Swimming performance and dispersal potential of larval Australian freshwater fish in a regulated riverscape

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Table of Contents

Certificate of Authorship ........................................................................................................ vii
Acknowledgements .............................................................................................................. viii
Animal Research Authority ................................................................................................. x
Abstract ............................................................................................................................ xi
Chapter 1: General Introduction .......................................................................................... 2
  1.1 River ecology at the riverscape scale ........................................................................ 2
      1.1.1 River ecosystems ........................................................................................... 2
      1.1.2 Riverscapes ..................................................................................................... 4
  1.2 Life history strategies at the riverscape scale ............................................................. 5
      1.2.1 Swimming capabilities and dispersal of the early life stages of fish ............... 7
      1.2.2 The effects of river regulation in the Murray-Darling Basin on the early life
          stages of fishes ......................................................................................................... 9
  1.3 Aims of the Thesis ....................................................................................................... 10
Chapter 2: Description of study area .................................................................................. 14
  2.1 Catchment characteristics ......................................................................................... 14
  2.2 Climate ..................................................................................................................... 15
  2.3 Geomorphology and hydrology .............................................................................. 16
  2.4 Fish fauna ................................................................................................................ 18
  2.5 Description of study reaches ................................................................................... 21
Chapter 3: Anabranches as habitat for larval fishes in regulated riverscapes ................. 28
  3.1 Introduction ............................................................................................................... 28
  3.2 Materials and methods ............................................................................................ 30
      3.2.1 Study Area ..................................................................................................... 30
      3.2.2 Study Design ................................................................................................ 33
3.2.3 Field Sampling ................................................................. 34
3.2.4 Laboratory Methods ........................................................ 35
3.2.5 Data Analysis ................................................................. 36

3.3 Results .............................................................................. 37
3.3.1 Study 1 .......................................................................... 37
3.3.2 Study 2 .......................................................................... 48

3.4 Discussion ......................................................................... 51
3.4.1 Comparisons among main stem and anabranches .......... 51
3.4.2 Comparisons within the Old Man Creek anabranch ....... 54
3.4.3 Consistency of habitat use ............................................. 55
3.4.4 Can anabranches provide a refuge for fish from modified flows? .... 56

Chapter 4: Ontogeny of critical and prolonged swimming performance for the larvae of six Australian freshwater fish species ......................................................... 59

4.1 Introduction .................................................................... 59
4.2 Materials and methods ...................................................... 62
4.2.1 Experimental setup and design ...................................... 65
4.2.2 Data analysis ................................................................. 69

4.3 Results .............................................................................. 70
4.3.1 Best predictors of critical and prolonged swimming performance ........ 70
4.3.2 Ontogeny in swimming performance .............................. 76
4.3.3 Comparisons of critical speed of average and best performers among species ......................................................... 79
4.3.4 Comparisons among life history strategies ...................... 82
4.3.5 Prolonged swimming ...................................................... 82

4.4 Discussion ........................................................................ 85
4.4.1 Comparisons of swimming performance of Murray-Darling Basin with other freshwater fishes ................................. 85
### 4.4.2 Ontogeny and swimming performance ...........................................86

### 4.4.3 Life history strategies and swimming performance .....................88

Chapter 5: The dispersal of experimentally released larvae of riverine fishes with contrasting life history strategies .................................................................93

5.1 Introduction ......................................................................................93

5.2 Materials and methods......................................................................96

5.2.1 Study site .....................................................................................96

5.2.2 Experimental release of fish larvae and passive particles ..............97

5.2.3 Laboratory methods .....................................................................102

5.2.4 Data Analysis ................................................................................102

5.2.5 Hydrodynamic modelling ..............................................................104

5.3 Results ............................................................................................104

5.4 Discussion .......................................................................................111

Chapter 6: Modelling hydraulic habitat for riverine fish larvae in relation to flow alteration ...........................................................................................................116

6.1 Introduction ......................................................................................116

6.2 Materials and methods......................................................................119

6.2.1 Study reaches ...............................................................................119

6.2.2 Data inputs for hydraulic modelling ............................................122

6.2.3 Hydraulic modelling .....................................................................127

6.2.4 Percent usable hydraulic habitat criteria .......................................129

6.3 Results ............................................................................................130

6.3.1 Modelled velocity in Old Man Creek under nine river discharge levels .. 130

6.3.2 Percent usable area of hydraulic habitat for four species of larvae ......133

6.4 Discussion .......................................................................................137

6.4.1 Modelled velocity in Old Man Creek under nine river discharge levels .. 137
6.4.2 Percent usable area of hydraulic habitat for the larvae of four species of fish.................................................................................................................................................................................. 138

6.4.3 Implications for larval fish in lowland rivers under river regulation ..... 139

Chapter 7: General Discussion.............................................................................................................................. 141

Appendix A: AIC value for the model factors: Section (S), Habitat (H), Depth (D), Velocity (V), with the best fitting modelled factor in bold, and................................................................. 151

the statistically significant model ***P<0.05, for individual species and total abundance of larvae for Study 1 and Study 2 by sampling date. ................................................................. 151

Appendix B: Photographs of laboratory flume (a) and set up (b) used in Chapter 4.... 152

Appendix C: Photographs of release site (a) and just after the release of larvae and passive particles (b and c) for experimental release described in Chapter 5. ......................... 153

Appendix D: Photographs of Murray cod larvae (a) with yolk sacs and (b) without yolk sacs, found in drift net samples described in Chapter 5................................. 154

Appendix E: Figure and table showing the total mean abundance of Murray cod larvae (—) and Murray cod larvae with yolk sac (— • • —) collected in drift nets over the sampling time (h), with 95% confidence limits for the overall mean catch (---) describing data from Chapter 5................................................................. 155

Appendix F: Murray cod null, Murray cod, golden perch null and golden perch linear mixed model results with variance and standard deviation of................................. 156

variance for random effects and estimated standard, error and t value for fixed effects for data described in Chapter 5. ................................................................................................. 156

Appendix G: Publication: Ontogeny of critical and prolonged swimming performance for the larvae of six Australian freshwater fish species............................................. 157

References.............................................................................................................................................................. 179
Certificate of Authorship

I hereby declare that this submission is my own work and to the best of my knowledge and belief, understand that it contains no material previously published or written by another person, nor material which to a substantial extent has been accepted for the award of any other degree or diploma at Charles Sturt University or any other educational institution, except where due acknowledgement is made in the thesis. Any contribution made to the research by colleagues with whom I have worked at Charles Sturt University or elsewhere during my candidature is fully acknowledged. I agree that this thesis be accessible for the purpose of study and research in accordance with normal conditions established by the Executive Director, Library Services, Charles Sturt University or nominee, for the care, loan and reproduction of thesis, subject to confidentiality provisions as approved by the University.

Stacey Kopf

17 December 2014
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Animal Research Authority

This study was undertaken in accordance with the Charles Sturt University Animal Care and Ethics Approval, approval numbers 09/108 and 08/102.
Abstract

Riverscape ecology aims to incorporate the biotic and abiotic patterns and processes at spatial and temporal scales appropriate to organisms of interest. Set within a riverscape ecology framework, and using life history traits as a basis for understanding, this thesis explores how fish larvae in a lowland river are affected by regulated flows.

This study investigated the potential of anabranches, or secondary channels, in the riverscape, to provide habitat for larval fish under regulated flows. The fish larvae of a highly flow-modified river (main stem), a highly flow-modified anabranch and an anabranch which has a less modified flow regime, were sampled during the normal breeding season in south-eastern Australia. The main stem supported a relatively high abundance of larvae, but the anabranch with a less modified flow regime, supported more species overall than the other river types. Anabranches may provide habitat heterogeneity and act as a refuge for larvae under regulated conditions.

To help understand limitations on habitat use in, and ability to move through, riverscapes by the early life history stages of fish the swimming capabilities of the larvae of six species of native fish were investigated in a laboratory flume. Swimming performances for species broadly corresponded with life history strategies: equilibrium species were the best swimmers, periodic species the poorest and opportunistic species in between. Swimming capability increased with ontogeny, and developmental stage better explained swimming ability than did length, size or age.
To investigate the implications of differential swimming performance in the wild, *in situ* dispersal experiments in a reach of the anabranch with a less modified flow regime were conducted with the larvae of two species of native fish - with different life history strategies and swimming abilities - and with sunflower seeds, as passive particles. Seventy-one per cent of released Murray cod larvae passed through the 500 m reach, whereas 16% of released golden perch larvae and 3-4% of passive particles did so. Furthermore, Murray cod did not drift in the same pattern as sunflower seeds, but golden perch larvae did, suggesting that the latter was more passive in its dispersal than the former.

Models were developed to determine how the distribution of current speeds throughout the experimental reach of the anabranch changes with discharge levels below bankful and how this in turn might affect the available hydraulic habitat available for fish larvae. As discharge increased, so did overall current speeds, resulting in a more homogeneous flow environment and decreasing available hydraulic habitat for all species examined. However, the relative impact of changes in discharge and current speeds is species-specific, depending on whether dispersal is active or passive or non-existent.

I conclude that under regulated, high flows, during the spawning season: (1) the larvae of *equilibrium* life history strategy fishes may have a reduced ability to actively disperse through the riverscape into suitable nursery habitat due to an increase in current velocity above critical swimming thresholds; (2) there may be an increase in prevalence of the larvae of *periodic* life history strategy fishes passively drifting through the riverscape into unsuitable habitat, because there are fewer
slow/no flow habitats; and (3) there may be an increase in occurrence of the larvae of *opportunistic* life history strategy fishes being washed out of suitable habitat for similar reasons. Under regulated high flows, a less modified anabranch may provide alternative, suitable nursery habitat within the main stem/anabranch riverscape.
Chapter 1: General Introduction

1.1 River ecology at the riverscape scale

1.1.1 River ecosystems

River systems are highly heterogeneous in space and time, geomorphologically, chemically and biologically (Ward, 1989, Thorp et al., 2006). Research initially focused on the longitudinal connection, relationships and interactions of abiotic and biotic communities within the river system from the head waters to the confluence (e.g. Vannote et al., 1980), and the effects of anthropogenic changes to these (e.g. Ward and Stanford, 1983). Soon after, concepts and research incorporated lateral connections and interactions between the channel and floodplain (Junk et al., 1989, Sedell et al., 1989), as well as the importance of the main channel (Thorp and Delong, 1994). Over time, river ecologists have acknowledged and incorporated more of the complexity of river ecosystems across more dimensions (Ward, 1989, Humphries et al., 2014).

River systems are hierarchical in nature, in which large-scale factors, such as climate, geology, and topography are the basis for hydrologic and geomorphic processes that produce and maintain habitat at smaller scales (Allen and Starr, 1982, Frissell et al., 1986, Montgomery, 1999). Apart from the main channel, river systems can also include an extensive network of side channels and floodplain landforms, including permanent or semi-permanent standing-water habitats: wetlands, side-arms, oxbow lakes, meander scroll depressions, and backwater swamps. Rivers are dynamic by nature and local habitat features and aquatic organisms are associated with, and affected by, the lateral and linear characteristics of river systems. In particular, the
exchange of sediment, nutrients, organic matter and biota between the main river channel and its side channels and/or floodplain habitats impact aquatic organisms by providing additional and/or different habitat or food sources (McGinness et al., 2002, Thoms et al., 2005, Thoms and Sheldon, 2000a).

In many floodplain river systems, one of the most common landscape features connected to the river by flow pulses below bankfull is the anabranch or side channel, which breaks out from the main channel, travels across the floodplain, and rejoins downstream (McGuiness, 2011). Indeed, side channels, also known as anabranches, anastomosing channels or side arms (hereafter, anabranches), are common features of lowland braided rivers and can be continuously or intermittently connected to the main channel. In Australian river systems, anabranches gradually dry out and disconnect during flood recession and low flow periods between flow pulses, often retaining water in small billabongs, pools or wetlands for months. When connected to the main channel, anabranches comprise a diversity of habitats, often at smaller scales than the main stem, which may provide important habitat and resources for particular species or life stages of organisms (Thoms et al., 2005). Understanding the importance and function of anabranches helps us understand river systems as a whole. However, the role of anabranches and tributaries has received relatively little attention from fish ecologists, especially in Australia (but see Thoms et al., 2005, Balcombe et al., 2011); this is especially in regard to the early life stages of fish, whose habitat and food requirements are quite different from juveniles and adults (see King et al., 2003).
1.1.2 Riverscapes

The hierarchical nature of streams, the spatial and temporal heterogeneity, structure, function and organization of the stream template (sensu Townsend, 1989), along with the pool of species available for colonization, influence the development and organization of stream communities (Frissell et al., 1986). Because of this inherent complexity, there is a need for a broad approach to river ecology that considers the responses of aquatic organisms to habitat heterogeneity at multiple spatial and temporal scales. According to Fausch et al. (2002), there are five principles to guide research in lotic ecosystems.

1) Choose the appropriate scale, possibly working at multiple scales;

2) Don’t simplify the complexity of lotic systems;

3) Consider unique attributes of lotic systems, because they can have overriding effects;

4) Recognise that anthropogenic alterations may have strong effects at distances far from their source; and

5) Match observations and predictions to the scale at which managers effect change.

However, most research has focused on questions that can be answered over small spatial (e.g. reaches of 50–500 m) and temporal (e.g. 2–4 years) scales (e.g. Angermeier et al., 2002). These scales may be only weakly linked to the problems at larger spatial and longer temporal scales, which are more relevant to the scales at which disturbance occurs, at which organisms respond and with which management must contend. In order to describe heterogeneity in rivers, researchers must make observations at the intermediate scale (1-100 km river segment) because populations
and communities of stream fishes generally carry out important aspects of their entire life histories at intermediate spatial scales and respond to habitat changes that often occur over long time periods (5-50 years) (Reeves et al., 1995, Mantua et al., 1997).

Within Australia, much of the fish ecology research that has purposely incorporated riverscape principals, at the intermediate scale, has taken place in northern dryland rivers (see Arthington et al., 2005, Boys and Thoms, 2006) and the northeastern coast (see Pusey et al., 2000) within a short time frame (<4 years). Within the Murray-Darling Basin, much research has examined movement and habitat available to adult fish within the riverscape, (see e.g. Koehn and Harrington, 2005, Crook and Koster, 2006, Humphries et al., 2008), but relatively little has been published on the movement and habitat available for larval fish, at intermediate scales within the riverscape (see, however, Humphries et al., 2002, King et al., 2003).

1.2 Life history strategies at the riverscape scale

Habitat use and movement – as well as many other behaviours and processes - during early life are inextricably linked to the life history strategy of species (Schlosser, 1991). Indeed, life history theory aims to explain the evolution of an organism’s morphological, developmental or behavioural traits as an adaptive response to environmental variation, resource allocation and/or differential mortality during life stages (Roff, 1992, Stearns, 1992, Winemiller, 2005). The most common illustration of life history strategies are $r$-selected and $K$-selected traits (MacArthur and Wilson, 1967, Pianka, 1970), where $r$-selected traits (high reproductive effort, little parental care, short lived) and $K$-selected traits (delayed reproduction, low fecundity, parental care, long lived) are shaped by stochastic (i.e. disturbances), and deterministic (i.e.
competition and predation) processes, respectively. The life history traits of aquatic organisms are forged, through evolution, by the physical habitat, water chemistry and flow characteristics found in lotic systems (Southwood, 1977, Southwood, 1988, Townsend, 1989, Lytle and Poff, 2004). Winemiller and Rose (1992) expanded the life history strategies of fish from \( r \)- and \( K \)-selection to include the effects of environmental gradients selecting for three endpoint strategies: opportunistic (colonising, similar to \( r \)-selection), periodic (inter-generational form of bet-hedging) or equilibrium (=\( K \)-selection). And Balon (1986a) developed ideas related to relationships between food acquisition and ontogeny: altricial (generalist, \( r \)-selection, opportunistic and periodic) or precocial (specialist, \( K \)-selection and equilibrium) species.

Early lotic fish ecology models incorporated aspects of landscape with riverine fish life histories by linking important physical and biotic processes of fish movement, survival and reproduction in rivers at scales relevant to the fish (Schlosser, 1991, Schlosser, 1995a, Schlosser, 1995b, Schlosser and Angermeier, 1995). Within Australia, the development of larvae at first feed, and spawning and recruitment characteristics of native freshwater fish have been used to describe the life history strategies of Murray-Darling Basin fishes (Humphries et al., 1999, Humphries et al., 2002, King et al., 2003, King, 2004). The resulting three life history strategies: Strategy 1 (sensu Humphries et al., 1999), precocial (sensu Balon, 1986a) or equilibrium (sensu Winemiller and Rose, 1992) are species that are well-developed at hatch and free embryos and larvae, that are able to drift actively downstream, after leaving a ‘nest’; Strategy 2 (sensu Humphries et al., 1999), altricial (sensu Balon, 1986a) or periodic (sensu Winemiller and Rose, 1992) species, with relatively
undeveloped planktonic free embryos at hatch, that have limited swimming capabilities when drifting; and *Strategy 3* (sensu Humphries et al., 1999), have *altricial* ontogeny (sensu Balon, 1986a) and are *opportunistic* species (sensu Winemiller and Rose, 1992), that have small, poorly-developed free embryos at hatch, have limited swimming capabilities, and are largely defined by their association with particular flows and habitats during the breeding period and early life. Although the life history strategies of south-eastern Australian freshwater fish and their use of habitat within the riverscape have been studied (Humphries et al., 1999, King et al., 2003, Mallen-Cooper and Stuart, 2003, King, 2004, Tonkin et al., 2008), other aspects of their ecology, such as the swimming capabilities and dispersal potential of the young stages of fishes, have received almost no attention.

1.2.1 *Swimming capabilities and dispersal of the early life stages of fish*

Spawning and early life stages in fish are critical periods that may serve as bottlenecks limiting recruitment and survival to reproductively mature life stages (May, 1974, Ludsin and Devries, 1997, Halpern et al., 2005). The early life stages of fish are critical because factors influencing growth and survival during this period largely determine population dynamics. Such factors include spatial and temporal environmental heterogeneity or the ability of the early life stages of fish to access high quality habitat or resources (King, 2004, King, 2005, Price, 2007). Life history theory can potentially be used to explain and understand many aspects of early life, including, perhaps, swimming ability and how fish access habitat and resources. Most riverine fish larvae are rheotactic (can orientate to the current) and have the ability to locate current speeds that allow them to maintain position, but fish larvae do not swim well, in general (Pavlov et al., 2008). Previously, researchers have studied the
swimming performance of the larvae of several species of freshwater fish in Europe and North America (see Wolter and Arlinghaus, 2003), but almost nothing is known about the swimming abilities of the larvae of native Australian freshwater fish. By determining the swimming abilities of larvae in the laboratory we gain better insight into the swimming capabilities of the larvae of native fish with different life history strategies and, therefore, an important step in our understanding of movement potential, especially dispersal, of larvae through the riverscape.

Postnatal dispersal, leaving one’s place of birth to breed elsewhere (Dingle and Drake, 2007), is an important aspect of landscape ecology and metapopulation biology, with gene flow among populations as the ultimate result (Hanski and Gilpin, 1997, Schlosser, 1991, Ronce, 2007, Stevens et al., 2012). Dispersal is not undirected movement, but movement that usually ends when habitat patches, with suitable resources, are met (Dingle, 1996). Dispersal links subdivided populations, and allows colonization of newly-created habitat patches and recolonisation of patches where there was disturbance (Van Kleunen et al., 2010, Berg et al., 2010, Stevens et al., 2012). Many lotic fishes disperse during early life, either passively or actively (Brown and Armstrong, 1985, Pavlov, 1994). Dispersal of early life strategies is usually downstream, but occasionally upstream (Zimmer et al., 2009, Schwalb et al., 2010, Schludermann et al., 2012). Most studies on larval dispersal recognize that there is an active component to drift - downstream, flow-mediated movement (Pavlov et al., 2008, Lechner et al., 2013, Schludermann et al., 2012) - but little is known about how swimming ability and swimming behaviour varies with ontogeny and how this affects dispersal or retention in river channels. As important as it is to understand swimming behaviour and dispersal capabilities of the early life stages of fish, it is
also important to look at the affect of highly regulated flows during spawning periods.

1.2.2 The effects of river regulation in the Murray-Darling Basin on the early life stages of fishes

The decline in abundance and distribution of fishes native in the Murray–Darling Basin, Australia, has been partly attributed to river regulation, with seasonal reversal of flow resulting in high summer irrigation discharge, within bank flows and reduced frequency and magnitude of flooding considered the main factors responsible (Cadwallader, 1978, Walker and Thoms, 1993, Gehrke et al., 1995). Previous research has found that flow regulation causes increased channelization, decreased geomorphic complexity, loss of connectivity between rivers and floodplains, and thus decreased habitat heterogeneity and negatively affecting the abundance and species richness of fish communities (Ward and Stanford, 1995, Kondolf et al., 2007). Since early life is considered a critical time in a fish’s life, understanding the impact of altered flow regimes is fundamental for the conservation and management of fish populations (Humphries et al., 1999, King et al., 2003, Balcombe et al., 2006). Several studies have described selection, shifts, preferences and use of lotic hydraulic habitats by larval fish, typically at the microhabitat scale (e.g. Copp, 1992a, Copp, 1992b, Scheidegger and Bain, 1995, Wintersberger, 1996, Garner, 1997, Jurajda, 1999, Gaudin, 2001, Scholten et al., 2003). Survival and mortality of the early life stages of fish can be influenced by spatial and temporal variability in hydraulic habitat, especially for those species that have limited swimming abilities (Price, 2007, Tonkin et al., 2008). For these poor swimming species, dispersal will depend largely on local hydrodynamic conditions (Shanks, 1995). Potentially, low-flow recruitment
strategy fish, using in-channel habitats under altered flows (Humphries et al., 1999, King et al., 2003) can have disrupted spawning cues, altered dispersal mechanisms and/or reduced area of suitable nursery habitats (Bain et al., 1988, Bunn and Arthington, 2002). Therefore, the present study looks to use life history strategy traits of fish set within a riverscape framework to explain how larvae are affected by highly regulated flows during spawning periods (e.g. Bain et al. 1988, Bunn and Arthington 2002, Freeman et al., 2001, Dudley and Platania 2007).

1.3 Aims of the Thesis

The overall aim of this thesis is: To assess the swimming performance and dispersal potential of larval fish in a regulated riverscape. The research was conducted at the mesohabitat, reach and river section scales and in a flume.

The specific aims are:

1. To compare the fish faunas of a highly flow-modified river, a highly flow-modified anabranch and an anabranch which has a less modified flow regime, during the breeding season; establish if habitat use of larval fishes is consistent between the main stem and its anabranches; determine whether the species richness, composition and abundance of larval fishes vary among reaches within the anabranch with a less modified flow regime; and assess the consistency of habitat use within the anabranch with a less modified flow regime.

2. Describe the critical (<30 min) and prolonged (>60 min) swimming performance of the larvae of six species of Murray-Darling Basin fish
representing the three life history strategies; determine which developmental characteristics (days after hatch, length, developmental stage) best explain critical and prolonged swimming performance; and establish if critical swimming speed and prolonged swimming performance vary with ontogeny, species and life history strategy.

3. To compare the timing of drift through a reach of an anabranch of larvae of Murray cod (representing equilibrium life history strategy) and golden perch (representing periodic life history strategy) with that of passive particles (sunflower seeds); and consider the role of swimming ability and active and passive dispersal in the proportion of larvae of each species retained within the reach.

4. To model patterns in current velocity at nine river discharges that reflect the range of flows that occur in an anabranch of the Murrumbidgee River; combine the modelled discharges with data on critical and prolonged swimming speed of the larvae of native fish (Chapter 4) to quantify the potential effects on available hydraulic velocity habitat for each larval developmental stage; and, in the light of my results, discuss the implications of flow regulation on usable hydraulic habitat for larval fish.

5. To discuss the overall outcomes from the research in this thesis and present a conceptual model on how larval fish of different life history strategies use the riverscape under different seasons (i.e. winter to spring, late spring to early summer and summer to autumn) and modified high flows during spawning.
Chapter 2 describes the location, climate, land use, geomorphology and hydrology and fish fauna of the selected study area, the mid-Murrumbidgee River, as well as a description of the study reaches which are the focus of each chapter of this thesis.

Chapter 3 compares the species richness, composition, abundance and habitat use of larval fishes among the main stem Murrumbidgee River and two of its anabranches, one highly flow-modified and one less modified. Research undertaken in Chapter 3 of this thesis, addresses several of the riverscape ecology principles and explicitly considers the role of anabranches in lowland river regulated riverscapes as habitat for the early life stages of fishes. Research was conducted at the mesohabitat, reach and river section scales.

Chapter 4 describes a series of flume experiments, assessing the swimming performance of the early life history stages of six native fish species and determines which developmental characteristics best explain the patterns observed. It contrasts the swimming capabilities of fishes from the three recognised life history categories (opportunistic, periodic and equilibrium) and follows four of the species through ontogeny, from hatch to metamorphosis. These finding are discussed in terms of ontogeny, species and life history strategy.

Chapter 5 takes the swimming capability findings into the field, where experimental releases of Murray cod larvae (representing the equilibrium life history strategy and competent swimmers) and golden perch larvae (representing the periodic life history strategy and poor swimmers) were made in a reach of the anabranch Old Man Creek.
Comparisons were made between dispersal of these larvae with passive particles (sunflower seeds), to test hypotheses about passive and active dispersal.

In Chapter 6, velocity in the anabranch Old Man Creek was modelled under nine river discharges, and the modelled discharges were combined with the swimming capability results from Chapter 4 to determine the amount of available hydraulic habitat for each larval developmental stage.

Finally, Chapter 7, draws together the results on the composition and habitat use of the young stages of fish in lowland riverscapes, to examine how flow regulation affects the hydraulics of rivers and the swimming capabilities of fish, resulting in implications for dispersal potential.

Although, Chapters 4, 5 and 6 do not strictly adhere to riverscape ecology principles stated by Fausch et al., 2002, determining the swimming abilities of larvae of native fish in the lab, testing their dispersal potential in the field and modelling the hydraulic habitat available to larvae based on their swimming ability during the dispersal stage in their life history, does further the understanding of the effects of flow on the most vulnerable life stage of fish and the impact flow alteration can have on larvae.
Chapter 2: Description of study area

2.1 Catchment characteristics

The Murrumbidgee River, in southern New South Wales, is one of Australia’s largest rivers, draining approximately 84,000 km² of the Murray-Darling Basin (Figure 2.1). The river rises in the Fiery Ranges of the Snowy Mountains and flows, firstly, to the south-east and then north through the Australian Capital Territory, through Burrinjuck Dam, to its confluence with the Murray River; a length of almost 1,700 km (DLWC, 1995). Below Burrinjuck Dam, the river emerges from a deep narrow gorge, to commence a low gradient and mostly westerly flow across the Riverine Plain to its confluence with the Murray River (Figure 2.1). Throughout the catchment, elevation ranges from 1395-61 m asl.

The Murrumbidgee River has a system of well developed floodplains, billabongs (oxbow lakes), distributaries and anabranches, connected or in association with the main channel. The main tributaries to the Murrumbidgee River include the Tumut River, Tarcutta Creek and Hillas Creek, and are all located upstream of Wagga Wagga, NSW (Figure 2.1). Downstream of Wagga Wagga, tributaries are minimal, with Yanco Creek a distributary and the Lachlan River is technically a tributary that rarely flows into the Murrumbidgee River. The lack of tributaries downstream of Wagga Wagga, in the mid and lower catchment, is a notable feature of the Murrumbidgee River system.
Figure 2.1: Murrumbidgee catchment in south-eastern Australia showing irrigation areas and two major upstream reservoirs, major towns are represented by black circles, research was conducted between Wagga Wagga and Narrandera (from Page et al., 2005).

2.2 Climate

Mean daily maximum and minimum temperatures at Wagga Wagga, NSW in January are approx. 32 °C and 16 °C, respectively, and in July are approx. 14 °C and 4 °C, respectively (Figure 2.2). Frosts occur throughout the valley, mostly between June and August in the lower valley, with an average of about one severe frost per year (DLWC, 1995, BOM, 2014).

Rainfall decreases across the catchment from east to west, with the annual mean of 1564 mm near the river source, including a significant snowfall component (Frazier, 2004). Further downstream, at lower elevations, the mean annual rainfall is little over 470 mm, but values range annually from 256-738 mm at Wagga Wagga (Figure 2.2). The mean monthly rainfall in January is approx. 28.3 mm, and in July is approx. 44.8
Evaporation exceeds precipitation, except for a small area of the upper catchment.

![Figure 2.2: (a) Mean monthly maximum (■) and minimum (▲) air temperatures and (b) mean monthly rainfall at Wagga Wagga, NSW.]

2.3 Geomorphology and hydrology

In the bedrock-confined valley upstream of Wagga Wagga, low river terraces with inundation return periods of between 10 and 20 years, border the active floodplain (Page et al., 2005). These terraces in turn extend laterally to the bedrock valley margins. Floodplain width varies from about 1-4 km between Wagga Wagga and Gundagai, but increases to about 10 km in the region upstream of Narrandera, where an extensive region of anabranches, palaeo-channel remnants and back swamps exists.
There are six distinctive, broad topographic regions along the length of the Murrumbidgee River, subdivided by floodplain morphology, geomorphology and the presence or absence of palaeo-channels (Schumm, 1968, Knight, 1997, Page and Nanson, 1996). The Murrumbidgee catchment can be divided into two geologic divisions, with this study located in the region comprising mainly hard, Palaeozoic rocks, which confine the margins of the Murrumbidgee floodplain. The active (late Holocene) floodplain is, for the most part, a horizontally-disposed surface formed by lateral channel accretion (Page et al., 2003). Scroll bars, concave benches and meander cut-offs are common (Page et al., 2005). The area that is the focus of the current research can be described as confined valley-wide valley with a channel width 70-80 m. Stream energy is generally low, with channel slope and specific stream power at bankfull stage 0.00025 W m$^{-2}$, and 15 W m$^{-2}$ at Gundagai (Page et al., 2005).

The Murrumbidgee is a heavily regulated river, with 26 dams and weirs and over 10,000 km of irrigation canals (Kingsford, 2003, DLWC, 1995). The river accounts for about 22% of all annual flows diverted from the Murray-Darling Basin (MDBMC, 1995) and the large capacity of the two dams on the river, Burrinjuck (1 026 000 Ml) and Blowering (1 600 000 Ml), provide irrigation releases to the Murrumbidgee and Tumut Rivers from the mountainous higher precipitation part of the catchment (Page et al., 2005). The Murrumbidgee River also supplies domestic and stock water to rural communities. Murrumbidgee flows have been augmented since around 1970 by 6365.74 m$^3$s$^{-1}$ per year due to water transferred from the east-flowing Snowy River into the upper Tumut River to generate hydroelectricity and
supply large irrigation areas downstream. The maximum mean discharge (1970–1998) of 147 m³ s⁻¹ occurs at Wagga Wagga, but downstream, a combination of irrigation diversions, the absence of significant tributaries and natural losses to evaporation, anabranches, distributaries and floodplain storage, results in the mean flow declining to 48.36 m³ s⁻¹ at Balranald (DLWC, 1995). The current altered flow regime has resulted in significant decreases in flood frequency, the magnitude and duration of flow peaks as well as over bank flow in the lowland section below Gundagai (Page et al., 2005). The flow regime of the Murrumbidgee River main stem has a seasonally inverted hydrograph, with high flows in late spring-summer, and low flows over winter (Page et al., 2005)(Figure 2.3).

![Mean monthly discharge for the Murrumbidgee River at Wagga Wagga (gauge # 410001), from January 2000 to December 2010. Grey bars denote sampling period.](image)

**Figure 2.3:** Mean monthly discharge for; the Murrumbidgee River at Wagga Wagga (gauge # 410001), from January 2000 to December 2010. Grey bars denote sampling period.

2.4 Fish fauna
Thirteen native and seven alien species of fish have been recorded in the Murrumbidgee River catchment, with 10 native and four alien species occurring in the region between Wagga Wagga and Narrandera NSW (Table 2.1). Overall, the fish community of the Murrumbidgee catchment is considered degraded, with a large number of alien fish species present in the catchment (33% of the species richness), which contribute a high relative abundance (70.77% of the total number of individuals) (Gilligan, 2005). Four native species, Murray cod, trout cod, silver perch and golden perch, have been stocked as juveniles, annually into the region where the current research occurred (Gilligan, 2005). There are few known collections of silver perch, golden perch and trout cod as larvae and juveniles in the Murrumbidgee around Wagga Wagga, inferring that there are few to no natural breeding populations in these systems (Gilligan, 2005).
Table 2.1: Common names, scientific names and relative abundances of fish species recorded from the Murrumbidgee River, based on Gilligan (2005). *The taxonomy of carp gudgeons is currently uncertain (Bertozzi et al., 2000).

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<tr>
<th>Common name</th>
<th>Scientific name</th>
<th>Abundance</th>
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<tr>
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</tr>
<tr>
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<td><em>Melanotaenia fluviatilis</em> (Castlenau)</td>
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<td>Australian smelt</td>
<td><em>Retropinna semoni</em> (Weber)</td>
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<td><em>Hypseleotris spp.</em></td>
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</tr>
<tr>
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</tr>
<tr>
<td>Golden perch</td>
<td><em>Macquaria ambigua</em> (Richardson)</td>
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</tr>
<tr>
<td>River blackfish</td>
<td><em>Gadopsis marmoratus</em> (Richardson)</td>
<td>Rare</td>
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<tr>
<td>Trout cod</td>
<td><em>Maccullochella macquariensis</em> (Cuvier)</td>
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<td>Gambusia</td>
<td><em>Gambusia holbrooki</em> (Girard)</td>
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2.5 Description of study reaches

The study reaches were located on three river sections between Wagga Wagga and Narrandera, NSW: the Murrumbidgee river main stem and two of its anabranches, Old Man Creek and Bundidgerry Creek (Figure 2.4). The Old Man Creek anabranch has a fixed weir at its upstream end, the flows are not specifically regulated for irrigation purposes, but due to the nature of the weir, the flow follows the regulated Murrumbidgee River hydrograph, with peak flows in the spring, at a much lower magnitude than the main stem, and low winter flows (Figure 2.5a and c). Bundidgerry Creek anabranch, also has a weir but by contrast, is highly regulated, with elevated, relatively constant, flows during the irrigation season and an artificially straightened section of the original riverbed, developed to divert water for the Murrumbidgee Irrigation Area (Figure 2.5a and b). Both anabranches have a constant flow from the main stem and do not undergo seasonal disconnection. The surrounding landscape of the river sections sampled in this study are characterised by agricultural production, livestock grazing and row cropping (Table 2.2). The Old Man Creek anabranch is approximately 70 km, and Bundidgerry Creek is approximately 36 km in length. The length of river reach sampled within the 5 river sections (one in each of the Murrumbidgee River and Bundidgerry Creek and three in Old Man Creek) varied from 300-315 m, with 17 of the 20 reaches extending 300 m (Table 2.2). River section length varied from 4137-6529 m among the three rivers, with the Murrumbidgee River section the shortest, and the longest sections on Old Man Creek. Stream width was similar during the sampling periods for Old Man Creek and Bundidgerry Creek, ranging from 20-27 m, but bankfull width was nearly three times greater for the Murrumbidgee River (61-75 m) (Table 2.2). River reaches were chosen based on the availability of common mesohabitat types found within: i.e. bare
bank, slackwater, open channel and woody debris (Figure 2.6). Field work for Chapter 3 was conducted at the riverscape scale, throughout all three rivers, while Chapter 5 field work was conducted at one reach on Old Man Creek and hydraulic modelling was performed for three reaches of Old Man Creek in Chapter 6 (Figure 2.6).
Figure 2.4: Research area for the Murrumbidgee River, Old Man Creek and Bundidgerry Creek with study reaches for experiments carried out in Chapter 3 (reaches 1-20), Chapter 5 (reach 10) and Chapter 6 (reach 3, 6 and 10).
Figure 2.5: Mean monthly discharge for; a) the Murrumbidgee River at Wagga Wagga (gauge # 410001), b) Bundidgerry Creek (gauge #410023) (there is no available data where there are breaks in the line) and c) Old Man Creek (gauge # 410137), from January 2000 to December 2010 with breeding season of fish in grey bars.
Figure 2.6: Examples of the four mesohabitat types sampled in the Murrumbidgee River system; (a) Bare Bank, (b) Slackwater, (c) Open Channel and (d) Woody Debris.
Table 2.2: Location, length (m), bankfull width (m), distance to upstream and downstream confluences (m), as well as name of confluence for the river and surrounding land use for the reaches and sections of the three rivers sampled; the Murrumbidgee River (MR), Bundidgerry Creek (BC) and Old Man Creek (OMC UP, OMC MD, and OMC LW) in this thesis.

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<th>Section/Reach</th>
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<th>Bankfull width (m)</th>
<th>Distance to upstream confluence (m)</th>
<th>Upstream confluence</th>
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Chapter 3: Anabranches as habitat for larval fishes in regulated river landscapes

3.1 Introduction

Lowland river systems typically comprise a complex network of main stem, tributaries, secondary channels and floodplain. Secondary channels, also known as anabranches, anastomosing channels or side arms (hereafter, anabranches), often make up a significant proportion of the overall channel length (Thoms and Sheldon, 2000b, Thoms, 2003, Thoms et al., 2005). When connected to the main channel, anabranches comprise a diversity of habitats, often at smaller scales than the main stem, and contribute sediment, nutrients and biota to the river system as a whole (Thoms and Sheldon, 2000a, McGinness et al., 2002, Thoms et al., 2005). During high flows, nutrients are transported from anabranches into the main stem, contributing to river productivity (Ward, 1989, Bunn and Arthington, 2002). During low flows, anabranches often become disconnected, forming chains of ponds, until higher flows reconnect them to the main stem of the river (Thoms et al., 2005). Despite their prevalence in the riverscape, and the fact that their hydrology diverges substantially from the main stem to which they connect at times, ecological relationships between anabranches and main stems are not well researched (Thoms, 2003).

In highly flow-modified systems, anabranches may act as refuges for flow-sensitive biota, by providing areas of slow-flowing or still habitat (Arthington et al., 2005). Small-bodied adults and the larvae and juveniles of all fishes are particularly susceptible to displacement by high flows, and so anabranches may be important for survival and growth of these under flow-modified conditions (Humphries et al., 2002). Typically, flow releases for consumptive water use in temperate Australia...
occur in late spring and summer, which is also the peak time for fish breeding (Humphries et al., 1999). Thus, the most vulnerable stages of fish –free embryos and larvae – often experience unnaturally high flows in their nursery habitats, which can potentially result in increased displacement and perhaps mortality (Humphries et al., 2002, Humphries et al., 2006).

Despite the potentially important role of anabranches for fish recruitment, little is known about the relationship between the flow regime of the main stem and how this affects the anabranches, or how in turn this affects habitat and habitat use by small fishes within the anabranches (Boys and Thoms, 2006). The Murrumbidgee River is an example of a highly flow-modified lowland river with a degraded fish fauna (Davies et al., 2008). The flow regimes of some of the anabranches (e.g. Bundidgerry Creek) in the Murrumbidgee system are significantly modified, whereas the flow regimes of others (e.g. Old Man Creek) are not as influenced by irrigation flows and may provide a more benign rearing environment for the young stages of fishes (Page et al., 2005). Thus, this provides an opportunity to compare and contrast the fish faunas in habitats of the main stem and its anabranches under various discharge and connectivity patterns.

This study aims to compare the fish faunas of a highly flow-modified river, a highly flow-modified anabranch and an anabranch which has a less modified flow regime during the breeding season of fishes. Specifically, comparing the species richness, assemblage composition and abundance of larval fishes in each system and assess whether use of habitats in each system is consistent. The hypothesis for this chapter is to determine if the anabranch with a less modified flow regime provides a more
benign environment for the young stages of fishes – and thus observe greater abundances and higher species richness there - because of the more heterogeneous flow and habitat conditions, relative to the highly flow-modified systems. The specific aims are to: 1) determine whether the species richness, composition and abundance of larval fishes differ in the main stem (highly flow-modified) and two anabranches (one highly flow-modified, one less modified) of the Murrumbidgee River; 2) establish if habitat use of larval fishes is consistent between the main stem and its anabranches; 3) determine whether the species richness, composition and abundance of larval fishes vary among reaches within the anabranch with a less modified flow regime; and 4) assess the consistency of habitat use within the anabranch with a less modified flow regime.

3.2 Materials and methods

3.2.1 Study Area

This study was conducted in the lowland reaches of the Murrumbidgee River, New South Wales, Australia (Figure 3.1a). The Murrumbidgee River has a total catchment area of about 84,000 km² and flows almost 1,700 km from its source in the Snowy Mountains, to its confluence with the Murray River in South Australia (Crabb and Milligan, 1997, Page et al., 2005). It contains 26 dams and weirs and over 10,000 km of irrigation channels, making this river a highly regulated system (Buchan, 1996, Kingsford, 2003). The current altered flow regime has resulted in significant decreases in flood frequency and flow peaks (Page et al., 2005). The Murrumbidgee River has a system of well developed floodplains, billabongs (oxbow lakes), distributaries and anabranches, connected or in association with the main channel.
Figure 3.1: (a) Location of the 20 study reaches (1-20) in the Murrumbidgee River system. Note: Beavers Creek anabranch becomes Old Man Creek anabranch near reach 4 and is referred to as Old Man Creek in this study. (b) The two study sampling designs, showing stratified sampling (three replicates of sweep-net electrofishing, SNE) in each discrete mesohabitat type (bare bank=BB, slackwater=SW, open channel=CH, woody debris=WD), in four river reaches, within each of five river sections. (i) Study 1 compares the main stem section, the Murrumbidgee River (reaches 13-16), with two anabranch sections, Bundidgerry Creek (reaches 17-20) and Old Man Creek middle (reaches 5-8). (ii) Study 2 compares sections within Old Man Creek; Middle (reaches 5-8), Upper (reaches 1-4) and Lower (reaches 9-12).

The study reaches were located on three river sections: the Murrumbidgee river main stem and two of its anabranches: Old Man Creek and Bundidgerry Creek. The flow regime of the Murrumbidgee River main stem has a seasonally inverted hydrograph, with high flows in late spring-summer, and low flows over winter (Page et al., 2005). The Old Man Creek anabranch has a fixed weir at its upstream end, the flows are not
specifically regulated for irrigation purposes, but due to the nature of the weir the flow in Old Man Creek follows the regulated Murrumbidgee River hydrograph, albeit at much lower magnitudes, with peak flows in the spring and low winter flows. Bundidgerry Creek anabranch, by contrast, is highly regulated, with elevated, relatively constant, flows during the irrigation season and an artificially straightened section of the original riverbed, developed to divert water for the Murrumbidgee Irrigation Area (Figure 3.2). Bundidgerry Creek has an artificially straightened confluence section, which in turn changes the river geomorphology and decreases habitat heterogeneity, but the anabranch still retains general characteristics of a lowland river of this area, with pools, riffles and runs as well as slackwaters, woody debris and shoreline vegetation. The surrounding landscape of the three river sections is characterised by agricultural production, livestock grazing and row cropping.

**Figure 3.2:** Hydrograph for rivers in this study; the Murrumbidgee River (MR=dashed line), Old Man Creek (OMC=dotted line) and Bundidgerry Creek (BC=grey line) from January 2000 to December 2010, which were the only dates data was available for Bundidgerry Creek. The grey bar denotes sampling season.
3.2.2 Study Design

Two studies were conducted within the Murrumbidgee River system: Study 1 compared aspects of the fish fauna among water bodies - Old Man Creek, the Murrumbidgee River and Bundidgerry Creek; and Study 2 compared aspects of the fish fauna within Old Man Creek.

Study 1 was conducted at the river section and mesohabitat scales. It addresses the first two aims of this chapter: examining the differences between the main stem and its anabranches. To accomplish this, three river sections - Old Man Creek middle, the Murrumbidgee River and Bundidgerry Creek - were sampled, totalling 12 study reaches and 4 reaches per section (Figure 3.1b(i)). The length of reaches normally encompassed three replicates of each of the four mesohabitats (see below). All reaches included in Study 1 were located in agricultural landscapes.

Study 2 was conducted within one anabranch of the Murrumbidgee River, Old Man Creek. Four reaches in each of three sections of Old Man Creek - Old Man Creek upper, Old Man Creek middle, and Old Man Creek lower - were sampled to address the third aim of this chapter (Figure 3.1b(ii)). Flow is consistent throughout the Old Man Creek anabranch. The Old Man Creek upper section occurs within a state forest, the Old Man Creek middle section is surrounded by agricultural land with intact riparian areas and the Old Man Creek lower section is bordered by degraded agricultural land with intermittent riparian areas. The Old Man Creek middle section was used for comparisons in both studies.
Four mesohabitat types were designated in both study designs, because they were the dominant habitats in each of the rivers, and were consistent with those sampled by other researchers (King, 2004, Crook et al., 2001): bare bank, slackwater, open channel and woody debris (Table 3.1). Although mesohabitat types were sampled equally throughout the study, it must be noted that the Murrumbidgee River is much larger than Old Man Creek and Bundidgerry Creek, and therefore a higher percentage of overall river was sampled in the two smaller creeks.

Table 3.1: Description, mean area sampled during the study and characteristics of mesohabitat types found in the Murrumbidgee River system.

<table>
<thead>
<tr>
<th>Mesohabitat</th>
<th>Area (m²)</th>
<th>Characterisation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bare bank</td>
<td>9.80</td>
<td>Bank without vegetation, woody debris or any other cover a meter into the water and onto the bank. Next to open channel mesohabitat</td>
</tr>
<tr>
<td>Slackwater</td>
<td>5.28</td>
<td>Still shallow water areas cut off from the river channel by a sandbar, large snag or obstruction and bordered by a bank on at least one side</td>
</tr>
<tr>
<td>Open channel</td>
<td>10.90</td>
<td>An area of free flowing river not characterised by any of the previously described habitat types</td>
</tr>
<tr>
<td>Woody debris</td>
<td>10.94</td>
<td>Woody debris with a diameter $\geq$15cm, either as a single large snag or a group of small diameter debris that formed an independent habitat area.</td>
</tr>
</tbody>
</table>

3.2.3 Field Sampling

Sampling was conducted from 28 September-26 October 2007 and repeated from 19 November-14 December 2007 for both Study 1 and Study 2, to correspond with peak larval fish occurrence (Humphries et al., 2002, King et al., 2003). Larval fishes were sampled using the sweep net electrofishing (SNE) method, a modified Smith-Root model 12 backpack electrofishing unit, with a 250 μm mesh net encompassing the anode (King and Crook, 2002). In addition, this study used a second non-electrified
sweep net to collect any fish missed during SNE. Larval fishes were preserved in 70% ethanol and brought back to the laboratory for identification using Serafini and Humphries (2004). Study 1 and Study 2 had a stratified sampling design, each reach contained four sections (numbered 1-20) and within each section three replicates of SNE were carried out for each of the four discrete mesohabitat types (bare bank, slackwater, open channel, woody debris (Figure 3.1a and b). This resulted in 12 mesohabitat samples per each of the 20 river sections (Figure 3.2b). This sampling regime was repeated over the two sampling periods resulting in 288 SNE samples per study.

Backpack electrofishing was performed on a single mesohabitat type in water ≤1 m deep and time it took to fish the mesohabitat was recorded in order to standardise the SNE samples. The area sampled depended to an extent on the size of the mesohabitat, but was normally approximately 10 m². Depth was measured with a surveying pole and velocity was measured at 0.4 of the depth with a velocity meter (FLO-MATE 2000). Three measurements of depth and velocity were taken within each mesohabitat area sampled. Values were then averaged to determine a mean depth and velocity for each mesohabitat. Mean depth, velocity and percent in stream structure were measured to compare among sections and mesohabitat types. Water quality data (temperature [°C], turbidity [NTU], dissolved oxygen [DO%], conductivity [mS.cm⁻¹] and pH) were recorded with a YSI Model 556 water quality monitor multiprobe, four times randomly throughout the reach and averaged.

3.2.4 Laboratory Methods
Samples were sorted under a dissecting microscope and identified. Most larval fish could be identified to species, except carp gudgeon (*Hypseleotris spp.*) the taxonomy of which is currently unresolved (Bertozzi et al., 2000) and therefore treated as a species complex as in other studies (e.g. King, 2004). Standard length (SL) was measured to 0.1 mm using an eyepiece graticule for fish <10 mm and vernier callipers for fish ≥10 mm. Fish were categorised as larvae because of no yolk sac, or incomplete formation of fins (King, 2004). Non-native eastern gambuisa (*Gambusia holbrooki*) (Girard) give birth to live young and therefore are classified as newly hatched if pelvic fin buds were absent.

### 3.2.5 Data Analysis

Data were checked for normality and log transformed for analysis due to lack of normality. Data were analysed separately for each study and sampling date, using generalized linear models and a Poisson distribution, for total abundance, where species with sufficient individuals were collected. To determine the best predictor of occurrence of larval fishes among the main stem and two anabranches the factors Section and Habitat and co-variates Depth and Velocity were included in the models. The hypothesise is that section will be a significant predictor of larval fish occurrence but due to the complexity of lotic systems, local habitat and flow characteristics (velocity and depth) will also affect occurrence. To determine the best predictor of occurrence and habitat use of larval fishes within the anabranche with a less modified flow regime the factors Section, or location within the anabranche, and Habitat and co-variates Depth and Velocity were included in the models. The hypothesise is that local habitat and flow characteristics (velocity and depth) will be a significant predictor of larval fish occurrence but due to the complexity of lotic systems, location
within the anabranch, i.e. proximity to the confluence, will also affect occurrence. Akaike Information Criterion (AIC) (Akaike, 1973), a model selection method that prioritizes models based on their fitting ability and level of parsimony, was used to determine which variable best predicted occurrence. The model with the lowest AIC value was selected for further modelling, i.e. Section (S), Habitat (H), Depth (D) or Velocity (V). A step-wise method was used to build models with several combinations of the four variables, i.e. S, S/H, S/H/D, S/V, S/VH, S/V/H/D. An analysis of variance (ANOVA) was computed to determine if there was a significant difference between the models at $\alpha=0.05$, and the simplest, significant model was used. Data were analysed using the R statistical package (R v2.9.0, R Development Core 2008).

Depth, velocity and water quality data were analysed using a two-way ANOVA. For depth and velocity analysis Section and Mesohabitat were fixed factors. Water quality analysis compared the mean temperature, conductivity, dissolved oxygen, pH and turbidity among Section and Date for each Study, as water quality variables did not typically vary among mesohabitats using Tukey’s tests. These data were analysed using SPSS 16.0 (SPSS Inc.).

3.3 Results

3.3.1 Study 1

3.3.1.1 Habitat characteristics and water quality

In comparisons among systems, mesohabitat depth and velocity varied significantly with Section and Habitat, with Habitat contributing the most to the variance in both
variables (2-way ANOVA, $P<0.001$; Table 3.2) (Appendix A). In each case, bare
bank and slackwater mesohabitats had similar depths (20-37 cm) but slackwaters had
the lowest velocity (0.0-0.01 ms$^{-1}$) (Figure 3.3). The woody debris mesohabitats were
intermediate (38-56 cm and 0.05-0.10 ms$^{-1}$) and channel was the deepest and fastest
(52-97 cm and 0.15-0.33 ms$^{-1}$). Old Man Creek was consistently the shallowest of
the three river sections (20-58 cm). Velocity was greatest either in the Murrumbidgee
River or Bundidgerry Creek (0.33 and 0.28 ms$^{-1}$, respectively), and was always the
lowest in Old Man Creek (0.20 ms$^{-1}$).

All water quality variables varied significantly with Date (Sept-Oct vs. Nov-Dec) (2-
way ANOVA; Table 3.3). The medians of temperature, dissolved oxygen and
turbidity generally increased, while that of conductivity generally decreased, between
Sept-Oct and Nov-Dec (Figure 3.4). All water quality variables also differed
significantly by Section, except for conductivity. Dissolved oxygen and pH were
significantly higher in the Murrumbidgee river than the Old Man Creek middle
section (Tukey: both $P<0.01$), and turbidity was significantly higher in the Old Man
Creek middle section than the Murrumbidgee River and Bundidgerry Creek section
(Tukey: both $P<0.001$). Results of the post hoc analysis for temperature failed the
$<0.05$ P-value level for normality and were not considered further.
**Table 3.2:** Mean squares and significance level for results of 2-way analysis of variance for habitat measurements depth and velocity of Study 1 and Study 2, with Section and Habitat as factors; **$P<0.01$, ***$P<0.001$  

<table>
<thead>
<tr>
<th>Factor</th>
<th>DF</th>
<th>MS</th>
<th>DF</th>
<th>MS</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Study 1</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Section</td>
<td>2</td>
<td>5013***</td>
<td>2</td>
<td>0.066***</td>
</tr>
<tr>
<td>Habitat</td>
<td>3</td>
<td>44000***</td>
<td>3</td>
<td>0.869***</td>
</tr>
<tr>
<td>Section*Habitat</td>
<td>6</td>
<td>2229***</td>
<td>6</td>
<td>0.022**</td>
</tr>
<tr>
<td><strong>Study 2</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Section</td>
<td>2</td>
<td>2298***</td>
<td>2</td>
<td>0.013</td>
</tr>
<tr>
<td>Habitat</td>
<td>3</td>
<td>24309***</td>
<td>3</td>
<td>0.448***</td>
</tr>
<tr>
<td>Section*Habitat</td>
<td>6</td>
<td>667</td>
<td>6</td>
<td>0.007</td>
</tr>
</tbody>
</table>
Figure 3.3: Mean (+ S.E.) (a) Depth (cm) and (b) Velocity (ms$^{-1}$) by four mesohabitat types: bare bank, slackwater, channel and woody debris for Study 1 and Study 2.
Table 3.3: Mean squares and significance level for results of 2-way ANOVA test for water quality measurements; temperature (temp), conductivity, dissolved oxygen (DO), pH and turbidity for Study 1 and Study 2, with Section, and Date (Sept-Oct and Nov-Dec) as factors; *P< 0.05, **P<0.01, ***P<0.001

<table>
<thead>
<tr>
<th>Factor</th>
<th>Temp</th>
<th>Conductivity</th>
<th>DO</th>
<th>pH</th>
<th>Turbidity</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>DF</td>
<td>Mean Square</td>
<td>DF</td>
<td>Mean Square</td>
<td>DF</td>
</tr>
<tr>
<td>Study 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Section</td>
<td>2</td>
<td>6.131***</td>
<td>2</td>
<td>0.001</td>
<td>2</td>
</tr>
<tr>
<td>Date</td>
<td>1</td>
<td>202.763***</td>
<td>1</td>
<td>0.028***</td>
<td>1</td>
</tr>
<tr>
<td>Section*Date</td>
<td>2</td>
<td>8.932***</td>
<td>2</td>
<td>0.001</td>
<td>2</td>
</tr>
<tr>
<td>Study 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Section</td>
<td>2</td>
<td>46.683***</td>
<td>2</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Date</td>
<td>1</td>
<td>360.59***</td>
<td>1</td>
<td>1.50E-05</td>
<td>1</td>
</tr>
<tr>
<td>Section*Date</td>
<td>2</td>
<td>15.321*</td>
<td>2</td>
<td>0.039***</td>
<td>2</td>
</tr>
</tbody>
</table>
3.3.1.2 Comparisons of species richness, composition and abundance

In total, the larvae of seven species of fish were collected over the two sampling periods (Tables 3.4 and 3.5). Of the three river sections compared for Study 1, Old
Man Creek middle had the greatest number of species as larvae (5) and Bundidgerry Creek section the fewest (2). However, there was no statistical difference in mean species richness among the three river sections ($P>0.05$). Murray cod, rainbowfish, carp gudgeon and gambusia larvae were only found in the anabranch (Old Man Creek middle) with a less modified flow regime but not in the regulated main stem of the Murrumbidgee River or the highly regulated anabranch of Bundidgerry Creek. Australian smelt larvae were found in all three sections, and common carp were only found in the Murrumbidgee River and Bundidgerry Creek section. The larvae of native species dominated the total abundance (65-85%) in all sections, with Australian smelt being the most abundant in the Murrumbidgee River and Bundidgerry Creek section, but in Old Man Creek this species was in similar proportions to gambusia. Raw and adjusted abundances of larvae were greatest in the Murrumbidgee River section, intermediate in Bundidgerry Creek section, and lowest in Old Man Creek.

Table 3.4: Raw abundance of larval fish (n per 10 m$^2$) collected over in Sept-Oct and Nov-Dec from the Murrumbidgee River, Bundidgerry Creek and Old Man Creek.

<table>
<thead>
<tr>
<th>Larvae</th>
<th>Sept-Oct</th>
<th>Nov-Dec</th>
</tr>
</thead>
<tbody>
<tr>
<td>Murray cod (<em>Maccullochella peeli</em>)</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>Murray rainbowfish (<em>Melanotaenia fluviatilis</em>)</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>River blackfish (<em>Gadopsis marmoratus</em>)</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Carp gudgeon (<em>Hypseleotris spp.</em>)</td>
<td>0</td>
<td>146</td>
</tr>
<tr>
<td>Australian smelt (<em>Retropinna semoni</em>)</td>
<td>173</td>
<td>49</td>
</tr>
<tr>
<td>Common carp (<em>Cyprinus carpio</em>)</td>
<td>55</td>
<td>6</td>
</tr>
<tr>
<td>Gambusia (<em>Gambusia holbrooki</em>)</td>
<td>0</td>
<td>9</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>229</strong></td>
<td><strong>219</strong></td>
</tr>
</tbody>
</table>
Table 3.5: Percent composition, abundance and species richness for larvae (n per 10 m$^2$) found within Study 1 and Study 2

<table>
<thead>
<tr>
<th>Species</th>
<th>Murrumbidgee River</th>
<th>Bundidgerry Creek</th>
<th>Old Man Creek Middle</th>
<th>Old Man Creek Upper</th>
<th>Old Man Creek Lower</th>
</tr>
</thead>
<tbody>
<tr>
<td>Native</td>
<td>73.6</td>
<td>85.1</td>
<td>65.4</td>
<td>98.0</td>
<td>89.2</td>
</tr>
<tr>
<td>Murray cod</td>
<td>-</td>
<td>-</td>
<td>11.5</td>
<td>-</td>
<td>2.7</td>
</tr>
<tr>
<td>Rainbowfish</td>
<td>-</td>
<td>-</td>
<td>15.4</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>River blackfish</td>
<td>0.6</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>2.7</td>
</tr>
<tr>
<td>Carp gudgeon</td>
<td>-</td>
<td>-</td>
<td>11.5</td>
<td>90.5</td>
<td>24.3</td>
</tr>
<tr>
<td>Australian smelt</td>
<td>73.0</td>
<td>85.1</td>
<td>26.9</td>
<td>7.4</td>
<td>59.5</td>
</tr>
<tr>
<td>Alien</td>
<td>26.4</td>
<td>14.9</td>
<td>34.6</td>
<td>2.0</td>
<td>10.8</td>
</tr>
<tr>
<td>Common carp</td>
<td>26.4</td>
<td>14.9</td>
<td>-</td>
<td>2.0</td>
<td>10.8</td>
</tr>
<tr>
<td>Gambusia</td>
<td>-</td>
<td>-</td>
<td>34.6</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Total no. of larvae</td>
<td>163</td>
<td>74</td>
<td>26</td>
<td>148</td>
<td>37</td>
</tr>
<tr>
<td>Adjusted: total no. of larvae (per 10 m$^2$)</td>
<td>113</td>
<td>52</td>
<td>17</td>
<td>97</td>
<td>24</td>
</tr>
<tr>
<td>Total no. of spp</td>
<td>3</td>
<td>2</td>
<td>5</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>Total no. of samples</td>
<td>90</td>
<td>85</td>
<td>95</td>
<td>96</td>
<td>100</td>
</tr>
</tbody>
</table>
In general, very few species were collected as larvae from any one mesohabitat type (Table 3.6). However, the greatest abundances of fish species as larvae were collected from woody debris (Figure 3.5). All sections and habitats were dominated by native species, except for the Murrumbidgee River bare bank and slackwater and Old Man Creek middle slackwater mesohabitats. Australian smelt was the most widespread species collected as larvae, found in every mesohabitat type in all river sections. There was little consistency in relative abundance of larvae in mesohabitats across sections, with the greatest abundance being in woody debris in the Murrumbidgee River, in channel in Bundidgerry Creek section and in slackwater in Old Man Creek middle. The modified anabranch, Bundidgerry Creek, was the only section in which larvae were collected from all mesohabitat types.

Overall, GLMs indicated that Section best explained the abundance of larvae of each species in Study 1 (Table 3.7). Section best described the abundance of larvae of common carp and all species combined (total abundance) for the September/October, and Australian smelt for the November/December sampling periods, explaining between 38% and 65% of the variance. Australian smelt, from September/October, was the only species not to have Section explaining most of the variance in larval abundance; instead Habitat was the best explainer of abundance of this species ($R^2=0.59$). Section was included in all GLMs describing the abundance of the larvae of each species, with Habitat in most models and Velocity and Depth contributing to about half. There were no significant models for total abundance of larvae from November/December.
Table 3.6: Percent composition, abundance and species richness for larvae found in the four mesohabitat types; bare bank (BB), slack water (SW), channel (CH) and woody debris (WD) sampled for Study 1 and Study 2

<table>
<thead>
<tr>
<th>Species</th>
<th>Murrumbidgee River</th>
<th>Bundidgerry Creek</th>
<th>Old Man Creek Middle</th>
<th>Old Man Creek Upper</th>
<th>Old Man Creek Lower</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>BB</td>
<td>SW</td>
<td>CH</td>
<td>WD</td>
<td>BB</td>
</tr>
<tr>
<td>Native</td>
<td>15.4</td>
<td>16.2</td>
<td>100.0</td>
<td>99.1</td>
<td>92.9</td>
</tr>
<tr>
<td>Murray cod</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Rainbowfish</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>River blackfish</td>
<td>-</td>
<td>-</td>
<td>0.9</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Carp Gudgeon</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Australian smelt</td>
<td>15.4</td>
<td>16.2</td>
<td>100.0</td>
<td>98.2</td>
<td>92.7</td>
</tr>
<tr>
<td>Alien</td>
<td>84.6</td>
<td>83.78</td>
<td>-0.89</td>
<td>7.14</td>
<td>10.0</td>
</tr>
<tr>
<td>Common carp</td>
<td>84.6</td>
<td>83.78</td>
<td>-0.89</td>
<td>7.14</td>
<td>10.0</td>
</tr>
<tr>
<td>Gambusia</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Total no. of larvae</td>
<td>13</td>
<td>37</td>
<td>1</td>
<td>112</td>
<td>14</td>
</tr>
<tr>
<td>Adjusted: total no. of larvae (per 10m²)</td>
<td>36</td>
<td>164</td>
<td>2</td>
<td>259</td>
<td>35</td>
</tr>
<tr>
<td>Total no. of spp</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Total no. of samples</td>
<td>24</td>
<td>19</td>
<td>24</td>
<td>23</td>
<td>24</td>
</tr>
</tbody>
</table>
Table 3.7: Results for Poisson GLM models with deviance residual (D.R.), degrees of freedom residual (D.F.), pseudo $R^2$, deviance, $P$-value, AIC value for the four model factors: Section (S), Habitat (H), Depth (D), Velocity (V), with the best fitting modelled factor in bold, and the statistically significant model, for individual species and total abundance of larvae for Study 1 and Study 2 by sampling date, N = abundance.

<table>
<thead>
<tr>
<th>Study 1</th>
<th>Date</th>
<th>N</th>
<th>D.R.</th>
<th>D. F.</th>
<th>Pseudo $R^2$</th>
<th>Deviance</th>
<th>$P$-value</th>
<th>Section</th>
<th>Habitat</th>
<th>Depth</th>
<th>Velocity</th>
<th>Best model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Australian smelt</td>
<td>Sept-Oct</td>
<td>145</td>
<td>9.23</td>
<td>27</td>
<td>0.59</td>
<td>170</td>
<td>0.0024</td>
<td>449</td>
<td>405</td>
<td>481</td>
<td>425</td>
<td>H/V/S/D</td>
</tr>
<tr>
<td>Common carp</td>
<td>Sept-Oct</td>
<td>50</td>
<td>40.50</td>
<td>29</td>
<td>0.38</td>
<td>123</td>
<td>8.50E-09</td>
<td>198</td>
<td>198</td>
<td>227</td>
<td>230</td>
<td>S/H</td>
</tr>
<tr>
<td>Total abundance</td>
<td>Sept-Oct</td>
<td>196</td>
<td>7.92</td>
<td>27</td>
<td>0.53</td>
<td>189</td>
<td>0.0049</td>
<td>430</td>
<td>472</td>
<td>499</td>
<td>458</td>
<td>S/V/H/D</td>
</tr>
<tr>
<td>Australian smelt</td>
<td>Nov-Dec</td>
<td>44</td>
<td>12.40</td>
<td>22</td>
<td>0.65</td>
<td>24.9</td>
<td>0.002</td>
<td>84.8</td>
<td>99.5</td>
<td>104.3</td>
<td>111.4</td>
<td>S/H</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Study 2</th>
<th>Date</th>
<th>N</th>
<th>D.R.</th>
<th>D. F.</th>
<th>Pseudo $R^2$</th>
<th>Deviance</th>
<th>$P$-value</th>
<th>Section</th>
<th>Habitat</th>
<th>Depth</th>
<th>Velocity</th>
<th>Best model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carp gudgeon</td>
<td>Nov-Dec</td>
<td>146</td>
<td>28.71</td>
<td>33</td>
<td>0.52</td>
<td>127</td>
<td>&lt;2e-16</td>
<td>303</td>
<td>322</td>
<td>346</td>
<td>312</td>
<td>S/H/V</td>
</tr>
<tr>
<td>Total abundance</td>
<td>Nov-Dec</td>
<td>171</td>
<td>5.89</td>
<td>32</td>
<td>0.49</td>
<td>102</td>
<td>0.015</td>
<td>310</td>
<td>288</td>
<td>315</td>
<td>283</td>
<td>V/H/S/D</td>
</tr>
</tbody>
</table>
3.3.2 Study 2

3.3.2.1 Habitat characteristics and water quality

Within Old Man Creek, mesohabitat depth varied significantly with Habitat and Section, but velocity only varied significantly with Habitat (Table 3.2). Habitat contributed most to the variance in depth. Again, bare bank mesohabitats were consistently the shallowest (19-30 cm), slackwaters had the lowest velocity of all the habitats (0.0-0.01 m s\(^{-1}\)) and channel was deepest (52-59 cm) and had the fastest velocity (and 0.15-0.20 m s\(^{-1}\)) (Figure 3.3). Old Man Creek middle was the deepest of the three sections (59 cm), followed by Old Man Creek lower (56 cm). As with study 1, velocity was greatest in channel mesohabitat and was always lowest in slackwater.

Temperature, pH and dissolved oxygen varied significantly with Date (2-way ANOVA; Table 3.3). Generally, temperature and dissolved oxygen increased, whereas pH marginally decreased between Sept-Oct and Nov-Dec (Figure 3.4). Only temperature also varied significantly with Section, with Old Man Creek lower cooler than Old Man Creek upper and Old Man Creek middle (Tukey: both \(P<0.001\)).

3.3.2.2 Comparisons of species richness, composition and abundance

The larvae of 5 species of fish were collected throughout the three anabranch sections in Old Man Creek (Table 3.5). Of the three anabranch sections, Old Man Creek upper had the fewest species as larvae (3) with Old Man Creek middle and lower both having the larvae of 5 species. Carp gudgeon and Australian smelt larvae were found in all three sections, whereas gambusia was only found in Old Man Creek middle. Native fish dominated the total abundance of larvae (65-98%) in all sections, with Australian smelt being the most abundant in Old Man Creek middle and lower, but in
Old Man Creek upper carp gudgeon dominated abundance. Raw and adjusted abundances of larvae were greatest in Old Man Creek upper, intermediate in Old Man Creek lower, and lowest in Old Man Creek middle.

Very few species were collected as larvae from any one mesohabitat type within the Old Man Creek anabranches (Table 3.6). However, larvae of the greatest number of species were collected from woody debris in Old Man Creek middle and Old Man Creek lower (4) and bare bank in Old Man Creek upper (3) (Figure 3.5). All sections and habitats were dominated by native species (60-100%), except for Old Man Creek middle slackwater. Australian smelt was the most widespread species collected as larvae, found in every mesohabitat type in all sections, except for channel habitat in Old Man Creek upper. Collectively, Australian smelt and carp gudgeon dominated abundances throughout the anabranch. The greatest adjusted abundance of larvae were found in woody debris in Old Man Creek upper and Old Man Creek middle and in slackwater in Old Man Creek middle.

GLM indicated that Section, Habitat and Velocity best explained larval abundance of each species in Study 2 (Table 3.7). Section best explained abundance of carp gudgeon and Velocity best explained total abundance for the November/December sampling period, explaining between 52% and 49% of the variance. Section, Habitat and Velocity were included in the model for carp gudgeon, whereas all variables were included in the model for total abundance. There were no significant models for Australian smelt and total abundance of larvae from September/October.
Figure 3.5: Mean (± 1 SE) number for a) Species richness, b) Total abundance, c) Australian smelt, and d) carp gudgeon larvae within mesohabitat types; bare bank, slackwater, channel and woody debris for Study 1 and Study 2.
3.4 Discussion

3.4.1 Comparisons among main stem and anabranches

Overall, in the present study, the total number of species of fish at the larval stage was greater in the less flow-modified anabranch, Old Man Creek, than in the main stem Murrumbidgee River or highly flow-modified anabranch Bundidgerry Creek. This was not reflected, however, in mean species richness among the three river sections, where no differences were found. It is commonly reported that there is a positive relationship between species richness and stream order (see Matthews, 1986, Oberdoff et al., 1995), although this is for adults rather than larvae. The underlying reasons for this relationship are not straightforward, but are likely to relate to diversity of habitat (Gorman and Karr, 1978), opportunities for immigration and emigration (Power et al., 1988) or geomorphological characteristics. Patterns of greater species richness in anabranches than main stems are consistent with findings elsewhere (Simons et al., 2001, Grift et al., 2003), and are thought to occur because anabranches typically provide more heterogeneous flow and habitat conditions, and enhanced lateral connectivity with the floodplain, than their regulated main stems: something potentially important for the young stages of fishes. Simons et al. (2001), for example, found that man made anabranches with less modified flow regimes than the main stem, can act as nursery areas for larval fish, due to the connectivity of no-flow habitat with flowing habitat and this finding is plausible for naturally occurring anabranches as well. This heterogeneous habitat arrangement may aid in the longitudinal and transverse movement and dispersal of young-of-year and larval fish; especially considering that the latter may have relatively poor swimming capabilities (Simons et al., 2001, Grift et al., 2003, Chapter 4).
It should be noted that the multiple factors in Bundidgerry Creek (i.e. the anabranches overall higher flows and artificially straightened channel) may have confounding affect on the results. It must be borne in mind that some of the differences between Bundidgerry Creek and Old Man Creek may be due to the straightening of the former, which would likely have the effect of reducing habitat heterogeneity. In rivers, the interaction between discharge and channel morphology create a heterogeneous mosaic of habitat (Schlosser 1991; Wiens 2002; Thorp et al. 2006). In a flow modified system, such as Bundidgerry Creek, with alterations to channel morphology, and constant high velocities during spawning periods, slackwaters and woody debris mesohabitats, with slow to no flow, can become degraded due to scouring and filling or flooding/overtopping (King 2004). When looking at the multiple factors affecting habitat heterogeneity in Bundidgerry Creek it is apparent flow alteration can affect habitat, but it is likely that flow will not directly affect the amount of woody debris in a system, but the hydraulic environment around it. Woody debris will moderate hydraulics, but only to a limited extent. With very high flow, woody debris is still not going to be a great habitat for fish larvae.

Regardless of the degree of flow alteration, however, the larvae of native species dominated all river sections in the present study. This result was mostly because of large numbers of Australian smelt, a common, widespread, tolerant, pelagic species (Lintermans, 2007), with an opportunistic (sensu Winemiller and Rose, 1992) life history strategy, that can take advantage of a range of conditions in which to spawn and recruit (Humphries et al., 1999, Tonkin et al., 2011, Humphries et al., 2013). The anabranch with a less modified flow regime, Old Man Creek, in fact supported the lowest total abundance of larvae of all sections, and the heavily regulated
Murrumbidgee River, the most. This may reflect the fact that the anabranch plays an important role in maintaining fish populations and increasing diversity of habitats used by different species of larvae, but the main stem is an important source for recruits (Pollux et al., 2006). Several native species – Murray cod, Murray rainbowfish and carp gudgeons – were only collected as larvae in Old Man Creek and never in the other more regulated river sections. Murray cod care for eggs and larvae in a hollow or nest for 2-3 weeks and normally spawn between October and mid-December, when high flows are less common than at other times of the year in this region (Humphries, 2005). Indications are that unseasonably high flows may wash larvae prematurely from the nest (Humphries, 2005). Furthermore, Murray rainbowfish and carp gudgeons are considered low-flow specialists and typically spawn during the warmer months of the year in lowland rivers, where there is a relatively low chance of disturbance by high flows (Humphries et al., 1999, King, 2004, McCasker, 2010). The lower, relatively stable flows of the Old Man Creek anabranch during the spawning season may therefore provide more suitable rearing and nursery habitats for these species than the other more regulated river sections. It must be noted that this study did not directly determine the importance anabranches in native fish recruitment (i.e. tagging of juveniles) to the main stem but instead is making suggestions about the possible recruitment scenarios based on the findings in the results.

Consistent elevated base flows during summer are considered unfavourable for maintenance of position and survival of the early life history stages of fish (Bunn and Arthington, 2002, Humphries et al., 2002, Humphries et al., 2006). Furthermore, changes to natural patterns of flow, and to the connectivity of the main stem with
secondary channels, are likely to limit the resistance and resilience of native species, generally (Bunn and Arthington, 2003). This is because species diversity peaks along a connectivity gradient within the riverine landscape, suggesting that habitat patches across a broad range of connectivity will optimise community diversity (Ward et al., 2002, Schlosser, 1991). Indeed, the inherent complexity of riverine system helps to maintain populations and assemblages, through movement and recruitment (Junk et al., 1989, Schlosser, 1995a, Grossman et al., 1998, Puckridge et al., 2000, Balcombe et al., 2006, Balcombe et al., 2007, Balcombe and Arthington, 2009), whereas reductions of that complexity risk declines in populations and abundance.

3.4.2 Comparisons within the Old Man Creek anabranch

The composition, abundance and overall species richness of larval fish varied less among reaches within Old Man Creek, but still broadly showed the same patterns, as the among-sections comparison of Study 1. Thus, native species similarly dominated the larval fauna in all reaches as they did across river sections. Similar to Study 1, abundance was greatest at the location where overall species richness was lowest. Results also show that the upper reach of Old Man Creek had the highest occurrence of non-native species and the lowest species richness, suggesting that non-native fish may move from the Murrumbidgee River main stem into Old Man Creek or that the local habitat features within Old Man Creek upper, such as deeper mesohabitat depths, may benefit non-native fish.

Location within the anabranch relative to the confluence with the main stem is only one factor that might affect the composition, richness and abundance of larval fish. Local features, such as geomorphology, instream vegetation and habitat, adjacent
land use and riparian zone quality and quantity, are all likely to influence these measures of the fish assemblage (Growns et al., 2003, Nerbonne and Vondracek, 2001). Interestingly, Australian smelt was the most abundant species at Old Man Creek lower and Old Man Creek middle, whereas carp gudgeon was the most abundant taxon at Old Man Creek upper. So, while results from Study 1 suggested that Old Man Creek overall supported the richest fish assemblage, there were some substantial differences within the system, suggesting that local features affect overall diversity and abundance trends within the riverscape.

3.4.3 Consistency of habitat use

Results demonstrated that low velocity habitats with instream structure (i.e., woody debris), supported more larvae and higher species richness than those which typically had higher velocities and no structure (i.e. open channel). Indeed, habitat use by larvae was consistent, regardless of river section. Woody debris mesohabitats supported more larvae than slackwater mesohabitats, indicating that structure likely plays a part in larval retention. Fish larvae are often associated with structure in inshore riverine habitats (Lonzarich and Quinn, 1995): structure acts as a refuge from the current and from predators and also allows the young stages of fish to orientate visually (Blaxter, 1969, Copp, 1992a, Scheidegger and Bain, 1995, King, 2004, Price, 2007). High densities of prey for small fish are also often associated with woody debris and vegetation, so these habitats are typically rich sources of food (Benke, 1969).

Slackwater habitats are commonly used by riverine fishes as nurseries because they protect early life stages from washout during changing water levels, have high
retention of organic material and high densities of prey (Schiemer et al., 2001, King, 2004, King, 2005). A combination of slow-to-zero flow and structure may provide essential conditions for larvae in rivers lacking substantial off-channel backwater habitats (Scheidegger and Bain, 1995). Furthermore, during low-flow events of late spring and summer in Mediterranean climates, water temperatures increase and flows decline, and prey items are concentrated to the extent that densities may be sufficient for first-feeding larvae (Humphries et al., 1999, Ning et al., 2010, Ning et al., 2013, King, 2005).

3.4.4 Can anabranches provide a refuge for fish from modified flows?

When looking at a regulated riverscape, this study found that connectivity and flow characteristics may be more important in understanding the overall species richness, and rehabilitation efforts should include aspects of connectivity and not just habitat improvements. Since tributaries and anabranches are part of the lowland river complex and perform many of the same functions within the riverscape, this study considers comparisons between them similar in terms of benefit for fish. Results indicate that anabranch connection with the main stem may be a more important factor in species abundance and occurrence than mesohabitat type and structure. Indeed, Pollux et al. (2006) found that fish can use tributaries during different life stages (as larvae, juveniles and adults) for different reasons (e.g. reproduction, growth, food, shelter) and at different periods (e.g. different seasons). This is supported by the results of Study 1, where section was the best descriptor of larval abundance and occurrence, and in Study 2, with the upper and lower reach of Old Man Creek containing 97% of the total abundance for carp gudgeon. Movement
during different life stages of fish, between a main river channel and a tributary is common. For example, Nunn et al. (2010) found that cyprinids moved from the main stem river to a tributary in response to increasing river discharge and decreased water velocity within the tributary, and speculated that increasing river discharge and water velocity within the main stem stimulated the young or small fishes, due to their poor swimming ability, to seek shelter in the tributary. Gardner et al. (2013) found that adult common bream (*Abramis brama*) moved from the main stem to a tributary following rising temperatures, and Koster et al. (2014) found that adult golden perch (*Macquaria ambigua*) movement from the main stem to a tributary occurred during or soon after changes in flow. Maintaining main stem connectivity with secondary channels seems to result in higher habitat heterogeneity and provides complementary habitats that are required for the completion of either part or all of riverine organisms’ life cycles (Amoros and Bornette, 2002, Ward et al., 2002).

The findings show that anabranches with a less modified flow regime may provide increased habitat heterogeneity that can be used as habitat for spawning, feeding and as refuge for larvae. Previous research has established that shallow, slow- or no-flow littoral habitats are commonly used by the early life stages of fishes in river systems (Schiemer and Spindler, 1989, Sempeski and Gaudin, 1995, Watkins et al., 1997), especially for low-flow recruitment specialists found in the lowland rivers of Australia (Humphries et al., 1999, King, 2004, Price et al., 2012). Due to river regulation and altered flow regimes, off-channel slow-flow nursery habitats are less common, and more homogenous in character (Bowen et al., 2003, Dieterman and Galat, 2004, Korman et al., 2004, Price et al., 2012). In large river systems, like the Mississippi and Colorado River, USA, research has found that shallow, riverine
shorelines provide critical nursery habitat for small-bodied riverine fishes (Dieterman and Galat, 2004, Korman et al., 2004) and, in the absence off-channel slow-flow habitat, perhaps, anabranches or unregulated secondary channels can act as suitable nursery habitat. As stated above, the findings in the present study and from previous research (Schiemer and Spindler, 1989, Sempeski and Gaudin, 1995, Watkins et al., 1997, Humphries et al., 1999, King, 2004, Price et al., 2012) have found that shallow, slow- or no-flow littoral habitats are potentially important as refuges and nursery habitats for the early life stages of fishes (King 2004). And given that river regulation in south-eastern Australia typically enhances discharge and increases current speeds during the spawning and rearing period of many native fishes, an obvious question to ask is: how capable are the larvae of native fishes at maintaining position and at swimming for short and prolonged periods? In other words, how critical are the slow-flow and slackwater environments for rearing of free embryos and larvae? This will be the topic of Chapter 4, which will examine the swimming capabilities of the larvae of six species of native fish under controlled, laboratory conditions.
4.1 Introduction

Downstream dispersal is common during the early life history of riverine fishes. Movement from breeding to nursery habitats is thought to provide enhanced conditions for feeding, while reducing cannibalism and competition (Lowe-McConnell, 1987, Pavlov, 1994). The mode of downstream dispersal, or drift, of free embryos and larvae differs according to a species’ life history strategy and stage of development, but is usually classified as passive (unorientated), active/passive (orientated upstream), or active (orientated downstream) drifting (Pavlov, 1994). Passive drift was considered the most common mode of dispersal for many years, but more recently this has been questioned (Copp, 1992a, Scheidegger and Bain, 1995, Wolter and Sukhodolov, 2008, Schludermann et al., 2012, Lechner et al., 2013). Indeed, the dispersal patterns during early life history and how fishes actively influence their position in lotic systems are generally poorly understood (Reichard et al., 2004, Korman et al., 2004, Zitek et al., 2004, Schludermann et al., 2012).

To understand how larvae influence the distance, speed and ultimate destination of their dispersal, it is important to know at what stage during ontogeny effective swimming - the ability to maintain position or orientate in the current - develops (Clark et al., 2005). Ontogenetic changes in swimming performance of free embryos and larvae are important to the survival of fishes, because this influences habitat use, feeding, escape from predators and ultimately survival. Swimming performance
depends on a variety of biological and physical factors (Webb, 1975), such as body shape (Wootton, 1990, Hammer, 1995), formation of fins (Webb, 1984, Plaut, 2001), muscle function (Hammer, 1995, Kieffer, 2000), swimming mode (e.g. undulatory swimming) (Müller et al., 2001), body condition (Wootton, 1990), and water temperature (Ojanguren and Brañta, 2000). Absolute swimming performance also increases with size (Webb, 1975, Domenici, 2001). However, the vast majority of free embryos and larvae of most riverine fishes die before they reach the juvenile stage, and therefore it is probably reasonable to assume that the larvae that survive in the wild are the best performers in a variety of critical capabilities, including swimming. For this reason, it may be informative to understand not only overall swimming performance of a cohort or species, but also variation in performance.

Variation in swimming performance exists within species, for the reasons mentioned above, but also among species, probably due to life history strategy-related differences. Winemiller and Rose (1992) recognize three endpoint life history strategies: opportunistic and periodic (=altricial, sensu Balon, 1986b), and equilibrium (=precocial, sensu Balon, 1986b). Species in the first two life history strategies tend to be pelagic broadcast spawners, usually have small eggs which typically hatch as planktonic larvae, and either occupy habitats with persistent, unpredictable fluctuations, or invade new habitats (Winemiller and Rose, 1992). Because of these factors, fishes with opportunistic and periodic life history strategies will probably be relatively poor swimmers early in ontogeny and be less likely to influence aspects of their dispersal in rivers. Equilibrium strategy species, on the other hand, tend to have larger amounts, or have greater density, of yolk as free embryos, have high investment per offspring, moderate to long generation time, and
low batch fecundity (Winemiller and Rose, 1992). Because of these factors, these fishes will probably be relatively competent swimmers early in ontogeny and have a relatively greater ability to influence aspects of their dispersal in rivers.

Dispersal during early life history is hazardous for riverine fishes even under the relatively benign conditions of rivers with natural flows. But unique challenges now exist in the form of river regulation and flow alteration. Enhanced flows, because of releases from dams, have been implicated in the demise of native fishes throughout the world (Bain et al., 1988, Bunn and Arthington, 2002, Hauer and Lorang, 2004). Such changes to river flow often result in increased in-channel flow volume and current speeds during the spring and summer growing seasons, which is also typically the peak spawning period of most species of native fishes in the Murray-Darling Basin, southern Australia (Murchie et al., 2008). However, most Murray-Darling Basin fishes apparently breed despite flow alteration, but the influence of flow alteration on recruitment is less certain (Walker and Thoms, 1993, Gehrke et al., 1995, Humphries et al., 1999, Humphries et al., 2002, King et al., 2009). One reason that native fishes may be in low abundances or absent from flow-altered rivers, is the inability during early life history to either maintain position or influence their dispersal when experiencing the high current speeds, typical of flow-altered rivers during spring and summer (Humphries et al., 2006).

The overall aim of this chapter was to: describe changes in critical and prolonged swimming performance during the early life history of six native fish species. Specifically, the aims were to: 1) determine which developmental characteristics (days after hatch, length, developmental stage) best explain critical and prolonged
swimming performance; and 2) establish if critical swimming speed and prolonged swimming performance vary with ontogeny, species and life history strategy.

4.2 Materials and methods

The free embryos and larvae of Murray cod *Maccullochella peeli* (Mitchell), trout cod *Maccullochella macquariensis* (Cuvier), silver perch *Bidyanus bidyanus* (Mitchell), golden perch *Macquaria ambigua* (Richardson), carp gudgeon *Hypseleotris spp* and Murray rainbowfish *Melanotaenia fluviatilis* (Castelnau) were used in swimming experiments, because they represent the three life history strategies defined for native fishes from the Murray-Darling Basin and a diversity of sizes and morphologies (Humphries et al., 1999) (Table 4.1). The first four species were spawned, reared and housed at the New South Wales Inland Fisheries Research Centre (IFRC), Narrandera, New South Wales from 1 October 2008 to 9 March 2009. *Maccullochella macquariensis* and *M. peelii* free embryos and larvae used in all flume trials came from one cohort, whereas *M. ambigua* and *B. bidyanus* free embryos and larvae came from two cohorts. *Hypseleotris spp* and *M. fluviatilis* larvae were collected using modified quatrefoil light traps (Floyd et al., 1984, Secor et al., 1992, Humphries et al., 2002), from ponds at the Inland Fisheries Research Centre on 9 and 12 December 2008. Traps were set at sunset for 10 h. Only metalarvae were able to be collected for these two species. Age (days after hatch) was not known and it was beyond the scope of this study to validate age increments and back calculate age using otoliths for these two species.

Fish were grouped into four developmental stages, determined by the state of flexion of the notochord and fin-ray development (preflexion, flexion, postflexion and
metalarvae), as proposed by Kelso et al. (1996). It is recognised, however, that there are other classifications (e.g. Balon, 1975), and this study endeavours to make terminology compatible with both. After each trial, larvae were preserved in 70% ethanol, standard length ($L_s$) was measured to 0.1 mm using vernier callipers and age was recorded in days after hatch (DAH).
Table 4.1: Life history strategy characteristics for larvae used in this experiment after Humphries et al. (1999), with comparisons to life history strategies described by Balon (1986) and Winemiller and Rose (1992).

<table>
<thead>
<tr>
<th>Characteristics</th>
<th>Strategy 1</th>
<th>Strategy 2</th>
<th>Strategy 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Life history type</td>
<td>Precocial, equilibrium</td>
<td>Altricial, periodic</td>
<td>Altricial, opportunistic</td>
</tr>
<tr>
<td>Adult size and longevity</td>
<td>Large, 25+ years</td>
<td>Medium, 7-10 years</td>
<td>Small, 2-3 years</td>
</tr>
<tr>
<td>Spawning</td>
<td>Short, single spawning, same time annually</td>
<td>Single variable spawning, October to March</td>
<td>Short single spawn</td>
</tr>
<tr>
<td>Eggs</td>
<td>up to 10,000s, demersal</td>
<td>100,000 semi-buoyant or planktonic</td>
<td>up to 1000s, planktonic or demersal</td>
</tr>
<tr>
<td>Embryo/larva parental care</td>
<td>yes</td>
<td>no</td>
<td>no</td>
</tr>
<tr>
<td>Development of larvae up to first feed</td>
<td>well developed, highly mobile</td>
<td>undeveloped, limited mobility</td>
<td>undeveloped, limited mobility</td>
</tr>
<tr>
<td>Example species</td>
<td>Trout cod (\text{Maccullochella maquariensis})</td>
<td>Golden perch (\text{Maquaria ambigua}) Silver perch (\text{Bidyanus bidyanus})</td>
<td>Carp gudgeon (\text{Hypseleotris} \text{spp.}) Murray River rainbowfish (\text{Melanotaenia fluviatilis})</td>
</tr>
</tbody>
</table>


4.2.1 Experimental setup and design

The swimming chamber used in this experiment was as described in Stobutzki and Bellwood (1997). This chamber was constructed from Perspex™, with six raceways, each measuring 30 W x 50 H x 180 L mm (Appendix B). Flow was controlled with T-piece diffuser and straighteners. Previous studies have established negligible boundary layers within raceways of this type of flume (Stobutzki and Bellwood, 1997, Stobutzki, 1998, Fisher et al., 2000). This study follows the design and principle of Stobutzki and Bellwood (1997), which has addressed boundary layer issues by using large swimming chambers relative to the size of the fish studied and videoing neutrally buoyant particles moving past a grid. Stobutzki and Bellwood (1997) found that interactions with the boundary layer were negligible, as the water velocity in the 0.5 cm closest to the wall was not significantly different to that in the centre of the chamber. Current speed was calibrated by recording the amount of time it took for water flowing out of the raceway to fill a container of a known volume. Fill time was divided by the cross-section area of the chamber. Each day an experiment was run, the chamber was calibrated three times for each of the five velocity increments used in the study.

Groundwater was used for the flume experiments and was the same water used to rear fishes in tanks and maintain them in ponds. Maccullochella peelii and M. macquariensis were free embryos and fed endogenously from their yolk sacs for the entire experiment, but gradually lost yolk as they developed. Bidyanus bidyanus and M. ambigua were not fed for the first three days, when they were free embryos feeding endogenously. They were then transferred into a pond with a self-sustaining,
unregulated population of zooplankton upon which they could feed freely. Bidyanus bidyanus and M. ambiguity did not have yolk sacs during swimming trials, whereas Maccullochella peelii and M. macquariensis transitioned from having relatively large yolk sacs at the start, to having very small yolk sacs at the end of the trials. This study chose to focus on comparing life stages, regardless of feeding strategy, even though the presence or absence of a yolk sac may influence swimming performance. The timing of transition from endogenous to exogenous feeding differs among individuals, making any comparison difficult and outside the scope of this study. Immediately before the experiments began, Maccullochella peelii and M. macquariensis larvae were transferred from rearing troughs and B. bidyanus and M. ambiguity were collected from ponds and acclimated for 5 minutes in the flume at a speed of 0·5 cm s⁻¹ with one individual in each raceway. Any fish exhibiting signs of stress during acclimation were removed and replaced.

Researchers routinely investigate swimming performance by determining critical (≤60 min), prolonged (>60–200 min,) or sustained (>200 min) swimming performance (Webb, 1975, Beamish, 1978, Leis et al., 2007). Critical and prolonged swimming trials were conducted separately (Table 4.2). For critical swimming experiments, six fish, each in separate raceways, were initially exposed to a current speed of 1·1 cm s⁻¹, with this speed increasing by 4·8 cm s⁻¹ every 5 min until fish could no longer maintain position and were forced against the rear screen of the flume. The time at which fish were unable to maintain position was recorded; critical swimming experiments did not exceed 30 min. Critical swimming trials were repeated five times, so that 30 fish of each stage of each species were swum, one species at a time. All individual fish were swum once only and not re-used in any
other experiments. Critical swimming speed ($U_{\text{crit}}$) was calculated following Brett (1964):

$$U_{\text{crit}} = U + (t/t_i \times U_i)$$

where, $U =$ penultimate speed, $U_i =$ velocity increment (4·8 cm s$^{-1}$), $t =$ time swum and $t_i =$ time interval at each speed increment (5 min). An advantage of using $U_{\text{crit}}$ to investigate ontogeny of swimming performance is the ability to compare swimming speed among developmental stages, and among species (Leis et al., 2007). Critical speed is a laboratory measure of forced performance over a relatively short period, and probably does not represent cruising speed of free embryos and larvae in the wild.

In the wild, prolonged swimming speed is difficult to separate from sustained swimming speed because true fatigue cannot be determined (Plaut, 2001, Beamish, 1978). With this in mind, prolonged swimming trials were conducted at two speeds, to represent more realistic in situ swimming and/or current speeds (Leis and Carson-Ewart, 1997, Leis and Stobutzki, 1999). Prolonged swimming capabilities were measured by swimming fish continuously at a single speed for 61 min. Replicate individual larvae ($n = 6$) of each species were swum, with no individual fish swum in more than one trial and not re-used in any other experiments (Table 4.2). Fish were initially swum at one increment (4·8 cm s$^{-1}$) lower than the fastest mean $U_{\text{crit}}$ of that species. Then, if they tired before 60 min, another prolonged swimming trial was completed with different individuals of the same species and was swum at two increments (9·6 cm s$^{-1}$) lower than the mean $U_{\text{crit}}$. Fish were swum until the speed at which 75% of individuals could swim for 61 min was determined.
Table 4.2: Number of individuals of each developmental stage of the six fish species included in swimming trials (number of cohorts in brackets), with ranges of days after hatch and standard lengths for the six species when known. Included are measurements taken during swimming trials.

<table>
<thead>
<tr>
<th>Developmental stages</th>
<th>Maccullochella macquariensis</th>
<th>Maccullochella peelii</th>
<th>Macquaria ambigua</th>
<th>Bidyanus bidyanus</th>
<th>Hypseleotris spp.</th>
<th>Melanotaenia fluviatilis</th>
</tr>
</thead>
<tbody>
<tr>
<td>preflexion</td>
<td>51 (1)</td>
<td>30 (1)</td>
<td>63 (1)</td>
<td>29 (1)</td>
<td>no data</td>
<td>no data</td>
</tr>
<tr>
<td>flexion</td>
<td>29 (1)</td>
<td>30 (1)</td>
<td>20 (1)</td>
<td>54 (2)</td>
<td>no data</td>
<td>no data</td>
</tr>
<tr>
<td>postflexion</td>
<td>30 (1)</td>
<td>30 (1)</td>
<td>39 (2)</td>
<td>31 (1)</td>
<td>no data</td>
<td>no data</td>
</tr>
<tr>
<td>metalarvae</td>
<td>29 (1)</td>
<td>30 (1)</td>
<td>31 (1)</td>
<td>28 (1)</td>
<td>36</td>
<td>21</td>
</tr>
</tbody>
</table>

Days after hatch (DAH) 3-14 3-17 10-25 3-15 unknown unknown

Standard length ($L_3$, mm) 6·3-10·9 7·4-10·6 4·5-11·9 4·7-11·4 9·1-14·6 9·8-12·1

Swimming trial measurements

Critical swimming (< 30 min)

$U_{crit} L_s s^{-1} = \text{number of body lengths that the individual fish can swim per second}$

$U_{crit} \text{ cm s}^{-1} = U + (t/t_i \times U_i)$, where, $U = \text{penultimate speed, } U_i = \text{velocity increment (4·8 cm s}^{-1})$, $t = \text{time swum}$ and $t_i = \text{time interval at each speed increment (5 min)}$

Prolonged swimming (> 60 min)

increment 1 = 4·8 cm s$^{-1}$ < mean $U_{crit}$ as cm s$^{-1}$
increment 2 = 9·6 cm s$^{-1}$ < mean $U_{crit}$ as cm s$^{-1}$
4.2.2 Data analysis

To establish the best predictor of swimming performance, generalized linear models (GLM) were developed for critical swimming speeds, using three variables potentially affecting swimming performance: size ($L_s$) which was transformed using natural log of standard length, age in days after hatch (DAH) and developmental stage (DS). These three variables are measures of growth, physically and physiologically. GLMs for critical swimming speeds used cm s$^{-1}$ because statistical comparisons showed little difference between $U_{crit}$ as measured in $L_h$ s$^{-1}$ or cm s$^{-1}$. $L_s$ and DAH are continuous data, whereas DS is categorical, and analysis and presentation of results take this into account by separating results into each stage. Akaike Information Criterion (AIC) (Akaike, 1973), one of many model selection methods that prioritize models based on their fitting ability and level of parsimony, was used to determine which variable was most efficient. The variable with the lowest AIC value was selected for further modelling. Three generalised linear models were developed, using the best variable and subsequent combinations of variables: e.g. 1/ DS, 2/ DS and $L_s$ or 3/ DS, $L_s$ and DAH. An analysis of variance (ANOVA, 95% C.I.) was undertaken to determine if there was a significant difference between the three models. If there was no significant difference among the models, the simplest model was used. Only metalarval Hypseleotris spp and M. fluviatilis were collected for swimming performance trials, so these species could not be included in GLM analysis. Data were analysed using the R statistical package (R v2.9.0, R Development Core 2008).
Macquaria ambiguа and B. bidyanus larvae came from 2 cohorts each. To determine if variation in swimming performance was greater within cohorts than among cohorts, cohorts were compared statistically using analysis of variance on log_{10}-transformed data. There was no significant difference in the swimming performance among cohorts for M. ambiguа or B. bidyanus larvae (P>0.05) and so the cohorts were not treated separately.

Swimming performance (U_{crit}) has been reported in this study as body lengths per second (L_b s^{-1}), a relative measurement and as swimming speed (cm s^{-1}), an absolute measurement because both of these measures are used commonly throughout the literature. Kruskal-Wallis tests were used to determine if there were differences in the swimming performance among species and among fishes from different life history strategies and, if significant, Mann-Whitney U-tests were used to make pairwise comparisons. Adjustments for multiple tests were made using the Bonferroni correction. To estimate performance of theoretical wild-surviving best performers, the top 25% swimming individuals for each development stage were also assessed for each species. Prolonged swimming speeds are expressed both as absolute speeds and as percentages of mean critical speeds, at which 75% of larvae of each species and developmental stage could swim for >60 min. All data were analysed at α=0.05 level, using SPSS 17.0 (SPSS Inc. http://www-01.ibm.com/software/au/analytics/spss/).

4.3 Results

4.3.1 Best predictors of critical and prolonged swimming performance

All fish showed rheotaxis when placed in the flume and swam against the current for the entire 5 min acclimation period. Maccullochella macquariensis and M. peelli
swam along the bottom, whereas the other species swam mostly in mid-water. Critical swimming speeds increased with age, size and development stage for all species (Figures 4.1 and 4.2). Metalarvae were able to swim against the fastest currents, with $U_{crit}$ ranging from 25.4-46.4 cm s$^{-1}$ and 23.3-44.6 $L_b$ s$^{-1}$ ($B. bidyanus$ and $M. macquariensis$, respectively), at sizes from 10.3-14.6 mm $L_s$ ($M. peelii$ and $Hypseleotris spp$, respectively). $Maccullochella macquariensis$ metalarvae were the fastest swimming larvae (max. 46.4 cm s$^{-1}$, 44.6 $L_b$ s$^{-1}$) while $B. bidyanus$ prefexion larvae were the slowest (min. 0.1 cm s$^{-1}$, 0.3 $L_b$ s$^{-1}$). The largest swimming larva was a $Hypseleotris spp$ metalarva (14.6 mm) and the smallest was a $B. bidyanus$ prefexion larva (4.7 mm). $Macquaria ambiguca$ metalarvae were the oldest larvae used in swimming trails (25 DAH) and $M. macquariensis$, $M. peelii$ and $B. bidyanus$ prefexion larvae were the youngest (3 DAH).

Generally, AIC indicated that developmental stage was overall the factor that best explained swimming performance for average and best performers (top 25%) (Table 4.3). Developmental stage best explained swimming performance for $M. peelii$ (AIC 747.96, 116, $P<0.001$), $B. bidyanus$ (AIC 655.90, 138, $P<0.001$), and $M. macquariensis$ (AIC 851.84, 133, $P<0.001$) and, alone, this factor explained 68% and 55% of the variance in swimming performance of $M. peelii$ and $B. bidyanus$, respectively. Variability in the critical swimming speed ($U_{crit}$, measured as cm s$^{-1}$) of $M. macquariensis$ was best explained by size, age and developmental stage ($R^2=0.69$). The only species not to include developmental stage as the best explainer of swimming speed was $M. ambiguca$ (AIC 908.93, 151, $P<0.001$), for which length was preeminent ($R^2=0.58$). Developmental stage was also included in all GLMs explaining the swimming speed of the best performers. Models using only
developmental stage explained the most variance in swimming speed of *M. peelii* (AIC 156.50, 34, \(P<0.001\)), *B. bidyanus* (AIC 193.52, 34, \(P<0.001\)) and *M. macquariensis* (AIC 208.39, 34, \(P<0.001\)) (\(R^2=0.96, 0.67, \text{ and } 0.78\), respectively), but the variance in swimming speed of larval *Macquaria ambigua* best performers (AIC 212.91, 38, \(P<0.001\)) was significantly better when length and stage (\(R^2=0.88\)) were included as predictors of swimming ability.
Figure 4.1: Age (days after hatch) and length (mm) for the larvae of a) *Maccullochella macquariensis* b) *Maccullochella peelii* c) *Macquaria ambiguа* and d) *Bidyanus bidyanus*.
Figure 4.2: Ontogeny of swimming speed ($U_{\text{crit}}$ cm s$^{-1}$) of four species a) *Maccullochella macquariensis* b) *Maccullochella peelii* c) *Macquaria ambiguа* and d) *Bidyanus bidyanus* at the preflexion (open diamonds) flexion (closed square) post flexion (grey triangles) and metalarvae (open circles) development stage.
Table 4.3: GLM relationship between growth characteristic \([L_s\) (standard length), DAH (days after hatch) and developmental stage described as; Pre (preflexion), Flex (flexion) Post (postflexion) and Meta (metalarvae)] and swimming performance \((U_{crit}\) in cm s\(^{-1}\)) for all larvae and only best performers, with \(n. Hypseleotris\) spp. and \(M. fluviatilis\) include only metalarvae developmental stage (see methods).

<table>
<thead>
<tr>
<th>Species</th>
<th>(R^2)</th>
<th>(n)</th>
<th>Critical speed (cm s(^{-1})) for all larvae</th>
<th>(R^2)</th>
<th>(n)</th>
<th>Critical speed (cm s(^{-1})) for best performers</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Macullochella macquariensis</em></td>
<td>0.69</td>
<td>139</td>
<td>(25\cdot2926\ L_s - 1\cdot5642\ DAH - 0\cdot1713\ Pre) (25\cdot2926\ L_s - 1\cdot5642\ DAH + (6\cdot0625 - 0\cdot1713)\ Flex) (25\cdot2926\ L_s - 1\cdot5642\ DAH + (11\cdot0640 - 0\cdot1713)\ Post) (25\cdot2926\ L_s - 1\cdot5642\ DAH + (31\cdot3128 - 0\cdot1713)\ Meta)</td>
<td>0.78</td>
<td>38</td>
<td>23\cdot0327 Pre (23\cdot0327 + 1\cdot4756\ Flex) (23\cdot0327 + 1\cdot4827\ Post) (23\cdot0327 + 16\cdot9357\ Meta)</td>
</tr>
<tr>
<td><em>Macullochella peelii</em></td>
<td>0.68</td>
<td>120</td>
<td>(11\cdot4748\ Pre) (11\cdot4748 + 8\cdot4248\ Flex) (11\cdot4748 + 17\cdot3623\ Post) (11\cdot4748 + 19\cdot4147\ Meta)</td>
<td>0.96</td>
<td>38</td>
<td>16\cdot3156 Pre (16\cdot3156 + 8\cdot6769\ Flex) (16\cdot3156 + 20\cdot1176\ Post) (16\cdot3156 + 20\cdot8244\ Meta)</td>
</tr>
<tr>
<td><em>Macquaria ambigua</em></td>
<td>0.58</td>
<td>150</td>
<td>(28\cdot799\ L_s - 12\cdot849)</td>
<td>0.88</td>
<td>43</td>
<td>21\cdot43 L_s - 2\cdot505 Pre (21\cdot43 L_s + (2\cdot421 - 2\cdot505)\ Flex) (21\cdot43 L_s + (5\cdot922 - 2\cdot505)\ Post) (21\cdot43 L_s + (12\cdot770 - 2\cdot505)\ Meta)</td>
</tr>
<tr>
<td><em>Bidyanus bidyanus</em></td>
<td>0.55</td>
<td>142</td>
<td>(0\cdot8061\ Pre) (0\cdot8061 + 1\cdot5289\ Flex) (0\cdot8061 + 1\cdot2041\ Post) (0\cdot8061 + 7\cdot3541\ Meta)</td>
<td>0.67</td>
<td>36</td>
<td>1\cdot849 Pre (1\cdot849 + 2\cdot565\ Flex) (1\cdot849 + 2\cdot593\ Post) (1\cdot849 + 12\cdot204\ Meta)</td>
</tr>
<tr>
<td><em>Hypseleotris spp.</em></td>
<td>0.24</td>
<td>54</td>
<td>(37\cdot488\ L_s - 29\cdot254)</td>
<td>0.75</td>
<td>10</td>
<td>52\cdot771 L_s - 40\cdot3</td>
</tr>
<tr>
<td><em>Melanotaenia fluviatilis</em></td>
<td>0.38</td>
<td>36</td>
<td>(52\cdot324\ L_s - 38\cdot404)</td>
<td>0.50</td>
<td>6</td>
<td>5\cdot261 L_s - 35\cdot753</td>
</tr>
</tbody>
</table>
4.3.2 Ontogeny in swimming performance

For *Maccullochella macquariensis*, *M. peelii*, *Macquaria ambigua* and *B. bidyanus*, critical swimming speeds differed among the four developmental stages (Kruskal-Wallis, 3, \( P < 0.001 \)) (Table 4.4, Figure 4.3). *Maccullochella macquariensis*, *M. peelii* and *B. bidyanus* each had two sequential developmental stages that did not vary significantly from each other in swimming performance, but the stages for which this occurred were not consistent. There was no significant increase in swimming performance of *M. macquariensis* and *B. bidyanus* larvae between the flexion and postflexion stages and for *M. peelii* between the postflexion and metalarvae stage. *Macquaria ambigua* larvae showed a significant difference in the critical swimming speed among all developmental stages (Figure 4.3).

Critical swimming speeds differed among the four developmental stages for best performers in a similar pattern to that of all individuals (Kruskal-Wallis, 3, \( P < 0.001 \)) (Table 4.4, Figure 4.3). The exceptions were that there were no significant differences in the swimming speeds between preflexion and flexion *M. ambigua* (\( P < 0.066 \)) and best performing *M. macquariensis* larvae showed no difference among the preflexion, flexion and postflexion development stages for \( U_{crit} \).
Table 4.4: Within species Mann-Whitney U-tests results of all and best performers $U_{crit}$ as cm s$^{-1}$ and $L_b$ s$^{-1}$ for the developmental stages of the four species studied, grouped by species; Bonferroni correction meant that only for $P<0.001$, were tests significant, *** $P<0.001$, # no significance in $L_b$ s$^{-1}$ comparisons at the $P<0.001$ level, ^ significance in $L_b$ s$^{-1}$ at the $P<0.001$ level but not for cm s$^{-1}$.

<table>
<thead>
<tr>
<th>Ontogeny</th>
<th>Macullochella macquariensis</th>
<th>Macullochella peelli</th>
<th>Macquaria ambigua</th>
<th>Bidyanus bidyanus</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Flex</td>
<td>Post</td>
<td>Meta</td>
<td>Flex</td>
</tr>
<tr>
<td>All performers</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Preflexion</td>
<td>439·5*** 479·5***</td>
<td>3·0***</td>
<td>80·0*** 25·0*** 600·0***</td>
<td>209·0*** 270·5*** 70·0***</td>
</tr>
<tr>
<td>Flexion</td>
<td>430</td>
<td>12·0***</td>
<td>93·5*** 600·0***</td>
<td>245·5 69·5***</td>
</tr>
<tr>
<td>Postflexion</td>
<td>870·0***</td>
<td>358</td>
<td>241·0***</td>
<td>3·0***</td>
</tr>
<tr>
<td>Best performers</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Preflexion</td>
<td>43</td>
<td>52</td>
<td>76·0*** 108·0*** 81·0***</td>
<td>125·0 8·0*** 180·0***</td>
</tr>
<tr>
<td>Flexion</td>
<td>30·5</td>
<td>64·0***</td>
<td>96·0*** 108·0***</td>
<td>10 50·0***</td>
</tr>
<tr>
<td>Postflexion</td>
<td>64·0***</td>
<td>33</td>
<td>100·0***</td>
<td>56·0***</td>
</tr>
</tbody>
</table>
Figure 4.3: Box plots (median, range, 1st quartile and 3rd quartile) for $U_{crit}$ (cm $s^{-1}$, $L_b$ $s^{-1}$) and $L_s$ (mm) for all larvae of six species and four developmental stages; preflexion (Pre), flex (Flexion), postflexion (Post) and metalarvae (Meta) for a) *Maccullochella macquariensis* b) *Maccullochella peelii* c) *Macquaria ambigua* d) *Bidyanus bidyanus* e) *Hypseleotris* spp. and f) *Melanotaenia fluviatilis*, with $n$ above x-axis.Only metalarvae were available for *Hypseleotris* spp. and *Melanotaenia fluviatilis*, and age was not known for these species (see methods). Numbers above the x-axis are $n$. 
4.3.3 Comparisons of critical speed of average and best performers among species

Comparisons of average and best performer critical swimming speeds for all life stages were made for *M. peelii*, *M. macquariensis*, *M. ambigua* and *B. bidyanus*, but only the metalarval stage was included for all six species (Table 4.5, Figure 4.4). Results indicated that there were almost always significant differences among all species within a life stage. In most cases, *M. macquariensis* and *M. peelii* had the highest average and best performer critical swimming speed of all species. However, although the speeds for *M. macquariensis* were initially similar or greater than *M. peelii*, swimming speeds for *M. peelii* postflexion larvae were significantly greater than *M. macquariensis* larvae at the same stage and reached similar levels to those of metalarvae. The next fastest swimmers were *Macquaria ambigua*, with *B. bidyanus* being the poorest swimmers overall. *Macquaria ambigua*, *Hypseleotris spp* and *Melanotaenia fluviatilis* metalarvae had similar swimming speeds, but these were significantly slower than for *Maccullochella macquariensis* and *M. peelii*.

Generally, critical swimming speed of the best performers (top 25%) of all species was considerably greater than for all larvae, at any given developmental stage (0.91-22.15 cm s\(^{-1}\) or 1.60-16.61 \(L_b\) s\(^{-1}\)) (Figures 4.3 and 4.4). The difference between all and best performers was least for *B. bidyanus* (0.91 cm s\(^{-1}\), 1.06 \(L_b\) s\(^{-1}\)). The greatest contrast was for *Hypseleotris spp* metalarvae best performers whose \(U_{\text{crit}}\) was 22.15 cm s\(^{-1}\) and 16.61 \(L_b\) s\(^{-1}\) faster than all larvae. Although *Hypseleotris spp*, *Macquaria ambigua* and *Melanotaenia fluviatilis* had similar swimming speeds, *Hypseleotris spp* had faster best performing swimmers than *Macquaria ambigua* and *Melanotaenia fluviatilis*. 
Table 4.5: Among species Mann-Whitney U-tests results of all and best performers for $U_{crit}$ as cm s$^{-1}$ and $L_b$ s$^{-1}$ for the six species studied:
Maccullochella peeli (Mp), Macquaria ambigua (Ma), Bidyanus bidyanus (Bb), Hypseleotris spp. (H) and Melanotaenia fluviatilis (Mf), grouped by developmental stage; Bonferroni correction meant that only for $P<0.0007$, were tests significant, ***$P<0.0007$, #no significance in $L_b$ s$^{-1}$ comparisons at the $P<0.0007$ level, ^significance in $L_b$ s$^{-1}$ at the $P<0.0007$ level but not for cm s$^{-1}$. Hypseleotris spp. and Melanotaenia fluviatilis were swum only at the metalarvae developmental stage (see methods).

<table>
<thead>
<tr>
<th>Species</th>
<th>Preflexion</th>
<th>Flexion</th>
<th>Postflexion</th>
<th>Metalarvae</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mp</td>
<td>Ma</td>
<td>Bb</td>
<td>Mp</td>
</tr>
<tr>
<td>All performers</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maccullochella macquariensis</td>
<td>521·0</td>
<td>229·0***</td>
<td>1479·0***</td>
<td>399·0***</td>
</tr>
<tr>
<td>Maccullochella peeli</td>
<td>153·0***</td>
<td>870·0***</td>
<td>15·0***</td>
<td>1620·0***</td>
</tr>
<tr>
<td>Macquaria ambigua</td>
<td>320·0***</td>
<td>73·0***</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bidyanus bidyanus</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hypseleotris spp.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Best performers</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maccullochella macquariensis</td>
<td>5·0***</td>
<td>216·0***</td>
<td>96·0***</td>
<td>28·5</td>
</tr>
<tr>
<td>Maccullochella peeli</td>
<td>11·5***</td>
<td>56·0***</td>
<td>60·0***</td>
<td>180·0***</td>
</tr>
<tr>
<td>Macquaria ambigua</td>
<td>144·0***</td>
<td>75·0***</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bidyanus bidyanus</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hypseleotris spp.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 4.4: Box plots (median, range, 1st quartile and 3rd quartile) for $U_{crit}$ (cm s$^{-1}$, $L_b$ s$^{-1}$) and $L_s$ (mm) for the best performers of six species and four developmental stages; preflexion (Pre), flex (Flexion), postflexion (Post) and metalarvae (Meta) for a) *Macullochella macquariensis* b) *Macullochella peelii* c) *Macquaria ambigu* d) *Bidyanus bidyanus* e) *Hypseleotris spp.* and f) *Melanotaenia fluviatilis*, with $n$ above x-axis. Only metalarvae were available for *Hypseleotris spp.* and *Melanotaenia fluviatilis*, and age was not known for these species (see methods). Numbers above the x-axis are $n$. 
4.3.4 Comparisons among life history strategies

There was a significant difference in average and best performer critical swimming speeds of metalarvae among almost all of the three life history strategies (Figure 4.5, Table 4.6). Only Strategy 2 and 3 metalarvae showed similar values and a non-significant difference. Of the three life history strategies, the fastest metalarvae were from Strategy 1 (25.3-46.4 cm s\(^{-1}\), 23\(\cdot\)8-44\(\cdot\)6 \(L_b\) s\(^{-1}\)), more than twice as fast as the average of Strategy 2 metalarvae (6\(\cdot\)0-26\(\cdot\)4 cm s\(^{-1}\), 5\(\cdot\)3-27\(\cdot\)9 \(L_b\) s\(^{-1}\)), the slowest life history strategy. The critical swimming speeds of Strategy 3 fish were intermediate between Strategy 1 and 2 fish.

4.3.5 Prolonged swimming

Overall, *M. macquariensis* had the highest prolonged swimming speeds, and *B. bidyanus* had the lowest prolonged swimming speeds, of all species tested (Table 4.7). Indeed, metalarval *M. macquariensis* could swim for >60 min at 44% of the mean critical speed. Preflexion, flexion and postflexion *B. bidyanus*, on the other hand, could not swim at any speed for >60 min. Generally the two cod species were able to swim at least 30% of the mean critical speed for >60 min, whereas for the two perch species, either prolonged swimming performance was variable among developmental stages or uniformly poor.
Figure 4.5: Box plots (median, range, 1st quartile and 3rd quartile) for metalarvae of three life history strategies for $U_{crit}$ (cm s$^{-1}$, $L_b$ s$^{-1}$) and $L_s$ (mm) for a) all larvae and b) best performers. Numbers above the x-axis are $n$. 
Table 4.6: Mann-Whitney U-tests results of all and best performers for $U_{crit}$ as cm s$^{-1}$ and $L_b$ s$^{-1}$ for the three life history strategies (LHS) studied: S1 (LHS 1), S2 (LHS 2) and S3 (LHS 3); Bonferroni correction meant that only for $P<0.008$, were tests significant, *** $P<0.008$, #no significance in $L_b$ s$^{-1}$ comparisons at the $P<0.008$ level.

<table>
<thead>
<tr>
<th>LHS</th>
<th>S2</th>
<th>S3</th>
<th>S2</th>
<th>S3</th>
</tr>
</thead>
<tbody>
<tr>
<td>S1</td>
<td>59·0***</td>
<td>237·0***</td>
<td>0·0***</td>
<td>13·0***</td>
</tr>
<tr>
<td>S2</td>
<td>1291·5</td>
<td></td>
<td>79·0***#</td>
<td></td>
</tr>
</tbody>
</table>

Table 4.7: Prolonged swimming performance speed (cm s$^{-1}$) at which more than 75% of larvae completed the 60 min swimming trial, with percent of the prolonged swimming speed compared to the mean $U_{crit}$ in brackets.

<table>
<thead>
<tr>
<th></th>
<th>Preflexion</th>
<th>Flexion</th>
<th>Postflexion</th>
<th>Metalarvae</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Maccullochella macquariensis</em></td>
<td>5·9 (26%)</td>
<td>5·9 (32%)</td>
<td>5·9 (32%)</td>
<td>15·4 (23%)</td>
</tr>
<tr>
<td><em>Maccullochella peelii</em></td>
<td>1·1 (10%)</td>
<td>5·9 (34%)</td>
<td>10·7 (27%)</td>
<td>10·7 (29%)</td>
</tr>
<tr>
<td><em>Macquaria ambiguа</em></td>
<td>1·1 (3%)</td>
<td>1·1 (10%)</td>
<td>1·1 (10%)</td>
<td>5·9 (32%)</td>
</tr>
<tr>
<td><em>Bidyanus bidyanus</em></td>
<td>0 (0%)</td>
<td>0 (0%)</td>
<td>0 (0%)</td>
<td>1·1 (8%)</td>
</tr>
</tbody>
</table>
4.4 Discussion

4.4.1 Comparisons of swimming performance of Murray-Darling Basin with other freshwater fishes

This is the first study to determine the critical and prolonged swimming speeds of the larvae of Australian riverine fishes, which means that comparisons with other Australian species is not possible. There are also few studies elsewhere in the world that have tested the swimming performance of larvae of comparable sizes to those included in the present chapter (Wolter and Arlinghaus, 2003). The six species, which included preflexion larvae to metalarvae (4.7 to 14.6 mm), had $U_{crit}$ (swam <60 minutes) values between 0.1 cm s$^{-1}$ or 0.3 $L_b$ s$^{-1}$ ($B. bidyanus$ preflexion) and 46.4 cm s$^{-1}$ or 44.6 $L_b$ s$^{-1}$ ($M. macquariensis$ metalarvae) and prolonged swimming (swam >60 minutes) values between 0 cm s$^{-1}$ or 0 $L_b$ s$^{-1}$ ($B. bidyanus$ preflexion, flexion and postflexion) and 15.6 cm s$^{-1}$ or 20.1 $L_b$ s$^{-1}$ ($M. macquariensis$ metalarvae). Of those studies which have tested larvae of comparable sizes and under comparable conditions, walleye $Stizostedion vitreum$ (Mitchill) ($L_s$ 10.5 mm, 13 °C) and yellow perch $Perca flavescens$ (Mitchill)($L_s$ 10.5 mm, 13 °C) swam at a mean $U_{crit}$ of 3.2 cm s$^{-1}$ for 10 min (Houde, 1969), European chub $Leuciscus cephalus$ (Linnaeus), dace $Leuciscus leuciscus$ (Linnaeus) and roach $Rutilus rutilus$ (Linnaeus) swam at $U_{crit}$ of 10.5, 20.9 and 11.26 cm s$^{-1}$ (8-22 °C, $U_{crit}$ derived from equations for $L_s$ 10 mm), respectively, for 3 min (Cowx and Welcomme, 1998, Garner, 1999) and Danube bleak $Alburnus chalcoides$, (Güldenstädt)($L_s$ 9 mm, 15-20 °C) swam at a mean $U_{crit}$ of 6.3-7.8 cm s$^{-1}$ (Wieser and Kaufmann, 1998). $Maccullochella macquariensis$ and $M. peelii$ larvae had faster mean $U_{crit}$ than the larvae of all of those species above. $Macquaria ambigu$ larvae had faster mean $U_{crit}$ than all species except $L. leuciscus$. 
and *B. bidyanus* larvae, the poorest swimmer, had faster mean \( U_{crit} \) than the larvae of *S. vitreum* and *P. flavescens*, but slower than the remaining.

### 4.4.2 Ontogeny and swimming performance

Critical speed increased with ontogeny for the larvae of species investigated in the present chapter, which agrees with trends found for other fishes (Wieser and Kaufmann, 1998, Garner, 1999, Fisher et al., 2000, Clark et al., 2005). Swimming performance was best explained by developmental stage for the majority of species, except *M. ambiguа*, for which length was the best explanatory variable. In general, age did not explain variation in swimming performance well. Whilst developmental stage is related to body length, there is considerable overlap in length for larvae at different stages, and it was apparent that transitions from one stage to the next influenced a larva’s swimming performance more than simply increase in length. Even though variation in length at age was higher in the two species that had larvae from more than one cohort (*B. bidyanus* and *M. ambiguа*) than the other species, this reinforces the findings that developmental stage is a better predictor of swimming performance. Yolk sac absorption was not uniform over time within species and may influence swimming ability because of drag. *Precocial* life history *Strategy I* fish, *M. macquariensis* and *M. peelii*, retain their yolk sacks longer than any of the other species in this chapter, and indeed still had vestiges of yolk throughout the trials. While the effects of yolk sac size on swimming performance was not measured in the current chapter, and is not commonly reported in similar experiments, it warrants further investigation in future research. Since larvae were used in only one trial, there is no effect of individual growth rate on results. Clark et al. (2005) also found that for the larvae of four species of temperate marine fishes, endurance swimming
performance increased after notochord flexion. However, many studies use only length to explain larval swimming performance (Houde, 1969, Wieser and Kaufmann, 1998, Garner, 1999, Wolter and Arlinghaus, 2003), which runs counter to what is known of patterns of ontogenesis in fishes. Balon (1986b) describes morphological and physiological changes during ontogeny as ‘bursts and intermissions’ or saltatory growth and development. Whilst rates of change during ontogeny remain an area of debate, and some contend that development is gradual (Fuiman and Werner, 2002), the consensus seems to be that there is constant development, interspersed with periods of more rapid change (Kamler, 2002). As a result, changes in performance through development are not a continuum of gradual improvements, but stepwise changes, as reflected in larvae development, and as demonstrated in this chapter.

Most species in the present chapter showed an ‘intermission’ in swimming performance - e.g. between flexion and postflexion in Maccullochella macquariensis - and only Macquaria ambigua showed consistent improved swimming performance through all developmental stages. Nevertheless, for each species, the overall improvement throughout ontogeny indicated little change between stages, but instead ‘bursts’ in performance associated with changes in morphology. While larvae grow, the notochord flexes, and, at the same time, fin ray development starts. These morphological changes provide support and an anchor point for developing muscle, increasing swimming capability of larvae (Webb, 1975).

Swimming performance increases predominately during the metalarval development stage for M. ambigua and B. bidyanus, when all fins are most developed. This may fit
the *altricial* life history strategy, *Strategy 2*, of broadcast spawners that require increased swimming performance at the end of larval development, when larvae are about to settle out of the pelagic drifting stage into habitat to transition to the juvenile life stage. *Maccullochella macquariensis* show the biggest increase in swimming performance at the metalarval stage, whereas *M. peelii* have the greatest increase between the flexion and postflexion stage. It would make sense for these species to have the biggest increase in swimming performance between parental care in the nest and entering the drift, since drifting is a targeted, purposeful event to disperse downstream, in contrast to the broadcast spawning strategy of *altricial* life history *Strategy 2* *M. ambigua* and *B. bidyanus* (Humphries et al., 1999). A burst in swimming performance during the metalarval stage of *M. macquariensis* larvae may be due to conditions in which larvae are found. They tend to occupy more upland stream habitat than do *M. peelii*, and the faster current velocities, cooler water and lower densities of food may make it advantageous to drift at a later, more developed stage (Harris and Rowland, 1996).

### 4.4.3 Life history strategies and swimming performance

The swimming performance of all species are consistent with what would be predicted by life history theory, which has correlates for other groups, such as salmonids in the northern hemisphere (Patterson et al., 2004, Eliason et al., 2011). A conceptual model was developed to link life history, swimming performance and dispersal patterns in riverine fishes, using species swum in this chapter as models (Figure 4.6). It must be borne in mind, however, that *M. macquariensis* and *M. peelii* share a similar life history strategy and are related phylogenetically, and so confound the comparison somewhat. These *Strategy 1* species (sensu Humphries et al., 1999),
can be classified as *precocial* (sensu Balon, 1986b) or *equilibrium* (sensu Winemiller and Rose, 1992) species. The larvae are well-developed at hatch, undergo parental care for a considerable period, and begin to disperse as relatively large larvae, with large pectoral fins and usually some development of the second dorsal and caudal fins (Cadwallader et al., 1979, Ingram and Rimmer, 1992, Humphries et al., 1999, Humphries, 2005, Koehn and Harrington, 2006). The critical swimming speeds of the metalarvae of *M. macquariensis* and *M. peelii*, *Strategy 1* species, suggest that larvae could influence their position in the river during downstream dispersal migration (Figure 4.6a). Certainly, *M. macquariensis* and *M. peelii* larvae are capable of swimming within slow-moving littoral zones in the Murray-Darling Basin and using main channels to drift between slow-water habitats (Humphries et al., 2005).

*Maccullochella macquariensis* and *M. peelii* undergo parental care during the free embryo stage, and the commencement of exogenous feeding is coincident with pectoral fin functionality and drifting behaviour. Delayed hatching, resulting in well developed larvae, is a common strategy of some demersal-spawning reef fishes, which allows for better swimming ability and more developed sensory systems, therefore enhancing retention and survival (Barlow, 1981, Hickford and Schiel, 2003, Jones et al., 2005).

Murray-Darling Basin life history *Strategy 2* fish (sensu Humphries et al., 1999) have *altricial* ontogenies (sensu Balon, 1986b) and are *periodic* species (sensu Winemiller and Rose, 1992), that enter the drift as fertilised eggs, have relatively under-developed planktonic free embryos at hatch, have limited swimming capabilities when drifting and have no parental care (Lake, 1967). The swimming performances of the free embryos and larvae of *M. ambigua* and *B. bidyanus* larvae were the
poorest of all the species in the present chapter, which indicates limited ability to swim against currents or influence dispersal in rivers (Figure 4.6b). They are considered pelagic-spawning, flood recruitment specialists (Lake, 1967, Harris and Gehrke, 1994, Schiller and Harris, 2001), although this may be region-specific (see King et al., 2009, Mallen-Cooper and Stuart, 2003, Balcombe et al., 2006). However, if these species do indeed - or historically, more commonly - spawn in response to high flows and flooding, pelagic spawning of large numbers of eggs and limited swimming capabilities of free embryos and larvae would mean that young would be distributed widely within the main channel and across the floodplain. Widespread dispersal may provide an advantage in that it scatters young across a diversity of habitat patches, with the high probability of some of these being favourable for survival and recruitment. Strategy 2 and the saltatory ontogeny of *M. ambigua* and *B. bidyanus* are similar to marine pelagic spawning fishes, where recruitment success has been related to broad-scale, long term environmental variables (Lasker, 1981, Borja et al., 2002). For this strategy to be successful, however, presumably there would have to be rapid improvement in swimming performance in post-larval fishes, so that fish could leave floodplain habitats before they dry or, if in the main channel, move between habitat patches of varying quality at smaller spatial scales (Lyon et al., 2008).

Life history Strategy 3 fish (sensu Humphries et al., 1999) have *altricial* ontogeny (sensu Balon, 1986b) and are *opportunistic* species (sensu Winemiller and Rose, 1992), that have small, poorly-developed free embryos at hatch, have limited swimming capabilities and no parental care (Humphries et al., 1999). Swimming performances of the metalarvae of Strategy 3 species, *Hypseleotris spp* and
*Melanotaenia fluviatilis*, were similar to that of *Strategy 2* fish. Opportunists can take advantage of a range of conditions in which to spawn and recruit and may be successful colonizers, especially in areas subjected to frequent and intense disturbance (Winemiller, 2005). The free embryos and larvae of *M. fluviatilis* and *Hypseleotris spp* are small and not known to disperse by drifting (Figure 4.6c). These species are considered low-flow specialists (Humphries et al., 1999) with spawning typically taking place during the summer, low-flow period. Furthermore, eggs and early life stages of these species typically occupy slackwater habitats, where they encounter rich food resources, avoid fast currents that might displace them, and presumably get protection from large-bodied predators (King, 2004)(Chapter 3). Females can lay several batches of eggs in one day or breeding season, spreading 100’s to 1000’s of eggs over several habitat patches, therefore potentially further increasing survival and recruitment. While it is important to understand the critical and prolonged swimming performance of larval fish, an obvious question to ask to further our understanding of swimming ability is: how do laboratory based swimming ability results translate to *in situ* conditions? In other words, can larvae that are capable of swimming and influencing their position, affect dispersal? This will the topic of Chapter 5, which will examine the dispersal capabilities of the larvae of two species of native fish with contrasting life history strategies.
Figure 4.6: Schematic representing hypothesized dispersal pathways for larvae of the three life history strategies used in this chapter based on swimming performance. Life history Strategy 1 species spawn at predictable times each year, larvae swim strongly and likely are able to determine their dispersal pathways into and out of slackwater habitats, as they move downstream and perhaps even move upstream. Life history Strategy 2 species may spawn in response to flow changes, including flooding, larvae swim weakly and are likely to have passive downstream dispersal, largely determined by stream flow, and may disperse during high flows into floodplain habitats. Life history 3 species spawn during low flow periods, larvae do not disperse by drifting, but colonise local patches of slow moving or slackwater habitats and may move between them.
Chapter 5: The dispersal of experimentally released larvae of riverine fishes with contrasting life history strategies

5.1 Introduction

The dispersal of the eggs, free embryos and larvae in river currents, or drift, is a feature of the early life history of many riverine fish species (Brown and Armstrong, 1985, Pavlov, 1994, Dudley and Platania, 2007). Downstream dispersal is thought to enhance survival, growth and sustainability of populations and promote gene mixing (Fuiman, 2002, Houde, 2002, Fuiman and Cowan, 2003, Pavlov, 1994). Fish larvae typically disperse from breeding grounds to nursery areas, presumably to settle and grow in favourable environmental conditions (Keckeis et al., 1997, Schiemer et al., 2003) and to avoid competition and cannibalism at spawning sites (Humphries, 2005). Since dispersing larvae are at a young, relatively vulnerable stage, they experience high rates of mortality (Harvey, 1987, Reichard et al., 2002).

Dispersal of free embryos and larvae downstream has been categorised as passive (unorientated), active (orientated downstream), or active/passive (orientated upstream), depending on a species’ life history strategy and stage of development (Pavlov, 1994, Reichard and Jurajda, 2007). It is uncertain the extent to which active and/or passive dispersal affect downstream movement of riverine fish larvae, but currently, most studies on larval dispersal recognize that there is a major active component to drift (Pavlov et al., 2008, Lechner et al., 2013, Schludermann et al., 2012). Pavlov (1994) stated that larval drift consists of an active component, because all fish larvae show rheotaxis (orientation into current) (Jurajda, 1998, Reichard and Jurajda, 2007, Robinson et al., 1998), but once threshold current speeds are reached, this rheotaxis is not possible and passive dispersal occurs. Robinson et al. (1998)
argued that if larvae used only passive dispersal then they would settle in inshore, low-speed, depositional habitats with a clumped distribution, but their study found larvae to be primarily randomly distributed in low-velocity near shore habitats, and attributed this finding to larvae actively seeking out nursery habitat during downstream dispersal. However, many studies, have reported clumped distributions of larval fish in rivers (e.g. Keckeis et al., 1997), suggesting numerous models of larval dispersal are possible.

Dispersal mode is intrinsically linked to overall life history strategy. Pelagic-spawning riverine fishes, are typically periodic strategy species (Winemiller and Rose, 1992), and comprise a reproductive guild whose undeveloped eggs and free embryos, with little yolk reserves, drift downstream for several days until they attain a free-swimming larval phase (Battle and Sprules, 1960, Balon, 1975, Araujo-Lima, 1994, Platania and Altenbach, 1998). Periodic species may spawn during elevated flows, when drifting early life stages would be transported downstream passively (Moore, 1944, Taylor and Miller, 1990, Platania and Altenbach, 1998), and it is hypothesized that they will settle out in a variety of habitats, much as passive particles would and, therefore, the rate of larvae passing through the reach will be similar to passive particles. In contrast, the larvae of equilibrium strategy species (Winemiller and Rose, 1992) are typically well developed, with larger amounts, or greater density, of yolk as free embryos, and so it is hypothesized that, because of substantial energy reserves and relatively good swimming ability, they can have relatively greater influence on their dispersal and settlement and may settle out in a variety of nursery habitats in greater densities to passive particles and, therefore, the
rate of larvae passing through the reach will be less than passive particles (e.g. Kaminskas, 2011).

Most research on dispersal of the early life stages of fishes focuses on environmental variables related to downstream movement, such as flow regime, current velocity, shear stress and turbulence (Korman et al., 2004, Reichard et al., 2004, Zitek et al., 2004, Wolter and Sukhodolov, 2008, Ellien et al., 2004, James et al., 2002, Speirs and Gurney, 2001), but the patterns, drivers and role of active/passive movement on larval dispersal are not well understood (Reichard and Jurajda, 2007, Reichard et al., 2004, Sonny et al., 2006). Gaps in the understanding of larval dispersal should deal with the questions of why larvae enter the drift and what larvae do once they are in the drift. Specifically, there is a need to understand the effects of larval swimming behaviour on active or passive dispersal or a combination of both. We also need to know more about the relationship among ontogeny, swimming ability, and swimming behaviour for different species (Reichard and Jurajda, 2007, Reichard et al., 2004, Sonny et al., 2006). Laboratory-based swimming trials are commonly used to determine larvae dispersal capabilities (Wolter and Arlinghaus, 2003, Wolter and Sukhodolov, 2008, Schludermann et al., 2012), but in situ dispersal capabilities may be quite different from those under controlled conditions. Knowing the critical threshold velocity and prolonged swimming performance results from Chapter 4 provides the opportunity to investigate in situ dispersal capabilities of fish larvae of species with different swimming abilities in lowland rivers, and to assess the implications of this for the ecology of these species in the Murray-Darling Basin.
The overall aim of this chapter, therefore, is to investigate dispersal of riverine fish free embryos and larvae through experimental releases of individuals from a species representing periodic (poor swimmers) and a species representing equilibrium (good swimmers) life history strategies in a small, lowland stream – the Murrumbidgee River anabranch, Old Man Creek. The specific aims of this chapter are to: (1) compare the time taken to drift through a river reach for larvae of species representing periodic and equilibrium life history strategies, and for passive particles; (2) determine the proportion of larvae of each group and of passive particles retained within the reach; and (3) to discuss the role of active-passive dispersal within a small stream.

5.2 Materials and methods

5.2.1 Study site

The study site was located in Old Man Creek, an anabranch, of the Murrumbidgee River in Southern New South Wales, Australia (Figure 5.1). The Murrumbidgee River has a system of well developed floodplains, billabongs, distributaries and anabranches, connected or in association with the main channel. The study site was a 500 m reach of the Old Man Creek anabranch, passing through agricultural land, including livestock grazing and row cropping. Old Man Creek anabranch has a fixed weir at the upstream end of the creek. The flow regime of Old Man Creek is controlled, and follows a hydrograph with peak flows in the spring and low winter flows. The average monthly discharge for Old Man Creek from 1990-2010 was 11.60 m$^3$s$^{-1}$, fluctuating from 0.00 to 86.27 m$^3$s$^{-1}$. The channels vary in width from 9.8-38.9 m, averaging 19.6 m.
Figure 5.1: (a) The Murrumbidgee River system examined in this study, showing the location of the release site on Old Man Creek within the Murray-Darling Basin, Australia and (b) the range of velocity (ms\(^{-1}\)) within the release site under 2.31 m\(^3\)s\(^{-1}\) discharge. The black square (■) represents the release point and the black circles (•) represent drift nets at 5, 50, 250 and 500 m downstream of the release point.

5.2.2 Experimental release of fish larvae and passive particles

Murray cod *Maccullochella peelii* (Mitchell) was used in this experiment to represent species with an *equilibrium* life history strategy: well-developed, large larvae that have the ability to influence their position in the river, and have the potential for active dispersal (Table 5.1). Golden perch *Macquaria ambigua* (Richardson) was used to represent species with a *periodic* life history strategy: poorly-developed, small larvae without the ability to influence their position in the river, and likely to
display passive dispersal (Table 5.1). In this Chapter ‘larvae’, will be used as the generic term for the free-swimming early life stages before juveniles.

Table 5.1: Life history strategy characteristics for species of larvae used in this experiment after Humphries et al. (1999), with comparisons to life history strategies described by Balon (1986b) and Winemiller and Rose (1992).

<table>
<thead>
<tr>
<th>Life history type</th>
<th>Murray cod (Maccullochella peeli)</th>
<th>Golden perch (Maquaria ambigua)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Life history type</td>
<td>Precocial, equilibrium</td>
<td>Altricial, periodic</td>
</tr>
<tr>
<td>Adult size and longevity</td>
<td>Large, 25+ years</td>
<td>Medium, 7-10 years</td>
</tr>
<tr>
<td>Spawning</td>
<td>Short, single spawning, same time annually</td>
<td>Single variable spawning, October to March</td>
</tr>
<tr>
<td>Eggs</td>
<td>up to 10,000s, demersal</td>
<td>100,000 semi-buoyant or planktonic</td>
</tr>
<tr>
<td>Embryo/larva parental care</td>
<td>yes</td>
<td>no</td>
</tr>
<tr>
<td>Development of larvae up to first feed</td>
<td>well developed, highly mobile</td>
<td>undeveloped, limited</td>
</tr>
</tbody>
</table>

Ten thousand Murray cod larvae were sourced from Grong Grong Fisheries in Narrandera, New South Wales, Australia. Murray cod larvae were eight days after hatch (DAH), with a mean (+ SE) length of 9.17 ± 0.01 mm and at the flexion-postflexion developmental stage, which is the stage when larvae would normally be drifting in the wild (Humphries, 2005). During the flexion-postflexion developmental stage, larvae are transitioning from endogenous to exogenous feeding and their yolk sac is conspicuous to inconspicuous, while the swim bladder is inconspicuous or absent. Their mean (+ SE) critical threshold velocity at these stages is 0.20 ± 0.008 - 0.29 ± 0.01 m.s⁻¹ (Chapter 4). Ten thousand golden perch larvae were sourced from the Narrandera Fisheries Centre, Narrandera, New South Wales, Australia. Golden perch larvae were four DAH, with a mean (+ SE) length of 4.38 ± 0.02 mm and at the preflexion-flexion developmental stage, which is the stage when larvae would
normally be drifting in the wild (Gehrke, 1991). These larvae have exogenous feeding and their swim bladders are inconspicuous or absent. Their mean (± SE) critical threshold velocity at these stages is 0.04 ± 0.004 - 0.06 ± 0.007 m.s⁻¹ (Chapter 4). Ten thousand heat-treated, coloured sunflower seeds were released simultaneously with the larvae of each species of fish. Sunflower seeds were used to represent drifting passive particles. Whilst they float, sunflower seeds provide an acceptable null model for entirely passive particles (Andersson et al., 2000, Merritt and Wohl, 2002, Groves et al., 2009). There was no substantial wind during the experiments.

Releases were conducted on 10 November 2009 for Murray cod and seeds and 17 November 2009 for golden perch and seeds and were sampled using drift nets (0.5 m diameter, 1.5 m long, and 500-μm mesh tapered, with a removable collection jar) over a three week period (10-24 November 2009), when the two species examined in this study are known to drift. A General Oceanics Inc. (FL, USA) flow meter was fixed in the mouth of each drift net to determine the volume of water filtered, therefore enabling raw catch data to be adjusted to a standard volume of filtered water (100 m³). Larvae and sunflower seeds were released mid-channel (release point) at the same time. Pairs of drift nets were set 5, 50, 250 and 500 m from the release point, except at the 500 m station, where 3 drift nets were deployed at a constricted part of the channel and represented the end of the experimental reach. One drift net was set 10 m upstream from the release point to determine if larvae were swimming upstream of the release point and to determine if larvae of either species was drifting into the experimental reach from upstream. All nets were set, and larvae and sunflower seeds were released, at 2000 h, at dusk (Appendix C). On the nights of the releases drift net samples were collected every 0.5 h until midnight and every hour
thereafter, until 0300 h, totalling 7 h. For two nights after each release, nets were set at dusk and retrieved three hours later. Sampled water depth ranged from 0.4 to 1.49 m. Larval fish samples were preserved in 95% ethanol in the field and returned to the laboratory for processing.

No golden perch larvae were collected at any time but immediately after releasing the experimental individuals and only in the experimental reach, so all larvae recaptured are presumed to have been released. However, wild and experimentally released Murray cod larvae were both collected in the experimental reach. A combination of methods was employed to determine if Murray cod larvae captured in the drift nets were from the experimental release or were hatched in situ in Old Man Creek. Hatchery larvae used for release were marked with calcein (Crook and Thurstan, 2009) to distinguish between released larvae and wild larvae. However, no mark could be found in a sample of non-released calcein-marked hatchery larvae, set aside for laboratory analysis. Consequently, calcein was not reliable in distinguishing between released and wild caught larvae in drift samples. Therefore, the presence of a yolk sac in the hatchery-reared (and experimentally-released) larvae was used as the distinguishing feature between wild caught and hatchery-reared larvae (Appendix D). This is based on the fact that larvae were collected in drift nets in Old Man Creek for six days post experimental release and all wild larvae collected during this time had no yolk sacs. Also, no larvae with yolk sacs were observed in the drift net set 10 m upstream of the release point on the night of the release, indicating no wild larvae drifting with a yolk sac. By contrast, all released hatchery larvae had yolk sacs. In addition, aging Murray cod larvae with and without yolk sacs using otolith daily increments, was attempted for age comparisons. Unfortunately, otoliths were all in
such poor condition when this was attempted, because of acidification of samples, that otoliths were unable to be used for age estimates.

Finally, if the larvae that were assumed to be experimentally released larvae, were in fact wild larvae, then their actual abundance distribution over time should show the same pattern as wild individuals. Although the abundance of wild drifting larvae does change during the night (Humphries, 2005), there is no evidence that there is an exponential decline in abundance after dusk, as is common when experimental releases of larvae are made at this time (see e.g. Schludermann et al., 2012). Therefore, all larvae, with and without yolk sac, for each time step were summed (see Appendix E). Using these 10 values as distributions, the lower and upper 95% confidence limits of this distribution were determined. Then 1000 simulations for each time step were run, choosing abundances randomly from between the 95% confidence limits, then taking a mean of these values and compared the mean, and lower and upper 95% confidence limits of the simulated abundance distribution with the actual abundances of larvae with yolk sac over time, that were hypothesized had been released. Results showed that the only overlap in recaptures of larvae with yolk sacs within the 95% confidence limits for the simulated abundance distribution was at the first sample period. Thus, the fact that (1) no wild larvae had yolk sacs that were collected upstream of the study reach on the night of the experimental release, or on subsequent nights, and (2) the fact that the actual distribution of abundances of the larvae presumed to have been released was well outside the simulated abundance distribution of all larvae collected, means that released larvae were identified correctly.
The following analyses and results are based on the assumption that one could correctly distinguished released from wild Murray cod larvae.

Sunflower seeds deposited on the banks of the 500 m reach were identified, and the location and number of seeds was recorded, the morning after the release. Sweep nets, with 250 µm mesh, were used to sample at random locations along the margins and slackwaters of the 500 m reach for two mornings after the release, and eight modified quatrefoil light traps (Floyd et al., 1984, Secor et al., 1992, Humphries et al., 2002), were set at sunset for 10 h on the two nights after the larvae release night, to try to capture any released larvae that might have settled.

Temperature, turbidity (NTU), dissolved oxygen (mg.L⁻¹), conductivity (µS.cm⁻¹) and pH were recorded with a YSI model 556 water quality monitor multiprobe each night before drift sampling started.

5.2.3 Laboratory methods

Samples were sorted under a dissecting microscope to find released seeds and identify larval fish. Fish identification was determined using Serafini and Humphries (2004). Standard length (SL) was measured to 0.1 mm using an eyepiece graticule for fish <10 mm and Vernier callipers for fish ≥10 mm.

5.2.4 Data Analysis

Drift data was standardized as number of individuals per standard volume of filtered water (100 m³). Data was log-transformed and linear mixed models (Distance and Time as random factors, Species, i.e. Murray cod, golden perch and seeds, as the fixed
factor) were carried out for each release date (Murray cod and seeds 1; golden perch and seeds 2) using the lme4 package in R. Two linear mixed models were performed for each release date, comparing the null model that did not differentiate between adjusted abundance of seeds and fish larvae with a model that did differentiate between seeds and fish larvae, using a Chi-squared test (Winter, 2013). These linear mixed models were used to test the hypothesis that larvae would move through the system in different abundances than passive particles (sunflower seeds), resulting in a significant difference between the null model (combined abundance of larvae and seeds) and the model with larvae and seeds abundances independent of one another.

All data were analysed using the R statistical package (R v2.9.0, R Development Core 2008). Adjusted abundance catch data from the 5 m nets was not included in analysis because current velocity was not fast enough for flow meters to rotate and accurately determine the volumes of filtered water. To determine the proportion of released particles moving through the reach I the number of released particles collected in all non-500 m nets were combined and subtracted the number from the release total (10,000): this determined the total potentially able to be caught in the 500 m nets. The area sampled by the 500 m drift nets to was adjusted to reflect the cross-sectional area, and to determine how many released particles would have been collected if the entire 500 m cross section was sampled. Then, the number of larvae collected in the 500 m nets was multiplied by the adjusted area sampled to reflect sampling the entire 500 m cross section. This number was divided by the total of released particles potentially able to be caught in 500 m nets and made into a proportion (%). This calculation assumes that larvae are evenly distributed across the cross section, both vertically and horizontally.
5.2.5 Hydrodynamic modelling

A hydrodynamic model was carried out for this reach as part of research for Chapter 6. This reach was modelled at a discharge of 2.31 m$^3$s$^{-1}$ and depth (m) and velocity (ms$^{-1}$) measurements presented in this chapter are based on Chapter 6 modelling and presented here to give context to the study. From the release location, water moved through the 500 m reach within or before 60 min, meaning released larvae and seeds had the potential to move out of the reach during the first two sampling times.

5.3 Results

The discharge varied from 2.42-2.60 m$^3$s$^{-1}$ during sampling, with the discharge at 2.49 m$^3$s$^{-1}$ during the release (Table 5.2). Water quality measurements were relatively stable during the two week sampling period, but overall water temperature and conductivity decreased, while dissolved oxygen and pH increased. Current velocity ranged from 0.01-0.66 ms$^{-1}$ and depth ranged from 0.04-1.61 m with the cross sections at distances with drift nets (Table 5.3). Depth and velocity profiles were similar for the release point (0), 5, 50 and 250 m cross section, whereas the 500 m cross section was shallower and had a faster current speed than the other cross sections.
Table 5.2: Daily mean discharge (ML/d), temperature (°C), Specific conductivity, dissolved oxygen (D.O.) in mg/L, pH, salinity, and turbidity (NTU) for the study reach. Add ± SE and range

<table>
<thead>
<tr>
<th>Date</th>
<th>Discharge (m$^3$s$^{-1}$)</th>
<th>Temp (°C)</th>
<th>Sp Cond</th>
<th>D.O. (mg/L)</th>
<th>pH</th>
<th>Salinity</th>
<th>Turbidity (NTU)</th>
</tr>
</thead>
<tbody>
<tr>
<td>10-Nov</td>
<td>2.49</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>11-Nov</td>
<td>2.60</td>
<td>27.20</td>
<td>0.079</td>
<td>6.66</td>
<td>8.40</td>
<td>0.04</td>
<td>104</td>
</tr>
<tr>
<td>12-Nov</td>
<td>2.60</td>
<td>24.31</td>
<td>0.077</td>
<td>6.35</td>
<td>8.16</td>
<td>0.04</td>
<td>106</td>
</tr>
<tr>
<td>17-Nov</td>
<td>2.42</td>
<td>26.51</td>
<td>0.071</td>
<td>7.00</td>
<td>8.54</td>
<td>0.04</td>
<td>107</td>
</tr>
<tr>
<td>18-Nov</td>
<td>2.48</td>
<td>24.36</td>
<td>0.072</td>
<td>7.37</td>
<td>8.65</td>
<td>0.04</td>
<td>107</td>
</tr>
<tr>
<td>19-Nov</td>
<td>2.49</td>
<td>25.93</td>
<td>0.071</td>
<td>7.27</td>
<td>8.74</td>
<td>0.04</td>
<td>120</td>
</tr>
<tr>
<td>24-Nov</td>
<td>2.55</td>
<td>24.50</td>
<td>0.066</td>
<td>7.74</td>
<td>8.77</td>
<td>0.04</td>
<td>105</td>
</tr>
</tbody>
</table>

Table 5.3: Hydromorphological characteristics of the release point (0 m) and four transects (5, 50, 250, 500 m) with drift nets.

<table>
<thead>
<tr>
<th></th>
<th>0</th>
<th>5</th>
<th>50</th>
<th>250</th>
<th>500</th>
</tr>
</thead>
<tbody>
<tr>
<td>Depth (m)</td>
<td>Velocity (m$^{-1}$)</td>
<td>Depth (m)</td>
<td>Velocity (m$^{-1}$)</td>
<td>Depth (m)</td>
<td>Velocity (m$^{-1}$)</td>
</tr>
<tr>
<td>Mean</td>
<td>0.79</td>
<td>0.08</td>
<td>0.64</td>
<td>0.08</td>
<td>1.03</td>
</tr>
<tr>
<td>Median</td>
<td>0.81</td>
<td>0.07</td>
<td>0.61</td>
<td>0.08</td>
<td>1.12</td>
</tr>
<tr>
<td>25$^{th}$ percentile</td>
<td>0.57</td>
<td>0.05</td>
<td>0.40</td>
<td>0.05</td>
<td>0.69</td>
</tr>
<tr>
<td>75$^{th}$ percentile</td>
<td>1.13</td>
<td>0.11</td>
<td>0.89</td>
<td>0.10</td>
<td>1.46</td>
</tr>
<tr>
<td>Minimum</td>
<td>0.06</td>
<td>0.01</td>
<td>0.04</td>
<td>0.02</td>
<td>0.12</td>
</tr>
<tr>
<td>Maximum</td>
<td>1.38</td>
<td>0.12</td>
<td>1.21</td>
<td>0.12</td>
<td>1.61</td>
</tr>
</tbody>
</table>
In total, the drifting larvae of five species of wild caught fish were collected over seven nights of sampling (Table 5.5). The highest abundances of Murray cod, common carp (*Cyprinus carpio*) and Australian smelt (*Retropinna semoni*) were collected on the first night of sampling, 10 November, 2009. In general, larval abundances decreased over sampling dates. Murray cod was the most common species collected, followed by common carp, Australian smelt, carp gudgeon (*Hypseleotris spp.*) and river blackfish (*Gadopsis marmoratus*). Yolk sac Murray cod larvae had a mean SL of 9.17 mm, ranging from 7.0-10.5 mm (SE ± 0.0107) and larvae without yolk sacs had a mean SL of 9.14 mm, ranging from 6.0-17.1 mm (SE ± 0.0034). No seeds from the first release, 10 November 2009, and 53 seeds from the second release, 17 November 2009, were collected on the banks within the reach the morning after their respective release dates. Sweep net and light trap samples were not included in the results, because no Murray cod or golden perch larvae were collected. Wild caught larvae have been reported in these results to show there were naturally occurring Murray cod larvae in the reach, that may confound results, but there were no wild caught golden perch larvae.

**Table 5.4:** Total raw abundance and adjusted abundance (number per 100 m$^3$) recaptures from releases of 10,000 Murray cod (*Maccullochella peeli*), golden perch (*Macquaria ambigua*), and seeds. The 5 m net results are not included (see methods).

<table>
<thead>
<tr>
<th></th>
<th>Murray cod</th>
<th>Golden perch</th>
<th>Seeds</th>
</tr>
</thead>
<tbody>
<tr>
<td>Raw abundance</td>
<td>1316</td>
<td>-</td>
<td>286</td>
</tr>
<tr>
<td>Adjusted abundance</td>
<td>1349</td>
<td>-</td>
<td>422</td>
</tr>
<tr>
<td>17-Nov 2009</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Raw abundance</td>
<td>-</td>
<td>294</td>
<td>234</td>
</tr>
<tr>
<td>Adjusted abundance</td>
<td>-</td>
<td>330</td>
<td>335</td>
</tr>
</tbody>
</table>

In all, during the first release of the 10,000 Murray cod and sunflower seeds, 1627 Murray cod (16%) and 335 seeds (3%) were recaptured with drift nets (Table 5.4).
During the second release of the 10,000 golden perch and sunflower seeds, 383 golden perch (4%) and 401 seeds (4%) were recaptured with drift nets. Murray cod larvae were collected at 4 to 5 times greater abundance than sunflower seeds and golden perch. Golden perch and both seed releases (Seeds 1 and Seeds 2) were collected with similar abundances (between 335-401 individuals or 3-4%).
Table 5.5: Total raw and adjusted abundance (number per 100 m$^3$) of the wild caught larvae of all species; Murray cod (*Maccullochella peeli peeli*), common carp (*Carpio cyprinus*), Australian smelt (*Retropinna semoni*), carp gudgeon (*Hypseleotris spp.*), and river blackfish (*Gadopsis marmoratus*), collected during drift net sampling dates. The 5 m net results are not included (see methods).

<table>
<thead>
<tr>
<th>Date</th>
<th>Murray cod</th>
<th>Common carp</th>
<th>A smelt</th>
<th>Carp gudgeon</th>
<th>River blackfish</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Raw</td>
<td>Adjusted</td>
<td>Raw</td>
<td>Adjusted</td>
<td>Raw</td>
</tr>
<tr>
<td>10-Nov</td>
<td>15689</td>
<td>11731</td>
<td>1804</td>
<td>1841</td>
<td>36</td>
</tr>
<tr>
<td>11-Nov</td>
<td>3126</td>
<td>2601</td>
<td>524</td>
<td>404</td>
<td>3</td>
</tr>
<tr>
<td>12-Nov</td>
<td>833</td>
<td>366</td>
<td>480</td>
<td>284</td>
<td>1</td>
</tr>
<tr>
<td>17-Nov</td>
<td>1291</td>
<td>914</td>
<td>860</td>
<td>583</td>
<td>24</td>
</tr>
<tr>
<td>18-Nov</td>
<td>155</td>
<td>146</td>
<td>57</td>
<td>32</td>
<td>2</td>
</tr>
<tr>
<td>19-Nov</td>
<td>130</td>
<td>89</td>
<td>55</td>
<td>21</td>
<td>0</td>
</tr>
<tr>
<td>24-Nov</td>
<td>208</td>
<td>216</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Totals</td>
<td>21432</td>
<td>16063</td>
<td>3782</td>
<td>3165</td>
<td>66</td>
</tr>
</tbody>
</table>

The 5 m net results are not included (see methods).
Recaptured larvae of both species were only found in drift nets on the day of release. Wild Murray cod larvae were collected on both release dates, but no wild golden perch were collected at any time. Ignoring distance from the release point and adjusting for multiple nets, maximum drift densities were observed in the 250 m nets in the first 30 min for both fish species and seeds (Figure 5.2). By multiplying up the area sampled at the 500 m drift nets to reflect the cross-sectional area and adjusting the number of released particles collected in all non-500 m nets by subtracting the number from the release total (10,000), it was estimated that 71% of Murray cod, 4-5% of seeds and 16% of golden perch were collected in or moving past the 500 m nets, representing the proportion of larvae moving through the reach, not settling from the drift or lost to predation (Table 5.6).
Figure 5.2: The adjusted abundance of released particles drifting through the reach: (a) distance (50m, 250m and 500m), by species (Seeds 1, Seeds 2, Murray cod and golden perch) and (b) hours after release, by species (Seeds 1, Seeds 2, Murray cod and golden perch)
Table 5.6: The proportion of released particles (Murray cod, Seeds 1, golden perch and Seeds 2) drifting through the reach, with the total number of released particles, total number of released particles caught in non-500 m nets, total number of released particles potentially able to be caught in 500 m nets, total number of released particles caught in the 500 m nets and adjusted (for cross-sectional area) total caught in the 500 m nets.

<table>
<thead>
<tr>
<th></th>
<th>Total released</th>
<th>Total caught in non-500 m nets</th>
<th>Total potentially able to be caught in 500 m nets</th>
<th>Total caught in 500 m nets</th>
<th>Adjusted total in 500 m nets for cross-sectional area</th>
<th>Proportion drifted through reach (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Murray cod</td>
<td>10000</td>
<td>774</td>
<td>9226</td>
<td>853</td>
<td>6581</td>
<td>71</td>
</tr>
<tr>
<td>Seeds 1</td>
<td>10000</td>
<td>282</td>
<td>9718</td>
<td>53</td>
<td>409</td>
<td>4</td>
</tr>
<tr>
<td>Golden perch</td>
<td>10000</td>
<td>174</td>
<td>9826</td>
<td>209</td>
<td>1612</td>
<td>16</td>
</tr>
<tr>
<td>Seeds 2</td>
<td>10000</td>
<td>341</td>
<td>9659</td>
<td>60</td>
<td>463</td>
<td>5</td>
</tr>
</tbody>
</table>

Linear models indicated that there was a significantly greater adjusted abundance of Murray cod larvae than seeds collected in the drift nets \( P<0.01 \); Figure 5.2, Table 5.7), with time and distance taken into account (Appendix F) compared to the model with combined abundance of Murray cod larvae and seeds collected in the drift. By contrast, there was no significant difference in the two models comparing combined adjusted abundance of golden perch larvae and seeds collected in the drift nets with independent abundances of golden perch larvae and seeds \( P>0.05 \).

Table 5.7: Linear mixed models testing the difference between the null model (Combined MC or GP + Seeds) with larvae and seeds differentiate between (independent MC or GP/Seeds) with AIC, Deviance, Chi squared (Chisq), degrees of freedom (DF) values and significance level for time and distance as random factors and species as a fixed factor; **\( P<0.01 \).

<table>
<thead>
<tr>
<th>Factor</th>
<th>DF</th>
<th>AIC</th>
<th>Deviance</th>
<th>Chisq</th>
</tr>
</thead>
<tbody>
<tr>
<td>Combined MC + Seeds</td>
<td>4</td>
<td>206.94</td>
<td>198.94</td>
<td></td>
</tr>
<tr>
<td>Independent MC/Seeds</td>
<td>5</td>
<td>201.83</td>
<td>191.83</td>
<td>7.1071**</td>
</tr>
<tr>
<td>Combined GP + Seeds</td>
<td>4</td>
<td>79.221</td>
<td>79.221</td>
<td></td>
</tr>
<tr>
<td>Independent GP/Seeds</td>
<td>5</td>
<td>79.189</td>
<td>79.189</td>
<td>0.0323</td>
</tr>
</tbody>
</table>

5.4 Discussion
Even though, in the present study, it was estimated that water would move through the experimental reach in Old Man Creek within 60 min, Murray cod larvae were found in drift nets up to 6 h after release, golden perch were found up to 2 h after and both seed releases were found in drift nets up to 7 h later. This likely indicates the effects of heterogeneity of the flow environment in the reach (i.e., dead zones and slow, moderate and fast currents) and, in the case of the free embryos and larvae, relative swimming ability. These are similar results to previous larval release and recapture experiments, which found that larvae were captured long after water would have moved through the reach, and indicating downstream dispersal was not entirely passive (Schludermann et al., 2012).

The means of how or why fish larvae ‘choose’ to drift or settle out in nursery or rearing habitats are not known. Results from the present experiment suggest that if larvae, such as those of Murray cod, have the ability to swim and to move within the reach, larvae can stay in the drift and actively disperse. If, on the other hand, larvae are poor swimmers, such as those of golden perch, dispersal is more likely to be passive, or at least more so. Thus it is likely that larval dispersal is not solely a passive process, but has an active component, influenced by swimming ability, which in turn is related to life history strategy. Murray cod larvae (equilibrium life history strategy) are better swimmers (Chapter 4), and more individuals, an estimated 71% of larvae released (assuming even spread through the cross section of Old Man Creek), reached the 500 m nets, compared to golden perch larvae (periodic life history strategy), of which, 16% of larvae released reached the 500 m. This is similar to others studies (Robinson et al., 1998, Schludermann et al., 2012) which found larger
larvae (>10 mm), with greater swimming ability exhibited an active component during drifting.

Current speeds at the drift nets did not always exceed critical threshold velocities or prolonged swimming velocities for Murray cod larvae, but did for golden perch (Chapter 4). Despite Murray cod larvae having the ability to avoid the channel and settle out into slow- or low-flow nursery habitat (Chapter 4), an estimated majority of released Murray cod larvae moved through the reach and Murray cod were found in higher abundances in all drift nets at all distances than golden perch or seeds. Therefore, it seems that Murray cod larvae are capable of orientating themselves in the water column and actively use the current as a means of transport, even if unable to swim directly into the current (i.e. active-passive drift sensu Pavlov, 1994). In experimental flumes, Murray cod larvae showed just such behaviour: once they had reached the postflexion developmental stage at 14 days after hatch, they oriented into the flow and drifted to stay in the current, avoiding refuges (Kaminskas, 2011). So what was seen in controlled laboratory conditions is likely reflected in the wild.

Although Murray cod larvae were found in significantly higher abundances than sunflower seeds in all nets at all distances downstream of release, adding further support to active dispersal, this was not true for golden perch. The abundance of golden perch larvae, by time and distance, did not differ significantly from that of sunflower seeds. Thus, it seems that golden perch disperse in a similar manner passive particles, but are likely not entirely passive as demonstrated in Chapter 4, which show the larvae’s ability to orientate into the current.
My results, related to how or where larvae drift during active dispersal, are not entirely supported by the findings of other studies. Robinson et al. (1998) and Schludermann et al. (2012) found that larvae swam lateral to currents after hatching, to seek out suitable low-velocity habitats. It seems that Murray cod larvae largely did not do this. They apparently actively dispersed in Old Man Creek, and were able to achieve this at least in part due to the creek’s relatively slow current velocity. It is likely that they would continue to drift until suitable nursery habitat is found or sufficient dispersal from parents, siblings or conspecifics is achieved (Humphries, 2005). Golden perch larvae, being poor swimmers, have more limited potential to influence downstream dispersal, and therefore these larvae probably disperse until geomorphic and hydrodynamic features deposit them in slackwater habitats or other dead zones. Robinson et al. (1998) and Schludermann et al. (2012) both suggest that larvae move towards the shore, where they are able to maintain position or move upstream into suitable nursery habitat. The environments in which Robinson et al. (1998) and Schludermann et al. (2012) conducted their studies are very different to Old Man Creek, an anabranch of the Murrumbidgee River, which is part of a lowland braided river system. The Little Colorado River is a transient desert river characterised by canyons of the American southwest (Robinson et al., 1998) and the Danube downstream of Vienna is still considered a mountain river (Schludermann et al., 2012). The current velocity of Old Man Creek is generally considerably slower than the Murrumbidgee River and the former could be considered a small creek compared to many North American and European river systems. Based on my results and those in other systems, it seems likely that dispersal is not only related to swimming ability and life history strategy, but also by the type of lotic system in
which the larvae are dispersing. Larvae may have the ability to influence their dispersal, but the extent to which it is done is undoubtedly context-dependent.

The *in situ* dispersal abilities of Murray cod and golden perch larvae, reported in this chapter, complement the species’ swimming performances described in Chapter 4. Specifically, species with well developed swimming ability, Murray cod, can actively disperse, whereas, golden perch, with poor swimming ability, likely have more limited abilities to influence their downstream dispersal and exhibit relatively greater passive dispersal. It is, therefore, important to look at the results of Chapter 4 and 5 in conjunction with the current altered flow regime found in the Murrumbidgee River system during times when the majority of native fish species are known to spawn. By modelling discharge and resulting current speeds within Old Man Creek, Chapter 6 will examine the changes in hydraulic habitat available for the larvae of fish species of varying swimming ability under an altered flow regime.
Chapter 6: Modelling hydraulic habitat for riverine fish larvae in relation to flow alteration

6.1 Introduction

Interactions between discharge and channel morphology in rivers create a heterogeneous hydraulic environment at multiple spatial and temporal scales (Price et al., 2012, Thorp et al., 2006, Humphries et al., 2014). This variability in hydraulic environment provides a diversity of conditions in rivers, enhancing biodiversity (Armitage and Pardo, 1995, Orth, 1987, Thorp et al., 2006). The young stages of fish are able to detect and respond to hydraulic habitat components, such as point velocity, velocity gradients, local depth, turbulence, shear stress and substrate particle size (Gore et al., 1981, Bovee, 1982, Statzner et al., 1988). As a result, these components appear to influence dispersal and distribution of the young stages of riverine fish (Lamouroux et al., 1998, Schludermann et al., 2012). In spite of recent advances in our understanding of the effects of hydrology and hydraulics on young fish in rivers, (Wolter and Sukhodolov, 2008, Speirs and Gurney, 2001, Korman et al., 2004), how the two are linked and how this influences the distribution and dispersal of young fish is not well understood (Reichard and Jurajda, 2007, Reichard et al., 2004, Schludermann et al., 2012).

In fishes, dispersal occurs primarily during the embryonic and larval periods (Brown and Armstrong, 1985, Pavlov, 1994) and facilitates population expansion, movement to suitable habitat and ensures gene mixing (Fuiman, 2002, Fuiman and Cowan, 2003, Pavlov, 1994). Seasonal patterns of larval fish drift abundance and composition in rivers are inevitably driven by the timing of reproduction (Humphries and Lake, 2000, Baumgartner et al., 2008), and more specifically by circannual rhythms,
photoperiod and temperature (Reichard et al., 2002). Free embryos and larvae of fish disperse to find productive, safe nursery habitats (Pavlov, 1994), but dispersal, at such vulnerable stages can result in high mortality (Harvey, 1987, Reichard et al., 2002). Mortality of the young stages of fish can occur because of starvation or predation or because of the inability to move to conditions conducive for growth and survival. Therefore, spatial and temporal variability in hydraulic habitat – which affect how free embryos and larvae disperse into nursery or rearing habitat – can influence recruitment (Price et al., 2012).

The swimming ability of larval fish varies by species and life history strategy, and therefore affects the movement or dispersal of species within lotic systems (Pavlov, 1994). For species with larvae that are weak swimmers, dispersal during the larval stage will depend mainly on local hydrodynamic features (Shanks, 1995), whereas species that are better swimmers can disperse actively. In Chapter 4, the swimming performance of the larvae of six species of native fish was examined to help understand their dispersal capability, results found that swimming performance broadly followed life history strategy, and that larvae more developed at hatch had faster swimming speeds and so, more potential to influence dispersal.

River regulation and fragmentation are known to alter seasonal flow patterns and affect downstream dispersal of larvae by altering the available time larvae can drift prior to being swept into unsuitable downstream environments, such as reservoirs or irrigation networks (Dudley and Platania, 2007). Events, like unseasonably elevated discharge, that occur during the early life stages of fish may have major impacts on populations by increasing mortality rates and affecting recruitment (Houde, 1989).
The relationships between drift densities and discharge have been documented in a range of rivers around the world (Johnston et al., 1995, Araujo-Lima and Oliveira, 1998, Copp et al., 2002, Reichard et al., 2004, Lechner et al., 2013). Previous research has used one-dimensional dispersion models (Wolter and Sukhodolov, 2008), two-dimensional hydrodynamic models (Ellien et al., 2004, James et al., 2002, Speirs and Gurney, 2001, Vietz et al., 2013) and particle tracing approaches to simulate larval movement (Korman et al., 2004). However, the link between discharge and preferred hydraulic habitat of larvae is not well understood (Reichard and Jurajda, 2007, Reichard et al., 2004, Schludermann et al., 2012). The lack of information available on the effect of flow regulation on larvae is due to: the paucity of information on the number and location of spawning areas; the dearth of knowledge of whether the initiation of larval dispersal is active by swimming or passive by dislodgement; the position and orientation of larvae in the water column; and the relationships among development, swimming ability, and swimming behaviour of different species (Reichard and Jurajda, 2007, Reichard et al., 2004).

This chapter aims to combine modelled hydraulic data with the swimming ability of larvae of four species of fish presented in Chapter 4 to investigate if larvae are able to maintain position and influence dispersal in a flow-modified system. A one-dimensional hydraulic model was used and field data from three study reaches in Old Man Creek to explore the percent usable area of hydraulic habitat for four developmental stages of the four species, under nine flow scenarios, ranging from baseflow, up to a typical regulated irrigation flow. At each stepped increment in discharge, the availability of suitable current speed was determined to establish the
potential effects of dispersal and maintenance of position. The specific aims of this chapter are to: (1) model patterns in current velocity at nine river discharges that reflect the range of flows that occur in the Old Man Creek anabranch; (2) combine the modelled discharges with data on critical \( U_{\text{crit}} \) and prolonged swimming speed of native fish larvae (Chapter 4) to quantify the effects on available hydraulic habitat for each larval developmental stage for four species of native fish; and (3) in the light of my results, discuss the implications of flow regulation on usable hydraulic habitat for larval fish.

6.2 Materials and methods

6.2.1 Study reaches

Old Man Creek is an anabranch of the Murrumbidgee River that receives regulated and unregulated flows (Figure 6.1). The anabranch flows out of the Murrumbidgee River approximately 20 km downstream of Wagga Wagga, NSW. There is a fixed-crest weir on the anabranch located 1025 metres downstream from the start of the anabranch. The anabranch begins to flow when the Murrumbidgee River has a discharge between 13.89 and 16.02 m\(^3\)s\(^{-1}\), and flow over the weir is estimated to start when the discharge at Wagga Wagga is approximately 115.74 m\(^3\)s\(^{-1}\). Although they are the same channel, Beavers Creek anabranch becomes Old Man Creek anabranch approximately 14 km downstream of the weir, however for simplicity, the whole system is hereafter referred to as Old Man Creek in this study. The length of Old Man Creek is 63.2 km where it rejoins the Murrumbidgee River. Additional water can enter the anabranch from the Murrumbidgee River via flood runners that commence to flow during flood events in the Murrumbidgee River, and from local catchments along the anabranch.
Blowering Dam was constructed in 1970 on the Murrumbidgee River. Flow records at the Wagga Wagga gauge on the Murrumbidgee River indicate that between 1970 and 2012, a discharge of 115.74 m$^3$s$^{-1}$ occurred more than 70% of the time during the high regulated season (October to March). Comparably, from 1900 to 1970 a discharge of 115.74 m$^3$s$^{-1}$ at Wagga Wagga occurred less frequently during the high regulated season (approximately 20% of the time). Similarly, the frequency of occurrence of a flow of 115.74 m$^3$s$^{-1}$ during the low regulated season (April to September) has not changed substantially pre and post 1970; frequency is estimated to vary from around 30% post 1970 to 20% pre 1970. The change in discharge in the Murrumbidgee River during the high regulation season potentially increases the opportunities for flow into the Old Man Creek anabranch during the high regulated season, compared to that prior to regulation.

This study looks at three study reaches along Old Man Creek (Figure 6.1). The upstream study reach (hereafter referred to as Old man Creek upper) flows through a state forest, the mid-section study reach is surrounded by agricultural land with intact riparian areas, and the downstream reach (hereafter referred to as Old Man Creek lower) study reach section is bordered by degraded agricultural land with intermittent riparian areas. Each study reach was 505 m in length and 30–108 m wide (Table 6.1). Fish and habitat associations for these three reaches were documented in Chapter 3. Habitat types among the three study reaches were similar, each including run, riffle and pool sequences; however, the channel morphology differed, in that the typical cross-sectional shape in some reaches was more incised or shallower than others (Figure 6.2).
Figure 6.1: The Old Man Creek anabranch examined in this study, showing the location of the three study reaches within the Murray-Darling Basin, Australia.

Table 6.1: Hydrological and geomorphic characteristics for each study reach.

<table>
<thead>
<tr>
<th></th>
<th>Old Man Creek upper</th>
<th>Old Man Creek middle</th>
<th>Old Man Creek lower</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nearest State Water gauge number</td>
<td>410137</td>
<td>410093</td>
<td>410093</td>
</tr>
<tr>
<td>Distance to gauge station (km)</td>
<td>13.36</td>
<td>21.34</td>
<td>0</td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>161.40</td>
<td>157.11</td>
<td>152.41</td>
</tr>
<tr>
<td>Mean annual discharge (m³ s⁻¹)</td>
<td>3.82</td>
<td>1.50</td>
<td>9.38</td>
</tr>
<tr>
<td>90% flow, high regulated period (m³ s⁻¹)</td>
<td>0.98</td>
<td>NA</td>
<td>1.50</td>
</tr>
<tr>
<td>Channel bed slope</td>
<td>0.0044</td>
<td>0.0038</td>
<td>0.0484</td>
</tr>
<tr>
<td>Study reach (m)</td>
<td>505</td>
<td>505</td>
<td>505</td>
</tr>
<tr>
<td>Mean bankfull width (range) (m)</td>
<td>44-90</td>
<td>32-108</td>
<td>30-52</td>
</tr>
<tr>
<td>Dominate substrate</td>
<td>gravel, sand</td>
<td>gravel, sand</td>
<td>gravel, sand</td>
</tr>
<tr>
<td>Dominate channel morphology</td>
<td>Riffer-pool</td>
<td>Riffer-pool</td>
<td>Riffer-pool</td>
</tr>
</tbody>
</table>

1 Based on gauge records from 1999 to 2012

2 Based on gauge records from 1976 to 2012
6.2.2 Data inputs for hydraulic modelling

Hydraulic modeling for this chapter was collated and performed by Donna Hughes and data was processed by Simon McDonald. The methods, data used and modeling performed by Donna Hughes and processed by Simon McDonald is described in the following sections (6.2.2.1-6.2.2.5 and 6.2.3).

6.2.2.1 Gauged flows

There are two stream gauging stations on Old Man Creek anabranch: one near the offtake regulator close to the Old Man Creek upper reach (NSW Office of Water gauge # 410137/Mundowey) and the other near the end of the anabranch at Old Man Creek lower reach (NSW Office of Water gauge #410093/Kywong) (Table 6.1). The discharge that occurred more than 50% of the time at Mundowey between 1999 and 2012 was approximately 1.74 m$^3$s$^{-1}$. This figure is expected to be lower than the long
term average daily discharge during this period, as this was three years of low flows
during the millennium drought in eastern Australia (Page et al., 2005). At the same
station and for same period, during the high regulated season, the discharge that
occurred more than 50% of the time was 3.82 m$^3$s$^{-1}$. This station, at Old Man Creek
lower, has been active since 1965.

6.2.2.2 Water depth and velocity survey

Depth and velocity measurements were taken at 25 m intervals along creek transects,
for each of the three study reaches (21 transects in each reach). Water depth and
velocity (0.4 of depth) measurements were taken at 1 m intervals along the transect
lines using a survey pole, and a FLO-MATE 2000 velocity meter, respectively.
Measured depths were not related to a survey datum. Survey sampling was completed
within a 10 h period, on the same day for each reach: Old Man Creek upper was
sampled on 6 June 2010 (between 0.05-0.07 m$^3$s$^{-1}$), Old Man Creek middle was
sampled on 3 June 2010 (0.38 m$^3$s$^{-1}$) and Old Man Creek lower was sampled on 5
Nov 2009 (2.06 m$^3$s$^{-1}$). Aerial laser survey (ALS) and measured depths in the each
reach were combined and the combined data points fitted well and therefore were
assumed to be an accurate representation of the creek invert (Figure 6.2).

There was little variation in the maximum survey depths of the three Old Man Creek
reaches, which varied from 1.3 m (Old Man Creek middle and lower) to 1.4 m (Old
Man Creek upper) whereas mean depth of Old Man Creek lower (0.2 m) was half the
mean depth of other two reaches (Old Man Creek upper, 0.54 m and Old Man Creek
middle 0.45 m). Unlike depth, max current velocity varied among reaches, ranging
from 0.17 (Old Man Creek upper), 0.60 (Old Man Creek middle) to 0.90 m$^{-1}$ (Old
Man Creek lower). Old Man Creek upper had the slowest mean velocity (0.05 ms\(^{-1}\)) and areas that pooled across the width of the reach and a more braided channel morphology (Figure 6.2). The mean current velocities of Old Man Creek middle and lower were similar (0.10 and 0.16 ms\(^{-1}\), respectively). There was noticeable variation of surveyed current velocities along Old Man Creek middle with the middle section of the reach (approximately 200 m in length) having lower velocities and shallower depths than the upper and lower sections, due to sedimentation and a blockage in the creek from vegetation. The current velocity and depths were relatively consistent along Old Man Creek lower, which is consistent with narrow channel morphology (Figure 6.2).

### 6.2.2.3 Digital Elevation Model

A 1 m gridded digital elevation model (DEM), based on ALS, was used for mapping the Old Man Creek anabranch and to extract cross sections for use in hydraulic modeling. As ALS does not penetrate water, and there were low flows in the channel at the time of the survey, the DEM did not include the channel invert. The channel invert levels were estimated using the DEM and water depths measured during field survey. The resultant DEM included interpretation due to combining the channel inverts and ALS data.

### 6.2.2.4 Selection of model parameters

Hydraulic roughness coefficients and Manning’s \(n\), were chosen with reference to modelling undertaken for the now defunct government organisation, Water for Rivers and validation of model results along Old Man Creek lower reach against gauged flows and water levels at the Kywong gauge, as it is within the modelled reach. The
Old Man Creek lower cross section survey data compared well with reported cross sections; therefore gauging station records of height and flow were used to calibrate the hydraulic model in this reach. Where possible, comparisons were made to measured velocities, and the differences in vegetation and channel geomorphology at each reach.

Discharge used for calibration considered a range of levels at time of sampling - 0.42, 1.66, 2.06 m³s⁻¹ - as well as a range of flows normally occurring in the reach under a managed flow regime: 1.50, 4.81, 11.39 and 25.23 m³s⁻¹. Manning’s parameter values of 0.042 for the channel bed and 0.055 on the banks reproduced observed water levels on average to within 10% of depths recorded at the gauge when comparing modelled values to survey data. This is considered a reasonable match, given the uncertainty of the DEM and cross sections. Additionally, results from the model run for flow of 2.06 m³s⁻¹ (flow at time of survey), were compared with surveyed depths and velocities. The modelled velocities were, on average, 20% slower than observed velocities, which may be due to the conflicts with combining survey and ALS without a common survey datum.

Selection of Manning’s value for the Old Man Creek upper reach and Old Man Creek middle reach was not possible by matching observed data, since at the time of sampling, flows were low, with areas of still water, and thus would not be represented accurately using HEC RAS (United States Army Corps of Engineers). A parameter value of 0.042 was adopted for in-channel hydraulic roughness for Old Man Creek upper and Old Man Creek middle reaches, as photographs taken during sampling indicated a consistent degree of debris and channel sinuosity compared with Old Man
Creek lower. The Manning’s value for the overbank at Old Man Creek lower (0.055) was adopted at Old Man Creek middle, as vegetation cover was consistent between these reaches. Old Man Creek upper reach is located in a forest where riparian zones are more densely vegetated than Old Man Creek lower or Old Man Creek middle; thus a value of 0.07 was adopted, which is a typical value for medium-to-dense vegetation on floodplains. Velocities sampled within the study reaches Old Man Creek upper and Old Man Creek middle were on average higher than velocities from modelling, which is somewhat anticipated, because the flow behaviour at very low flows (slow to no flow) is not represented within the model, i.e. the model cannot model for no flow, it assumes water is moving.

6.2.2.5 Selection of a range of flows

A range of discharges typical of gauged flows found in the Murrumbidgee River during the high regulated season were selected. Modelled discharges were 2.31, 4.63, 5.79, 7.75, 11.57 m$^3$s$^{-1}$, which occur 30-70% of time, and larger, less frequent flows, including 17.36, 23.15, 34.72 and 52.08 m$^3$s$^{-1}$. In Australia, discharge is typically measured in megalitres per day (ML$^3$ld$^{-1}$); therefore the values reported in this study have been converted to an international standard measurement (m$^3$s$^{-1}$), causing the modelled discharges to become fractional numbers. Extensive out-of-bank flow along the anabranch occurs for discharges above 52.08 m$^3$s$^{-1}$, so discharges were not modelled above this level. Water levels and discharge were used to determine the distribution of velocity across each cross section at 2 m intervals.
6.2.3 Hydraulic modelling

Steady state one-dimensional hydraulic modelling was undertaken at the three study reaches to estimate the velocity distribution across and along Old Man Creek for a range of flows. Modelling used HEC RAS (United States Army Corps of Engineers) software, which is a commonly used model package that represents one-dimensional flow behaviour. HEC RAS can be used with steady-state or unsteady flows and was considered appropriate for this study, as the objective was to assess flow characteristics that predominately occurred in channel. The choice of model enabled the actual survey points to be used and allowed for variation of hydraulic conveyance coefficients to be applied. Additionally, the accuracy of the DEM was not sufficient to enable a two-dimensional model that could assess minor flow paths within the channel that may occur during low flows or lateral movement within the channel or across floodplains. The model was run as a steady-state model. It is noted that this modelling approach does not allow for simulation of stagnant water that can occur at very low flows. The model type adopted represents flowing water along a water course, it is not suitable for modelling stagnant pools as was observed within the Old Man Creek upper and Old Man Creek middle study reaches.

Every opportunity was taken to use data and a modelling approach fit for purpose in this study, however, there were limitations to both available data and the model. Specifically, the calibration of model parameters was limited to one reach, and observed data was partially translated from an external location. The other two reaches had recorded data that was not suitable for comparison of flowing water. Also, the steady state model used assumes flows do not vary greatly over a number of days. This is assumed to be the typical of flow during a regulated season when water
is being delivered in the Murrumbidgee Rive to downstream users. Therefore, these limitations are to be considered when interpreting and using results.

### 6.2.3.1 Generation of velocities for nine flow events

Water levels and flow simulated in HEC RAS were used to determine the distribution of velocity across each cross section at 2 m intervals for each study reach. Thematic maps for these flows were produced by overlaying extended transect lines, for approximately 100 m either side of each transect and converting line to points using Hawth’s Analysis Tools for Arc GIS (spacing 2 m) and to extracted ALS values for each of the points. The analysis was completed in ArcMap, unless otherwise indicated. The ALS values, water depth and velocity survey measurements and x-y-z coordinates of each of the points were transformed using ArcGIS resulting in modelled velocities at each point for various flow events. ArcGIS was used to create TIN (triangulated irregular network) models of velocities and interpolate TIN models to smoothed grids cells (0.1 m cell) smoothed grids had a 20 cell circular mean. The Old Man Creek anabranch boundaries were determined by tracing the nearest 0.1 m contours to non-zero data values and the boundary grids were clipped using the boundaries from the smoothed grids. Velocity areas were calculated by multiplying the grids by 1000, turning those values into integers and dividing the value by 1000. The modelled reaches were divided into velocity categories, starting at 0.0 ms\(^{-1}\) and increased by 0.04 ms\(^{-1}\) with the last of the nine categories >0.35 ms\(^{-1}\). The nine velocity categories were determined with reference to critical swimming performance data of four species of larvae determined in Chapter 4 (Kopf et al., 2014), which found that some larvae could withstand speeds up to 0.35 ms\(^{-1}\). To determine the
percent of velocity categories for each reach under each modelled discharge (e.g. 2.31 m$^3$s$^{-1}$) the velocity category (e.g. 0.00-0.04 ms$^{-1}$) was divided by the total area (m$^2$).

6.2.4 Percent usable hydraulic habitat criteria

Usable hydraulic habitat was determined as the ability of larvae to affect their position in the current for either a short amount of time, $U_{crit}$ (<60 min) or a prolonged amount of time (>60 min). These swimming abilities were used to cover a range of behaviours larvae may exhibit, such as active or active passive dispersal downstream or upstream, burst swimming to capture food or avoid a location or event and the ability to maintain position. These are not an all encompassing list of larval behaviours or swimming abilities but provide a basis for understanding what velocity habitat is available to larvae and if they are capable of using it. $U_{crit}$ swimming performance (mean, best performers and prolonged speed) of free embryos and larvae of Murray cod, *Maccullochella peeli* (Mitchell 1838), trout cod, *Maccullochella macquariensis* (Cuvier 1829), silver perch, *Bidyanus bidyanus* (Mitchell 1838) and golden perch, *Macquaria ambigua* (Richardson 1845), were used to determine a reference for the percent usable hydraulic habitat in three modelled reaches of Old Man Creek. Four larval developmental stages (preflexion, flexion, post flexion and metalarvae) were used, because larvae are found drifting or dispersing at different developmental stages. Percent usable hydraulic habitat is considered for three measures of $U_{crit}$ - mean, best performers and prolonged swimming - to cover a range of indicators. Mean $U_{crit}$ represents the overall range in performance; best performers represent the top 25% or the most fit larvae and therefore most likely to survive in the wild; and prolonged $U_{crit}$ represent a more realistic demonstration of *in situ* swimming performance, or a representation of how well fish can swim over a +60
min period. Percent usable hydraulic habitat was determined for each reach under each of the nine discharge flows (2.31, 4.63, 5.79, 7.75, 11.57, 17.36, 23.15, 34.72 and 52.08 m$^3$s$^{-1}$). An upper and lower bound for the percent usable hydraulic habitat was determined by choosing the highest and the lowest percent area of usable hydraulic habitat for the mean $U_{crit}$, mean best performers $U_{crit}$, and prolonged speed ($U_{crit}$) among the three reaches.

6.3 Results

6.3.1 Modelled velocity in Old Man Creek under nine river discharge levels

Despite differences in channel morphology, the three reaches showed similar responses to modelled discharges (Figure 6.3). Overall, as modelled discharge increased, current velocity categories became more similar, with 56-79% of velocities within the fastest velocity category, >0.35 ms$^{-1}$, at the highest discharge (52.08 m$^3$s$^{-1}$). Hydraulic habitat was dominated by the fastest velocity category under all discharge levels for all three reaches, except for the lowest discharge 2.31 m$^3$s$^{-1}$, where the 0.05-0.09 and 0.1-0.14 m$^3$s$^{-1}$ velocity categories had the greatest percent hydraulic habitat. As discharge increased to 11.57 m$^3$s$^{-1}$ velocities became more uniform and in all three reaches the velocity categories <0.35 ms$^{-1}$, were consistently below 10% available hydraulic habitat. The no flow, or 0.0 ms$^{-1}$, velocity category had the least percent frequency for all three reaches under all modelled discharges. Pooling of slow flow water across the channel, or the width of the reach, stopped at a low discharge (5.79 m$^3$s$^{-1}$). Percent frequency of hydraulic habitat varied most at the lowest modelled discharge (2.31 m$^3$s$^{-1}$), with velocity categories ranging from 13-23% within each reach.
Figure 6.3: The percent frequency of velocity categories (velocity ms$^{-1}$) for each of the modelled reaches, Old Man Creek upper, Old Man Creek middle, Old Man Creek lower and percent frequency velocity categories histogram, comparing the three reaches (Old Man Creek upper: black bar, Old Man Creek middle: white bar and Old Man Creek lower: grey bar) for each modelled discharge; 2.31 ms$^{-1}$, 4.63 ms$^{-1}$, 5.79 ms$^{-1}$, 7.75 ms$^{-1}$, 11.57 ms$^{-1}$, 17.36 ms$^{-1}$, 23.15 ms$^{-1}$, 34.72 ms$^{-1}$ and 52.08 ms$^{-1}$.
Under the nine modeled discharges, within Old Man Creek upper, the mean velocity ranged from 0.21-0.57 m/s, with the greatest velocity, 2.38 m/s occurring at the 34.72 m³/s discharge (Figure 6.3). Mean velocity increased with an increase in discharge, and for all modeled discharges, except 52.08 m³/s, areas with zero current were apparent. The wider, shallower channel morphology of Old Mann creek upper, resulted in a larger area inundated under the higher modeled discharges. Percent frequency of hydraulic habitat varied most at the lowest modelled discharge (2.31 m³/s), with 7 out of 9 categories greater than 10%.

In Old Man creek middle, the mean velocity for the nine modeled discharges ranged from 0.15-0.58 m/s, with the greatest velocity, 1.54 m/s occurring at the 52.08 m³/s discharge (Figure 6.3). As with Old man Creek upper, mean velocity increased with increasing discharge but areas of zero current, were absent by the 23.15 m³/s discharge. Percent frequency of hydraulic habitat varied most at the second lowest modelled discharge (4.63 m³/s), with 7 out of 9 categories greater than 10%.

In Old Man creek lower, the mean velocity for the nine modeled discharges ranged from 0.20-0.83 m/s, with the greatest velocity, 2.57 m/s occurring at the 52.08 m³/s discharge (Figure 6.3). As with the other two reaches, mean velocity increased with increasing discharge. The only modeled discharge to include zero current in the Old Man Creel lower reach was the 2.31 m³/s discharge. Percent frequency of hydraulic habitat were more uniform within Old Man Creek lower, the discharges with the most variability (2.31, 4.63 and 5.79 m³/s) only had 4 out of 9 velocity categories greater than 10%. 

132
6.3.2 Percent usable area of hydraulic habitat for four species of larvae

In general, as discharge increased, the percent usable hydraulic habitat decreased for all species, all larval stages, and for the three measures of $U_{\text{crit}}$ (Figure 6.4). Percent usable hydraulic habitat bands (1-100%, lower to upper limits) were overall highest for best performers $U_{\text{crit}}$ and lowest for prolonged swimming (0-62%, lower to upper limits). Usable hydraulic habitat bands were the lowest and had the least variability for prolonged swimming performance, due to the fact larvae for all species and all stages had the poorest swimming ability. At larger, less frequent discharges (above 17.36 m$^3$s$^{-1}$), there was an overlap in the usable hydraulic habitat band for mean $U_{\text{crit}}$ among developmental stages for all species, with at least three of the four stages overlapping. In contrast, there was little to no overlap in the range of usable hydraulic habitat for mean $U_{\text{crit}}$ among developmental stages at modelled discharge levels which occur 30-70% of time (below 11.57 m$^3$s$^{-1}$), when there was a higher percent frequency of velocity categories <0.36 ms$^{-1}$.

Trout cod larvae usually drift during the postflexion and metalarvae developmental stage when larvae are most developed. These stages of trout cod larvae could potentially use at least 50% of the river reach at modelled discharge levels that are common (occurring 30-70% of the time) during a regulated season (up to 5.79 m$^3$s$^{-1}$), for mean $U_{\text{crit}}$ performance (Figure 6.5). For developmental stages of larvae known to drift, percent usable hydraulic habitat increased for best performers $U_{\text{crit}}$, with the potential to use all velocity categories for all modelled discharges. The percent usable hydraulic habitat was at least 10% for mean prolonged swimming $U_{\text{crit}}$, except at the highest modelled discharge (52.08 m$^3$s$^{-1}$).
Murray cod larvae, like trout cod larvae, usually drift during the postflexion and metalarvae developmental stage and results are similar to trout cod for available hydraulic habitat (Figure 6.4). Stages of Murray cod larvae commonly found drifting could potentially use at least 50% of the river reach at modelled discharge levels that are common (occurring 30-70% of the time) during a regulated season (up to 11.57 m$^3$s$^{-1}$), for mean $U_{crit}$ performance. Percent usable hydraulic habitat increased for best performers $U_{crit}$, with larvae able to use all velocity categories $\leq 0.35$ ms$^{-1}$ for all modelled discharges (Figure 6.5). Murray cod larvae at the drifting developmental stage had the highest percent usable hydraulic habitat among all species for prolonged swimming $U_{crit}$, with at least 10% usable hydraulic habitat for all modelled discharges.

Golden perch larvae are planktonic, and relatively undeveloped free embryos and larvae that drift from hatch, resulting in a lower percent of usable hydraulic habitat compared to trout cod and Murray cod (Figure 6.4) (Chapter 4). When comparing developmental stages of larvae that would be drifting, golden perch usable hydraulic habitat bands rarely overlapped trout and Murray cod bands, with overlap mostly occurring at the highest modelled, rarely occurring discharges (23.15-52.08 m$^3$s$^{-1}$) (Figure 6.5). The percent usable hydraulic habitat for developmental stages of golden perch commonly found drifting, was less than 50% for all modelled discharges, except for the upper bounds of best performers $U_{crit}$, at the lowest modelled discharge (2.31 m$^3$s$^{-1}$), which were 73% available hydraulic habitat available (Figure 6.5). Percent usable hydraulic habitat was $< 10\%$ for prolonged swimming $U_{crit}$ for all developmental stages commonly found drifting.
The larvae of silver perch, like those of golden perch, are planktonic, but silver perch are even poorer swimmers than golden perch. This means a lower percent of usable hydraulic habitat is able to be used by silver perch than golden perch (Figure 6.4). Overlap rarely occurred between best performing $U_{crit}$ silver perch and golden perch larvae at modelled discharge levels that are common (occurring 30-70% of the time) during a regulated season (up to 17.36 m$^3$s$^{-1}$), but was similar for the two species at higher modelled discharges (over 23.15 m$^3$s$^{-1}$). Usable hydraulic habitat was <25% for all discharges for mean and best performers $U_{crit}$, and percent usable hydraulic habitat was <5% for prolonged swimming $U_{crit}$ for developmental stages of silver perch larvae commonly found drifting (Figure 6.5).

When making comparisons among stages of larvae that are found in the drift, the species from the same life history strategy (trout cod and Murray cod; golden perch and silver perch) had similar or overlapping percent usable hydraulic habitat bands (Figure 6.5). Trout cod and Murray cod larvae had higher percent usable hydraulic habitat than golden and silver perch and there was never overlap between Murray cod and golden or silver perch percent usable hydraulic habitat bands.
Figure 6.4: Mean $U_{\text{crit}}$, best performer $U_{\text{crit}}$ and prolonged swimming hydraulic habitat availability bands (%) for trout cod, Murray cod, golden perch and silver perch under nine modelled discharges (m$^3$s$^{-1}$). Each line type represents a different developmental stage (Preflexion — , Flexion • • • •, Postflexion —, Metalarvae ‐ ‐ ‐ ‐). For each developmental stage, there are normally two lines: the upper representing the fastest and lower, representing the slowest velocities at which larvae can swim, among the three reaches modelled.
Figure 6.5: Mean $U_{crit}$, best performers $U_{crit}$ and prolonged swimming hydraulic habitat availability (%) for stages found drifting/dispersing of trout cod (postflexion and metalarvae developmental stage), Murray cod (postflexion and metalarvae developmental stage), golden perch (preflexion and flexion developmental stage) and silver perch (preflexion and flexion developmental stage), under nine modelled discharges (m$^3$s$^{-1}$). Each line type represents a different species (trout cod —, Murray cod - - -, golden perch — • —, silver perch • • • •). For developmental stages found drifting, there are normally two lines: the upper representing the the fastest and lower, representing the slowest velocities at which larvae can swim, among the three reaches modelled.

6.4 Discussion

6.4.1 Modelled velocity in Old Man Creek under nine river discharge levels

Results of modelled velocity with discharge for Old Man Creek showed that as channel discharge increased, across the range of in-channel flows examined in this study, not only did velocity increase, but so did the uniformity of velocity categories available: the river became more homogenous.

The three reaches investigated in this chapter had varying channel morphologies, but all responded in a similar way: as discharge increased, hydraulic habitat homogeneity increased. However, there was variation in the amount and configuration of hydraulic habitat categories within each reach, suggesting hydraulic habitat is mediated by geomorphology. This is in agreement with previous findings (e.g. Payne and Lapointe, 1997, Maddock et al., 2004, Moir et al., 2006, Price et al., 2012). Price et al. (2012) concluded that the differences in the temporal variability of low/no flow hydraulic habitat (slackwaters) among river reaches are related to channel characteristics (Maddock et al., 2004, Dyer and Thoms, 2006), suggesting that
channel morphology is a key driver of hydraulic habitat dynamics. This implies that the amount of habitat available to animals and plants varies at the relatively small, reach scale.

6.4.2 Percent usable area of hydraulic habitat for the larvae of four species of fish

The amount of usable hydraulic habitat increased as swimming ability – determined from Chapter 4 - increased. Swimming ability in turn increased with ontogeny. Several studies have documented major ontogenetic changes in habitat use for riverine fish species (Scott and Nielsen, 1989, Copp, 1990, Schiemer et al., 1991, King, 2004). Ontogenetic habitat changes for fishes can be related to changes in a fish’s morphology, such as the transition from larva to juvenile, or can be to minimise or avoid predation or competition for habitat or food (Werner and Gilliam, 1984).

Overall, useable hydraulic habitat reflected the life history strategies of each species of larvae, with trout cod and Murray cod defined as *equilibrium* (sensu Winemiller and Rose, 1992) species, *Strategy 1* (sensu Humphries et al., 1999) or *precocial* (sensu Balon, 1986a) that were well developed larvae able to drift downstream (Cadwallader et al., 1979, Ingram and Rimmer, 1992, Humphries et al., 1999, Humphries, 2005, Koehn and Harrington, 2006). Well-developed larvae of life history *equilibrium* fish were found to have higher useable hydraulic habitat compared to *periodic* species, inferring that the larvae of *equilibrium* species can potentially influence their dispersal under a greater range of in-channel velocities and therefore discharges. This may coincide with spawning periods. The prefexion and flexion larvae of *equilibrium* species, trout cod and Murray cod, are cared for in a nest until they are developed enough to enter the drift. Therefore, there is potentially
‘wash-out’ of larvae at this time under regulated high flow, during seasonal reversal of discharge. Golden and silver perch follow periodic (sensu Winemiller and Rose, 1992), Strategy 2 (sensu Humphries et al., 1999) or altricial (sensu Balon, 1986a) life history strategies, with relatively under-developed planktonic free embryos at hatch that have limited swimming capabilities when drifting (Lake, 1967).

6.4.3 Implications for larval fish in lowland rivers under river regulation

The results of this chapter showed that larvae of drifting equilibrium species could use 25-92% of hydraulic habitat under typical high regulated flows and 10-50% of hydraulic habitat under uncharacteristically high regulated flows, inferring that larvae of equilibrium species can potentially influence their dispersal under a greater range of in-channel velocities and therefore discharges than the larvae of periodic species. During high irrigation flows, occurring over the spawning seasons, trout cod and Murray cod can potentially use habitat within the channel as settlement/nursery habitat, such as sheltered bank areas or other with low/slow or no flow zones, because larvae have the potential to use burst swimming to orientate into slow flow habitat from the channel while drifting (Chapter 4). However, my results suggest that larvae of drifting periodic species have less hydraulic habitat available under typical regulated flows (0-46%), and under uncharacteristically high regulated flows (0-22%). Golden and silver perch are poor swimmers (Chapter 4) and, under a seasonal reversal of flow, resulting in high summer irrigation discharge and within bank flows, these species have less chance of reaching slackwater habitat that is found during overbank discharges or floods, or slow/no flow habitat that is more frequent in low discharges, at least in an anabranch like Old Man Creek. River regulation increased the downstream transport of pelagic-spawning cyprinid larvae into unsuitable
downstream environments, such as reservoirs or irrigation networks, where survival was lower, in a large river in the midwestern US (Dudley and Platania, 2007, Perkin and Gido, 2011). This may be a similar situation for Murray-Darling basin pelagic spawning larvae, like golden and silver perch, and may contribution to why silver perch populations are degraded. In the Broken River, northern Victoria, Vietz et al. (2013) found that as discharge increased, habitat became more homogenous, and areas important to larval fish for protection, feeding and rearing (slackwaters), decreased.

Results found that for all life history strategies, as discharge increase the usable hydraulic habitat decreases, meaning not only is downstream movement of pelagic spawned larvae, like golden and silver perch, affected by river regulation but the ability of larvae to settle out into suitable nursery habitat using swimming decreases. Research on the effects of river regulation in the Murrumbidgee River upstream and downstream of Old Man Creek has found that river regulation has dramatically reduced the frequency of moderate floods (Page et al., 2005).
Chapter 7: General Discussion

The broad aim of this thesis was to determine the swimming capabilities and dispersal potential of Australian freshwater fish in a regulated riverscape. This study used life history theory, set within a riverscape framework to explore how larvae are affected by high regulated flows during spawning periods. This study constituted the first attempt to determine the swimming capabilities of the larvae of several species of native Australian freshwater fish (Chapter 4). Additionally, this study tested the results of swimming performance findings in situ (Chapter 5) and modelled flow velocities to determine available hydraulic habitat using swimming performance results (Chapter 6).

A principal of riverscape ecology is that unique attributes within the lotic system can have over-riding effects on abiotic and biotic factors found in the riverscape (Fausch et al., 2002). This study demonstrated that anabranches, or secondary channels, may play an important role in the riverscape, because they have the potential to provide habitat for larval fish under high regulated flows and increase species abundance and diversity within the riverscape (Chapter 3). Pollux et al. (2006) also demonstrated that tributaries, like anabranches increase habitat heterogeneity resulting in increased habitat for larval fish. By comparing the fish faunas of a highly flow-modified river, a highly flow-modified anabranch and an anabranch which has a less modified flow regime, during the breeding season, this study found that the main stem had relatively high larval abundance, but that the anabranch with a less modified flow regime had higher overall number of species. Results suggest that anabranches can enhance overall habitat heterogeneity and potentially act as a refuge for the larvae of native
fishes in a regulated riverscape. It is important to note that anabranches must be periodically to continuously connected to the main stem in order to increase habitat heterogeneity and be useful to riverscape fish communities.

As well as understanding what riverscape attributes are important to larval fish, it is also important to understand what the movement capabilities of larvae are within the riverscape (Schlosser, 1991). Like Humphries et al. (1999) and King (2004), the findings presented in this thesis support the consideration and utility of life history theory in providing a basis for understanding how larvae move and behave within a riverscape. Similar to Patterson et al. (2004) and Eliason et al. (2011), a key finding of Chapter 4 was that, in general critical swimming speed and prolonged swimming performance of species followed patterns consistent with life history strategies (LHS). Murray cod and trout cod (*equilibrium* LHS) larvae were the best swimmers and have the greatest potential of all the species tested to influence how far they disperse and where they settle out in rivers. In contrast, golden perch and silver perch (*periodic* LHS) larvae were the poorest swimmers have the least potential to influence how far they disperse and where they settle out in rivers. Similarly, *opportunistic* LHS larvae (Murray rainbowfish and carp gudgeon) are relatively poor swimmers, but are not known to drift en masse like the other species and instead colonise slow/no flow habitats. This chapter also determined that developmental stage was the best at explaining critical and prolonged swimming performance, and established that critical swimming speed and prolonged swimming performance increase with ontogeny.
In order to better understand how drifting larvae, of different swimming abilities, species and life history strategies, move through rivers, \textit{in situ} experiments were performed in Old Man Creek anabranch and described in Chapter 5. This chapter demonstrated that a far higher proportion of released Murray cod larvae (representing \textit{equilibrium} LHS and good swimmers) (71%) passed through the experimental reach than golden perch larvae (representing \textit{periodic} LHS and poor swimmers) (16%), and passive particles (sunflower seeds) (4-5%). The superior swimming capability of Murray cod larvae apparently allows them to stay in the drift more readily, at least for the 500 m experimental reach, and actively disperse further under low-moderate flow conditions in the Old Man Creek anabranch. By contrast, the relatively poor swimming capability of golden perch larvae, under the low-moderate flow conditions, meant that a large proportion of this group did not disperse outside the 500 m reach. Of course, under higher flow conditions, to which spawning golden perch are likely to be better suited (Lake, 1967), the results may have been quite different. Under those conditions, it is expected that a greater proportion of golden perch larvae would disperse through the reach since current speeds would have been higher and retention zones fewer. It is possible that a similar proportion of Murray cod larvae would disperse through the reach under different flow conditions, since competent swimming and active dispersal (Kaminskas, 2011) gives them greater abilities to determine their movement path.

Regardless of life history strategy or swimming ability, if, during spawning season, altered flow regimes cause an increase in discharge and current velocities, larvae may be negatively affected by these increases with less available hydraulic habitat. Discharge models in Chapter 6, showed that as discharge increased, so did overall
current velocity within the Old Man Creek anabranch. The available hydraulic habitat decreased, and the hydraulic environment became more homogenous, for all species from all life history strategies, as found in Price et al. (2012) and Vietz et al. (2013). This undoubtedly means that discharge will influence the ability of larvae of all species to maintain position and so remain in preferred habitats, as well as influence their ability to direct where larvae disperse. The models indicate that at discharges comparable to regulation in rivers like the Murrumbidgee River, the vast majority of habitat in Old Man Creek would be above the critical threshold for the larvae of all species modelled.

Life history theory of freshwater fishes has provided a basis for understanding movement patterns of the early life stages of Murray-Darling Basin fishes throughout the riverscape and in the context of river regulation (Figure 7.1). In the absence of river regulation, a south-eastern Murray-Darling Basin lowland river would typically experience: high and often overbank flows at times between late autumn and winter (May-September) (Figure 7.1a); within-bank flows and connectivity among the main stem, anabranches and tributaries, during late spring/early summer (October-December) (Figure 7.1b); and low-flow periods, characterised by reduced mainstem flow and some disconnection with anabranches or tributaries during late summer/early autumn (January-April) (Figure 7.1c). River regulation in the south-eastern region of the Murray-Darling Basin, largely involving releases from instream storages for abstraction downstream, typically results in enhanced, but within-bank flows, coinciding with the spawning season of many species of native fish (Cadwallader, 1978, Walker and Thoms, 1993, Gehrke et al., 1995) (Figure 7.1d).
Overall, this type of river regulation results in an increase of within-bank velocities, which can cause an increase in mortality and affect downstream dispersal.

The larvae of *equilibrium* life history strategy fishes, typically, do not spawn during autumn and winter months (Figure 7.1a) (Lintermans, 2007). Therefore, apart from freshwater catfish, perhaps (Lintermans, 2007), they are not found using floodplain habitat available at this time of the year. Spawning of species in this life history strategy generally occurs from October-December (Figure 7.1b) (Lintermans, 2007), when flows are typically within bank, declining from winter/spring maxima but there is connectivity among the main stem, anabranches and tributaries. As they leave the ‘nest’, larvae would disperse through the system, staying mostly in the main flow path, actively assisting their dispersal downstream by swimming when the current naturally moves them into slackwater patches and dead zones. Larvae will actively disperse at this time, irrespective of the current speed, to find suitable nursery habitat. By mid-late summer (Figure 7.1c), when the main stem flow is reduced and there is limited connectivity between the main stem and its anabranches and tributaries, larvae will have settled out into nursery habitat, generally in flowing areas in the main stem and anabranches (Humphries et al., 1999, Chapter 3). Under modified high flows during the typical spawning period (October–December; Figure 7.1d) (Lintermans, 2007), it is speculated that the larvae of *equilibrium* species would disperse through the riverscape into suitable nursery habitat in a similar way as if the river was unregulated (Figure 7.1b). The main difference between these two scenarios is that regulated high flows would involve faster currents and greater areas of the channel bed would be inundated. Above a threshold, this would lead to an overall homogenisation of, and reduction in, hydraulic habitat where larvae would be able to
maintain position without refuge. This may result in larvae dispersing further in order to find suitable habitat in which to settle. Under river regulation, anabranches, with less flow modification, may have more heterogeneous hydraulic habitat and provide a greater area of suitable nursery habitat in the riverscape than the main stem.

The larvae of periodic life history strategy fishes are typically pelagic spawned, usually during late spring/early summer (Figure 7.1b), when drifting eggs, free embryos and larvae are confined to within-bank habitat. Spawning may also occur in late winter/early spring (Figure 7.1a), when eggs are broadcast during high flows, and if flows are large enough, eggs, free embryos and larvae can disperse widely - longitudinally downstream and laterally on flood plains, - exploiting rich food sources. Because of the poor swimming capability of free embryos and larvae, dispersal is largely passive. Since free embryos and larvae of periodic species have limited ability to swim out of even moderate currents, they will be deposited in slackwater patches and deadzones, some that may be suitable nursery habitat and others not. The distance drifted downstream and laterally will largely depend on the nature of the flows at that time. Periodic species do not usually spawn from late summer-autumn (Figure 7.1c), but if spawning occurred during low flows, it is likely that they would have limited dispersal and, those that survived, would settle out relatively close to where they were spawned. Under a regulated, enhanced flow scenario, during the late spring/summer period (Figure 7.1d), if the eggs, free embryos and larvae of periodic species occur, it is speculated that there will be substantial longitudinal dispersal, as larvae are entrained in the current and unable to maintain position in super-critical current speeds. The quality of habitat where larvae settle – those that survive – will likely be highly uncertain, but is unlikely to be of the
same quality, in terms of hydraulics or food, as the floodplain. Studies have shown elsewhere that river regulation increases the downstream transport of pelagic-spawning cyprinid larvae into unsuitable environments, such as reservoirs or irrigation networks, where survival is lower (Dudley and Platania, 2007, Perkin and Gido, 2011). Under river regulation conditions, with high within bank flows, anabanches, with less flow modification, may, like with *equilibrium* species, provide greater heterogeneity of hydraulic habitat, and therefore larvae may have more potential to passively drift into more suitable nursery habitat.

Fish of *opportunistic* life history strategy species have a variable spawning season, and so larvae can be found throughout most of the year, and under a range of flow conditions. Larvae have relatively poor swimming ability, like those of *periodic* species, but generally do not disperse en mass downstream. Instead larvae typically colonise local suitable habitat. It is uncommon for the larvae of *opportunistic* life history strategy fish to be spawned during overbank flows common in late winter/early spring (Figure 7.1a), but certain species, like pygmy perch, may be found, and eggs, free embryos and larvae have the potential to move laterally on flood plains spawning habitat, to exploit rich food sources as well as colonising local slackwater habitat (Tonkin et al., 2008). Spawning for these species generally peaks in late spring/early summer (Figure 7.1b), when there is within-bank flows and high connectivity among the main stem, anabanches and tributaries. During the spawning season eggs, free embryos and larvae have potential to move within slackwater habitat in which they were spawned, or perhaps drift into new slackwater/slow flow nursery habitat. Spawning may also occur from late summer-autumn (Figure 7.1c), under low flow conditions, and like the late spring/early summer spawning season,
eggs, free embryos and larvae will likely either stay in local nursery habitat or colonise new suitable habitat, but with less connectivity within the riverscape, there is less opportunity for movement or colonisation. Under a regulated, enhanced flow scenario, during the late spring/summer period (Figure 7.1d), it was speculated that there will be greater longitudinal dispersal, as eggs, free embryos and larvae are washed out of local slackwater habitats. Due to poor swimming ability, free embryos and larvae will tend to end up in habitats that may be less optimal for survival.

In conclusion, when looking at this thesis as a body of knowledge, the results from each data chapter form pieces of a puzzle, that when examined together, in a broader context, give a more complete picture of the swimming abilities and dispersal potential of the early life stages of fish and the potential impacts of how the currently managed flow regime of the Murrumbidgee River system affects larvae. By examining research with riverscape ecology principles, over the broad scale, and underpinned by life history traits and behaviours, research can give insight into smaller scale issues, which may be at the scale management can affect change. The results of this thesis can give managers information on how to manage flow regimes for the drifting stages of larval fish and shed light on how anthropogenic disturbances like seasonal flow reversal may be impacting these larvae. One limitation of this thesis is that it does not cover a long time period (5-50 yrs), as suggested by Fausch et al. (2002), to address gaps in the understanding of species over their life time, but this research may add to a body of information to be collected and analysed over that time scale.
Figure 7.1: A conceptual model representing the riverscape of an Australian low land river with the main stem and anabanches under four flow scenarios: (a) High
overbank flows throughout the autumn and winter months (March to September), (b) Within bank flows and connectivity among the main stem, anabranches and tributaries, during late spring/early summer (October to December), (c) Low flow periods, characterised by reduced main stem flow and some disconnection with anabranches or tributaries and during summer months (January to March) and (d) River regulation during typical spawning season with high within bank flows and flow modification of some anabranches (black triangle ▲). Dispersal patterns of three life history strategies (equilibrium, periodic and opportunistic) are show for each flow scenario. Equilibrium life history strategy larvae typically disperse passively and actively through the riverscape during spawning seasons but river regulation and modification to anabranches reduces the ability of larvae to actively disperse. Periodic life history strategy larvae have little swimming ability and rely on passive dispersal to move to suitable nursery habitat. Under river regulation and modification to the flow regime of anabranches there is a likely increase in the downstream transport of larvae into unsuitable nursery habitat. Opportunistic life history strategy larvae can be found spawning in all four flow scenarios and colonising local suitable nursery habitat. During river regulation and modification to anabranches there is a likely increase in larvae being washed out of suitable habitat and a reduction in the ability of larvae to colonise new habitat.
**Appendix A:** AIC value for the model factors: Section (S), Habitat (H), Depth (D), Velocity (V), with the best fitting modelled factor in bold, and the statistically significant model ***$P<0.05$***, for individual species and total abundance of larvae for Study 1 and Study 2 by sampling date.

<table>
<thead>
<tr>
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<tbody>
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<td><strong>Study 1</strong></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carp</td>
<td>Sept-Oct</td>
<td>198</td>
<td>163***</td>
<td>164</td>
<td>164</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Total abundance</td>
<td>Sept-Oct</td>
<td>430</td>
<td>472</td>
<td>499</td>
<td>458</td>
<td>-</td>
<td>-</td>
<td>356</td>
<td>307</td>
<td>301***</td>
</tr>
<tr>
<td>A smelt</td>
<td>Nov-Dec</td>
<td>84.8</td>
<td>76.3**</td>
<td>77.2</td>
<td>78.3</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><strong>Study 2</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C gudgeon</td>
<td>Nov-Dec</td>
<td>303</td>
<td>322</td>
<td>346</td>
<td>312</td>
<td>256</td>
<td>229***</td>
<td>229</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><strong>Study 1</strong></td>
<td>H</td>
<td>H/V</td>
<td>H/V/S</td>
<td>H/V/S/D</td>
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<tr>
<td>A smelt</td>
<td>Sept-Oct</td>
<td>405</td>
<td>283</td>
<td>263</td>
<td>256**</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td><strong>Study 2</strong></td>
<td>V</td>
<td>V/H</td>
<td>V/H/S</td>
<td>V/H/S/D</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Total abundance</td>
<td>Nov-Dec</td>
<td>283</td>
<td>266</td>
<td>239</td>
<td>235*</td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tbody>
</table>
Appendix B: Photographs of laboratory flume (a) and set up (b) used in Chapter 4.
Appendix C: Photographs of release site (a) and just after the release of larvae and passive particles (b and c) for experimental release described in Chapter 5.
Appendix D: Photographs of Murray cod larvae (a) with yolk sacs and (b) without yolk sacs, found in drift net samples described in Chapter 5.
Appendix E: Figure and table showing the total mean abundance of Murray cod larvae (—) and Murray cod larvae with yolk sac (— • • —) collected in drift nets over the sampling time (h), with 95% confidence limits for the overall mean catch (---) describing data from Chapter 5.

Table showing the total mean abundance of Murray cod larvae and Murray cod larvae with yolk sac collected in drift nets over the sampling time (h), with 95% confidence limits for the overall mean catch from data described in Chapter 5.

<table>
<thead>
<tr>
<th>Time (h)</th>
<th>2000-2100</th>
<th>2100-2200</th>
<th>2200-2300</th>
<th>2300-2400</th>
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<tbody>
<tr>
<td>Mean total larvae</td>
<td>740</td>
<td>751</td>
<td>738</td>
<td>740</td>
<td>744</td>
</tr>
<tr>
<td>- 95%</td>
<td>479</td>
<td>494</td>
<td>479</td>
<td>482</td>
<td>486</td>
</tr>
<tr>
<td>+ 95%</td>
<td>1005</td>
<td>1013</td>
<td>1007</td>
<td>1006</td>
<td>1004</td>
</tr>
<tr>
<td>Yolk sac larvae</td>
<td>550</td>
<td>94</td>
<td>11</td>
<td>2</td>
<td>2</td>
</tr>
</tbody>
</table>
Appendix F: Murray cod null, Murray cod, golden perch null and golden perch linear mixed model results with variance and standard deviation of variance for random effects and estimated standard error and t value for fixed effects for data described in Chapter 5.

<table>
<thead>
<tr>
<th>Murray cod null model</th>
<th>Murray cod model</th>
</tr>
</thead>
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<tr>
<td><strong>Random effects:</strong></td>
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<tr>
<td>time</td>
<td>0.13678</td>
</tr>
<tr>
<td>distance</td>
<td>0.01981</td>
</tr>
<tr>
<td>Residual</td>
<td>0.22275</td>
</tr>
<tr>
<td><strong>Fixed effects:</strong></td>
<td></td>
</tr>
<tr>
<td>Estimate Std.</td>
<td>Error</td>
</tr>
<tr>
<td>0.3866</td>
<td>0.1489</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Golden perch null model</th>
<th>Golden perch model</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Random effects:</strong></td>
<td></td>
</tr>
<tr>
<td>time</td>
<td>0.08889</td>
</tr>
<tr>
<td>distance</td>
<td>0.01071</td>
</tr>
<tr>
<td>Residual</td>
<td>0.07769</td>
</tr>
<tr>
<td><strong>Fixed effects:</strong></td>
<td></td>
</tr>
<tr>
<td>Estimate Std.</td>
<td>Error</td>
</tr>
<tr>
<td>0.1381</td>
<td>0.1103</td>
</tr>
</tbody>
</table>
Appendix G: Publication: Ontogeny of critical and prolonged swimming performance for the larvae of six Australian freshwater fish species.

Ontogeny of critical and prolonged swimming performance for the larvae of six Australian freshwater fish species

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Critical (<30 min) and prolonged (>60 min) swimming speeds in laboratory chambers were determined for larvae of six species of Australian freshwater fishes: trout cod Maccullochella macquariensis, Murray cod Maccullochella peeli, golden perch Macquaria ambigua, silver perch Bidyanus bidyanus, carp gudgeon Hypseleotris spp, and Murray River rainbowfish Melanotisca fluviatilis. Developmental stage (preflexion, flexion, postflexion and metalarval) better explained swimming ability than did length, size or age (days after hatch). Critical speed increased with larval development, and metalarvae were the fastest swimmers for all species. Maccullochella macquariensis larvae had the highest critical [maximum absolute 46:4 cm s\(^{-1}\) and 44.6 relative body lengths (\(L_b\) s\(^{-1}\)) and prolonged (maximum 15.6 cm s\(^{-1}\), 15.6 \(L_b\) s\(^{-1}\)) swimming speeds and B. bidyanus larvae the lowest critical (minimum 0.1 cm s\(^{-1}\), 0.3 \(L_b\) s\(^{-1}\)) and prolonged swimming speeds (minimum 1.1 cm s\(^{-1}\), 1.0 \(L_b\) s\(^{-1}\)). Prolonged swimming trials determined that the larvae of some species could not swim for 60 min at any speed, whereas the larvae of the best swimming species, M. macquariensis, could swim for 60 min at 44% of the critical speed. The swimming performance of species with preocial life-history strategies, with well-developed larvae at hatch, was comparatively better and potentially had greater ability to influence their dispersal by actively swimming than species with altricial life-history strategies, with poorly developed larvae at hatch.

Key words: 0+ year fishes; dispersal; larval development; life-history strategy; rivers.

INTRODUCTION

Downstream dispersal is common during the early life history of riverine fishes. Movement from breeding to nursery habitats is thought to provide enhanced conditions for feeding, while reducing cannibalism and competition (Lowe-McConnell, 1987; Pavlov, 1994). The mode of downstream dispersal, or drift, of free embryos and larvae differs according to a species’ life-history strategy and stage of development but is usually classified as passive (unoriented), active or passive (orientated upstream), or active (orientated downstream) drifting (Pavlov, 1994). Passive drift was considered the most common mode of dispersal for many years, but more recently, this has been questioned (Copp, 1992; Scheidegger & Bain, 1995; Wolter & Sukhodolov, 2008; Schluderer, et al. 2012; Lehner, et al. 2013). Indeed, the dispersal patterns during early life history and how fishes actively influence their position in lotic systems are generally poorly

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understood (Korman et al., 2004; Reichard & Jurajda, 2004; Zitek et al., 2004; Schludermann et al., 2012).

To understand how larvae influence the distance, speed and ultimate destination of their dispersal, it is important to know at what stage during ontogeny effective swimming, the ability to maintain position or orientate in the current develops (Clark et al., 2005). Ontogenetic changes in swimming performance of free embryos and larvae are important to the survival of fishes because this influences habitat use, feeding, escape from predators and ultimately survival. Swimming performance depends on a variety of biological and physical factors (Webb, 1975), such as body shape (Wootton, 1990; Hammer, 1995), formation of fins (Webb, 1984; Plaut, 2001), muscle function (Hammer, 1995; Kieffer, 2000), swimming mode (e.g. undulatory swimming) (Müller et al., 2001), body condition (Wootton, 1990) and water temperature (Ojanguren & Braña, 2000). Absolute swimming performance also increases with size (Webb, 1975; Domenici, 2001). The vast majority of free embryos and larvae of most riverine fishes, however, die before they reach the juvenile stage, and therefore, it is probably reasonable to assume that the larvae that survive in the wild are the best performers in a variety of critical capabilities, including swimming. For this reason, it may be informative to understand not only overall swimming performance of a cohort or species but also variation in performance.

Variation in swimming performance exists within species, for the reasons mentioned above, and among species, probably due to life-history strategy-related differences. Winemiller & Rose (1992) recognize three endpoint life-history strategies: opportunistic and periodic (altricial, Balon, 1986) and equilibrium (precocial, Balon, 1986). The species in the first two life-history strategies tend to be pelagic broadcast spawners, usually have small eggs that typically hatch as planktonic larvae, and occupy habitats with persistent, unpredictable fluctuations or invade new habitats (Winemiller & Rose, 1992). Because of these factors, fishes with opportunistic and periodic life-history strategies will probably be relatively poor swimmers early in ontogeny and be less likely to influence aspects of their dispersal in rivers. Equilibrium strategy species, on the other hand, tend to have larger amounts, or have greater density, of yolk as free embryos, have high investment per offspring, moderate to long generation time and low batch fecundity (Winemiller & Rose, 1992). Because of these factors, these fishes will probably be relatively competent swimmers early in ontogeny and have a relatively greater ability to influence aspects of their dispersal in rivers.

Dispersal during early life history is hazardous for riverine fishes even under the relatively benign conditions of rivers with natural flows. But unique challenges now exist in the form of river regulation and flow alteration. Enhanced flows, because of releases from dams, have been implicated in the demise of native fishes throughout the world (Bain et al., 1988; Bunn & Arthington, 2002; Hauer & Lorang, 2004). Such changes to river flow often result in increased in-channel flow volume and current speeds during the spring and summer growing seasons, which is also typically the peak spawning period of most species of native fishes in the Murray–Darling Basin, southern Australia (Murchie et al., 2008). Most Murray–Darling Basin fishes apparently breed despite flow alteration, but the influence of flow alteration on recruitment is less certain (Walker & Thoms, 1993; Gehrke et al., 1995; Humphries et al., 1999, 2002; King et al., 2009). One reason that native fishes may be in low abundances or absent from flow-altered rivers is the inability during early life history to either maintain position or influence
their dispersal when experiencing the high current speeds, typical of flow-altered rivers during spring and summer (Humphries et al., 2006).

The overall aim of this study was to describe changes in critical and prolonged swimming performance during the early life history of six native fish species. Specifically, the aims were to (1) determine which developmental characteristics (days after hatch, length and developmental stage) best explain critical and prolonged swimming performance and (2) establish if critical swimming speed and prolonged swimming performance vary with ontogeny, species and life-history strategy.

MATERIALS AND METHODS

The free embryos and larvae of Murray cod *Maccullochella peeli* (Mitchell 1838), trout cod *Maccullochella macquariensis* (Cuvier 1829), silver perch *Bidyanus bidyanus* (Mitchell 1838), golden perch *Macquaria ambigua* (Richardson 1845), carp gudgeon *Hypseleotris* spp. and Murray rainbowfish *Melanotaenia fluviatilis* (Castelnau 1878) were used in swimming experiments because they represent the three life-history strategies defined for native fishes from the Murray–Darling Basin and a diversity of sizes and morphologies (Humphries et al., 1999) (Table 1). The first four species were spawned, reared and housed at the New South Wales Inland Fisheries Research Centre (IFRC), Narrandera, New South Wales, from 1 October 2008 to 9 March 2009. The *M. macquariensis* and *M. peeli* free embryos and larvae used in all flume trials came from one cohort, whereas *M. ambigua* and *B. bidyanus* free embryos and larvae came from two cohorts. *Hypseleotris* spp., and *M. fluviatilis* larvae were collected using modified quatrefoil light traps (Floyd et al., 1984; Secor et al., 1992; Humphries et al., 2002), from ponds at the Inland Fisheries Research Centre on 9 and 12 December 2008. Traps were set at sunset for 10 h. Only metalarvae were able to be collected for these two species. Age (A) (days post hatch, d.p.h.) was not known and it was beyond the scope of this study to validate age increments and hackcalculate A using otoliths for these two species.

Fish were grouped into four developmental stages, determined by the state of flexion of the notochord and fin-ray development (preflexion, flexion, postflexion and metalarvae), as proposed by Kelso & Rutherford (1996). It is recognized, however, that there are other classifications (Balon, 1975), and this study endeavours to make terminology compatible with both. After each trial, larvae were preserved in 70% ethanol, standard length (Ls) was measured to 0.1 mm using vernier callipers and A was recorded (d.p.h.).

EXPERIMENTAL SETUP AND DESIGN

The swimming chamber used in this experiment was as described in Stobutzki & Bellwood (1997). This chamber was constructed from Perspex, with six raceways, each measuring 30 W×50 H×180 L mm. Flow was controlled with T-piece diffuser and straighteners. Previous studies have established negligible boundary layers within raceways of this type of flume (Stobutzki & Bellwood, 1997; Stobutzki, 1998; Fisher et al., 2000). This study follows the design and principle of Stobutzki & Bellwood (1997), which has addressed boundary layer issues using large swimming chambers relative to the size of the fish studied and videoing neutrally buoyant particles moving past a grid. Stobutzki & Bellwood (1997) found that interactions with the boundary layer were negligible, as the water velocity in the 0.5 cm closest to the wall was not significantly different from that in the centre of the chamber.

Current speed was calibrated by recording the amount of time it took for water flowing out of the raceway to fill a container of a known volume. Fill time was divided by the cross-section area of the chamber. Each day an experiment was run, the chamber was calibrated three times for each of the five velocity increments used in the study.

Groundwater was used for the flume experiments and was the same water used to rear fishes in tanks and maintain them in ponds. *Maccullochella peeli* and *M. macquariensis* were free embryos and fed endogenously from their yolk sacs for the entire experiment, but gradually lost yolk as they developed. *Bidyanus bidyanus* and *M. ambigua* were not fed for the first 3 days,
TABLE I. Life-history strategy characteristics for six species of larvae used in this experiment after Humphries et al. (1999), with comparisons to the life-history strategies described by Balon (1986) and Winemiller & Rose (1992)

<table>
<thead>
<tr>
<th>Characteristics</th>
<th>Strategy 1</th>
<th>Strategy 2</th>
<th>Strategy 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Life-history type</td>
<td>Precocial, equilibrium</td>
<td>Altricial, periodic</td>
<td>Altricial, opportunistic</td>
</tr>
<tr>
<td>Adult size and longevity</td>
<td>Large, 25+ years</td>
<td>Medium, 7–10 years</td>
<td>Small, 2–3 years</td>
</tr>
<tr>
<td>Spawning</td>
<td>Short, single spawning, same time annually</td>
<td>Single variable spawning, October to March</td>
<td>Short single spawn</td>
</tr>
<tr>
<td>Eggs</td>
<td>Up to 10,000 s, demersal</td>
<td>100,000 semi-buoyant or planktonic</td>
<td>Up to 1000 s, planktonic or demersal</td>
</tr>
<tr>
<td>Embryo and larva parental care</td>
<td>Yes</td>
<td>No</td>
<td>No</td>
</tr>
<tr>
<td>Development of larvae up to first feed</td>
<td>Well developed, highly mobile</td>
<td>Undeveloped, limited mobility</td>
<td>Undeveloped, limited mobility</td>
</tr>
<tr>
<td>Example species</td>
<td>Maccullochella macquariensis, Maccullochella peelli</td>
<td>Macquaria ambiguа, Bidyatus bidyanus</td>
<td>Hypleotris spp., Melanotaenia fluitatilis</td>
</tr>
</tbody>
</table>

when they were free embryos feeding endogenously. They were then transferred into a pond with a self-sustaining, unregulated population of zooplankton upon which they could feed freely. *Bidyatus bidyanus* and *M. ambiguа* did not have yolk sacs during swimming trials, whereas *M. peelli* and *M. macquariensis* changed from having relatively large yolk sacs at the start to having very small yolk sacs at the end of the trials. This study chose to focus on comparing life stages, regardless of feeding strategy, even though the presence or absence of a yolk sac may influence swimming performance. The timing of the change from endogenous to exogenous feeding differs among individuals, making any comparison difficult and outside the scope of this study. Immediately before the experiments began, *M. peelli* and *M. macquariensis* larvae were transferred from rearing troughs and *B. bidyanus* and *M. ambiguа* were collected from ponds and acclimated for 5 min in the flume at a speed of 0.5 cm s\(^{-1}\) with one individual in each raceway. Any fish exhibiting signs of stress during acclimation were removed and replaced.

Researchers routinely investigate swimming performance by determining critical (≤60 min), prolonged (>60–200 min) or sustained (>200 min) swimming performance (Webb, 1975; Beamish, 1978; Leis et al., 2007). Critical and prolonged swimming trials were conducted separately (Table II). For critical swimming experiments, six fish, each in separate raceways, were initially exposed to a current speed of 1.1 cm s\(^{-1}\), with this speed increasing by 4-8 cm s\(^{-1}\) every 5 min until fish could no longer maintain position and were forced against the rear screen of the flume. The time at which fish were unable to maintain position was recorded; critical swimming experiments did not exceed 30 min. Critical swimming trials were repeated five times, so that 30 fish of each stage of each species were swum, one species at a time. All individual fish were swum only once and not re-used in any other experiments. Critical swimming speed (\(U_{\text{crit}}\)) was calculated following Brett (1964): \(U_{\text{crit}} = U + [t (t_i U_i)^{-1}]\), where \(U = \) penultimate speed, \(U_i = \) velocity increment (4-8 cm s\(^{-1}\)), \(t = \) time swum and \(t_i = \) time interval at each speed increment (5 min). An advantage of using \(U_{\text{crit}}\) to investigate ontogeny of swimming performance is the ability to compare swimming speed among developmental stages and among species (Leis et al., 2007). Critical speed is a laboratory measure of forced
Table II. Number of individuals of each developmental stage of the six fish species included in swimming trials (number of cohorts in parentheses), with ranges of days post hatch (d.p.h.) and standard lengths ($L_s$) for the six species when known. Included are measurements taken during swimming trials.

<table>
<thead>
<tr>
<th>Developmental stages</th>
<th>Macquaria macquariensis</th>
<th>Macquaria peeli</th>
<th>Macquaria ambigua</th>
<th>Bidyanus bidyanus spp.</th>
<th>Hyseleotris spp.</th>
<th>Melanotaenia fluviatilis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Preflexion</td>
<td>51 (1)</td>
<td>30 (1)</td>
<td>63 (1)</td>
<td>29 (1)</td>
<td>No data</td>
<td>No data</td>
</tr>
<tr>
<td>Flexion</td>
<td>29 (1)</td>
<td>30 (1)</td>
<td>20 (1)</td>
<td>54 (2)</td>
<td>No data</td>
<td>No data</td>
</tr>
<tr>
<td>Postflexion</td>
<td>30 (1)</td>
<td>30 (1)</td>
<td>39 (2)</td>
<td>31 (1)</td>
<td>No data</td>
<td>No data</td>
</tr>
<tr>
<td>Metalarvae</td>
<td>29 (1)</td>
<td>30 (1)</td>
<td>31 (1)</td>
<td>28 (1)</td>
<td>36</td>
<td>21</td>
</tr>
<tr>
<td>Age (d.p.h.)</td>
<td>3–14</td>
<td>3–17</td>
<td>10–25</td>
<td>3–15</td>
<td>Unknown</td>
<td>Unknown</td>
</tr>
<tr>
<td>$L_s$ (mm)</td>
<td>6–3–10.9</td>
<td>7.4–10.6</td>
<td>4.5–11.9</td>
<td>4.7–11.4</td>
<td>9.1–14.6</td>
<td>9.8–12.1</td>
</tr>
</tbody>
</table>

performance over a relatively short period and probably does not represent cruising speed of free embryos and larvae in the wild.

In the wild, it is difficult to separate prolonged swimming speed from sustained swimming speed because true fatigue cannot be determined (Beamish, 1978; Plaut, 2001). With this in mind, prolonged swimming trials were conducted at two speeds, to represent more realistic in situ swimming and current speeds (Leis & Carson-Ewart, 1997, Leis & Stobutzki, 1999). Prolonged swimming capabilities were measured by swimming fishes continuously at a single speed for 61 min. Replicate individual larvae ($n = 6$) of each species were swum, with no individual fish swum in more than one trial and not re-used in any other experiments (Table II). Fishes were initially swum at one increment (4.8 cm s$^{-1}$) lower than the fastest mean $U_{crit}$ of that species. Then, if they tired before 60 min, another prolonged swimming trial was completed with different individuals of the same species and was swum at two increments (9.6 cm s$^{-1}$) lower than the mean $U_{crit}$. Fishes were swum until the speed at which 75% of individuals could swim for 61 min was determined.

DATA ANALYSIS

To establish the best predictor of swimming performance, generalized linear models (GLMs) were developed for $U_{crit}$, using three variables potentially affecting swimming performance: $L_s$ that was transformed using ln, $A$ (d.p.h.) and developmental stage ($S_p$). These three variables are measures of growth, physically and physiologically. GLMs for $U_{crit}$ used cm s$^{-1}$ because statistical comparisons showed little difference between $U_{crit}$ as measured in body lengths ($L_B$) cm s$^{-1}$ or cm s$^{-1}$. $L_s$ and $A$ are continuous data, whereas $S_p$ is categorical, and analysis and presentation of results take this into account by separating results into each stage. Akaike information criterion (AIC) (Akaike, 1973), one of the many model selection methods that prioritize models based on their fitting ability and level of parsimony, was used to determine which variable was most efficient. The variable with the lowest AIC value was selected for further modelling. Three GLMs were developed, using the best variable and subsequent combinations of variables, e.g. model 1: $S_p$, model 2: $S_p$ and $L_s$ or model 3: $S_p$, $L_s$ and $A$. An ANOVA (95% c.t.) was undertaken to determine if there was a significant difference between the three models. If there was no significant difference among the models, the simplest model was used. Only metalarval Hyseleotris spp. and M. fluviatilis were collected for swimming performance trials, so these species could not be included in GLM analysis. Data were analysed using the R statistical package (R 2.9.0, R Development Core Team; www.r-project.org).

Macquaria ambigua and B. bidyanus larvae came from two cohorts each. To determine if variation in swimming performance was greater within cohorts than among cohorts, cohorts were compared statistically using ANOVA on log$_{10}$-transformed data. There was no significant difference in the swimming performance among cohorts for M. ambigua or B. bidyanus larvae ($P > 0.05$) and so the cohorts were not treated separately.

Swimming performance ($U_{crit}$) has been reported in this study as $L_B$ s$^{-1}$, a relative measurement, and as swimming speed, cm s$^{-1}$, an absolute measurement because both of these measures are used commonly throughout the literature. Kruskal–Wallis tests were used to determine if there were differences in the swimming performance among species and among fishes from different life-history strategies and, if significant, Mann–Whitney U-tests were used to make pair-wise comparisons. Adjustments for multiple tests were made using the Bonferroni correction. To estimate performance of theoretical wild-surviving best performers, the top 25% swimming individuals for each development stage were also assessed for each species. Prolonged swimming speeds are expressed both as absolute speeds and as percentages of mean critical speeds, at which 75% of larvae of each species and developmental stage could swim for $>60$ min. All data were analysed at $\alpha = 0.05$ level, using SPSS 17.0 (SPSS Inc.; http://www-01.ibm.com/software/analytics/spss/).

RESULTS

BEST PREDICTORS OF CRITICAL AND PROLONGED SWIMMING PERFORMANCE

All fishes showed rheotaxis when placed in the flume and swim against the current for the entire 5 min acclimation period. *Maccullochella macquariensis* and *M. peelli* swam along the bottom, whereas the other species swam mostly in mid-water. $U_{crit}$ increased with age, size and development stage for all species (Figs 1 and 2). Metalarvae were able to swim against the fastest currents, with $U_{crit}$ ranging from 25.4 to 46.4 cm s$^{-1}$ and 23.3 to 44.6 L$B$ s$^{-1}$ (*B. bidyanus* and *M. macquariensis*), at $L_S$ from 10.3 to 14.6 mm (*M. peelli* and *Hypseleotris* spp.). *Maccullochella macquariensis* metalarvae were the fastest swimming larvae (maximum 46.4 cm s$^{-1}$, 44.6 L$B$ s$^{-1}$) while *B. bidyanus* preflexion larvae were the slowest (minimum 0.1 cm s$^{-1}$, 0.3 L$B$ s$^{-1}$). The largest swimming larva was a *Hypseleotris* spp. metalarva (14.6 mm) and the smallest was a *B. bidyanus* preflexion larva (4.7 mm). *Macquaria ambigua* metalarvae were the oldest larvae used in swimming trials (25 d.p.h.) and *M. macquariensis*, *M. peelli* and *B. bidyanus* preflexion larvae were the youngest (3 d.p.h.).

Generally, AIC indicated that $S_D$ was overall the factor that best explained swimming performance for average and best performers (top 25%) (Table III). $S_B$ best explained swimming performance for *M. peelli* (AIC 747.96, 116, $P < 0.001$), *B. bidyanus* (AIC 655.90, 138, $P < 0.001$) and *M. macquariensis* (AIC 851.84, 133, $P < 0.001$); and, alone, this factor explained 68 and 55% of the variance in swimming performance of *M. peelli* and *B. bidyanus*. Variability in $U_{crit}$ of *M. macquariensis* was best explained by $L_S$, $A$ and $S_D$ ($r^2 = 0.69$). The only species not to include $S_D$ as the best explainer of swimming speed was *M. ambigua* (AIC 908.93, 151, $P < 0.001$), for which $L_S$ was pre- eminent ($r^2 = 0.58$). $S_D$ was also included in all GLMs explaining the swimming speed of the best performers. Models using only developmental stage explained the most variance in swimming speed of *M. peelli* (AIC 156.50, 34, $P < 0.001$), *B. bidyanus* (AIC 193.52, 34, $P < 0.001$) and *M. macquariensis* (AIC 208.39, 34, $P < 0.001$) ($r^2 = 0.96, 0.67$ and $0.78$), but the variance in swimming speed of larval *M. ambigua* best performers (AIC 212.91, 38, $P < 0.001$) was significantly better when $L_S$ and $S_D$ ($r^2 = 0.88$) were included as predictors of swimming ability.
ONTOPGENY IN SWIMMING PERFORMANCE

For *M. macquariensis*, *M. peelli*, *M. ambiguus* and *B. bidyanus*, $U_{\text{crit}}$ differed among the four developmental stages (Kruskal–Wallis, d.f. = 3, $P < 0.001$) (Table IV and Fig. 3). *Maccullochella macquariensis*, *M. peelli* and *B. bidyanus* each had two sequential developmental stages that did not vary significantly from each other in swimming performance, but the stages for which this occurred were not consistent. There was no significant increase in swimming performance of *M. macquariensis* and *B. bidyanus* larvae between the flexion and postflexion stages and for *M. peelli* between the postflexion and metalarval stage. *Macquaria ambiguus* larvae showed a significant difference in $U_{\text{crit}}$ among all developmental stages (Fig. 3).

$U_{\text{crit}}$ differed among the four developmental stages for best performers in a pattern similar to that of all individuals (Kruskal–Wallis, d.f. = 3, $P < 0.001$) (Table IV and Fig. 3). The exceptions were that there were no significant differences in the swimming speeds between preflexion and flexion *M. ambiguus* ($P > 0.05$) and best performing *M. macquariensis* larvae showed no difference among the preflexion, flexion and postflexion development stages for $U_{\text{crit}}$.

COMPARISONS OF CRITICAL SPEED OF AVERAGE AND BEST PERFORMERS AMONG SPECIES

Comparisons of $U_{\text{crit}}$ of average and best performer for all life stages were made for *M. peelli*, *M. macquariensis*, *M. ambiguus* and *B. bidyanus*, but only the metalarval stage was included for all the six species (Table V and Fig. 4). Results indicated that there were almost always significant differences among all species within a life stage. In most cases, *M. macquariensis* and *M. peelli* had the highest average and best performer $U_{\text{crit}}$ of all species. Although the speeds for *M. macquariensis* were initially
similar or greater than those of *M. peeli*, swimming speeds for *M. peeli* postflexion larvae were significantly greater than for *M. macquariensis* larvae at the same stage and reached similar levels to those of metalarvae. The next fastest swimmers were *M. ambiguа*, with *B. bidyanus* being the poorest swimmers overall. *Macquaria ambiguа*, *Hypseleotris* spp. and *M. fluviatilis* metalarvae had similar swimming speeds, but these were significantly slower than for *M. macquariensis* and *M. peeli*.

Generally, *U*\textsubscript{crit} of the best performers (top 25%) of all species was considerably greater than for all larvae, at any given developmental stage (0-91-22-15 cm s\textsuperscript{-1} or 1-60-16-61 L\textsubscript{B} s\textsuperscript{-1}) (Figs 3 and 4). The difference between all and best performers was least for *B. bidyanus* (0-91 cm s\textsuperscript{-1}, 1-06 L\textsubscript{B} s\textsuperscript{-1}). The greatest contrast was for *Hypseleotris* spp. metalarvae best performers whose *U*\textsubscript{crit} was 22-15 cm s\textsuperscript{-1} and 16-61 L\textsubscript{B} s\textsuperscript{-1} faster than all larvae. Although *Hypseleotris* spp., *M. ambiguа* and *M. fluviatilis* had similar swimming speeds, *Hypseleotris* spp. had faster best performing swimmers than *M. ambiguа* and *M. fluviatilis*.

**Comparisons Among Life-History Strategies**

There was a significant difference in average and best performer *U*\textsubscript{crit} of metalarvae among almost all the three life-history strategies (Fig. 5 and Table VI). Only strategies 2 and 3 metalarvae showed similar values and a non-significant difference. Of the three life-history strategies, the fastest metalarvae were from strategy 1 (25-3-46-4 cm s\textsuperscript{-1}, 23-8-44-6 L\textsubscript{B} s\textsuperscript{-1}), more than twice as fast as the average of strategy 2 metalarvae (6-0-26-4 cm s\textsuperscript{-1}, 5-3-27-9 L\textsubscript{B} s\textsuperscript{-1}), the slowest life-history strategy. The *U*\textsubscript{crit} of strategy 3 fish was intermediate between strategy 1 and 2 fish.
**Table III.** Generalized linear model (GLM) relationships between growth characteristic [standard length ($L_S$), age ($A$; days post hatch, d.p.h.) and developmental stage ($S$) described as $S_{Dpre}$ (preflexion), $S_{Dflex}$ (flexion), $S_{Dpost}$ (postflexion) and $S_{DMeta}$ (metalarvae)] and critical swimming speed ($U_{crit}$) for all larvae and only best performers; *Hypseleotris* spp. and *Melanotaenia fluviatilis* include only metalarvae developmental stage.

<table>
<thead>
<tr>
<th>Species</th>
<th>$r^2$</th>
<th>$n$</th>
<th>$U_{crit}$ (cm s$^{-1}$) for all larvae</th>
<th>$r^2$</th>
<th>$n$</th>
<th>$U_{crit}$ (cm s$^{-1}$) for best performers</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Maccullochella macquariensis</em></td>
<td>0.69</td>
<td>139</td>
<td>25.2926 $L_s$ -1.5642 $A$ -0.1713 $S_{Dpre}$</td>
<td>0.78</td>
<td>38</td>
<td>23.0327 $S_{Dpre}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>25.2926 $L_s$ -1.5642 $A + (6.0625 - 0.1713) S_{Dflex}$</td>
<td></td>
<td></td>
<td>23.0327 + 1.4756 $S_{Dflex}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>25.2926 $L_s$ -1.5642 $A + (11.0640 - 0.1713) S_{Dpost}$</td>
<td></td>
<td></td>
<td>23.0327 + 1.4827 $S_{Dpost}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>25.2926 $L_s$ -1.5642 $A + (31.3128 - 0.1713) S_{DMeta}$</td>
<td></td>
<td></td>
<td>23.0327 + 16.9357 $S_{DMeta}$</td>
</tr>
<tr>
<td><em>Maccullochella peeli</em></td>
<td>0.68</td>
<td>120</td>
<td>11.4748 $S_{Dpre}$</td>
<td>0.96</td>
<td>38</td>
<td>16.3156 $S_{Dpre}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>11.4748 + 8.4248 $S_{Dflex}$</td>
<td></td>
<td></td>
<td>16.3156 + 8.6769 $S_{Dflex}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>11.4748 + 17.3623 $S_{Dpost}$</td>
<td></td>
<td></td>
<td>16.3156 + 20.1176 $S_{Dpost}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>11.4748 + 19.4447 $S_{DMeta}$</td>
<td></td>
<td></td>
<td>16.3156 + 20.8244 $S_{DMeta}$</td>
</tr>
<tr>
<td><em>Macquaria ambigu</em></td>
<td>0.58</td>
<td>150</td>
<td>28.7990 $L_s$ -12.8490</td>
<td>0.88</td>
<td>43</td>
<td>21.4300 $L_s$ -2.5050 $S_{Dpre}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>21.4300 $L_s + (2.4210 - 2.5050) S_{Dflex}$</td>
<td></td>
<td></td>
<td>21.4300 $L_s + (5.9220 - 2.5050) S_{Dpost}$</td>
</tr>
<tr>
<td><em>Bidyanus bidyanus</em></td>
<td>0.55</td>
<td>142</td>
<td>0.8061 $S_{Dpre}$</td>
<td>0.67</td>
<td>36</td>
<td>1.8490 $S_{Dpre}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.8061 + 1.5289 $S_{Dflex}$</td>
<td></td>
<td></td>
<td>1.8490 + 2.5650 $S_{Dflex}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.8061 + 1.2041 $S_{Dpost}$</td>
<td></td>
<td></td>
<td>1.8490 + 2.5930 $S_{Dpost}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.8061 + 7.5341 $S_{DMeta}$</td>
<td></td>
<td></td>
<td>1.8490 + 12.2040 $S_{DMeta}$</td>
</tr>
<tr>
<td><em>Hypseleotris</em> spp.</td>
<td>0.24</td>
<td>54</td>
<td>37.4880 $L_s$ -29.2540</td>
<td>0.75</td>
<td>10</td>
<td>52.7710 $L_s$ -40.3000</td>
</tr>
<tr>
<td><em>Melanotaenia fluviatilis</em></td>
<td>0.38</td>
<td>36</td>
<td>52.3240 $L_s$ -38.4040</td>
<td>0.50</td>
<td>6</td>
<td>5.2610 $L_s$ -35.7530</td>
</tr>
</tbody>
</table>

$n$, sample size.
Table IV. Within species Mann-Whitney U-test results of all and best performers for critical swimming speeds (Ucrit) as cm s\(^{-1}\) and body lengths (L\(_B\)) s\(^{-1}\) for the developmental stages of the four species studied, grouped by species; Bonferroni correction meant that only for P<0.001 were tests significant (***) ; # non-significant in L\(_B\) s\(^{-1}\) comparisons at the P<0.001 level; † significant in L\(_B\) s\(^{-1}\) at the P<0.001 level but not for cm s\(^{-1}\).

<table>
<thead>
<tr>
<th>Ontogeny</th>
<th>M. macquariensis</th>
<th>M. peelli</th>
<th>M. ambigua</th>
<th>B. bidyanus</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Flex</td>
<td>Post</td>
<td>Meta</td>
<td>Flex</td>
</tr>
<tr>
<td>All performers</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Prefixon</td>
<td>439.5***</td>
<td>479.5***</td>
<td>3.0***</td>
<td>80.0***</td>
</tr>
<tr>
<td>Flexion</td>
<td>430.0</td>
<td>12.0***</td>
<td></td>
<td>93.5***</td>
</tr>
<tr>
<td>Best performers</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Prefixon</td>
<td>43.0</td>
<td>52.0</td>
<td>76.0***</td>
<td>108.0***</td>
</tr>
<tr>
<td>Flexion</td>
<td>30.5</td>
<td>64.0***</td>
<td></td>
<td>96.0***</td>
</tr>
<tr>
<td>Postflexion</td>
<td>64.0***</td>
<td></td>
<td>33.0</td>
<td></td>
</tr>
</tbody>
</table>
Fig. 3. Box plots (median, range, first quartile and third quartile) for critical swimming speed ($U_{cr}$, cm s$^{-1}$) and body lengths ($L_y$) s$^{-1}$ and standard length ($L_o$) for all larvae of six species and four developmental stages (Pre, prefexion; Flex, flexion; Post, postflexion; Meta, metamorphosis) for (a) Macquodella macquariensis, (b) Macquodella pecki, (c) Macquaria ambigua, (d) Bidyanus bidyanus, (e) Hypselotris spp., and (f) Melanotaenia fluviatilis (numbers are sample sizes). Only metamorphs were available for Hypselotris spp. and M. fluviatilis, and age was not known for these species.
<table>
<thead>
<tr>
<th>Species</th>
<th>Prefixon</th>
<th>Flexion</th>
<th>Postflexion</th>
<th>Metalarvae</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All performers</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maccullochella macquariensis</td>
<td>521.0</td>
<td>229.0***</td>
<td>1479.0***</td>
<td>399.0***</td>
</tr>
<tr>
<td>Maccullochella peelli</td>
<td>153.0***</td>
<td>870.0***</td>
<td>15.0***</td>
<td>1620.0***</td>
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<tr>
<td>Macquaria ambigua</td>
<td>320.0***</td>
<td>73.0***</td>
<td>31.0***</td>
<td>98.0***</td>
</tr>
<tr>
<td>Bidyanus bidyanus</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hypseleotris spp.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Best performers</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maccullochella macquariensis</td>
<td>5.0***</td>
<td>216.0***</td>
<td>96.0***</td>
<td>28.5</td>
</tr>
<tr>
<td>Maccullochella peelli</td>
<td>11.5***</td>
<td>56.0***</td>
<td>60.0***</td>
<td>180.0***</td>
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<tr>
<td>Macquaria ambigua</td>
<td>144.0***</td>
<td>75.0***</td>
<td>80.0***</td>
<td>70.0</td>
</tr>
<tr>
<td>Bidyanus bidyanus</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Hypseleotris spp.</td>
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</tbody>
</table>
Fig. 4. Box plots (median, range, first quartile and third quartile) for critical swimming speed ($U_{crit}$) in cm s$^{-1}$ and body lengths ($L_B$) s$^{-1}$ and standard length ($L_S$) for the best performers of six species and (Pre, preflexion; Flex, flexion; Post, postflexion; Meta, metalarva) for (a) Macullochella macquariensis, (b) Macullochella peeli, (c) Macquaria ambiguus, (d) Bledanus bidyanus, (e) Hypseleotris spp. and (f) Melanotaenia fluviatilis (numbers are sample sizes). Only metalarvae were available for Hypseleotris spp. and M. fluviatilis, and age was not known for these species.
PROLONGED SWIMMING

Overall, _M. macquariensis_ had the highest prolonged swimming speeds, and _B. bidyanus_ had the lowest prolonged swimming speeds, of all species tested (Table VII). Indeed, metalarval _M. macquariensis_ could swim for >60 min at 44% of the mean _U_crit. Preflexion, flexion and postflexion _B. bidyanus_, on the other hand, could not swim at any speed for >60 min. Generally, _M. macquariensis_ and _M. peelii_ were able to swim at least 30% of the mean critical speed for >60 min, whereas for _M. ambiguus_ and _Bidyanus bidyanus_, either prolonged swimming performance was variable among developmental stages or uniformly poor.

| Table VI. Mann–Whitney _U_-test results of all and best performers for critical swimming speeds [ _U_ \_crit \_ cm s\^\-1 and body lengths ( _L_ 3) \_ s\^\-1] for the three life-history strategies (LHS) studied: S1 (LHS 1), S2 (LHS 2) and S3 (LHS 3); Bonferroni correction meant that only for _P_ \_< 0.01 were tests significant (**); *non-significant in _L_ 3 \_ s\^\-1 comparisons at the _P_ \_< 0.01 level |

<table>
<thead>
<tr>
<th></th>
<th>All performers</th>
<th>Best performers</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LHS</td>
<td>S2</td>
<td>S3</td>
</tr>
<tr>
<td>S1</td>
<td>59.0**</td>
<td>237.0**</td>
</tr>
<tr>
<td>S2</td>
<td>1291.5</td>
<td>79.0**</td>
</tr>
<tr>
<td>S3</td>
<td>0.0**</td>
<td>13.0**</td>
</tr>
</tbody>
</table>

SWIMMING PERFORMANCE OF AUSTRALIAN FISHES

Table VII. Prolonged swimming performance speed (cm s\(^{-1}\)) at which > 75% of larvae completed the 60 min swimming trial, with per cent of the prolonged swimming speed compared with the mean critical swimming speed in parentheses

<table>
<thead>
<tr>
<th>Species</th>
<th>Preflexion</th>
<th>Flexion</th>
<th>Postflexion</th>
<th>Metalarvae</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Maccullochella macquariensis</em></td>
<td>5.9 (26)</td>
<td>5.9 (32)</td>
<td>5.9 (32)</td>
<td>15.4 (23)</td>
</tr>
<tr>
<td><em>Maccullochella peeli</em></td>
<td>1.1 (10)</td>
<td>5.9 (34)</td>
<td>10.7 (27)</td>
<td>10.7 (29)</td>
</tr>
<tr>
<td><em>Macquaria ambiguа</em></td>
<td>1.1 (3)</td>
<td>1.1 (10)</td>
<td>1.1 (10)</td>
<td>5.9 (32)</td>
</tr>
<tr>
<td><em>Bidyanus bidyanus</em></td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>1.1 (8)</td>
</tr>
</tbody>
</table>

DISCUSSION

COMPARISONS OF SWIMMING PERFORMANCE OF MURRAY-DARLING BASIN WITH OTHER FRESHWATER FISHES

This is the first study to determine the critical and prolonged swimming speeds of the larvae of Australian riverine fishes, which means that comparisons with other Australian species are not possible. There are also few studies elsewhere in the world that have tested the swimming performance of larvae of comparable sizes to those included in this study (Wolter & Arlinghaus, 2003). The six species, which included preflexion larvae to metalarvae (4.7–14.6 mm), had \( U_{crit} \) (swam <60 min) values between 0.1 cm s\(^{-1}\) or 0.3 \( L_B \) s\(^{-1}\) (B. bidyanus preflexion) and 46.4 cm s\(^{-1}\) or 44.6 \( L_B \) s\(^{-1}\) (M. macquariensis metalarvae) and prolonged swimming (swam >60 min) values between 0 cm s\(^{-1}\) or 0 \( L_B \) s\(^{-1}\) (B. bidyanus preflexion, flexion and postflexion) and 15.6 cm s\(^{-1}\) or 20.1 \( L_B \) s\(^{-1}\) (M. macquariensis metalarvae). Of those studies that have tested larvae of comparable sizes and under comparable conditions, walleye *Sander vitreus* (Mitchell 1818) (\( L_B \) 10.5 mm, 13° C) and yellow perch *Perca flavescens* (Mitchell 1814) (\( L_B \) 10.5 mm, 13° C) swam at a mean \( U_{crit} \) of 3.2 cm s\(^{-1}\) for 10 min (Houde, 1969), European chub *Leuciscus cephalus* (L. 1758), dace *Leuciscus leuciscus* (L. 1758) and roach *Rutilus rutilus* (L. 1758) swam at \( U_{crit} \) of 10.5, 20.9 and 11.26 cm s\(^{-1}\) (8–22° C, \( U_{crit} \) derived from equations for \( L_B \) 10 mm) for 3 min (Cowx & Welcomme, 1998; Garner, 1999) and Danube bleak *Alburnus chalcoides* (Güldenstädt 1772) (\( L_B \) 9 mm, 15–20° C) swam at a mean \( U_{crit} \) of 6.3–7.8 cm s\(^{-1}\) (Wieser & Kaufmann, 1998). *Maccullochella macquariensis* and *M. peeli* larvae had faster mean \( U_{crit} \) than the larvae of all of those species above. *Macquaria ambiguа* larvae had faster mean \( U_{crit} \) than all species except *L. leuciscus*, and *B. bidyanus* larvae, the poorest swimmer, had faster mean \( U_{crit} \) than the larvae of *S. vitreum* and *P. flavescens*, but slower than the remaining.

ONTOGENY AND SWIMMING PERFORMANCE

Critical speed increased with ontogeny for the larvae of species investigated in this study, which agrees with trends found for other fishes (Wieser & Kaufmann, 1998; Garner, 1999; Fisher et al., 2000, Clark et al., 2005). Swimming performance was best explained by developmental stage for the majority of species, except *M. ambiguа*, for which length was the best explanatory variable. In general, age did not explain variation in swimming performance well. While developmental stage is related to body length, there is considerable overlap in length for larvae at different stages, and it was
apparent that changes from one stage to the next influenced a larva’s swimming performance more than simply increase in length. Even though variation in length at age was higher in the two species that had larvae from more than one cohort (B. bidyanus and M. ambiguus) than the other species, this reinforces the findings that developmental stage is a better predictor of swimming performance. Yolk sac absorption was not uniform over time within species and may influence swimming ability because of drag. Precocial life-history strategy 1 fish, M. macquariensis and M. peeli retain their yolk sacks longer than any of the other species in this study and indeed still had vestiges of yolk throughout the trials. While the effects of yolk sac size on swimming performance were not measured in the current study and is not commonly reported in similar experiments, it warrants further investigation in future research. As larvae were used in only one trial, there is no effect of individual growth rate on results. Clark et al. (2005) also found that for the larvae of four species of temperate marine fishes, endurance swimming performance increased after notochord flexion. Many studies use only length to explain larval swimming performance (Houde 1969; Wieser & Kaufmann, 1998; Garner, 1999; Wolter & Arlinghaus, 2003), which runs counter to what is known of patterns of ontogenesis in fishes. Balon (1981, 1986) describes morphological and physiological changes during ontogeny as ‘bursts and intermissions’ or saltatory growth and development. While rates of change during ontogeny remain an area of debate, and some contend that development is gradual (Fuiman & Werner, 2002), the consensus seems to be that there is constant development, interspersed with periods of more rapid change (Kamler, 2002). As a result, changes in performance through development are not a continuum of gradual improvements, but stepwise changes, as reflected in larvae development and as demonstrated in this study.

Most species in this study showed an intermission in swimming performance, e.g. between flexion and postflexion in M. macquariensis, and only M. ambiguus showed consistent improved swimming performance through all developmental stages. Nevertheless, for each species, the overall improvement throughout ontogeny indicated little change between stages, but instead bursts in performance associated with changes in morphology. While larvae grow, the notochord flexes and, at the same time, fin ray development starts. These morphological changes provide support and an anchor point for developing muscle, increasing swimming capability of larvae (Webb, 1975).

Swimming performance increases predominately during the metalarval development stage for M. ambiguus and B. bidyanus, when all fins are most developed. This may fit the altricial life-history strategy, strategy 2, of broadcast spawners that require increased swimming performance at the end of larval development, when larvae are about to settle out of the pelagic drifting stage into habitat to change to the juvenile life stage. Macullochella macquariensis show the largest increase in swimming performance at the metalarval stage, whereas M. peeli have the greatest increase between the flexion and postflexion stage. It would make sense for these species to have the largest increase in swimming performance between parental care in the nest and entering the drift, as drifting is a targeted, purposeful event to disperse downstream, in contrast to the broadcast spawning strategy of altricial life history strategy 2 M. ambiguus and B. bidyanus (Humphries et al. 1999). A burst in swimming performance during the metalarval stage of M. macquariensis may be due to conditions in which larvae are found. They tend to occupy more upland stream habitat than do M. peeli, and the faster current velocities, cooler water and lower densities of food
may make it advantageous to drift at a later, more developed stage (Harris & Rowland, 1996).

**LIFE-HISTORY STRATEGIES AND SWIMMING PERFORMANCE**

The swimming performances of all species are consistent with what would be predicted by life-history theory, which has correlates for other groups, such as salmonids in the northern hemisphere (Patterson *et al.*, 2004; Eklason *et al.*, 2011). This study has developed a conceptual model to link life history, swimming performance and dispersal patterns in riverine fishes, using species swum in this study as models (Fig. 6). It must be borne in mind, however, that *M. macquariensis* and *M. peeli* share a similar life-history strategy and are related phylogenetically and so confound the comparison somewhat. These strategy 1 species (Humphries *et al.*, 1999) can be classified as precocial (Balon, 1986) or equilibrium (Winemiller & Rose, 1992) species. The larvae are well developed at hatch, undergo parental care for a considerable period and begin to disperse as relatively large larvae, with large pectoral fins and usually some development of the second dorsal and caudal fins (Cadwallader *et al.*, 1979; Ingram & Rimmer, 1992; Humphries *et al.*, 1999; Humphries, 2005; Koehn & Harrington, 2006). The $U_{crit}$ of the metalarvae of *M. macquariensis* and *M. peeli*, strategy 1 species,

Fig. 6. Schematic representing hypothesized dispersal pathways for larvae of the three life-history strategies used in this study based on swimming performance. (a) Life-history strategy 1 species spawned at predictable times each year, larvae swim strongly and are probably able to determine their dispersal pathways into and out of slackwater habitats, as they move downstream and perhaps even move upstream. (b) Life-history strategy 2 species may spawn in response to flood changes, including flooding, larvae swim weakly and are likely to have passive downstream dispersal, largely determined by stream flow and may disperse during high flows into floodplain habitats. (c) Life-history 3 species spawn during low flow periods, larvae do not disperse by drifting but colonize local patches of slow moving or slackwater habitats and may move between them.


173
suggest that larvae could influence their position in the river during downstream dispersal migration [Fig. 6(a)]. Certainly, *M. macquariensis* and *M. peeli* larvae are capable of swimming within slow-moving littoral zones in the Murray–Darling Basin and using main channels to drift between slow water habitats. *Maculovella macquariensis* and *M. peeli* undergo parental care during the free embryo stage, and the commencement of exogenous feeding is coincident with pectoral fin functionality and drifting behaviour. Delayed hatching, resulting in well-developed larvae, is a common strategy of some demersal-spawning reef fishes, which allows for better swimming ability and more developed sensory systems, therefore enhancing retention and survival (Barlow, 1981; Hickford & Schiel, 2003; Jones et al., 2005).

Murray–Darling Basin life-history strategy 2 fish (Humphries et al., 1999) have altricial ontogenies (Balon, 1986) and are periodic species (Winemiller & Rose, 1992) that enter the drift as fertilized eggs, have relatively under-developed planktonic free embryos at hatch, have limited swimming capabilities when drifting and have no parental care (Lake, 1967). The swimming performances of the free embryos and larvae of *M. ambigua* and *B. bidyanus* larvae were the poorest of all the species in this study, which indicates limited ability to swim against currents or influence dispersal in rivers [Fig. 6(b)]. They are considered pelagic-spawning, flood recruitment specialists (Lake, 1967; Harris & Gehrke, 1994; Schiller & Harris, 2001), although this may be region specific (Mallen-Cooper & Stuart, 2003; Balcombe et al., 2006; King et al., 2009). If these species do indeed, or historically, more commonly, spawn in response to high flows and flooding, pelagic spawning of large numbers of eggs and limited swimming capabilities of free embryos and larvae would mean that young would be distributed widely within the main channel and across the floodplain. Widespread dispersal may provide an advantage in that it scatters young across a diversity of habitat patches, with the high probability of some of these being favourable for survival and recruitment. Strategy 2 and the saltatory ontogeny of *M. ambigua* and *B. bidyanus* are similar to marine pelagic spawning fishes, where recruitment success has been related to broad-scale, long-term environmental variables (Lasker, 1981; Borja et al., 2002). For this strategy to be successful, however, presumably there would have to be rapid improvement in swimming performance in post-larval fishes, so that fish could leave floodplain habitats before they dry or, if in the main channel, move between habitat patches of varying quality at smaller spatial scales.

Life-history strategy 3 fish (Humphries et al., 1999) have altricial ontogeny (Balon, 1986) and are opportunistic species (Winemiller & Rose, 1992) that have small, poorly developed free embryos at hatch, have limited swimming capabilities and no parental care (Humphries et al., 1999). Swimming performances of the metalarvae of strategy 3 species, *Hypleotris* spp. and *M. fluviatilis*, were similar to those of strategy 2 fishes. Opportunists can take advantage of a range of conditions in which to spawn and recruit and may be successful colonizers, especially in areas subjected to frequent and intense disturbance (Winemiller, 2005). The free embryos and larvae of *M. fluviatilis* and *Hypleotris* spp. are small and not known to disperse by drifting [Fig. 6(c)]. These species are considered low-flow specialists (Humphries et al., 1999) with spawning typically taking place during the summer, low-flow period. Furthermore, eggs and early life stages of these species typically occupy slackwater habitats, where they encounter rich food resources, avoid fast currents that might displace them and presumably get protection from large-bodied predators (King, 2004). Females can lay several batches.
of eggs in one day or breeding season, spreading 100–1000s of eggs over several habitat patches, therefore potentially further increasing survival and recruitment.

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