-7 months annually and there is abundant spawning habitat in shallow, off-stream wetlands (Chapter 6). I anticipated that in the prior studies, the duration and frequency of spawning were under-estimated.

My work has revealed significant new information about the spawning dynamics and early survivorship and growth of carp, from macroscopic and histological staging of gonads and analyses of the gonadosomatic index and monthly samples of young-of-the-year (YOY) fish. The key findings are outlined below.

8.1.1. *Key findings*

1. Age determination in YOY carp, via enumeration of daily otolith (lapilli) increments under light microscopy, is a valid, relatively straight-forward process. This is indicated by the high precision (IAPE and CV < 3 %) and accuracy (\pm 0-3 days) of the post-hatch age estimates. Before aging, lapilli should be ground to thin-sections in the sagittal plane, and age estimates need to be adjusted because one increment is already present at the time of hatching (Chapter 4).

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2. Preserving YOY carp in 70 or 95% ethanol causes body shrinkage. Shrinkage was inversely proportional to initial (pre-preservation) size, and weight shrinkage was more pronounced than shrinkage in length. Indices of growth or condition based on preserved specimens therefore must be corrected (Chapter 5).
 3. Carp are asynchronous, multiple-batch spawners. Their annual fecundity depends on the number of batches of eggs spawned annually by individuals and on the number of eggs in each batch (rather than the number of mature oocytes at the time of capture, as in prior work) (Chapter 6).
 4. The annual 'window of opportunity' for carp spawning in south-eastern Australia was at least six months during 2001-2003: from October to March. Spawning may also occur during cooler months (September, April, May), but YOY survivorship then may be moderated by low temperatures (Chapter 7).
 5. Reproduction was relatively continuous throughout the spawning period, but YOY production peaked between mid-October and December and mid-January and mid-March. Thus, most females probably spawned twice annually: once at onset and again 3-4 months later, when the gonads re-matured (Chapter 7).
 6. YOY production is likely to be greatest at onset, when the gonadosomatic index (GSI) is maximal. This prediction was not confirmed, however, as only the relative abundance, not the total abundance, of age groups of YOY carp was compared between sites and times (Chapter 7).
 7. The relatively continuous nature of spawning, indicated by the near-continuous time series of hatch-dates, may indicate a) females from previous year-classes maturing and spawning asynchronously throughout the spawning period, or b) variation in the timing of spawning in separated areas, mediated by pheromones which synchronised reproduction in cohabiting individuals. Neither possibility was confirmed, but both are plausible as females in any one population had gonads at a range of developmental stages during each month of spawning (Chapter 7).

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8. Complementary analyses of YOY and gonad samples provided significantly more information than either kind of analysis in isolation. Gonad staging revealed the duration and approximate timing of reproduction, and YOY samples better indicated the seasonal patterns of spawning and YOY survivorship (e.g. Chapter 7).
 9. The length and width of otoliths are better predictors of YOY age than measurements of body length and body weight. In the lower Murray in 2001-2003, more than 85% of the variation in age between years and locations was explained by its relationship with otolith size (Appendix 1).
 10. The growth of YOY carp was spatially and temporally variable, and in 2002-2003, annual growth rates increased as the spawning season progressed. Although early-spawned fish grow relatively slowly, their survival may be enhanced because they develop over a longer period, attain a larger body size and accumulate more energy reserves before winter (Appendix 1).

8.2. REFLECTIONS

8.2.1. *Potential sampling bias in histological studies*

In Chapter 6, I explored the reproductive biology of carp via macroscopic and histological staging of gonads. Whilst the former is rapid and inexpensive, histological staging is laborious and costly. *A priori*, I chose to limit monthly histological sample sizes to 20 fish (10 ♀, 10 ♂). Sex determination in carp is error prone, however, as males and females are not sexually dimorphic for much of the year. Consequently, upon capture, the fish were sorted into two groups of 10 fish containing ‘probable females’ and ‘probable males’. Fish of less-certain gender were discarded. Although this method was essentially random, sorting could have biased the results. That is, females with obviously distended abdomens and males extruding milt were targeted. Not surprisingly, most females were categorized as ‘late-developing’ and few were ‘regressing’ or ‘spent’ (with post-ovulatory follicles). Similarly, most males were ‘developing’ or ‘developed’ and few were ‘spent’. To avoid these potential biases, it would be desirable to randomly sample more fish than are required, and to process these until sufficient numbers of each sex are obtained.

8.2.2. *Validation of daily otolith increments*

Studies to validate the daily deposition of otolith increments often utilise laboratory-reared larvae, as wild-caught larvae of known age are difficult to obtain. Under optimal laboratory conditions, daily increment deposition usually is confirmed (Radtke 1989; Vilizzi 1998; Campana 2001; Smith and Walker 2003b), but non-daily deposition may occur under abnormal or extreme conditions (Geffen 1982; Mugiya and Uchimura 1989; Radtke 1989; Tzeng and Yu 1992; Bestgen and Bundy 1998). Accordingly, the extrapolation of information from laboratory to field is suspect; ideally, validation should be conducted under both conditions (Jones 1986).

Whilst validation is essential in age-based studies, I doubt the need for field confirmation of laboratory results. For most species, this would require multi-factorial experiments that would be extremely difficult, if not impossible (Letcher *et al.* 1996). This is because a) natural environments experience a myriad of depth, flow, light, temperature, salinity, food and chemical conditions that could not be simulated in the laboratory, and b) the conditions experienced by individual YOY fish before capture are impossible to quantify, particularly for species with protracted breeding cycles, or those that are highly mobile or elusive. In addition, other factors such as the reader's experience, degree of otolith preparation, resolution limitations and sub-daily increments, accessory primordia, growth checks and/or discontinuities all may confound the interpretation of an otolith's microstructure (see further Campana and Neilson 1985; Jones 1986; Campana 2001). Thus, ages from field-captured fish can only be estimates, regardless of the validation method.

8.2.3. In support of histological studies

Given the precarious status of many native fish species in the Murray-Darling Basin, it would be prudent to monitor populations using basic histological methods. Information on reproductive seasonality and gonad development would elucidate recruitment processes and, perhaps, strategies for the allocation of 'environmental flows'. Histological studies of this kind, so far, have been limited mainly to the larger species, including golden perch (*Macquaria ambigua* Richardson, Mackay 1973a), freshwater catfish (*Tandanus tandanus* Mitchell, Davis 1977a), European perch (*Perca fluviatilis* Linnaeus., Treasurer and Holliday 1981), Murray cod (*Maccullochella peelii* Mitchell, Gooley *et al.* 1995), Australian bass (*Macquaria novemaculeata* Steindachner, Harris 1986), Macquarie perch (*Macquaria australasica* Cuvier, Appleford *et al.* 1998) and carp (Sivikumaran *et al.* 2003; Smith and Walker 2004a). Among the small native fish, only the common jollytail (*Galaxias maculatus* Jenyns, Pollard 1972), firetailed gudgeon (*Hypseleotris galii* Ogilby, Mackay 1973b, 1973c) and Australian smelt (*Retropinna semoni* Weber, Leigh 2002) have received attention.

8.3. PROSPECTUS

'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).

Despite recent large-scale field studies, there are comparatively few data on the population structure, recruitment (including 'hot-spots'), age and movements of carp in South Australia and the northern Murray-Darling Basin (MDB). In the following, I suggest six priorities for future research, designed to address these knowledge gaps but also to complement research now underway on the genetic 'Daughterless Carp' technology (review by Thresher 2001). Although the Daughterless technology is unproven and speculative, if successful, it will be a key aspect of any integrated and strategic approach, which is needed to control carp and rehabilitate native fish population in the MDB (Harris 1995; MDBMC 2003).

1) *Population structure*

The Daughterless Carp (DC) program assumes that we are able to monitor the spread of the Daughterless Gene (DG) after release. To do this, a genetic marker will be required to identify DC under field conditions. With that, we may address three critical questions, bearing in mind that the time for propagation is estimated to be decades, with constant re-introduction of the DG:

1. Is the DG propagating over space and time?
2. Has the DC technology reduced carp abundance, or altered population sex ratios?
3. What proportion of new recruits are females, compared to the pre-release condition?

Ecosystem-level responses should also be examined, as carp are thought to increase turbidity, undermine aquatic macrophytes and prevent the establishment of plant seedlings.

2) *Modelling the influence of stochasticity on recruitment*

CSIRO Marine & Primary Industries and Resources Victoria are developing carp population models to 1) establish release strategies for DC, 2) indicate the spread of DG post-release, and 3) test complementary control scenarios as part of an integrated pest management program (Haddon 2003). At present, a Ricker Stock-Recruitment (S/R) function drives the output of each model (Haddon 2003), although no such model has been validated for any freshwater fish, particularly carp (see Mraz and Cooper 1957). Indeed, to a large extent, annual carp recruitment depends on the duration of the spawning season and the environmental conditions to which early life stages are exposed (Harris 1992; Smith and Walker 2004a,b). Thus, model outputs should reflect stochastic environmental effects and not assume density dependence. It will be necessary to:

1. Further evaluate temporal and spatial variability in carp recruitment. For example: does recruitment occur uniformly throughout a river or only in restricted reaches ('Hot-Spots', see below)?
2. Describe the 'Environment-Recruitment' (E/R) relationship i.e., what environmental factors govern variability in carp recruitment?

3) *Confirmation and identification of 'Hot Spots' for carp breeding*

A 'hot spot' is a suspected location where adult carp congregate in unusually large numbers for spawning and from which young carp disperse and 'recruit' to adult populations (for example: Barmah-Millewa Forest, New South Wales and Walker Flat, South Australia: Stuart and Jones 2002; Smith and Walker 2004a). These sites are obvious targets for intensive studies, because:

1. Investigations of carp reproduction, sex ratios, abundance, habitat preferences, behaviour, genetic diversity, environmental effects, spawning migrations, dispersal and other life history traits would be most cost-effective.
2. They would be potentially targeted as release sites for DC, as they would promote the propagation of the DG.

-
3. Complementary control methods like pheromone attractants, commercial harvesting, carp separation cages and carp specific biocides, included as part of an integrated pest management program, would be most effective.

There has been no investigation of carp recruitment amongst disparate spawning localities, however, so even the *idea* of 'hot spots' remains speculative and must be confirmed. In doing this, the following questions may be addressed:

1. What are the physical characteristics of a 'hot spot' (for example, number of floodplain access points, surface area, depth, substrate type or the abundance of riparian vegetation)?
2. Are 'hot-spots' identifiable from unique water-chemistry signatures, reflected in the otolith microchemistry of newly recruited carp?

4) *The accuracy of ageing methods*

Accurate age estimates are crucial for assessments of recruitment and derived biological/ecological measures (i.e., age-length relationships, growth rates, longevity, age-at-maturity). However, mature carp are difficult to age (Jones 1974; Hume *et al.* 1983; Gehrke *et al.* 1995a; Vilizzi and Walker 1998), and only one study specifies tolerable *precision* (Brown *et al.* 2004). This may be a reflection of the methods used, rather than of the interpretability of carp otoliths. Regardless, the *accuracy* of the age estimates remains uncertain because validation methods for annuli have only confirmed the regular formation during the years of study (Brown *et al.* 2004). Thus, confirming annual increment formation over a longer time frame and for older age groups (age 15+ years) is required.

A secondary concern is that 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: regardless of their date-of-birth, it is unknown whether all YOY carp deposit an annual increment in their first year.

5) *Novel methods to exploit patterns of spawning and dispersal*

Trials of the 'Williams Carp Separation Cage', separating carp from native fish as they move upstream through fishways, have been successful (Stuart and Jones 2002, 2003). Improvements to the existing design should follow from additional information about the season, sex, diel-patterns, size and age of dispersing carp, and the timing and triggers of mass movements through fishways in the main-channel and from the main-channel to key spawning areas in off-stream wetlands.

Another behaviour that shows promise in separating carp from natives is their 'burrowing' behaviour (Champion *et al.* 2001). Carp in the laboratory show a tendency to force their way underneath fixed barriers to avoid unfavourable (in this case, well-lit) habitat, and there may be scope to exploit this behaviour in a manner similar to the carp separation cages.

Finally, pheromone attractants for carp are being investigated to complement the DC technology. Although pheromone attractants are little used in fisheries management, they may increase the efficiency of commercial harvesting operations (Sorensen and Stacey 2004).

6) *Movement patterns*

An early tagging study suggested that wild carp in Australia are essentially non-migratory, making only short-random movements (Reynolds 1983). A more recent study using radio-tracking of adults and juveniles, however, indicated long-distance dispersal by juveniles (especially small males) and annual migrations from the main-channel to off-stream spawning habitat by adults (Stuart and Jones 2002). This must be clarified, as the extent to which carp disperse will affect decisions regarding the release of DC.

9. REFERENCES

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10. APPENDIX 1. RECRUITMENT, AGE AND GROWTH OF YOUNG-OF-THE-YEAR CARP IN SOUTH AUSTRALIA

Abstract. Young-of-the-year (YOY) carp, *Cyprinus carpio* L., were monitored in two backwaters of the River Murray, South Australia, during August 2001-2003. The post-hatch age was estimated from daily increments in thin-sectioned otoliths (lapilli). Otolith length and width proved to be better predictors of age ($r^2 = 0.76 - 0.93$) than body length or body weight ($r^2 = 0.64 - 0.85$). Growth rates varied between sites and years, and in 2001-2002, accelerated as the spawning season progressed. Spawning was continuous from onset to completion each year, but the estimated production of YOY carp varied daily. YOY carp were most abundant when there were stable flows and stable atmospheric conditions during the periods of spawning, egg-incubation and larval development. Complex interactions between environmental variables, however, precluded development of a simple model to predict the timing of spawning.

Extra keywords: *Cyprinus carpio*, cohort, otolith, flow, spawning, environment.

10.1. INTRODUCTION

Variation in recruitment, indicated by changes in the abundance of catchable fish (Nilo *et al.* 1997; Gundersen and Gjosaeter 1998; Maceina and Bettoli 1998) remains one of the least understood problems in fisheries science, even after a century of research (Houde 1987). Traditional models assume that recruitment increases with adult biomass until survival of young-of-the-year (YOY) fish is constrained by density-dependent effects (e.g. Ricker 1975). Meta-analysis supports this assumption where the range in biomass of spawners (S) is large ($S_{\max}/S_{\min} > 10$; Myers 1997), but for smaller stocks the S/R relationship is variable and usually unknown (e.g. Helbig *et al.* 1992; Koslow 1992; Karjalainen *et al.* 2000).

Variable S/R relationships may be caused by sampling error in large, dynamic systems, or from the variable production of offspring, caused by density-independent climatic and hydrological events that interrupt spawning or kill early life-stages (Schlosser 1985; Copp and Penaz 1988; Cushing 1990; Johnston *et al.* 1995; Nilo *et al.* 1997; Karjalainen *et al.* 2000; Grenouillet *et al.* 2001). Early

survival depends on the intrinsic attributes of species, and on habitat conditions including food (Tomasson *et al.* 1984; Garner 1996; Bass *et al.* 1997; DeVries *et al.* 1998), protective cover (Paller 1987; Copp and Penaz 1988; Copp 1992; Garner 1996; Jurajda 1999), flow conditions (Copp 1997; Maceina 1997; Sommer *et al.* 1997; Freeman *et al.* 2001; Grenouillet *et al.* 2001) and predation (Tonn and Paszkowski 1992; Myers *et al.* 1997). Even small variations in the survivorship of eggs, larvae and early juveniles are likely to be significant (Thorrald 1988; Koslow 1992; Houde 1997). In common carp (Cyprinidae: *Cyprinus carpio* L.), the vulnerability of these stages is confirmed by field experiments (Mraz and Cooper 1957; Shields 1957).

In wild populations of carp, much is known of the pattern and distal cues for spawning (Swee and McCrimmon 1966; Crivelli 1981; Guha and Mukherjee 1991; Smith and Walker 2004a), but less is known of proximate cues ('spawning triggers') or the survivorship of eggs, larvae and juveniles (Crivelli 1981). In this paper, we attempt to characterize the 'window of opportunity' for spawning, relate the abundance of the early life stages to key environmental conditions, and examine spatial and temporal variation in YOY growth at two sites in the River Murray, South Australia. We begin by reviewing prior knowledge of the spawning behaviour and early life history of carp.

10.2. SPAWNING AND EARLY LIFE HISTORY

Carp are heterosexual, non-guarding, open-substratum, obligatory plant-spawners ('phytophils') (Alikunhi 1966; Balon 1985a). Their preferred spawning sites ('nursery' habitats) are among littoral plants in slow-flowing, shallow (<1 m), warm water (Mills 1991; Garner 1996). Spawning occurs when the mean photoperiod and temperature exceed 10-12 h light and 15-16°C, respectively, and generally involves groups of one female and several males (Shields 1957; Swee and McCrimmon 1966; Crivelli 1981; Santos *et al.* 1997). Depending on body size, the females produce from 500,000 to 2 million eggs per spawning (Alikunhi 1966; Horvath 1985). The eggs hatch within 60-80 degree-days, or 2.5-5 days at 16-28°C (English 1951; Alikunhi 1966; Verma 1970; Ahmed *et al.* 1989). The larvae attach to vegetation (Sigler 1958) for 4-5 days while remaining yolk is absorbed (Verma 1970), and they undergo organogenesis and other ontogenetic changes (Balon 1985b). Exogenous feeding begins before the complete exhaustion of yolk, when the gape is about 300 µm (Billard *et al.* 1995; DeVries *et al.* 1998). The larvae are zooplanktivores, but commence benthic feeding when they become juveniles, at 20-25 days (Vilizzi and Walker 1999).

YOY carp remain in their nursery habitat until they are about 70 mm TL or 4-6 months of age (Shields 1957; Swee and McCrimmon 1966; Paller 1987; Jurajda 1999). During this period they are vulnerable to local environmental changes. For example, low-salinity water exposes fertilised eggs to increased risk of fungal infection (Whiterod 2001¹), cool water slows egg development and reduces food acquisition, metabolism and the growth of larvae and juveniles (Houde 1987; Downing and Plante 1993; Hurst and Conover 1998; Hall and Rudstam 1999), water-level fluctuations and wave action expose spawned eggs (Shields 1957) and impair foraging by small fish unable to hold station against currents and turbulence (Mann and Bass 1997) and low water-levels expose shoreline vegetation, the preferred nursery habitat (Jurajda 1999). The hydrological and climatic variables most likely to influence the survivorship of YOY carp, therefore, are temperature, barometric pressure, river level, river flow, salinity, barometric pressure and wind speed and wind direction. Lunar phase also may be significant, although this is speculative and less well-documented for riverine fish than some tropical marine teleosts (e.g. *Herklotsichthys castelnaui*: Thorrald 1988; Sponagule and Cowen 1997; Takegaki 2000).

10.3. PHYSICAL SETTING

Two backwaters on the River Murray, South Australia, namely Punyelroo (PUN) and Walker Flat ('Walker Flat South', WFS), were chosen for sampling, as these are locations where carp were known to spawn in large numbers (Smith 2004²), and they appeared to be ideal nursery habitats. Each site has abundant submerged and emergent riparian vegetation and broad expanses (50-90 ha) of open, shallow water (mean <1 m, maximum 1.8 m) over a muddy substratum. They remain isothermal throughout the year. The sites occupy swales alongside the main river channel, and usually are directly connected. They are located on an intensively regulated river reach that is bounded to the north by Lock 1 at Blanchetown and to the south by barrages in Lake Alexandrina (Fig. 1). Water-level fluctuations result from changes in river flows and variable winds that may raise and lower river levels by up to 0.3 m (Webster *et al.* 1997). Rainfall is typically light and

¹Whiterod, N. (2001). Ecological consequences of rising salinity for common carp (*Cyprinus carpio*) populations in the Murray-Darling Basin. Unpub. BSc (Honours) thesis, Department of Environmental Biology, The University of Adelaide. 54 p.

² Smith, B. B. (2004). The state of the art: a synopsis of biological information on carp in Australia. Unpub. Technical Report. Primary Industries and Resources South Australia, South Australian Research and Development Institute, Aquatic Sciences Division, Adelaide. 65 pp.

sporadic, and confined to the cooler months (mean 350mm y⁻¹ at Murray Bridge: Bureau of Meteorology data); it does not affect water levels and was therefore excluded from the following analysis.

10.4. FIELD SAMPLING AND LABORATORY ANALYSIS

At each location (PUN, WFS), YOY sampling occurred every 4-6 weeks over 24 months (August 2001 to August 2003). Details of sampling and laboratory processing, including methods for estimating the age, hatch-date and growth rate of sampled fish, are provided by Smith and Walker (2004a). Briefly, post-hatch ages were estimated from thin-sectioned otoliths (lapilli) via enumeration of daily growth increments. Estimated hatch-dates were then calculated for each fish by subtracting the final age estimate from the date of capture. A further 3 days (the duration of egg-incubation: Alikunhi 1966) was subtracted from the estimated hatch-date to estimate the date of spawning. Spawn-date distributions were plotted separately for each backwater (Figs 2a-b) and for pooled data (Fig. 2c). Mean instantaneous growth rates were calculated from the final post-hatch age estimate and the shrinkage-corrected length (standard length, SL) at capture, with regard for the mean length at hatch:

$$\text{Mean growth rate (mm} \cdot \text{d}^{-1}) = \frac{\text{'initial' length at capture} - \text{mean length at hatch}}{\text{final age estimate}}$$

.....Equation 1.

A managed water drawdown in the Murray below Lock 1, from October 2002 (Higham et al. 2004³), made consistent sampling difficult. Littoral vegetation was exposed by falling water at Punyelroo in May and September 2001, and again in January-August 2003, and spawning habitat was restricted. Spawning ceased and/or YOY carp retreated into deeper, open water where they could not be adequately sampled using a small seine (Smith and Walker 2004a). Thus, a partial data set is available for 2002-2003, and a more complete time-series for 2001-2002 (Table 1).

³ Higham, J., Ye, Q. and Smith, B. B. (2004). Murray-Darling Basin drought monitoring: monitoring the response of lower Murray fish communities to reduced water flow and river levels. Unpublished report. Primary Industries and Resources South Australia, South Australian Research and Development Institute, Adelaide. 43 pp.

10.5. HYDROLOGICAL, CLIMATIC AND WATER QUALITY DATA

The spawning-date frequency distributions at the two sites were correlated (Pearson's $r = 0.22$, $P < 0.01$; cf. Figs 2a-b), suggesting that regional (not local) conditions most influenced spawning and YOY abundance. Thus, environmental data were obtained from nearby recording stations. Mean daily records of air temperature, wind speed and direction, and barometric pressure at Murray Bridge (Station 024521), were obtained from the Bureau of Meteorology. Daily records of flow, water levels and salinity immediately downstream of the weir, were obtained from the Department of Water, Land & Biodiversity Conservation, Berri, South Australia. Daily records of nutrients (N, P) and chlorophyll were not available. Information about photoperiod and lunar phase was obtained from Geoscience Australia (<http://www.ga.gov.au>, accessed February 2004).

10.6. ANALYSIS

10.6.1. *Spawning period*

The spawn-date distributions of YOY abundances (Figs 2a-c) are assumed to represent 'windows of opportunity' for carp spawning, and variation in the 'strength' of daily cohorts (relative number of fish spawned on a day) is assumed to reflect differences in YOY survivorship rather than patterns of egg production. To elucidate factors that may have contributed to daily variation, the cohorts were sorted into four categories reflecting the numbers of YOY carp born each day: nil (0 fish), low (1-4 fish), moderate (5-8) and strong (9-14) (Table 2) (Donald 1997; Maceina and Bettoli 1998).

10.6.2. *YOY abundance and environmental conditions*

Analysis of these data is a two-step process, including correlation of abundances (or another index of recruitment, e.g. year-class strength) with biotic or abiotic factors, and regression (following Ricker 1975; Beentjes and Renwick 2001). Difficulties may arise, however, from (1) autocorrelation, (2) spurious correlations from lack of prior theoretical justification for selection of independent variables, or by not adjusting the statistical P values for multiple tests on the same data set, (3) not reporting non-significant correlations and (4) overlooking complex correlations (see further Ricker 1975; Helbig *et al.* 1992; Myers 1997; Beentjes and Renwick 2001).

Autocorrelation, evident in repeated samples of one system, is unavoidable in large-scale field studies. We chose independent variables after *a priori* consideration of factors likely to be important for early survivorship (and thereby have assumed that we have included all important variables). We report all non-significant correlations, and have adjusted nominal *P* values using a modified Bonferroni procedure (Howell 2002). The temporal distribution of relative YOY abundances has a high 'signal amplitude', which reduces the possibility of spurious correlations (Beentjes and Renwick 2001). It covers more than six periods of increasing and decreasing abundance (Figs 2a-c).

Correlations between environmental parameters were examined to identify and discard redundant variables. For example, river flow, wind direction and salinity are positively related to river level (Pearson's $r > 0.16$, $P < 0.001$, $n = 761$), and barometric pressure is negatively related to temperature ($r = -0.4$, $P < 0.001$, $n = 754$). River level and temperature are considered primary factors because of their critical role in determining the availability of spawning and nursery habitat, and in controlling YOY metabolism and growth, respectively. Thus, river flow, wind direction, salinity and barometric pressure data were excluded from further analysis.

Correlations between the spawn-date distribution of YOY carp (Fig. 2c) and remaining parameters (temperature, river level, wind speed, lunar phase), recorded on the day of spawning and averaged over the duration of the critical larval phase (about 20 d post-spawning: Vilizzi and Walker 1999) were analysed using SAS JMP-IN v 4.04 (Table 3). Significant ($P < 0.05$) or suggestive correlations ($0.10 > P > 0.05$) were further analysed by multiple linear regression, using $\alpha = 0.10$ and 0.25 as entry and exit criteria, respectively.

10.6.3. Age and growth

Temporal and spatial variation in age-SL relationships was compared among years (2001-2002, 2002-2003) and locations (PUN, WFS) via Analysis of Covariance (ANCOVA: slopes, intercepts, r^2) (Narimatsu and Munehara 1999) after log-linear transformation (Table 4). Age-SL relationships were also compared within years, whereby YOY carp were grouped into three cohorts of fish, each spawned over *c.* 2 months. The Early Cohort includes fish estimated to have been spawned between the onset of reproduction and 10 December, the Middle

Cohort from 11 December to 10 February, and the Late Cohort from 11 February to 1 April (Table 5). There was no Late Cohort for the within-year comparison of 2002-2003, as estimation suggested that no YOY carp were spawned after 28 January 2003 (Fig 2c).

Relationships between the estimated post-hatch age and SL, body weight and otolith length and width were also examined by non-linear, least-squares regression using SigmaPlot v.8.0 (Fig. 3, Table 6). Subsequently, stepwise multiple linear regression using SAS JMPIN v.4.0.1 (after log-linear transformation), was used to identify the best age-prediction formula for each year and location (Table 7).

10.7. RESULTS

10.7.1. *Spawning period*

Figures 2a-c show estimated spawn-dates for YOY carp sampled in August 2001-2003. Spawning was evident over at least 7 months in 2001-2002, from 24 September to 27 March, but not from April to September 2002. In 2002-2003, spawning was evident over 5 months, from 4 October until 1 February. Spawning generally was continuous from onset until completion. Reproductive events lasted 2-10 days, and were separated by up to 2 weeks. Over the entire period, 34 successful events were apparent, 20 of them synchronous between the two locations. YOY production was greatest in mid-October and December, and mid-January and mid-March.

‘Windows of opportunity’ for carp spawning, noted above, were characterised by mean air temperature (10.5-31.2°C), photoperiod (11h54min-14h 30min), river level (0.57-1.2m ASL), river flow (2685-8372 ML d⁻¹), salinity (476-671 EC units), barometric pressure (1002-1029 Hpa), wind speed (0-28 km h⁻¹) and wind direction (0-360°TN) (Table 2). Within these ‘windows’, the relative number of YOY carp estimated to have been spawned each day was variable. For days where few or no YOY carp ($n < 4$) were estimated to have been spawned, the range in environmental conditions was broad, comparable to the range for the entire spawning period (Table 2). Conversely, on days where moderate ($n = 5-8$) and high ($n = 9-14$) numbers of YOY carp were estimated to have been spawned, environmental conditions were constrained: mean air temperature (15.9-25.1°C), photoperiod (12h 45min-14h15min), river level (0.66-1.06 m ASL), river flow

(3036-6071 ML d⁻¹), salinity (494-617 EC units) barometric pressure (1008-1019 Hpa), wind speed (1-19 km h⁻¹) and wind direction (0-230°TN) (Table 2).

10.7.2. YOY abundance and environmental conditions

Only wind speed showed a statistically significant (negative) correlation with the spawn-date distribution of YOY carp (relative number of YOY spawned each day) (Pearson's $r = -0.15$, $P = 0.008$, $n = 306$; Table 3). However, although the slope of the linear regression was significant ($t_b = 2.66$, $P = 0.01$), the relationship was highly variable (YOY abundance = $2.91 - 0.065 \times \text{mean daily wind speed}$, $r^2 = 0.023$). For the remaining parameters, there was no relationship (e.g. lunar phase: $r = -0.006$, $P = 0.915$) and/or the relationships were dome-shaped and highly variable (e.g. water level, temperature: Fig. 4). For the latter, the data were not suitable for transformation. Polynomial ($y = a + bx + cx^2$; Ricker 1975) and step-wise multiple linear regressions were considered, but all explained <4% of the variation in relative YOY abundance and further analyses were abandoned.

10.7.3. Age and growth

Mean instantaneous growth rates for individual YOY carp ranged from 0.23-1.25mm d⁻¹ (mean = $0.5\text{mm d}^{-1} \pm 0.12 \text{ S.D.}$, $n = 657$), depending on the initial age and size at capture. Population growth rates (indicated by age-SL relationships) were consistently highest at WFS (Fig. 3, Table 4), where visual inspection indicated a greater abundance of submerged nursery habitat than at PUN. Growth also was highest in 2001-2002 (Fig. 3, Table 4), when river-levels remained comparatively high, and mean monthly temperatures were more moderate and stable than in 2002-2003 (Fig. 5a-b). Growth was similar between the Early and Middle Cohorts, but in 2001-2002 when YOY carp were estimated to have hatched after 10 February, it was significantly faster for this Late Cohort (Table 5). Despite this, mean daily temperatures were significantly lower for the Early Cohorts than for the Middle Cohorts (2001-2002, Student's $t = 7.58$, $df = 134$, $P = <0.001$; 2002-2003, $t = 7.47$, $df = 119$, $P = <0.001$), and in 2001-2002, there were no temperature differences between the Middle and Late cohorts ($t = 0.90$, $df = 102$, $P = 0.37$).

Non-linear regression equations, relating estimated age and each of four fish (SL; weight, Wt) and otolith (length, width) parameters, typically explained >70% of the variation in age-at-size (Table 6). However, step-wise multiple linear regression indicated that otolith size was the best predictor of age, and >85% (up to 94%) of the variation in age between locations and years was explained by its relationship with otolith size (Table 7). Adding multiple parameters failed to improve their fit (r^2) beyond 5%. Thus, the regressions remain as simple linear models.

10.8. DISCUSSION

In this study, the aims were to characterise the ‘windows of opportunity’ for spawning, identify possible environmental factors important in the survivorship of YOY carp, and examine spatial and temporal variation in YOY growth.

10.8.1. Spawning period

Spawning lasted from September to March in 2001-2002 and October to February in 2002-2003. Young-of-the-year production was greatest in late (austral) spring (November) and late summer (February). These periods coincide with peaks in the gonadosomatic index for wild carp in the Murray (Hume *et al.* 1983; Sivakumaran *et al.* 2003; Smith and Walker 2004b; Smith and Walker 2004a), and are separated by about 3 months, the time required for the ovaries to re-mature after spawning (Davies and Hanyu 1986; Davies *et al.* 1986).

The environmental data recorded annually over spawning were highly variable. However, relatively strong cohorts of YOY carp were allied with stable flows and atmospheric conditions during the egg incubation and larval stages. During these periods, mean daily air temperatures were 15.9-25.1°C, the barometric pressure ranged between 1008-1019 Hpa, the photoperiod was >12.5 h light, river levels were 0.66-1.06 m ASL and wind speeds were 1-19 km h⁻¹. This concurs with laboratory data indicating a minimal photoperiod of 10-12h light for ovulation (Davies and Hanyu 1986; Davies *et al.* 1986; Brzuska 1989), and field data suggesting that spawning intensity is low from 15-18°C, optimal at 18-23°C and ceases at 28°C (Shields 1957; Swee and McCrimmon 1966; Fernandez-Delgado 1990).

10.8.2. YOY abundance and environmental conditions

The advantages of warm, lentic, riparian habitat and stable environmental conditions for teleost early life stages are well documented (Hall and Rudstam 1999). In the present study, however, variation in the spawn-date distribution of YOY carp was not strongly associated with any of the hydro-climatic factors recorded at the time of spawning, nor with those averaged over the duration of the critical larval phase. Thus, the spawn-date distribution may indicate the pattern of spawning- and egg production, rather than environment-mediated variation in survivorship. It may also be governed by other, unaccounted factors such as food, habitat, disease or predation (Shepherd *et al.* 1984; Houde 1987; Houde 1997). Alternatively, the apparent lack of association may be because the relationships between reproductive activity and hydro-climatic parameters are complex rather than simple, as the analyses here presume. For example, it could be insufficient to have stable water levels and calm weather if there is insufficient food due to a preceding period of low water temperatures or variable flows (Maceina *et al.* 1996; Copp 1997; Maceina and Bettoli 1998). Variable, dome-shaped relationships support this hypothesis (Fig. 4).

Survival is highest when optimal conditions prevail during the course of the egg, larval and early-juvenile stages (Sommer *et al.* 1997; Freeman *et al.* 2001). The duration of this period is about 15-18 days for largemouth bass (*Micropterus salmoides*, Maceina 1997; Maceina and Bettoli 1998) and 30 days for goldeyes (*Hiodon alosoides*, Donald 1997). As indicated, YOY carp probably require more than 25-30 days of calm, warm weather and abundant submerged vegetation for optimal survival.

10.8.3. Age and growth

Population growth rates were highest at WFS, where there was most submerged vegetation. Submerged vegetation provides the young fish with shelter from currents, refuge from predators and a source of food, through associated invertebrates (Floyd *et al.* 1984; Copp 1992; Freeman *et al.* 2001). Growth rates were also highest in 2001-2002, when river-levels remained high, and mean monthly temperatures were more moderate and stable than in 2002-2003. High river-levels and warm temperatures are likely to have promoted the recruitment of YOY carp by increasing the availability of nursery habitat and increasing their metabolism (Houde 1987; Downing and Plante 1993; Hurst and Conover 1998; Hall and Rudstam 1999). Indeed, after January 2001 when river

levels receded to 25cm below the annual average of 0.6-0.7m ASL, and most submergent shoreline vegetation was exposed (Higham *et al.* 2004³), there apparently was no spawning.

Protracted spawning over 2001-2003 meant that YOY carp with different spawn dates experienced different environmental conditions at the same age. Yet, growth of the Early and Middle Cohorts was statistically similar, and faster only for the Late Cohort in 2001-2002. Regardless, early-spawned fish probably are advantaged in the long term because they are larger at hatch (mean egg-size diminishes over the spawning season in multiple-batch spawners: Trippel *et al.* 1997), have a longer growing season (Limburg *et al.* 1997; Narimatsu and Munchara 1999), accumulate more energy reserves (Tonn *et al.* 1994) and thereby attain a larger body size (with lower metabolism) before winter.

Aging YOY carp via daily otolith increment counts is a valid, relatively straightforward process (Vilizzi 1998; Smith and Walker 2003, 2004a). Although time-consuming, the procedure may be streamlined by calibrating regression relationships between age- and fish (SL, Wt) and otolith (length, OL; width, OW) size for a small sub-sample, which may later be used for whole-samples (Worthington *et al.* 1995a,b). These have been calculated previously for YOY carp, but the relationships were modelled separately for larvae and juveniles, otolith size was not considered and the explained variation was typically <80% (Vilizzi 1998). In this study, relationships were calibrated for YOY carp of 10-45 mm SL (larvae and early-juveniles) using SL and Wt and OL and OW as independent variables. Step-wise multiple linear regression indicated that otolith size (OL and OW) was the best predictor of age and the explained variance was high ($r^2 = 0.85-0.94$: Table 7). However, as the relationships were spatially and temporally variable, frequent re-calibration is necessary.

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10.11. LIST OF FIGURES

Figure 1. Map of Australia (inset) showing sampling locations at Punyelroo and Walker Flat on the River Murray floodplain, South Australia.

Figure 2. Estimated spawn-date distributions of YOY carp sampled every 4-6 weeks from August 2001 to August 2003 at (a) Walker Flat South ($n = 355$), (b) Punyelroo ($n = 324$) and (c) Walker Flat South and Punyelroo combined ($n = 679$). No sampled fish were estimated to have been spawned prior to 27 September 2001, between 27 March and 4 October 2002 or after 29 January 2003. Minor ticks on abscissa are at 5-d intervals. Moon phase is indicated (\circ = full moon, \bullet = new moon).

Figure 3. Age-length relationships for YOY carp at Punyelroo (PUN) and Walker Flat South (WFS) during 2001/2002 and 2002/2003.

Figure 4. Relationships between mean air temperature ($^{\circ}\text{C}$) and water level (ASL, m), and the relative number of YOY carp estimated to have been spawned each day.

Figure 5. Mean daily a) temperatures and b) river levels, averaged over each month during August 2001-2003.

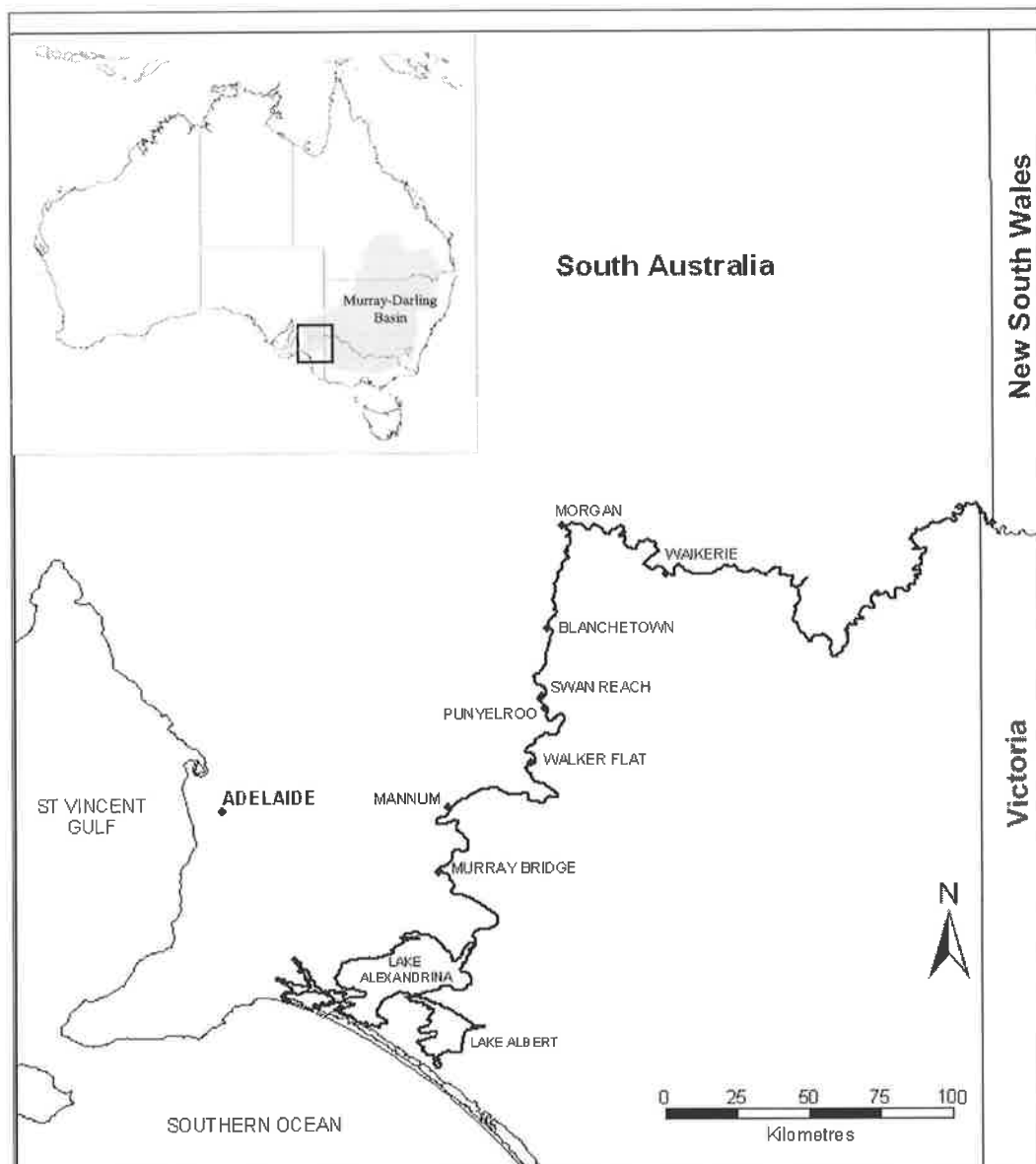


Figure 1.

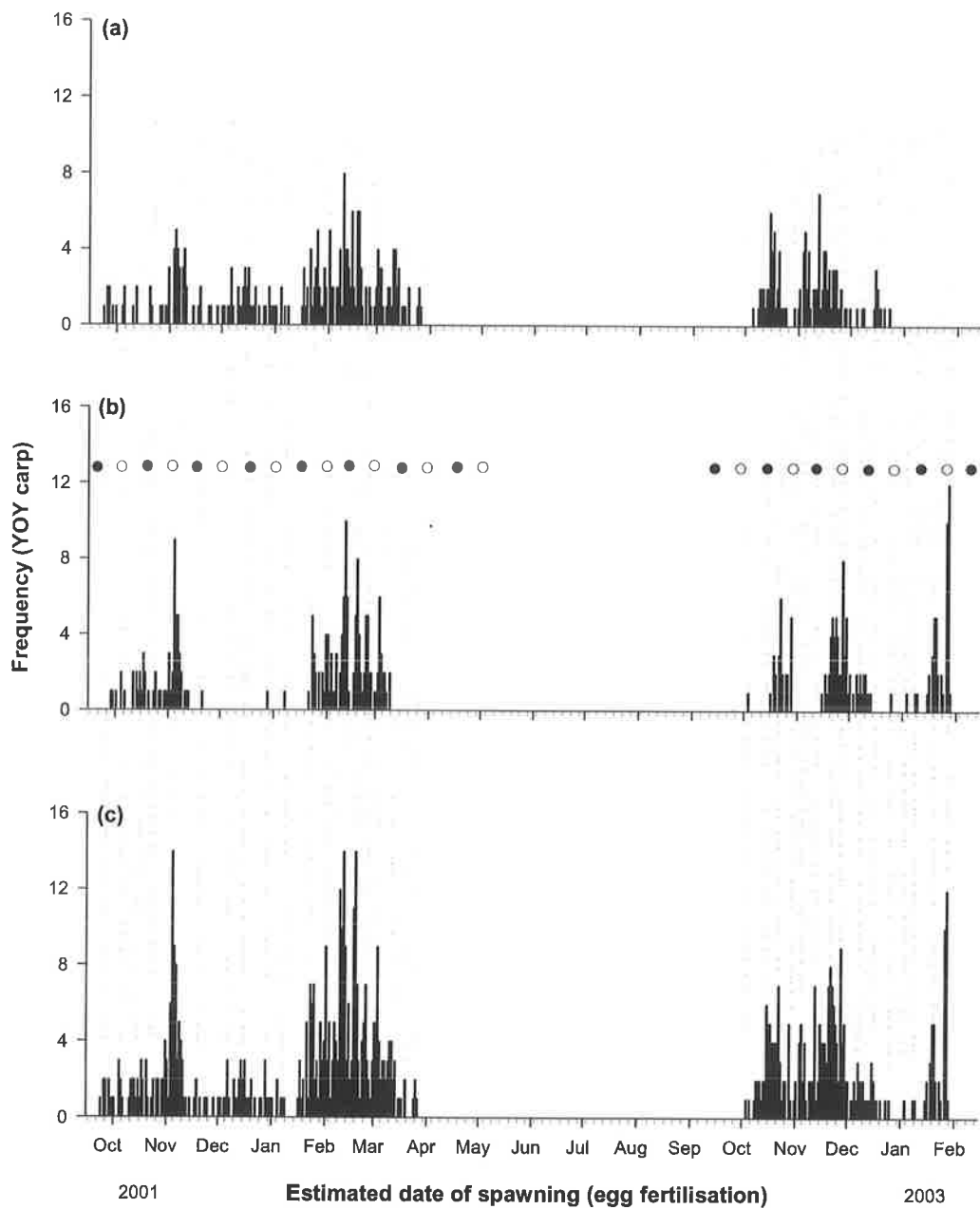


Figure 2.

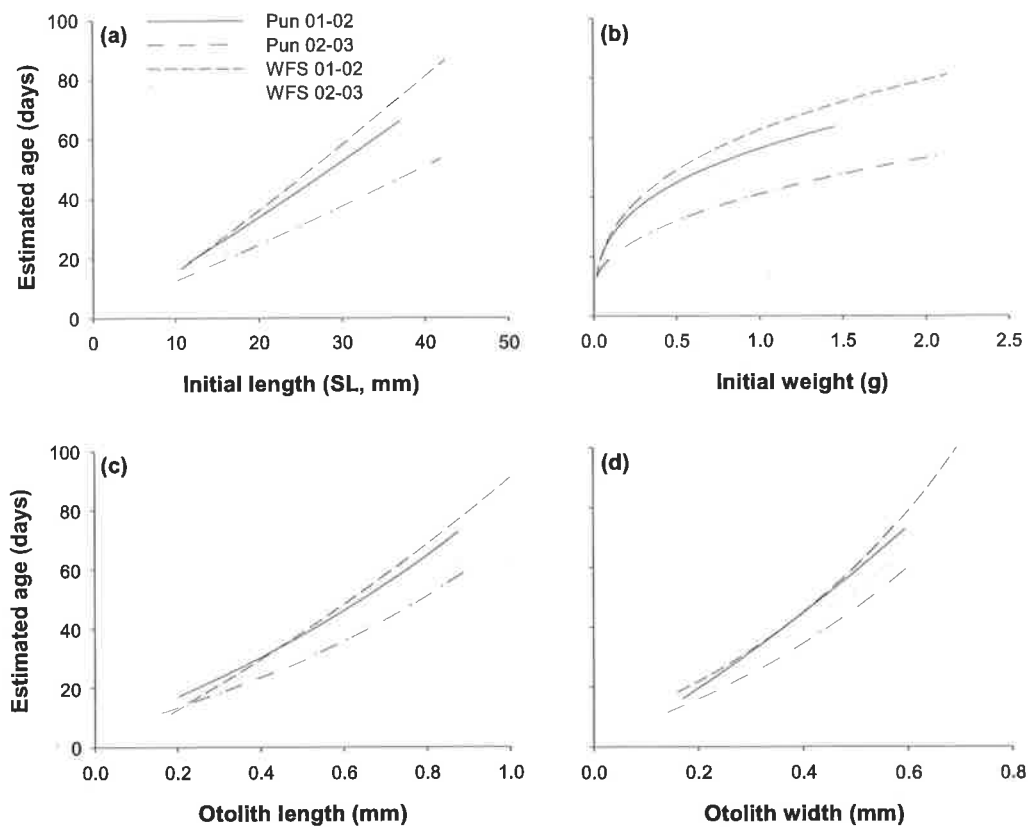


Figure 3.

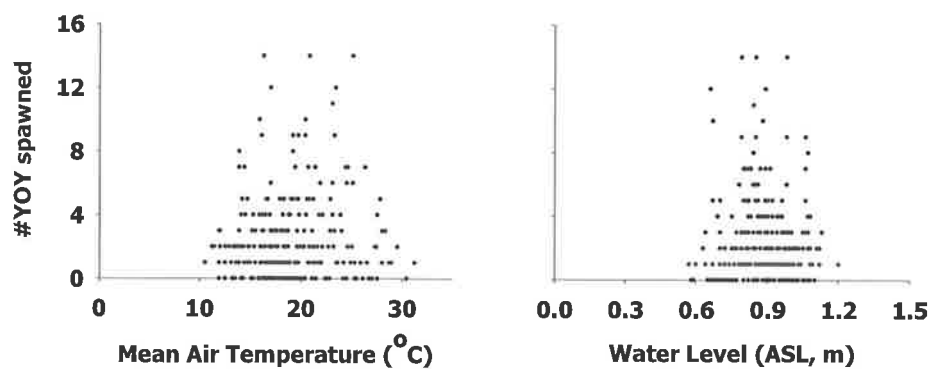


Figure 4.

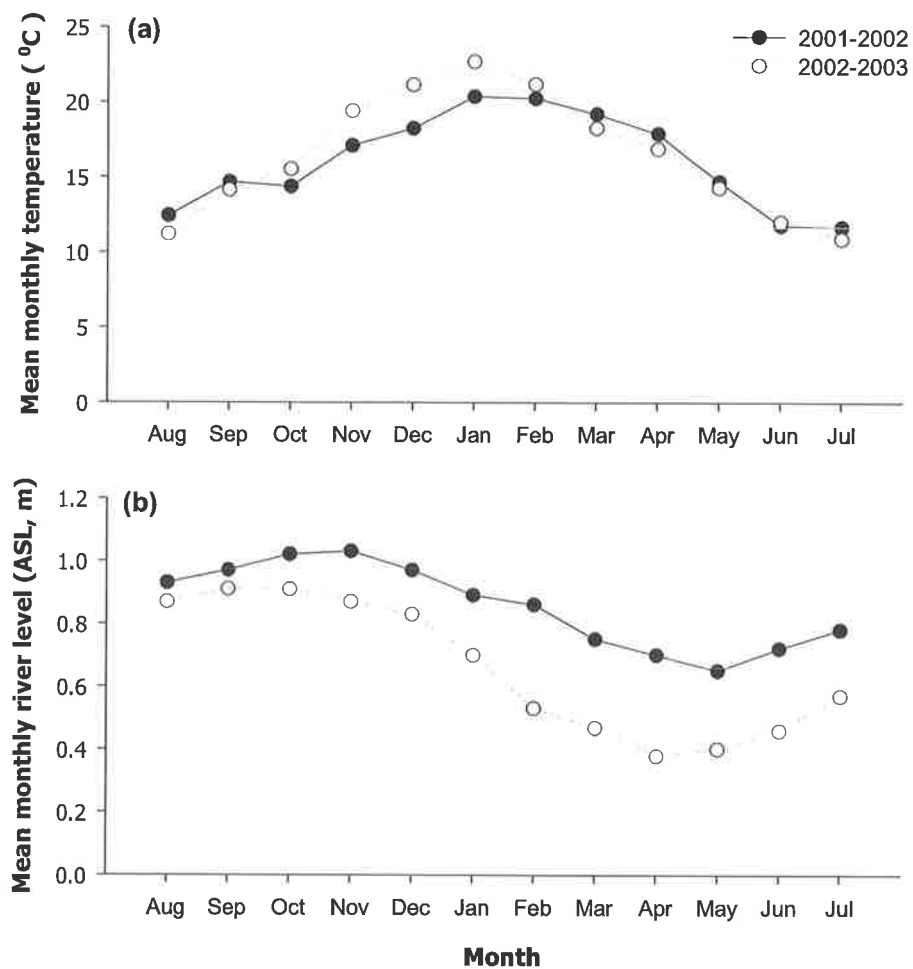


Figure 5.

LIST OF TABLES

Table 1. Numbers of YOY carp sampled at Punyelroo and Walker Flat South during August 2001-2003. No YOY carp were caught before November 2001, between June 2002 and October 2002, or after February 2002. *, $n < 5$.

Season	Location	Number of fish sampled per month											
		Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul
2001-2002	Walker Flat South	-	-	-	24	50	50	50	50	49	50	-	-
	Punyelroo	-	-	-	28	50	*	30	50	49	*	-	-
2002-2003	Walker Flat South	-	-	-	50	50	50	*	*	-	-	-	-
	Punyelroo	-	-	-	27	50	22	50	*	-	-	-	-

Table 2. Summary of the environmental conditions recorded (a) over the entire year, (b) over the spawning periods (viz the 'windows of opportunity'), and (c-f) on days within the spawning period, where there were nil, low, moderate and high numbers of YOY carp estimated to have been spawned.

		Temperature (°C)			Photoperiod (hh:mm)			River Level (ASL, m)			River Flow (ML/d ¹)		
		Min	Max	Range	Min	Max	Range	Min	Max	Range	Min	Max	Range
(a)	Entire year	5.6	31.2	25.6	949	1430	481	0.31	1.20	0.89	1160	8372	7212
(b)	Spawning period	10.5	31.2	20.7	1154	1430	276	0.57	1.20	0.63	2685	8372	5688
(c)	Nil (0)	11.9	30.4	18.5	1201	1430	229	0.58	1.10	0.52	2824	8372	5548
(d)	Low (1-4)	10.5	31.2	20.7	1154	1430	276	0.57	1.20	0.63	2685	8349	5665
(e)	Moderate (5-8)	13.9	27.8	13.9	1247	1416	169	0.67	1.07	0.41	3028	6540	3512
(f)	Strong (9-14)	15.9	25.1	9.2	1245	1415	170	0.66	1.06	0.40	3036	6071	3036

		Wind Speed (km/h ⁻¹)			Barometric Pressure (Hpa)			Salinity (EC units)			Wind Direction (°TN)		
		Min	Max	Range	Min	Max	Range	Min	Max	Range	Min	Max	Range
(a)	Whole year	0	44	44	996	1034	38	378	674	295	0	360	360
(b)	Spawning period	0	28	28	1002	1029	27	476	671	195	0	360	360
(c)	Nil (0)	2	28	26	1003	1024	21	476	668	192	0	360	360
(d)	Low (1-4)	0	28	28	1002	1029	27	477	671	194	0	360	360
(e)	Moderate (5-8)	0	28	28	1005	1024	19	492	656	164	0	360	360
(f)	Strong (9-14)	1	19	18	1008	1019	11	494	617	123	0	230	230

Table 3. Summary of correlations between the spawn-date distribution of YOY carp and selected environmental parameters recorded on the day of spawning *and* averaged over the duration of the critical larval phase (*).

Test	Correlation	P	α - modified	Significant
YOY abundance v Wind Speed	-0.1510	0.008	0.011	yes
YOY abundance v WindSpeed*	-0.1380	0.016	0.014	no
YOY abundance v Temperature	0.0870	0.134	0.020	no
YOY abundance v Water Level*	-0.0520	0.361	0.025	no
YOY abundance v Water Level	-0.0470	0.410	0.033	no
YOY abundance v Lunar Phase	-0.0006	0.915	0.050	no
YOY abundance v Temperature*	0.0005	0.931	0.100	no

Table 4. Linear regression equations relating age and initial length for YOY carp sampled from Punyelroo and Walker Flat South during August 2001-2003. The slope, intercept and fit of each regression are compared between locations and years via ANCOVA.

Location	Year	Relationship	r^2	n
Punyelroo	2001-2002	Estimated age = $0.096 + 1.097 (\pm 0.047 \text{ S.E.}) \times \text{IL}$	0.77	161
	2002-2003	Estimated age = $0.160 + 0.941 (\pm 0.061 \text{ S.E.}) \times \text{IL}$	0.63	141
Walker Flat	2001-2002	Estimated age = $-0.100 + 1.197 (\pm 0.040 \text{ S.E.}) \times \text{IL}$	0.79	237
	2002-2003	Estimated age = $-0.013 + 1.135 (\pm 0.040 \text{ S.E.}) \times \text{IL}$	0.88	118
Slopes comparison:		$F_{3,649} = 5.624, P = <0.0001$		
Intercept comparison:		$F_{3,654} = 179.4, P = <0.0001$		
r^2 comparison:		$F_{1,654} = 2129.5, P = <0.0001$		
Common slope:		$1.104 (\pm 0.024 \text{ S.E.}), df = 652$		

Table 5. Summary table of growth comparisons for YOY cohorts. EC, early-spawned cohort (onset - 10 Dec); MC, middle-spawned cohort (11 Dec - 10 Feb); LC, late-spawned cohort (11 Feb – 01 Apr); IL, initial fish length (SL, mm).

Location	Year	Cohort	Relationship	r^2	n
Punyelroo	2001-2002	EC	Estimated age = $0.775 + 0.598(\pm 0.116 \text{ S.E.}) \times \text{IL}$	0.42	39
		MC	Estimated age = $0.372 + 0.836(\pm 0.105 \text{ S.E.}) \times \text{IL}$	0.80	18
		LC	Estimated age = $-0.047 + 1.214(\pm 0.048 \text{ S.E.}) \times \text{IL}$	0.86	104
		Slopes comparison:	$F_{2,155} = 16.026, P = <0.0001$		
		Intercept comparison:	$F_{2,159} = 11.11, P = <0.0001$		
		r^2 comparison:	$F_{1,159} = 545.86, P = <0.0001$		
		Common slope:	$1.080 (\pm 0.046 \text{ S.E.}), df = 157$		
	2002-2003	EC	Estimated age = $0.175 + 0.928(\pm 0.061 \text{ S.E.}) \times \text{IL}$	0.63	140
		MC	Estimated age = $0.140 + 0.932(\pm 0.146 \text{ S.E.}) \times \text{IL}$	0.39	65
		Slopes comparison:	$F_{1,201} = 0.001, P = 0.978$		
		Intercept comparison:	$F_{1,204} = 4.730, P = 0.031$		
Punyelroo	2001-2002	EC	Estimated age = $0.313 + 0.945(\pm 0.060 \text{ S.E.}) \times \text{IL}$	0.83	55
		MC	Estimated age = $0.193 + 1.033(\pm 0.049 \text{ S.E.}) \times \text{IL}$	0.87	71
		LC	Estimated age = $-0.244 + 1.381(\pm 0.069 \text{ S.E.}) \times \text{IL}$	0.78	111
		Slopes comparison:	$F_{2,231} = 12.69, P = <0.0001$		
		Intercept comparison:	$F_{2,235} = 17.11, P = <0.0001$		
		r^2 comparison:	$F_{1,235} = 893.49, P = <0.0001$		
		Common slope:	$1.158 (\pm 0.039 \text{ S.E.}), df = 233$		
	2002-2003	EC	Estimated age = $-0.052 + 1.161(\pm 0.042 \text{ S.E.}) \times \text{IL}$	0.88	104
		MC	Estimated age = $0.277 + 0.932(\pm 0.169 \text{ S.E.}) \times \text{IL}$	0.72	14
		Slopes comparison:	$F_{1,114} = 1.255, P = 0.2658$		
		Intercept comparison:	$F_{1,117} = 3.672, P = 0.058$		
		r^2 comparison:	$F_{1,117} = 790.91, P = <0.0001$		
		Common slope:	$1.151 (\pm 0.041 \text{ S.E.}), df = 115$		

Table 6. Non-linear regression equations relating age and fish and otolith size for YOY carp sampled from Punyelroo and Walker Flat South during 2001-2003.

Regression	Location	Year	Equation	r^2
Estimated age v Initial length	Punyelroo	2001-2002	Age = $0.8358 + 1.171 \times IL^{1.113}$	0.74
		2002-2003	Age = $2.068 + 0.7916 \times IL^{1.117}$	0.64
	Walker Flat	2001-2002	Age = $-2.635 + 1.383 \times IL^{1.111}$	0.74
		2002-2003	Age = $-2.578 + 1.373 \times IL^{1.050}$	0.85
Estimated age v Initial weight	Punyelroo	2001-2002	Age = $-0.9708 + 57.21 \times IW^{0.3224}$	0.70
		2002-2003	Age = $7.955 + 32.99 \times IW^{0.4550}$	0.68
	Walker Flat	2001-2002	Age = $-5.228 + 67.72 \times IW^{-0.3209}$	0.73
		2002-2003	Age = $-10.66 + 60.27 \times IW^{0.2573}$	0.82
Estimated age v Otolith length	Punyelroo	2001-2002	Age = $-55.69 + 61.43 \times e^{0.8404 \times OL}$	0.83
		2002-2003	Age = $-28.63 + 34.13 \times e^{1.060 \times OL}$	0.91
	Walker Flat	2001-2002	Age = $-150.4 + 148.0 \times e^{0.4893 \times OL}$	0.78
		2002-2003	Age = $-128.0 + 131.1 \times e^{0.4232 \times OL}$	0.93
Estimated age v Otolith width	Punyelroo	2001-2002	Age = $-154.3 + 151.9 \times e^{0.6756 \times OW}$	0.87
		2002-2003	Age = $-31.36 + 34.44 \times e^{1.632 \times OW}$	0.87
	Walker Flat	2001-2002	Age = $-25.62 + 32.02 \times e^{1.974 \times OW}$	0.76
		2002-2003	Age = $-157.8 + 156.5 \times e^{0.5911 \times OW}$	0.93

Table 7. Results of step-wise multiple linear regressions, relating age and each of four fish and otolith parameters for Walker Flat and Punyelroo during 2001-2003. Addition of multiple parameters failed to increase the “fit” of any regression by more than 5%. Thus, regression equations for each location and year include only one predictor (x) variable.

Location	Year	Relationship	r^2	n
Punyelroo	2001-2002	$\log(\text{Estimated age}) = 2.140 + 1.227 (\pm 0.035 \text{ S.E.}) \times \log OW$	0.87	184
	2002-2003	$\log(\text{Estimated age}) = 1.745 + 0.916 (\pm 0.030 \text{ S.E.}) \times \log OL$	0.87	140
Walker Flat	2001-2002	$\log(\text{Estimated age}) = 2.126 + 1.220 (\pm 0.038 \text{ S.E.}) \times \log OW$	0.85	184
	2002-2003	$\log(\text{Estimated age}) = 1.845 + 1.030 (\pm 0.035 \text{ S.E.}) \times \log OL$	0.94	118

11. APPENDIX 2. EXAMINER COMMENTS RELATING TO APPENDIX 1

Appendix 1 is an unpublished manuscript that, in its current state, was deemed unacceptable for publication by both examiners of this thesis. Their primary concerns are listed below, and because this manuscript is no longer being pursued for publication, none of these have been addressed.

Readers of this thesis should consider the following comments when evaluating Appendix 1.

- *“There is the assumption that YOY fish stay around as they grow and therefore that the number of recruits can be accurately determined. Although it is mentioned that they moved into deeper water, there is no consideration on the possibility of emigration generally”.*
- *“I would have liked to have seen a data analysis section, since in Chapter 10.5 we launch straight into the statistics, without any indication of whether data needed to be transformed or whether they have been transformed”.*
- *“The r-value indicates that only about 5% of the variation of one site can be explained by the other, and the high significance is most likely due to the large n – so this does not really support the conclusion of regional influences”.*
- *“It is common, despite it having been stated on several occasions, for the terms ‘spawning production’ or ‘number of YOY spawned each day’ to be used, when in fact the results are telling us how many fish survived i.e., recruits. Without the knowledge of the number of newly hatched larvae (or, indeed, the number of eggs), it is impossible to conclude about numbers spawned. Survival is critical and may be related to spawning numbers, but there is no guarantee. In fact, I have seen several sets of data suggesting disproportionate recruitment”:*
- *“There is no real indication in the introduction section about why comparisons were made between SL, weight and otolith length and width with age. We are left until the Discussion to find out the reasons”:*
- *“Spawning can’t be continuous and be separated by up to two weeks”*
- *“It is hard to see how the data can be interpreted to show numbers of events and their synchronicity – this conclusion needs detailed validation. What defines an event?”*

-
- *“The ‘windows of opportunity’ concept has not proved fruitful. The ranges of conditions are extremely broad, there is no equivalent test of alternative conditions that close the ‘window’, and no clear separation of events other than the limits of the spawning season. I consider the data allow the long spawning season to be defined in terms of these environmental variables, but there is little basis for much finer scale resolution”.*
 - *“Water temperature would be a much more reliable predictor than air temperature, especially as no relationship has ever been established between the two and it is uncertain how greatly main-channel conditions control conditions in the backwater recruitment sites”.*
 - *“‘Australia’ is missing something”.*
 - *“With the benefit of hindsight it is tempting to ponder whether an alternative approach to some of this work might have been better. The vigorous spawning behaviour of large carp in shallow, calm water is often a highly visible phenomenon. An approach which invested field-sampling resources into simply observing and recording this behaviour, together with direct, on-the-spot recording of critical environmental data might have been more productive than the far more technically elegant back-calculation approach used. Perhaps this idea might be considered for the future”.*