

## **Fish, flows and flood plains: links between freshwater fishes and their environment in the Murray-Darling River system, Australia**

Paul Humphries<sup>a</sup>, Alison J. King<sup>a</sup> & John D. Koehn<sup>b</sup>

<sup>a</sup>*Cooperative Research Centre for Freshwater Ecology, Department of Biological Sciences, Monash University, c/- Murray-Darling Freshwater Research Centre, GPO Box 921, Albury, NSW 2640, Australia (e-mail: hump@mdfrc.canberra.edu.au)*

<sup>b</sup>*Freshwater Ecology Division, Marine and Freshwater Research Institute, Department of Natural Resources and Environment, 123 Brown Street, Heidelberg, Victoria 3084, Australia*

Received 11 August 1998

Accepted 18 December 1998

*Key words:* floods, low flow recruitment hypothesis, recruitment, life cycles, spawning, lowland rivers, fish larvae

### **Synopsis**

Knowledge of the biology of native fishes of the Murray-Darling Basin is based largely on studies conducted under hatchery conditions and on a limited number of recreationally important species. From observations that increases in water level in aquaculture ponds initiate spawning in some species, and from limited studies of wild fishes and studies in overseas floodplain river systems, a perception has emerged of the importance of flooding and the flood plain in the life cycles of Murray-Darling fishes in general. However, there is little confirmatory evidence of the use of temporary floodplain habitats by larvae, juveniles or adults. The significance of in-channel habitats, especially for rearing, has received little attention. Murray-Darling fish species can be placed into three life history modes, based mainly on spawning style and time and developmental intervals of larvae at first feeding. Fish in each group may be able to take advantage of floods if the timing is right and prey are plentiful, however, the larvae of some species are able to recruit under non-flood conditions within the main river channel. This forms the basis of the 'low flow recruitment hypothesis', which attempts to explain why some species spawn during the warmest months and lowest flows and how they are able to recruit under these conditions. This hypothesis is then placed in the context of the current state of knowledge of the relationships between flow and the biology of Murray-Darling fishes, specifically cues for spawning, movement and recruitment. The lack of widespread evidence for floodplain use by any life history interval of fish may be due to a paucity of study, however, there are some fundamental factors, such as the predictability of timing and duration of high flow events as well as the lack of coincidence of high flows and high temperatures in some regions of the Basin, which may be important in determining the use of floodplain habitats by fish.

### **Introduction**

The Murray-Darling Basin (Figure 1) drains an area of 1.073 million km<sup>2</sup>, with the Murray and Darling rivers alone comprising approximately 5300 river km. Interannual flow variability, especially within the drier and temperate regions of the basin, is extremely high (Walker 1986, Walker et al. 1995, Puckridge

et al. 1998). It is this highly variable flow, together with Australia's long isolation from the rest of the world, which is thought to have played a major role in maintaining a depauperate native fish fauna (Lake 1971, Harris 1984, Allen 1989). Indeed only 26 native species from 12 families spend their entire lives within the Murray-Darling Basin, and of these, only 10 are endemic (Cadwallader & Lawrence 1990). Despite the

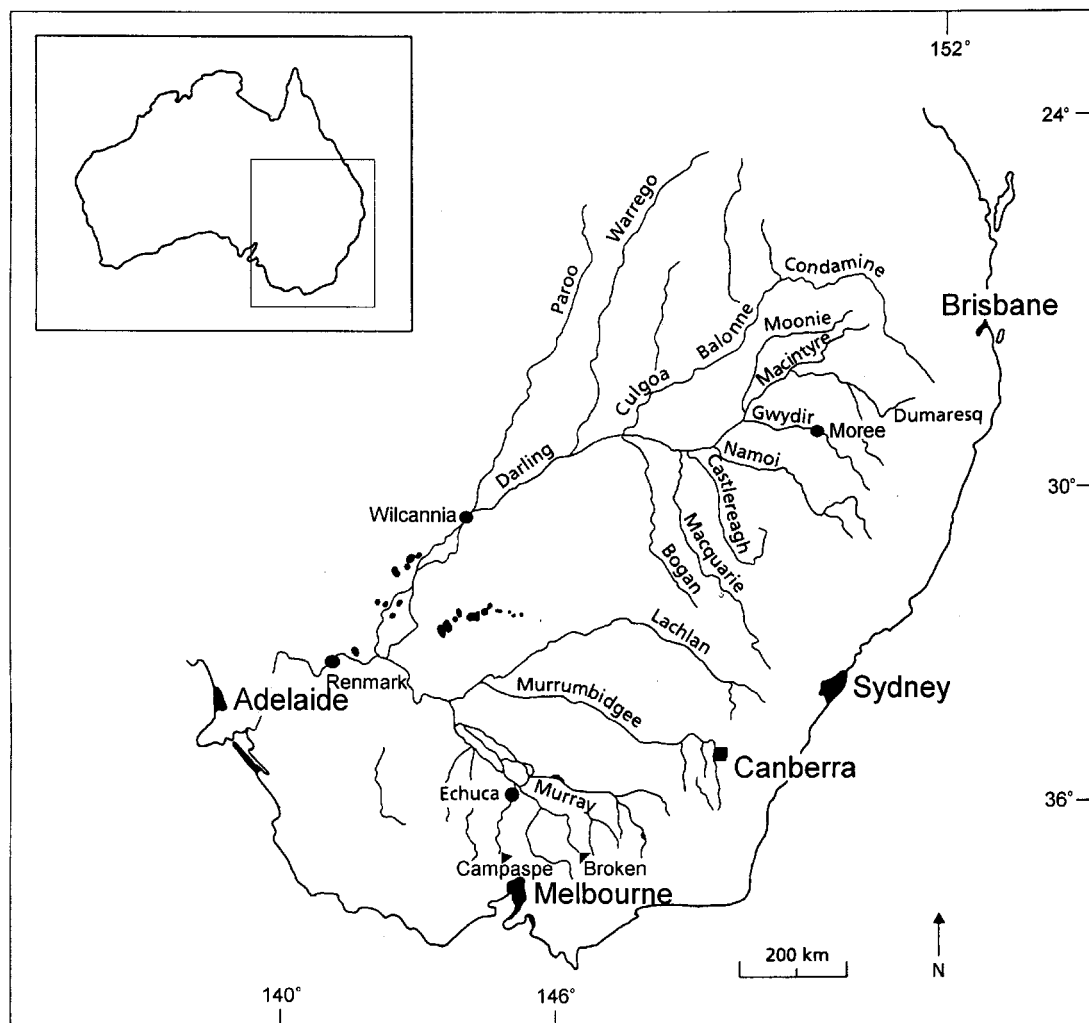


Figure 1. The Murray-Darling Basin.

paucity of species, the fish fauna exhibits a diverse range of sizes, forms and life cycle modes (Merrick & Schmida 1984). For example, some gudgeon species (Eleotridae) rarely exceed 50 mm in length and 2 g in weight and live for little more than two years, whereas Murray cod, *Maccullochella peelii peelii* (Mitchell), has been known to grow to 2 m in length, can weigh in excess of 100 kg and live for more than 30 years (McDowall & Fulton 1996).

Murray-Darling fish, such as Murray cod, have traditionally played a major role as a food source and as a cultural icon for indigenous Australians (Lawrence 1971). These traditions were carried over to early European settlers (see Rowland 1989). Early

commercial operations exploited the bountiful fishery resource, especially Murray cod, golden perch, *Macquaria ambigua*, and Macquarie perch, *Macquaria australasica* (Cuvier)<sup>1</sup> (Cadwallader 1978, Rowland 1989) and exploitation continues mainly through an enormously popular recreational fishery. Despite sporadic observations and anecdotal evidence, it was not until the late 1940s that the first systematic survey was done of the Murray-Darling fish fauna by J.O. Langtry.<sup>1</sup> Unfortunately this was well after the introduction of a

<sup>1</sup> Cadwallader, P.L. 1977. J.O. Langtry's 1949–50 Murray River investigations. Fisheries and Wildlife paper 13, Victoria. 70 pp.

number of exotic fish, including Eurasian perch, *Perca fluviatilis*, tench, *Tinca tinca*, brown trout, *Salmo trutta*, and rainbow trout, *Oncorhynchus mykiss*. Langtry's study and past fisheries catch data suggested that intense commercial fishing, river regulation, barriers to fish movement and the introduction of exotics, had already contributed to a decline in the abundance and range of native fish<sup>1</sup> (Whitely 1937, Rowland 1989). Carp, *Cyprinus carpio*, have since been introduced and now make up a large proportion of fish populations.

Much initial work on the breeding biology of Murray-Darling native fish was performed in the 1960s and 1970s, in aquaculture rearing ponds (Lake 1967a,b, Llewellyn 1971, 1973, 1974). Conclusions from this work, combined with hypotheses from studies overseas (Welcomme 1985, Junk et al. 1989), have resulted in speculation that over-bank flows and inundation of the flood plain are important for Murray-Darling fish, both as a cue for final maturation and spawning of some species (Lake 1967a), and for the subsequent survival of larvae and successful recruitment into juvenile stocks<sup>2</sup> (Lake 1967a, Arumugam & Geddes 1987, Lloyd et al. 1989, Puckridge & Walker 1990, Rowland 1992). Indeed, Harris & Gehrke (1994) have proposed the 'flood recruitment model' to describe how some species, such as golden perch, respond to rises in flow and flooding and how flooding provides the high densities of food for recruitment of this species.

Recent work on wild populations, however, has begun to put into question some of the hatchery-derived assumptions of the nature of the relationship between the biology of Murray-Darling fishes and their environment. Studies of life history traits<sup>3</sup> (Humphries 1995), spawning cues (Mallen-Cooper et al. 1995), movement and migration<sup>3,4</sup> habitat use<sup>3,4</sup> (Gehrke 1991) and

recruitment (Mallen-Cooper et al. 1995), have provided evidence that traits vary widely among species and may not even be consistent for one species across different regions. It is becoming increasingly apparent that reliance on hatchery-based studies as a major source of information is an unsound foundation upon which to base river management and that a better understanding of how fish interact with, and respond to, their environment is needed. Furthermore, whilst not a novel idea, the evidence is mounting that many species spawn independently of high flows and flooding and can successfully recruit during low flow periods (Humphries unpublished data).

Few studies of wild populations have found evidence that fish adults and larvae use non-permanent floodplain habitats.<sup>5</sup> The fact that the Murray-Darling Basin is not homogeneous climatically, but includes a range of zones, some where the highest flows occur in summer and some where the highest flows occur in winter and early spring, may mean that the flood plain is inundated at times not necessarily optimal for the breeding of fish or for recruitment of young. It is logical to infer, then, that a variety of life history and recruitment styles may have evolved to deal with a range of conditions encompassed in the Murray-Darling Basin and that some involve use of the flood plain and others do not. Spawning of adults or rearing of larvae on the flood plain may be advantageous if flooding coincides with warm temperatures, and flooding initiates blooms of microscopic animals, as some suggest (Arumugam & Geddes 1987). However, if flooding and warm temperatures do not coincide, as for the southern Mediterranean region of the Murray-Darling Basin, it may be more advantageous for a fish to spawn within the main channel of the river. Indeed, periods of low flow during summer, in rivers in these regions, are more predictable from year to year and generally of longer duration than floods at this time of the year.

The aim of this paper is to assess the adequacy of current ideas relating to the importance of flooding and the flood plain in the biology of Murray-Darling fishes and to propose the 'low flow recruitment hypothesis' as a way of explaining how some native species are able to spawn and recruit during periods when flows

<sup>2</sup> Geddes, M.C. & J.T. Puckridge. 1988. Survival and growth of larval and juvenile native fish – the importance of the floodplain. pp. 101–114. *In*: Proceedings of the Workshop on Native Fish Management, Murray-Darling Basin Commission, Canberra.

<sup>3</sup> Koehn, J. & S. Nicol. 1999. Habitat and movement requirements of fish. *In*: R.J. Banens & R. Lehane (ed.) Riverine Environment Research Forum, Proceedings of the Riverine Environment Research Forum of MDBC Natural Resource Management Strategy Funded Projects, Brisbane.

<sup>4</sup> Koehn, J.D. 1997. Habitats and movements of freshwater fish in the Murray-Darling Basin. pp. 27–32. *In*: R.J. Banens & R. Lehane (ed.) Riverine Environment Research Forum, Proceedings of the Inaugural Riverine Environment Research Forum of MDBC Natural Resource Management Strategy Funded Projects, Attwood.

<sup>5</sup> McKinnon, L.J. 1997. The effects of flooding on fish in the Barmah forest. pp. 1–8. *In*: R.J. Banens & R. Lehane (ed.) Riverine Environment Research Forum, Proceedings of the Inaugural Riverine Environment Research Forum of MDBC Natural Resource Management Strategy Funded Projects, Attwood.

are low, but temperatures are high. We begin by categorising Murray-Darling fishes into one of four life history modes in an attempt to understand how different species achieve successful recruitment under what are often highly variable hydrological conditions. We then describe the 'low flow recruitment hypothesis' and provide some justification for it from our own observations and from the literature. We then compare the conditions experienced by Murray-Darling fishes with those of other floodplain systems throughout the world and question whether concepts such as the 'flood pulse concept' of Junk et al. (1989) are appropriate for all regions of a climatically heterogeneous river basin like the Murray-Darling Basin. Finally, we suggest subjects for future study and emphasise the need to be vigilant against complacency that our knowledge of the relationships between fishes and the Murray-Darling riverine environment is adequate to manage this large and complex system.

#### **Life cycles of Murray-Darling Basin fishes and influences on recruitment**

Murray-Darling fishes have been grouped previously into four categories related to their spawning style, association or lack of association with flooding and significance for recruitment.<sup>6</sup> The 'flood recruitment model' (Harris & Gehrke 1994) has attempted to deal with the group of Murray-Darling fishes for which flow appears to initiate spawning and for which the flood plain may be important as a habitat of larvae, but this model is inadequate for many species of Murray-Darling fishes for which flow may not play a major role. We propose four categories of Murray-Darling fishes based on life history traits and emphasising spawning style and the importance of the developmental interval of larvae at first feeding as well as the differential ability that this confers on larvae, within each group, to ingest prey of various sizes. In constructing these categories, we also consider that the timing and duration of the spawning period is crucial to understand various styles for successful recruitment. Another important

trait is the occurrence of parental care of eggs and larvae. Finally, adopting Balon's (1984) methodology of describing the early life stages of fish, it is important to determine whether species go through a larva period or metamorphose directly from an embryo to a juvenile.

*Mode 1.* Includes the largest species in the Murray-Darling Basin (Table 1). These species: tend to spawn once only in late spring/early summer in a relatively short breeding period; have demersal eggs which number in the thousands to tens of thousands; have young that hatch well developed, with pigmented eyes: exhibit parental care after hatching; at the time they lose their yolk sac and begin feeding, generally at about 20 days of age, have developed all their fins and can swim well; and have large gapes (>1 mm) at first feeding. Spawning may or may not coincide with high flows, but is not apparently initiated by it. According to Balon's (1984) definition, each species in Mode 1 develops straight from the embryo to the juvenile, bypassing the larva period.

We suggest that, because of the advanced developmental interval at which fish in Mode 1 first begin feeding, they are able to pursue and ingest relatively large prey items, including early instars of macroinvertebrates and large potamoplankton. These are in high abundance within the main channel of rivers, especially in backwaters and slow-flowing or still sections of large lowland rivers (Thorp et al. 1994, King unpublished data). Although the breeding season of these species encompasses at least part of the time when floods may occur in some parts of the Murray-Darling Basin, we suggest that floods are not, as a rule, important for maintaining populations. However, if floods coincide with spawning, it may be that food on the flood plain proper is washed into the river channel from backwaters, billabongs (oxbow lakes) and anabranches, might enhance conditions for species in this group and greater recruitment would result. It is also possible that large floods at the time of spawning may actually displace eggs, embryos and larvae from nests or nurseries and cause higher than normal mortalities.

*Mode 2.* Fishes also grow to a relatively large size as adults (Table 1). These species: spawn once only, between late spring and early autumn and can apparently delay spawning until the appropriate conditions occur; some species, such as golden perch, are known to resorb gonads if the right conditions do not occur;

<sup>6</sup> Lloyd, L., J. Puckridge & K. Walker. 1989. The significance of fish populations in the Murray-Darling system and their requirements for survival. pp. 86-99. In: T. Dendy & M. Coombe (ed.) Conservation and Management of the River Murray System - Making Conservation Count, Proceedings of the Third Fenner Conference on the Environment, Canberra.

Table 1. Life cycle styles for several Murray-Darling Basin fishes.

Variable	Mode 1	Mode 2	Mode 3a	Mode 3b
Duration of spawning	short	variable	long	short
Spawning style	Single spawning, approx. same time each year	Single spawning, timing, can delay	Protracted, serial or repeat	Single spawning
Spawning time	October–December	October–March	September–March	Late winter or summer
Cues for spawning	Circannual and min. temp.	Rising water level? and min. temp.	Uncertain	Uncertain
Number of eggs	1000s–10 000s	100 000s	100s–1000s	100s–1000s
Type of egg	Demersal	Semi-buoyant or planktonic	Planktonic or demersal	Planktonic or demersal
Parental care of embryo/larva	Yes	No	No	No
Incubation period	10+ days	Hours	<10 days	<10 days
Size of embryo at hatching	6–9 mm	3–6 mm	3–4 mm	2–7 mm
Time to first feeding	ca. 20 days	ca. 5 days	ca. 3 days	ca. 3 days
Development of embryo/larva at first feeding	Advanced, large gape, well-formed fins, highly mobile	Undeveloped, small gape, limited mobility	Undeveloped, small gape, limited mobility	Undeveloped, small gape, limited mobility
Examples of species	Murray cod <sup>(a,e,i,m,u,v)</sup> Trout cod <sup>(d,j)</sup> Freshwater catfish <sup>(f,i,m)</sup> River blackfish <sup>(k)</sup>	Golden perch <sup>(c,g,l,m)</sup> Silver perch <sup>(l,m)</sup>	Australian smelt <sup>(a,n,q,r)</sup> Flat-headed gudgeon <sup>(a,n)</sup>	Carp gudgeons <sup>(a,b,l,m,n)</sup> <i>Galaxias olidus</i> <sup>(a,s)</sup> <i>G. rostratus</i> <sup>(n)</sup> Crimson-spotted rainbowfish <sup>(a,d,p,t)</sup> Southern pygmy perch <sup>(h,n,o)</sup>

<sup>a</sup>Humphries unpublished data, <sup>b</sup>Anderson et al. 1991, <sup>c</sup>Arumugam & Geddes 1987, <sup>d</sup>Backhouse & Frusher 1980, <sup>e</sup>Cadwallader et al. 1979, <sup>f</sup>Davis 1977, <sup>g,2</sup>Humphries 1995, <sup>i</sup>Ingram & Rimmer 1992, <sup>j</sup>Ingram & Douglas 1995, <sup>k</sup>Jackson 1978, <sup>l</sup>Lake 1967a, <sup>m</sup>Lake 1967b, <sup>n</sup>Llewellyn 1971, <sup>o</sup>Llewellyn 1974, <sup>p</sup>Milton & Arthington 1984, <sup>q</sup>Milton & Arthington 1985, <sup>r</sup>Milward 1969, <sup>s</sup>O'Connor & Koehn 1991, <sup>t</sup>Reid & Holdway 1995, <sup>u</sup>Rowland 1983, <sup>v</sup>Rowland 1992.

eggs number in the hundreds of thousands and are either semi-buoyant or planktonic; incubation is very short, a matter of hours in some cases; embryos hatch at a relatively small size, are not well developed and do not have pigmented eyes; there is no parental care of either eggs, embryos or larvae; larvae first start feeding after about five days, and the gapes of first feeding larvae are moderate in size (~ 500 µm). Spawning has been thought to be linked to rises in flow and later flooding. Species in this group have a definite larva period.

Mode 2 fish produce large numbers of eggs and must experience very high mortality of eggs, embryos and larvae. This is consistent with general patterns observed in marine and freshwater invertebrates and vertebrates that have planktonic larvae. It is also consistent with

life in an unpredictable environment, where the densities of food required for larvae may be extremely patchy in space and time. Species in this group attempt to cope with climatic and hydrological unpredictability by apparently tracking key environmental variables, such as temperature and flow rises. These fish are able to delay spawning and may not spawn at all if the conditions are not right. Gape size and undeveloped fins at first feeding would probably restrict the size of prey caught and ingested to rotifers and small planktonic crustacea. If zooplankton blooms do occur during flooding, as under aquaculture conditions,<sup>2</sup> than this might ensure high enough densities for larvae of this group to utilise. Otherwise, other habitats that might provide high densities of prey would be backwaters

and potentially impoundments, where water residence time is relatively long.

*Mode 3a.* Fishes are mostly small, have either protracted, serial or repeat spawning and the breeding season extends from early spring to early autumn (Table 1). Spawning of these species seems unrelated to flow, although breeding may occur during high flows; there may be a threshold temperature above which fish can begin spawning; eggs number in the hundreds to thousands and are mostly demersal and adhesive; incubation is less than 10 days; embryos hatch at a small size, are not well developed but do have pigmented eyes; there may be parental care of eggs (flathead gudgeons, *Philypnodon grandiceps*), but not of embryos and larvae; larvae first start feeding within 2–3 days after hatching, and the gapes of first feeding larvae are small (~200 µm). Species in this group have a definite larva period.

The key feature of Mode 3a is that fishes are able to spawn over an extended period. To date, there is not sufficient knowledge of their reproductive styles to determine whether each species is: a protracted spawner, a serial spawner, a repeat spawner or simply that females come into maturity and spawn haphazardly throughout the breeding season. Despite this uncertainty, species such as flathead gudgeons and Australian smelt, *Retropinna semoni*, spawn, and recruitment occurs, for approximately six months of the year, although the most successful recruitment times may be limited (Milton & Arthington 1985), and it is likely that in most years larvae have to contend with both high and low flows. The developmental stages and extremely small gape size of fish in this group at first feeding, means that they are restricted to ingesting very small prey and possibly even phytoplankton. Thus, they are reliant on high densities of minute prey to get them through the critical stages of first feeding.

*Mode 3b.* Fishes are similar to those in Mode 3a in regard to numbers and type of eggs, incubation period, size at hatching and developmental stages at first feeding (Table 1). However, they differ markedly in that they are single spawners and their breeding season is short, typically two months or less. Species either spawn in late winter/early spring or in summer, and gapes of first feeding larvae in this group are small (approximately 200 µm). Spawning is apparently unrelated to high flows and indeed, for some species, takes place during periods of low flow. Species in this group also have a definite larva period.

Since Mode 3b fish spawn for only a short period and have small gapes, they are very much dependent on high densities of microinvertebrates or algae at first feeding. Many galaxiids (*Galaxias*) spawn in later autumn/early winter and larvae spend some months at sea during the winter (McDowall & Fulton 1996). This is thought to have been a style to ensure adequate food for the early intervals of life. The spawning time of freshwater species of galaxiids and of normally diadromous species have shifted to early spring, presumably for similar reasons (Humphries 1989). Some Mode 3b species only spawn in summer and during low flows. In the 1995/1996 and 1996/1997 breeding seasons, crimson-spotted rainbowfish, *Melanotaenia fluviatilis*, larvae have been collected from the Broken River, north-eastern Victoria only in December, January and February and carp gudgeons, *Hypseleotris* spp., have been collected from the Campaspe, north-eastern Victoria and Broken Rivers only in the summer months (Humphries unpublished data).

#### **‘Low flow recruitment hypothesis’**

Spawning of adults and recruitment into juvenile stocks of flathead gudgeon, Australian smelt, crimson-spotted rainbowfish, and three species of carp gudgeon can occur in mid summer, when the prospect of flooding is remote, but the predictability of high temperatures and low flows are high (Milton & Arthington 1984, 1985, Humphries unpublished data). These species have small gapes at first feeding and fall into our Mode 3a and 3b, initially requiring extremely small prey. Thus, they must encounter high densities of small prey during periods of low flow in the main stem of rivers.

The ‘low flow recruitment hypothesis’ postulates that some species of fishes take advantage of the extended low flow period of the rivers in certain regions of the Murray-Darling Basin to spawn, because of the concentrations of appropriately-sized prey. This prey is of sufficient size and density to allow larvae of these species to make the transition from endogenous to exogenous feeding without recourse to the flood plain.

As flows decrease over late spring and into summer and temperatures warm, a smaller volume of water would concentrate the prey to such an extent that densities may increase to a level which would be sufficient for feeding of larvae. This would most likely occur in backwaters, pools and other still habitats which are common during low flow periods in lowland rivers in

many regions of the Murray-Darling Basin. Justification for this hypothesis is based on previous studies in rivers and observations detailed below.

Zooplankton biomass has been shown to be positively correlated with water residence time (Basu & Pick 1996), negatively correlated with flow (Pace et al. 1992, Thorp et al. 1994) and positively correlated with temperature (Thorp et al. 1994) in the main stem of large rivers. Similar results have been found for phytoplankton (Wehr & Thorp 1997), since there is a direct relationship between biomass of zooplankton and chlorophyll *a* (Basu & Pick 1997). Ferrari et al. (1989) showed that under summer low flow conditions, the zooplankton community of the Po River tended to become highly stable and very productive with flooding creating a destabilising effect, leading to increased diversity but reduced density of rotifers. Thus, the greatest biomass of zooplankton in the main stem of rivers will tend to occur during the lowest flows of each year (Ferrari et al. 1989, Pace et al. 1992, Thorp et al. 1994, Basu & Pick 1996). This is also presumably the explanation for the occurrence of maximum densities of zooplankton given by Welcomme (1985) in some tropical systems at low flow.

Although the above studies have shown that the biomass of zooplankton, by definition occurring in the water column, is greatest at times of low flow, in some cases densities are relatively low (Thorp et al. 1994). We suggest, however, that there is an alternative food source, potentially more abundant and of an ingestible size for fish larvae, which also occurs in slow-flowing or still habitats in the main stems of lowland rivers. This food resource consists predominantly of rotifers and benthic microcrustaceans, including cladocerans, copepods and their nauplii and ostracods. The benthic microcrustacean fauna of lotic systems has received little attention relative to its lentic counterpart (e.g. Williams 1982). However, recent evidence suggests that it may play important roles in riverine food webs (Perlmutter & Meyer 1991). Indeed, benthic microcrustaceans are a significant component of both invertebrate (Hildrew et al. 1985, Lancaster & Robertson 1995) and fish diets (Rundle & Hildrew 1992). Robertson (1990) found peaks in abundance of chydorids in summer in the benthos of the River Thames at levels of 50 000 individuals per m<sup>2</sup>, which coincided with maximum daily production and biomass (Robertson 1995). The maximum densities of three chydorid species each reached between 2000 and 8000 individuals m<sup>-2</sup> at this time (Robertson 1995).

Collections of benthic microfauna from the Campaspe and Broken rivers, northern Victoria, suggests that there is an extremely rich and abundant fauna occurring on or near the substratum (King & Humphries unpublished data). This fauna is not sampled adequately using conventional zooplankton sampling techniques and therefore is easily missed. Many of these taxa are entirely benthic and typically associated with lentic water bodies such as billabongs (R.J. Shiel personal communication) and many fall into the size range able to be ingested by fish larvae with gapes of 200 µm. There are no data on the densities of benthic microcrustaceans and rotifers from backwaters of the main stems of Murray-Darling rivers and how these are affected by declining discharge and increasing temperatures. However, studies overseas have suggested that such littoral habitats support greater densities of potamoplankton than main channel habitats and may support even greater densities of benthic organisms (Thorp et al. 1994).

The use of in-channel habitats by fish embryos and larvae has been documented in other large rivers throughout the world. In general, fish larvae have been shown to use still or slow flowing littoral areas, backwaters and shallow embayments as nursery habitats (Sager 1987, Schiemer & Spindler 1989, Schiemer et al. 1991, Sempeksi & Gaudin 1995, Watkins et al. 1997, Sempeksi et al. 1998). Their need for low velocity habitats is thought to be related to their poor swimming ability (Lightfoot & Jones 1996, Mann & Bass 1997), with some researchers noting an ontogenetic habitat shift for faster velocity water as the larvae develop (Schiemer & Spindler 1989, Schiemer et al. 1991, Sempeksi & Gaudin 1995, Mann & Bass 1997, Watkins et al. 1997).

There are clearly also potential disadvantages with spawning and recruiting during low flow periods. As discharge decreases and temperature warms, there is potential for pools to stratify and dissolved oxygen levels to fall to lethal levels for fishes. With evaporation and smaller volumes of water, concentrations of solutes, such as salt, may also increase to harmful, if not lethal levels. Extended periods of dry, warm weather would increase the risk of desiccation, although in most large lowland rivers, large pools would remain as refuges for fishes. However, the decreasing volume of water and concentration of food would also mean a concentration of aquatic predators and potentially easier access to small fish by aerial and terrestrial predators (Copp 1992). Competition for resources may also be

exacerbated, since a decrease in the volume of water may reduce overall area of available habitat and therefore increase the amount of overlap in microhabitat use by larvae and juveniles (Copp 1992).

### **Murray-Darling fishes and the riverine environment**

There is a current perception that for some species of Murray-Darling fishes, increases in flow may provide a cue to initiate maturation and spawning, and flooding may open up important spawning and rearing habitat<sup>2,6</sup> (Lake 1967a, Harris & Gehrke 1994). For others, despite the fact that they spawn independent of high flows, flooding may indirectly benefit them through the input of nutrients or food. However, it is also apparent that there are many species for which there has been no relationship established between high flows and maturation, spawning and rearing of young. Despite this diversity of styles, the management literature often lumps Murray-Darling fishes together when making recommendations for managing rivers within this system<sup>6</sup>. This is highly unsatisfactory, especially, as often happens, the significance of in-channel processes are downplayed or even ignored. If the 'low flow recruitment hypothesis' has some validity, than the lack of recognition of the importance of in-channel habitats may be detrimental to recruitment for several native species. If we are ever to manage Murray-Darling rivers in an ecologically sustainable way, than it is imperative to understand the role that flow, both within and outside the channel, plays in the biology of native fishes. In this section, we examine the evidence for the influence of flow and other environmental variables on maturation, spawning and movement of Murray-Darling fishes and what role the flood plain plays in the biology of fishes in general. We begin by examining whether flow has a role in the cuing of fish to mature and spawn, and what implications this has for the conditions likely to be encountered by larvae and juveniles in the wild. We then look at the question of the movement of adult and fish larvae in relation to flow and postulate on the adaptive significance of this. We then proceed with an examination of the nature of Murray-Darling Basin flood plain and the evidence for its direct use by fishes, what role the flood plain plays here and overseas for fishes and ask whether riverine ecosystem theories, such as the 'flood pulse concept', are appropriate for all regions of the Murray-Darling Basin.

### *Cues for spawning*

The role of the environment in influencing gametogenesis, maturation, ovulation and spawning of fishes has received much attention (see Jobling 1995). Considerable progress in the understanding of the effects of photoperiod, temperature, food availability and water level changes has been made by experimental investigations (see reviews: de Vlaming 1972, Bye 1984). Such controlled studies have so far been lacking for Murray-Darling fishes, with our knowledge of spawning cues relying heavily on data gained from hatchery studies in aquaria and ponds (Table 2), concentrating mostly on a few commercial or recreationally important species such as Murray cod and golden perch (Lake 1967a,b, Llewellyn 1971). Hatchery studies, however, cannot hope to mimic fully conditions in the wild, particularly the types and quantities of available food, diel variation in temperature, a lentic rather than lotic environment and the fact that a water level change in ponds is unlikely to be an adequate substitute for river flow variations. Despite these concerns, information gained from aquaculture studies can indicate which variables may play a role in initiating spawning.

Only temperature, flow changes or fluctuations in water level and photoperiod have been considered as potential cues associated with spawning in Murray-Darling fishes, although Lake (1967a) mentioned the presence of food for young fishes as being coincident with the onset of spawning in several species in ponds (Table 2). Variables such as moon phase and chemical cues have not been studied.

A change in water level has been suggested as a cue for spawning in five of the 13 species studied (Table 2). This has been taken as circumstantial evidence for the significance of a flow rise, which would presumably then lead to flooding in a main stem river. This apparently confirmed Langtry's observations that golden perch in the Murray River spawned in spring if the weather was warm, when the first water level rise occurred<sup>5</sup>. Langtry notes, however, that golden perch can spawn in response to both a rise and a fall in river height, and observed that fish spawned all together, for a short time, in the river proper. Mackay (1973) documented spawning of golden perch in January and February in a tributary of the Lachian River during extensive flooding and found that in the absence of flooding, few fish spawned. His results suggested that spawning is tied to flooding and that the lack of flooding in any year would coincide with poor recruitment.

Table 2. Evidence from scientific literature on the importance of temperature, flow or water level change and photoperiod as spawning cues for Murray-Darling native fish. Note that gaps in the table may indicate the documented lack of significance of a specific variable as a cue or simply a lack of sufficient data to assess the significance of that variable. ↑ = increase; ↓ = decrease; min = threshold minimum; min, ↑ = threshold minimum followed by an increase; Vic = Victoria, Qld = Queensland, SA = South Australia, NSW = New South Wales, Tas = Tasmania.

Species	Temp	Flow/ water level	Photo period	Study environment	Reference
Murray cod ( <i>Maccullochella peeli peeli</i> )	min min min, ↑ ↑ min	↑, slight ↑↓ No No	Likely Likely	Pond Murray R Pond Broken R, Vic Pond	Lake 1967a <sup>1</sup> Cadwallader et al. 1979 Rowland 1983 Humphries unpub. data <sup>16</sup>
Trout cod ( <i>Maccullochella macquariensis</i> )	min		Likely	Pond	Ingram & Rimmer 1992
Golden perch ( <i>Macquaria ambigua</i> )	min min	↑ ↑ ↑ or ↓		Pond Trib. of Lachlan R Murray R	Lake 1967a Mackay 1973 <sup>1</sup>
Macquarie perch ( <i>Macquaria australasica</i> )	min min			Lake Eildon Lake Eildon	Wharton 1968 Cadwallader & Rogan 1977
Silver perch ( <i>Bidyanus bidyanus</i> )	min	↑		Pond	Lake 1967a
Spangled perch ( <i>Leiopotherapon unicolor</i> )	min	↑		Pond Black R, NE Qld	Llewellyn 1973 Beumer 1979 <sup>2</sup>
Bony herring ( <i>Nematalosa erebi</i> )	min min	No No		Cooper Ck, SE Qld Lower River Murray, SA	Puckridge & Walker 1990 Llewellyn 1971
Australian smelt ( <i>Retropinna semoni</i> )	min min min			Pond Goulburn R, Vic Moggill Ck, SE Qld	Llewellyn 1971 Hume et al. 1983 Milton & Arthington 1985
Freshwater catfish ( <i>Tandanus tandanus</i> )	min	No		Pond Gwydir R, NSW	Lake 1967a Davis 1977
Crimson-spotted rainbowfish ( <i>Melanotaenia fluviatilis</i> )	min min, ↑	No		Aquaria Enoggera Ck, SE Qld	Backhouse & Frusher 1980 Milton & Arthington 1984
Southern pygmy perch ( <i>Nannoperca australis</i> )	min ↑ min	No		Pond Pond Macquarie R, Tas.	Llewellyn 1971 Llewellyn 1974 Humphries 1995
Southern purple-spotted gudgeon ( <i>Mogurnda adspersa</i> )	min			Pond/aquaria	Llewellyn 1971
Flathead gudgeon ( <i>Philypnodon grandiceps</i> )	min			Pond/aquaria	Llewellyn 1971
Western carp gudgeon ( <i>Hypseleotris klunzingeri</i> )	min			Pond	Lake 1967a
Murray jolytail ( <i>Galaxias rostratus</i> )	min			Pond	Llewellyn 1971
Murray hardyhead ( <i>Craterocephalus fluviatilis</i> )	min			Pond	Llewellyn 1971
Olive perchlet ( <i>Ambassis agassizii</i> )	min min, ↑	↑ No		Pond Brisbane R, SE Qld	Cadwallader & Backhouse 1983 Milton & Arthington 1985

Cadwallader, P.L. & G.J. Gooley. 1985. Propagation and rearing of Murray cod *Maccullochella peeli* at the warmwater fisheries station pilot project Lake Charleygrark. Fisheries and Wildlife Service, Department of Conservation, Forests and Lands, Melbourne. 189 pp.

The 'flood recruitment model' (Gehrke 1994, Harris & Gehrke 1994) emphasised the flood stimulus as the key to spawning and the resorption of gonad if this did not occur. By contrast, recent work has indicated that strong year classes of golden and silver perch in one section of the Murray River were associated with spring flows that were contained within the river channel and poor year classes were associated with high spring flows that inundated flood plains<sup>7</sup>.

Lake (1967a) suggested that Murray cod may require a rise in water level as a spawning cue, and Langtry<sup>1</sup> observed that they may spawn on either a rise or a fall in water level<sup>3</sup>. However, later pond experiments indicated that spawning was induced by a rise in water temperature during spring, and that an associated rise in water level was not required (Rowland 1983, Cadwallader & Lawrence 1990). Although 'minimum' temperatures of around 20°C are often mentioned for breeding, spawning has been observed to occur at lower temperatures<sup>4</sup>.

Beumer (1979) found that spangled perch, *Leiopotherapon unicolor*, require increasing water temperature and day length to initiate gonad development, with spawning probably being induced by the onset of the 'wet' season. It has been suggested that bony herring, *Nematalosa erebi*, spawn in backwaters during floods<sup>8</sup>, however, more recent evidence from south-east Queensland and the lower River Murray suggests that this species spawns well before a rise in flow and that it is the juveniles only which are able to utilise the newly inundated flood plain<sup>2</sup> (Puckridge & Walker 1990).

In general, workers on Murray-Darling fishes have tended to assign a minimum or threshold temperature as a cue for the spawning, whereas the important component of flow as a cue tends to be a rise or rarely a fall. This may reflect the nature of the experiments, since studies in ponds typically manipulated water levels, but were unable to control for temperature, which was apparently increasing during the trials (Lake 1967a). To our knowledge, no spawning cue experiments have manipulated one variable while controlling for others. Thus, it is difficult to determine exactly

the relationship between gametogenesis, final stages of maturation, ovulation and release of eggs and environmental variables, such as temperature, water level rises, food densities and photoperiod.

Despite these uncertainties, it is likely that temperature does play a significant role in the onset of gonadal development and in final maturation and spawning of many Murray-Darling fishes. Much of the Basin experiences distinct seasonal patterns in temperature which would be predictable from year to year and it is these types of patterns of which fish tend to make use to initiate gametogenesis (Bye 1984).

### Movement

Rises in flow have long been thought to initiate upstream pre-spawning movements in several of the larger Murray-Darling fish species (Cadwallader & Rogan 1977, Reynolds 1983, Llewellyn & MacDonald 1980). The hypothesis has been that fishes move upstream in response to increasing flows and then move laterally on to the flood plain to spawn or that they spawn mid-channel and free embryos are washed downstream to inundated nursery areas (Lake 1967b). Such upstream movement of adults would compensate for the downstream drift of embryos and larvae and prevent larvae from being washed down to unfavourable areas such as the lower reaches of the Murray River or even out to sea.

Although the migratory nature of some fish species in the Murray-Darling Basin has long been recognised by Aborigines and professional fishermen<sup>7</sup>, our knowledge of movement is generally poor. Studies have tended to concentrate on large fishes and on large-scale migrations (Koehn & O'Connor 1990). Several studies have tagged large numbers of fishes and recorded subsequent recaptures<sup>5</sup> (Llewellyn 1968, Reynolds 1983), whereas more recently, monitoring of fishways<sup>7</sup> and radiotracking have provided insights into both small and larger-scale fish movements<sup>3,4</sup>.

Adult golden perch have been shown to move large distances both upstream and downstream<sup>5</sup> (Llewellyn 1968, Reynolds 1983), with maximum reported distances of 1000 km upstream (Reynolds 1983) and 900 km downstream<sup>5</sup>. Large numbers of juvenile golden perch have been recorded moving upstream through the fishway at Torrumbarry Weir on the Murray River, possibly recolonising from rearing habitats<sup>7</sup>. Results from radiotracking indicated that this species is highly mobile in the Murray River for much of the

<sup>7</sup> Mallen-Cooper, M., I.G. Stuart, F. Hides-Pearson & J.H. Harris. 1995. Fish migration in the Murray River and assessment of the Torrumbarry fishway. Final report for the Natural Resources Management Strategy Project N002, NSW Fisheries, Sydney. 149 pp.

<sup>8</sup> Llewellyn, L.C. 1983. The distribution of fish in New South Wales. Australian Society for Limnology Special Publication 7. 23 pp.

year<sup>3</sup>. Llewellyn (1968) suggested that the upstream movement of golden perch was related to warm water temperatures and increases in river height, whereas Reynolds (1983) was uncertain of the cause of movement, although large-scale movements were coincident with large floods. Adult silver perch have been reported moving more than 200 km (Reynolds 1983) and juveniles of this species were also recorded passing upstream through the Torrumbarry Weir in large numbers<sup>7</sup>.

Reynolds (1983) concluded from his tagging study, that freshwater catfish, *Tandanus tandanus*, and Murray cod were non-migratory and that these species were essentially sedentary. It has been found recently, however, that Murray cod can make relatively large (up to 120 km) upstream movements prior to spawning before making a return journey<sup>4</sup>. Movement of Murray cod was largely seasonal and in an overall upstream direction. Once preceded by an upstream movement, however, movement occurred both upstream and downstream. Distances moved were greater in an unregulated than a regulated river and were greater during high flow than low flow years<sup>3</sup>. Such movements may indicate behaviour to compensate for the drift of fish larvae, but there is no direct evidence for this. The distance that larvae drift is likely to be related to discharge conditions at the time and so, if there is some cue to which a fish may respond, fishes may vary the distance that they migrate prior to spawning to compensate.

Koehn (1986) suggested that river blackfish, *Gadopsis marmoratus*, undertook only limited movements and had a small home range in the order of 10–20 m. Trout cod, *Maccullochella macquariensis*, showed similar limited movements and were territorial around home areas of large woody debris. Movement of this species appeared to be related to season and flow rather than water temperature<sup>3</sup>.

A recent study of a fishway on the Murray River found that increases in water levels, both large and small stimulated movement<sup>7</sup>. Migration was primarily seasonal, but river flow was found to be an important stimulus for movement for many species. In many instances large numbers of small fishes moved through the fishway following changes in river levels of less than 0.2 m per day.

Those species of Murray-Darling fishes for which there is evidence of large-scale upstream movements, are known to have drifting eggs, embryos or larvae<sup>3</sup> (Humphries unpublished data). The large distances

sometimes travelled by adult golden and silver perch may relate to their relatively small and buoyant eggs, embryos and larvae which may be expected to drift greater distances than Murray cod larvae, which are relatively much larger. The absence of golden perch above some artificial barriers from rivers within their range suggests that movement both upstream by juveniles and adults and downstream by eggs, embryos and larvae may be a significant component of their overall life history style<sup>9</sup>. Aside from recent stockings, silver perch have been similarly absent in the Murray River above the barriers that form Lake Mulwala and Lake Hume (Koehn unpublished data). Although there have been few recorded captures of the free embryos or larvae of golden and silver perch, these buoyant embryos and larvae will drift and the eggs of these species have been collected recently in drift samples<sup>3</sup>. Similarly, until recently Murray cod larvae had not been collected in the wild<sup>3</sup> (Humphries unpublished data), and this reflects the paucity of studies that have focussed on fish embryos and larvae of the Murray-Darling Basin.

There is thus, to date, evidence of large-scale movements (10's of km) for only three of the 26 freshwater species of Murray-Darling fishes. The smaller species of fish have been largely ignored in movement studies and this is clearly a major gap in our knowledge. We can make guesses as to why some individuals of the three species migrate large distances, but we are a long way from being able to provide a definitive answer to such an important question. In tropical floodplain rivers elsewhere in the world, it has been postulated that adult fish of some species migrate upstream to spawn in temporary habitats that are potentially important to the early intervals of fishes (P.B. Bayley personal communication). Subsequent drift of juveniles takes them to more substantial floodplain habitats, where food is plentiful and predators are scarce. Whilst we have some knowledge of longitudinal movements of Murray-Darling fishes in response to changes in flow, lateral movement into the flood plain remains a vexed question.

<sup>9</sup> Brumley, A.R., A.K. Morison & J.R. Anderson 1987. Revision of the conservation status of several species of warmwater native fish after surveys of selected sites in northern Victoria (1982–1984). Arthur Rylah Institute for Environmental Research Technical Report Series No.33, Melbourne.

*The floodplain environment and its use by fishes*

Floodplain rivers have longitudinal, as well as lateral linkages. The periodic pulsing of flows into the flood plain is thought to underpin the food webs of many flood plain rivers (Junk et al. 1989). Fish are typically prominent higher-order consumers within such food webs. The flood plain can be defined in an ecological sense as: 'areas that are periodically inundated by the lateral overflow of rivers or lakes, and/or by direct precipitation or groundwater; the resulting physico-chemical environment causes the biota to respond by morphological, anatomical, physiological, phenological and/or ethological adaptations and produce characteristic community structures' (Junk et al. 1989, p. 112). This definition stresses the importance of periods of wetting and drying as being of primary significance in defining the flood plain, in contrast to other definitions, which may include permanently inundated areas. Welcomme (1985) describes several different habitat types within the floodplain environment of rivers, which include flooded grassland, lagoons and depressions, lakes, flooded forest and flood areas outside the main flood area.

Fish may potentially use a range of floodplain habitats, such as ephemeral anabranches, permanent and ephemeral billabongs and the flood plain proper, but since some of the habitats are temporary and some permanent, each may be used by different species or life intervals for different purposes and varying durations. Thus, permanent billabongs may have permanent fish communities, and may or may not experience immigration and emigration during connection with the river channel. Temporary floodplain habitats, on the other hand, can only be used either while there is connection with the river channel or while water persists in that habitat. Since no Murray-Darling fishes have desiccation resistant life stages, it is likely that fish using temporary floodplain habitats move into that habitat as long as the connection between it and the river channel persists, but move out before the connection is severed.

There are few published studies that have documented the occurrence of native Murray-Darling fishes in floodplain habitats. Some data are available on the fish faunas of billabongs<sup>10</sup> and from the Barmah Forest

in the south-eastern region of the Basin<sup>4</sup>, but virtually nothing about the use of the flood plain proper. Several species have been recorded from billabongs, with some species abundant in permanent waters, including various species of carp gudgeon, crimson-spotted rainbowfish and Australian smelt<sup>10</sup> (Cadwallader & Lawrence 1990, Balcombe unpublished data). It is likely that most of these species can complete their entire life cycle within billabongs and do not require connection with the river proper. Indeed, larger native fish species, with the exception of bony herring, seem to prefer mainstream habitats rather than billabongs. Golden perch, flathead gudgeon and Murray cod also have been collected from billabongs, but generally prefer lotic environments (Cadwallader & Lawrence 1990). Bony herring have been observed spawning in shallow backwaters during floods<sup>8</sup> and, although flooding did not coincide with the occurrence of larvae, juveniles of this species colonised floodplain habitats in Cooper Creeks in large numbers.<sup>2</sup> Freshwater catfish have been recorded as spawning in flooded and shallow portions of main rivers or in quiet backwaters (Lake 1967a). Langtry<sup>1</sup> documented spawning of Murray cod in the main channels and major anabranches of the Murray River. He cites fishermen saying that they have never caught juvenile Murray cod in billabongs. No published work has recorded the presence of larvae of any species of Murray-Darling native fishes in temporary billabongs or the flood plain proper.

Gehrke (1990a,b, 1991, 1992, 1994, Gehrke et al. 1993) has attempted to elucidate the role of the floodplain in the ecology of some species of Murray-Darling fishes through a series of studies, which have included experiments in artificial flood plains. Whilst acknowledging the lack of empirical data on floodplain use by fishes, Gehrke has nevertheless attempted to determine the suitability of the floodplain environment for golden perch, silver perch, and gudgeon larvae (Gehrke 1990b, 1991, 1992). His results indicated that, although golden perch larvae are attracted to chemical leachates from river redgum wood, a common riparian and floodplain tree, these leachates can sometimes be lethal to fish larvae and that the poor water quality of the floodplain environment may have a greater effect on the distribution of golden perch larvae than the abundance of food (Gehrke 1990b, 1991). Low dissolved oxygen levels and high concentrations of tannins and lignins on the flood plain make it an unattractive environment for young stages of this and potentially other species.

<sup>10</sup> Hume, D.J., A.R. Fletcher & A.K. Morison. 1983. Final Report: Carp Program 10. Arthur Rylah Institute for Environmental Research, Melbourne. 213 pp.

McKinnon (1995) has similarly shown that low oxygen levels and adverse water quality conditions associated with inundation of a floodplain forest can be harmful for aquatic species, such as the Murray crayfish, *Euastacus armatus*. McKinnon & Shephard (1995) also reported a large fish kill which resulted from the return of oxygen depleted water from pastured flood plain. Anecdotal evidence from several sources indicated that rises in water levels and floods earlier this century in the Lachlan River coincided with staining of the water, large fish kills and subsequent low abundance of fishes for many years (Roberts & Sainty 1996). These examples suggest that flooding and floodplain habitats may not always provide conditions suitable for fish and fish larvae.

Despite the paucity of data which links Murray-Darling fishes to the floodplain environment, apart from permanent billabongs, the flood plain has been proposed by many researchers in Australia as playing a significant role in the life cycle of several species of Murray-Darling fish<sup>2</sup> (Lake 1967a, Arumugam & Geddes 1987, Rowland 1992, Gehrke 1990a,b, 1991, 1992, 1994). This suggestion has come about for several reasons. It stems partly from patterns observed in floodplain systems throughout the world (Welcomme 1985), partly from the perceived applicability of the 'flood pulse concept' (Junk et al. 1989) to the Murray-Darling Basin and partly from the perception that for successful recruitment of fishes at the larva period, the only environment that would provide sufficient sizes and concentrations of food would be newly inundated flood plain<sup>2</sup>. We will examine each of these issues below, assess the quantity and quality of evidence in support of their applicability to the Murray-Darling Basin and, where they are deemed wanting, provide some alternative explanations.

#### *The role of the flood plain in the biology of fishes*

A variety of species of fishes in floodplain river systems, such as the Amazon and the Mississippi-Missouri rivers, make use of the flood plain at times of high flow, for feeding and/or spawning. According to Welcomme (1985), all insect and plant foods consumed by fishes originate from overhanging vegetation, and he cites examples from the Amazon, Zaire and Mekong River systems<sup>11</sup> (Roberts 1973, Goulding 1980, 1981).

<sup>11</sup> Geisler, R., H.A. Knoppel & H. Sioli. 1973. The ecology of freshwater fishes in Amazonia; present status and future tasks

Indeed, several families of fishes in the Amazon rely heavily on fruits and seeds at times of high flows (Goulding 1980). Fruits, seeds and flowers are important to species of fishes in other floodplain systems as well (see Welcomme 1985). Detritivores and predators are also well represented in floodplain systems (see Lowe-McConnell 1975, Welcomme 1985) and take advantage of flooding to gain access to accumulations of detritus on the floodplain, for the former group<sup>12</sup> (Almeida 1980, Bowen 1984), and to make use of the large amount of terrestrial insects falling from forests for the latter group (Goulding 1980).

The majority of Murray-Darling Basin fishes are opportunistic carnivores, with few known to consume plant material or detritus (Merrick & Schmida 1984). Furthermore, the floodplain environments encountered by Murray-Darling fishes do not support the types of plants that have large quantities of edible fruits or seeds. Unlike rivers in the world whose riparian trees and shrubs are dominated by deciduous species, annual litter fall in much of the Murray-Darling peaks in summer (Lake 1995). No fish species are known to feed on fallen leaves or the seeds and flowers of riparian plants. Nevertheless, there would be a large quantity of terrestrial insects potentially available to fishes should they use the flood plain. While the importance of this type of food for Murray-Darling fishes is largely undocumented, some species of freshwater fish will take advantage of this resource when it is available (e.g. Cadwallader et al. 1980). It would be likely that, within a forested floodplain environment there would be more terrestrially-derived food available to fishes than there would be in the main stem river, because of the amount of vegetation per unit area of water. It is also likely that flood waters would wash floodplain food into the main river channel and other habitats<sup>5</sup> and so make it potentially available to fishes that do not directly use the flood plain themselves. There is no doubt that the

for research. pp. 144–162. In: Applied Sciences and Development, Vol. 2, Institute for Scientific Cooperation, Tübingen (cited In: R.L. Welcomme. 1985. River fisheries. Food and Agriculture Organization of the United Nations, FAO Fisheries Technical Paper 262).

<sup>12</sup> Santos, G.M. 1981. Estudos de alimentacao e habitos alimentares de *Schizodon fasciatus* Agassiz, 1829, *Rhytiodus microlepis* Kner, 1859 e *Rhytiodus argenteofuscus* Kner, 1859, do lago Janauca (Osteichthyes, Characoidei, Anostomidae). Acta Amazonica 11: 267–283 (cited In: W.J. Junk, P.B. Bayley & R.E. Sparks. 1989. The flood pulse concept in river-floodplain systems. Can. Sp. Publ. Fish. Aquat. Sci. 106: 110–127).

periodic connection between the main channel of rivers and their flood plains has an extremely important role in riverine trophic processes (see Junk et al. 1989), but the nature of the relationship between fish feeding and the flood plain in the Murray-Darling is unresolved.

Many species of fish in floodplain systems spawn during high flows, thus ensuring a variety of spawning sites and an abundance of food for their larvae (Bayley 1983, 1988a, Holland et al. 1983, Welcomme 1985). River fishes are typically seasonal in their breeding habits, with temperature and flow seeming to be the two major factors that dictate when fish spawn. In temperate systems, flow and temperature both have significant roles in the timing of spawning. In the tropics, however, where seasonally contrasting temperatures are not as marked, flow, and especially flooding, is the dominant factor. In most of the temperate systems that Welcomme (1985) uses as examples, temperature and flooding tend to coincide. This is also the case in the examples provided within the framework of the 'flood pulse concept' (Junk et al. 1989). The link between flooding and breeding of river fishes is well documented for tropical rivers in Asia, Africa, South America and Northern Australia (Welcomme 1985). The relationship is so tight, that in some cases where the flood wave takes time to move down a river, fish spawning follows the wave downstream (Welcomme 1985). It is important to note, however, that in cases where high temperatures and flows do not coincide, temperature will often be the dominant variable that influences the timing of spawning. An example of this is from the Okavango Delta, where for the most part the flood occurs at the coldest time of the year, and so the fish spawn during low water (Welcomme 1985). Although spawning modes of flood plain fishes are diverse, the use of the flood plain seems for the majority to be initiated by adults. Adults move on to the flood plain as the flood rises and spawn in a variety of habitats (Welcomme 1985, Lowe-McConnell 1975). The adults place their larvae in optimal habitats, rather than relying on the larvae to get there themselves.

The spawning styles of Murray-Darling fish species are varied, yet again our knowledge is mostly from aquaculture studies (Lake 1967a, Llewellyn 1973, Cadwallader et al. 1979, Koehn & O'Connor 1990, Ingram & Rimmer 1992) conducted on only a few species. What happens in the wild is much less certain. Langtry<sup>1</sup> describes his observations of spawning Murray cod and notes depressions made '... in pans and on mud banks situated on the downstream side of a bend,

sheltered from the main current' (p. 28). He also notes that golden perch spawn in the river or in lagoons when the water is rising, but that in the Murrumbidgee River, both Murray cod and golden perch are thought not usually to spawn in the anabranch-billabong systems adjacent to this river. Some suggestions by Australian workers have been that fishes spawn in the main stem of rivers and either the eggs, embryos or larvae are washed on to the flood plain as the flood waters rise. No Murray-Darling fishes have been observed spawning on the flood plain proper and we reiterate that no larvae have ever been collected from seasonally inundated floodplain habitats.

*The 'flood pulse concept' (FPC) and environmental prerequisites for use of the flood plain*

The FPC states that: '... in unaltered large river systems with floodplains in the temperate, subtropical, or tropical belt, the overwhelming bulk of the riverine animal biomass derives directly or indirectly from production within the floodplains and not from downstream transport of organic matter produced elsewhere in the basin' (Junk et al. 1989, p. 112). This is an alternative to the 'river continuum concept' (Vannote et al. 1980), where the emphasis is on longitudinal transport of organic material, not lateral. Many river fisheries are dominated by those species that seasonally colonise the flood plain (Bonnetto et al. 1969, Welcomme 1979, Bayley 1981, 1983, Goulding 1981). The FPC emphasises the role of the flood plain in the ecology of fishes in providing a benign spawning environment and bountiful food for juveniles, adults, and larvae. However, periods of low flow are also common in floodplain rivers in all climatic zones and fishes in these rivers exhibit a diversity of life history styles, some of which involve spawning within the main river channel (Junk et al. 1989, Junk et al. 1997).

Nevertheless, one of the main points of the FPC is that the best conditions for fish spawning is when high flows and high temperatures coincide (Junk et al. 1989). An example is of the relative dominance of spring vs. summer spawners being controlled by the timing and duration of flooding in Missouri floodplain forests (Finger & Stewart 1987). If floods are of only short duration during the warm period of the year, then recruitment can suffer (Junk et al. 1989). The inter-annual predictability of floods is critical. For fish to make use of flood plains for spawning purposes, floods need to be at the same time each year or fish have to have

a flexible life cycle, such as proposed for golden perch in the Murray-Darling Basin. Puckridge et al. (1998) showed clearly that flow variability, at a number of temporal scales, elicits major biological responses by a variety of riverine fishes throughout the world. These responses can be proximate responses (poor recruitment, local extinctions, different levels of migration) or ultimate ones (long breeding seasons, flexible life histories, wide physiological tolerances), depending on the nature of the flow variability.

Fish tend to spawn during the warmest months of the year, partly because rates of egg, embryo and larva development are positively correlated with temperature, and partly because it is at this time of the year that in temperate systems food for larvae and juveniles is most abundant (Jobling 1995). Rates of development and growth are critical to the survival of larvae, since the larger a fish is, the greater the swimming speed and the greater the volume of water able to be searched for food (Bone et al. 1995). Furthermore, the longer

an individual spends as a highly vulnerable larva, the greater the risk of predation by larger fish (Jobling 1995). A number of studies have indeed found that larger larvae are able to respond better to an attack from a predator and that the probability of capture decreases with increasing larva size (Butler & Pickett 1988, Fuiman 1989, Margulies 1990). It has even been suggested that survival in the early intervals of life is a direct function of growth rate (Houde 1987). On the other hand, others have suggested that larger larvae are more conspicuous to predators and provide more net energy gain than small larvae (Fuiman 1989, Litvak & Legett 1992).

High flows in the Murray-Darling Basin do not necessarily coincide with high temperatures. In the south-eastern temperate regions of this river system, flows tend to peak in mid-winter to early spring, before the water has warmed significantly (Figure 2). Flooding may occur during this time, whereas temperatures usually peak well after flows have declined dramatically,

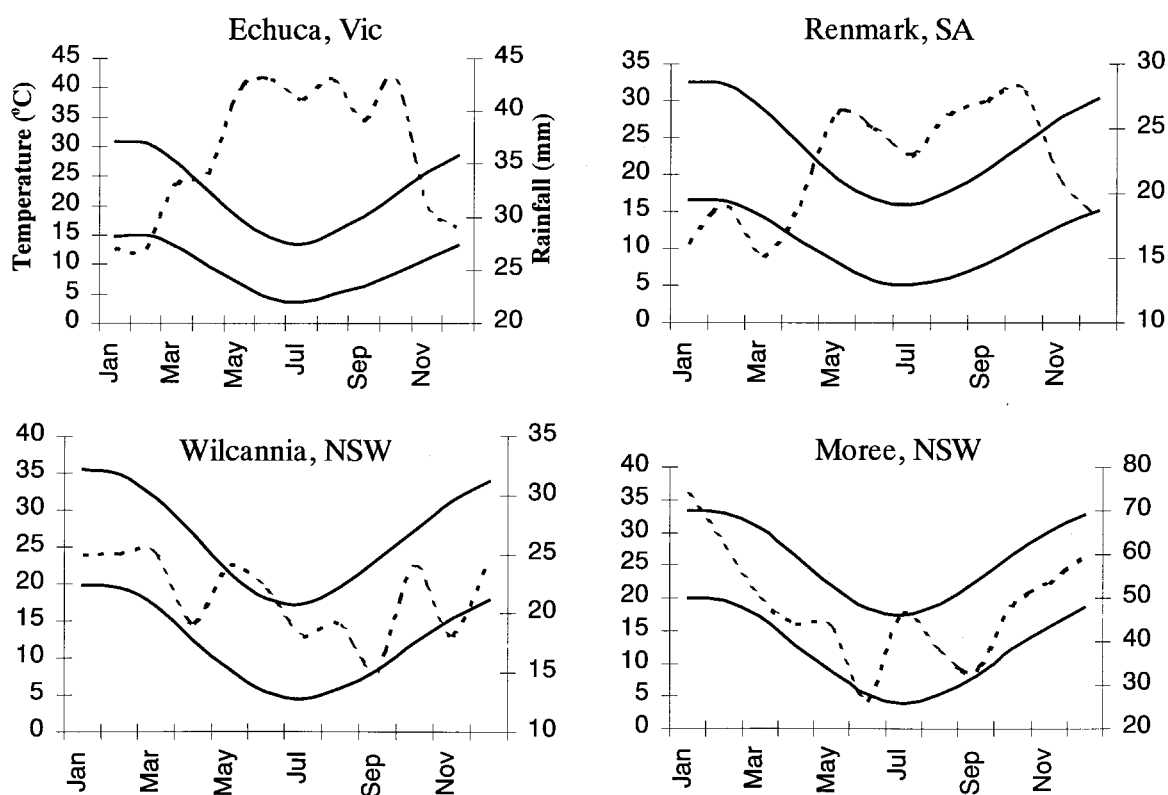


Figure 2. Average monthly rainfall and temperature for four localities in the basin. Solid line = maximum/minimum temperature, dashed line = rainfall. Echuca and Renmark = Murray River, southern Murray-Darling Basin, Wilcannia = Darling River, central-west Murray-Darling Basin, Moree = Gwydir River, north-eastern Murray-Darling Basin. See Figure 1.

certainly well below flood levels. It is clear, however, that as the flood wave passes down the Murray River, there is a shift in the timing of peak flows to later in spring. Therefore, in the lower Murray, floods may coincide with higher temperatures. This is also true of the sub-tropical regions of the Darling River and their major tributaries like the Gwydir, where floods tend to occur during summer when temperatures are high.

Thus, in regions of the Murray-Darling Basin where high flows and high temperatures coincide, fish have optimal conditions for breeding. However, in those regions of the basin where temperature and flow do not coincide, there may be a conflict. Clearly, evidence from studies to date have emphasised temperature more than flows in cues for spawning of native Murray-Darling fishes (Table 2). Furthermore, there is some evidence to suggest that temperature is the overriding parameter that determines timing of spawning elsewhere in the world when this non-coincidence occurs (Welcomme 1985). Since it is not possible to treat the Murray-Darling Basin as climatically homogeneous, it is possible that fish which occur in different regions of this system may have adapted to disparate climatic and hydrological influences and so may make use of different cues and environments for spawning.

The high interannual variability of discharge in rivers in the Murray-Darling Basin (Walker 1992, Walker et al. 1995, Puckridge et al. 1998) has been suggested as one of the contributing factors for the depauperate freshwater fish fauna (Harris 1984, Allen 1989). This extreme variability makes the Murray-Darling Basin a harsh environment for fishes and may limit the diversity of successful life history styles. If the appropriate environmental conditions, a flood, are unpredictable both interannually and seasonally, then it would be an advantage to have a life history style that would allow either a flexible spawning time, an extended spawning period so that a subset of the progeny are likely to encounter favourable conditions, or considerable longevity and so reduce the need to breed every year.

An alternative to relying on breeding during a highly unpredictable event is to breed under other conditions which are more predictable. This forms the basis of the 'low flow recruitment hypothesis' proposed earlier. While the timing of floods is often unpredictable, the timing of low flows can often be relatively predictable<sup>13</sup>. Spawning during stable low-flow times has

<sup>13</sup> Nathan, R.J. & P.E. Weinmann. 1992. Low flow atlas for Victorian streams. Long term planning guidelines background report, L3. Department of Conservation and Natural Resources, Melbourne. 42.

also been suggested to be adaptive for crimson-spotted rainbowfish (Milton & Arthington 1984) and Australian smelt (Milton & Arthington 1985) in coastal streams in the Brisbane area.

The other aspect of unpredictability is that of flood duration. It is risky for a fish to move on to the floodplain to spawn if the high flows are potentially of only short duration. This is especially so if spawning involves nest building, adhesive eggs and/or protracted larva period or parental care. In floodplain rivers in other regions of the world, especially in the tropics, the flood plain may be reliably inundated for six months (Goulding 1980, Welcomme 1985) and the risk of desiccation is slight compared with the conditions encountered throughout much of the Murray River (Walker 1986).

#### *Food for fish larvae*

The significance of high concentrations of food for fish larvae during the critical transition from endogenous to exogenous feeding has received much attention (see Bone et al. 1995). It is at this time that mortality due to starvation is thought to be at its highest. Fish larvae are generally visual predators and when small, can only search a relatively small volume of water. Furthermore, their gapes are generally very small, often in the order of 200–500  $\mu\text{m}$  (Table 3). Thus, to get through this critical transition interval, larvae must generally encounter dense concentrations of appropriately sized prey taxa. This subject has been the focus of many studies and much speculation in marine systems (e.g. Frank 1988, Miller et al. 1988, Pepin & Shears 1995, Gotceitas et al. 1996), with several hypotheses proposed that relate to the relationship between first-feeding larvae and their food, the most notable of which is the match/mismatch hypothesis (Cushing 1990). This hypothesis states that recruitment is governed by the relative timing of the occurrence of larvae relative to the occurrence of their prey. The key assumption is that fish spawn, and therefore larvae occur, at approximately the same time each year, but that the peak prey density is more influenced by relatively unpredictable environmental conditions. If it is possible to predict when and where high densities of food will occur, say on newly inundated flood plain, then some of the uncertainties in matching progeny with prey are alleviated.

The hypothesis proposed by several workers has been that the main stem of rivers in the Murray-Darling Basin generally do not support high densities

Table 3. Gape of larvae of some Murray-Darling Basin fish at first feeding (SL = standard length, TL = total length).

Species	Length at first feeding (mm)	Gape (mm)	Reference
Australian smelt	4.1–8.8 (SL)	0.16–0.52	Humphries & King unpublished data
Flathead gudgeon	3.7–5.3 (SL)	0.24–0.51	Humphries & King unpublished data
Murray cod	8.5–10.0 (SL)	1.0–1.2	Humphries & King unpublished data
Crimson-spotted rainbowfish	3.2–5.6 (SL)	0.2–0.3	Humphries & King unpublished data
Golden perch	4.7–4.9 (TL)	0.5	Arumugam & Geddes (1987)
Silver perch	4.6–5.4 (TL)	0.4	Arumugam & Geddes (1987)

of zooplankton and that the blooms of zooplankton that are thought to occur in newly inundated flood plain may provide the best environment for rearing of young fish<sup>2,6</sup> (Lake 1967a, Arumugam & Geddes 1987, Rowland 1992). To date, the diets of the larvae of only a few species have been studied (Lake 1967a, Arumugam & Geddes 1987, Gehrke 1992, Rowland 1992) with only one of these conducted in a natural system (Gehrke 1992). Concentrations of between 100 and 1000 individuals per litre have variously been proposed as being necessary for the survival of first-feeding larvae (Bone et al. 1995). Rowland (1992) found that hatchery-reared Murray cod survived well if exposed to 250 zooplankton per litre when they first started feeding, but that a delay of only a few days in encountering food increased the mortality rate of larvae exposed to 250 zooplankton per litre relative to a group exposed to 3000 zooplankton per litre.

The importance of the flood plain in providing high concentrations of prey for larvae rests on the assumption that inundated flood plain supports such densities. Welcomme (1985) provides numerous examples of the density of zooplankton in floodplain rivers. In some cases, densities were highest at high flows<sup>14</sup> (Welcomme 1985) and in others densities were highest

at low flows<sup>15</sup> (Holden & Green 1960, Welcomme 1985). There is generally a direct relationship between water residence time and zooplankton biomass (Basu & Pick 1996) and therefore lentic water bodies will tend to be more productive than rivers (Pace et al. 1992, Thorp et al. 1994). Inundation of the flood plain can release nutrients and the resting stages of a variety of invertebrates (Crome 1986, Crome & Carpenter 1988, Boulton & Lloyd 1992, Tan & Shiel 1993), but responses to changing water levels are not simple. Crome (1986) reported that the concentration effects of declining water levels meant that many groups of microcrustacea peaked in a swamp immediately before drying, whilst Crome & Carpenter (1988) showed that chironomids bloomed following the subsequent inundation, presumably as a result of nutrient release. Tan & Shiel (1993) showed that inundation of a billabong resulted in increases in the densities of some rotifer taxa, whereas this was not the case for the zooplankton fauna in general. High densities of zooplankton in the newly flooded Barnah Forest were suggested to have originated upstream and were washed into the forest by the flood waters<sup>5</sup>. The inundation of aquaculture ponds to provide food for hatchery-bred native fish larvae has been used as a model for inundation of the

<sup>14</sup> CECOAL, 1977. Estudios ecologicos en el area de Yacyreta: informe de avance, 2. Argentina, Corrientes, Centro de Ecologia Aplicada del Litoral (cited in: R.L. Welcomme. 1955. River fisheries. Food and Agriculture Organization of the United Nations, FAO Fisheries Technical Paper 262).

<sup>15</sup> Arias, P.A. 1977. Evaluacion limnologica de las planicies inundables de la cuena norte del Rio Magdalena. Proyecto para el desarrollo de la pesca continental en Colombia, Catagena, Inderena-FAO (cited in: R.L. Welcomme 1985. River fisheries. Food and Agriculture Organization of the United Nations, FAO Fisheries Technical Paper 262).

flood plain<sup>2</sup>. They found that there was a succession of phytoplankton and zooplankton taxa (from rotifers through to large zooplankters) through time. They suggest that a similar pattern of emergence and succession in flood plains would provide ideal nursery conditions for the larvae of native fishes. There is currently insufficient data to compare densities of microinvertebrates in the main stem of rivers with those of inundated flood plain and results of floodplain sampling do not provide enough evidence to indicate that blooms after flooding are consistent throughout the basin, nor that the densities of zooplankton are high enough to provide for the requirements of fish larvae. However, anecdotal evidence suggests that the microfauna of backwaters and similar habitats in lowland rivers are sufficiently dense and small to be useful for fish larvae and, therefore, the 'low flow recruitment hypothesis' should receive serious consideration.

The other assumption relating to the feeding of fish larvae is that they all require extremely small prey items to get them through the critical interval from endogenous to exogenous feeding. Whilst many species have small gapes, this is by no means universal (Table 3). It has already been suggested that the well developed larvae of Mode 1 fish, such as Murray cod, may be able to consume relatively large prey at first feeding. A lack of empirical data on the diets of fish larvae in the wild, however, again leads to a reliance on results from aquaculture studies.

Lake (1967a) described the food of several species of native fishes reared in ponds. Some species, such as silver perch and western carp-gudgeons begin feeding

after only a few days on algae, before switching to microcrustacea (Table 4). Others, such as freshwater catfish and Murray cod, have large yolksacs and begin feeding much later at relatively large sizes on zooplankton and chironomids (Rowland 1992). The only study performed under natural conditions found that eleotrid larvae less than 5 mm in length consumed only rotifers, whereas larger larvae switched to larger prey, such as calanoid copepods and cladocerans (Gehrke 1992).

Gape size is a major limiting factor in the consumption of prey for a wide range of species of marine and freshwater fishes (Bone et al. 1995). This may mean that there is a reduction or entire elimination of the dependence of those species of Murray-Darling Basin fishes that, as first-feeding larvae, have large gapes, on the very small prey which have generally been assumed to be significant in getting larvae through the critical endogenous/exogenous feeding interval. This may explain why, for species like Murray cod and freshwater blackfish, spawning may be unrelated to flooding, since the larvae may be able to obtain sufficient food in the main stem of rivers via relatively large zooplankton, benthic microfauna, and smaller instars of benthic macroinvertebrates.

### Concluding remarks

The fish faunas of most major river systems in the world have been affected adversely by river regulation, barriers to movement, riparian clearing, habitat alteration, the introduction of exotic species and declining water

Table 4. Food of the larvae of some Murray-Darling fish.

Species	Age at feeding (days)	Length at feeding (mm)	Prey consumed	Reference
Silver perch	6* 7		phytoplankton copepods & cladocerans	Lake (1967a)
Catfish	19*		zooplankton	Lake (1967a)
Murray cod	27*	12–14	chironomids, <i>Daphnia</i> & copepods	Lake (1967a)
Western carp-gudgeon	5*	3.4	Algae	Lake (1967a)
Golden perch			<i>Artemia</i> nauplii	Arumugam & Geddes (1987)
Gudgeons	<5		rotifers	Gehrke (1992)

\*First feeding.

quality. Attempts to redress many of these problems are underway, but to be successful, a good understanding of the relationship between fishes and their environment is vital. This paper has identified three life history modes of Murray-Darling native fish species, some of which may have strong links with the flow environment and others which may not. There is clearly a group of species whose spawning period is unrelated to high flows and flooding and seems to occur during the low flow period in summer. We have proposed the 'low flow recruitment hypothesis' as an explanation for why these species may spawn and how they can recruit during the warm, low flow periods of some Murray-Darling Basin lowland rivers. The widespread acceptance of the importance of flooding and the flood plain for successful recruitment of Murray-Darling fishes and virtual disregard of a rearing role for the in-channel environment has led us to review the status of our knowledge of the biology of Murray-Darling fishes, especially the presumed links with flow and the flood plain. Information on the use of floodplain habitats, and particularly the flood plain proper during inundation, by all stages of Murray-Darling Basin fishes, is either totally lacking, based on studies of limited taxonomic or geographic scope, or based solely on aquaculture studies. It should be a priority for future research to address these gaps in our knowledge. Some suggestions for research are: properly controlled and rigorously designed experiments investigating spawning cues, preferably in conjunction with long-term intensive studies of fish breeding in the wild; further studies into the movement of free embryos, larvae, juveniles and adults of small and large Murray-Darling fish species; sampling of floodplain habitats for emerging zooplankton, zoobenthos and fish larvae over large spatial scales; investigation of the size and composition of the diets of fish larvae in a range of habitats and under a variety of temperature and flow conditions; and studies of the population dynamics of small and large species of Murray-Darling fishes. In addition, our categories of life history modes of Murray-Darling fishes are based on insufficient data and require additional information, refinement and evaluation. The 'low flow recruitment hypothesis' is also as yet untested. Research is required into the relative importance of in-channel versus floodplain habitats as nursery areas, and also the influence of fluctuations in water level on the density and composition of zooplankton and benthic microfauna in these nursery habitats. One could conceive of a rigorous test of the 'low flow recruitment hypothesis' involving

investigation of recruitment patterns of fishes in the different life history modes under a variety of experimental flow releases. It should be possible to hypothesize that those species that recruit during low flow times will recruit well if low flows are maintained for several months during the summer, whereas the opposite will occur if flows fluctuate or are stable and high during this same period.

We are a long way from being able to state definitively what the significance of flow and the flood plain are to Murray-Darling fishes, let alone what the major environmental variables that influence recruitment are. It is incumbent on fisheries biologists to be cautious when ascribing unfettered significance of flooding and the flood plain to the biology of Murray-Darling fishes, since this has likely encouraged complacency in managers that our knowledge of the ecology of fishes is adequate. It may have also diverted attention from other important habitats such as those within the main channel of lowland rivers, as well as relegated to low priority other natural components of the hydrological cycle such as low flows. Indeed, river regulation that involves using rivers as irrigation conduits during periods when flows would normally have been low, has undoubtedly affected adversely those species which use in-channel habitats for rearing. Current stream ecosystem discussions constantly reinforce the importance of longitudinal as well as lateral and vertical linkages (Bayley 1988b, Junk et al. 1989, Thorp & DeLong 1994, Ward & Stanford 1995, Neiff 1996) and the need to understand the significance of many facets of the hydrology of rivers (Walker et al. 1995, Richter et al. 1996, Puckridge et al. 1998). Until we accept for ourselves, and convince resource managers, of the importance of the entire riverine ecosystem and its associated hydrology, there is a danger of establishing priorities based on inadequate knowledge and potentially condemning some of our native fish species to extinction in the process.

### Acknowledgements

We would like to thank the many people who discussed various aspects of this paper during its preparation, in particular Luciano Serafini and Jane Grown and in general staff at the Murray-Darling Freshwater Research Centre. For comments on drafts of the paper, we are grateful to Jane Grown, Simon Nicol, Andrew Boulton and Sam Lake. This paper was written while

AK was funded by the Land and Water Resources Research and Development Corporation through Environment Australia.

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