



Floodplain inundation and fish dynamics in the Murray-Darling Basin

Current concepts and future research: a scoping study



Natural Heritage Trust
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Cooperative Research Centre for Freshwater Ecology

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Abbreviations used in this report

ASL	Australian Society for Limnology
DO	dissolved oxygen
FPC	Flood Pulse Concept
MDB	Murray-Darling Basin
MDBC	Murray-Darling Basin Commission
RCC	River Continuum Concept
RPM	Riverine Productivity Model

Summary

Water in the MDB is a valuable and increasingly contested commodity. As demand for the resource escalates, it is becoming necessary for river regulators and water users to do more with less. This requirement for greater efficiency applies equally to the allocation of water for environmental flows. An improved understanding of the roles of floodplain inundation in the dynamics of freshwater fish populations would serve the interests of a wide variety of Murray-Darling Basin (MDB) stakeholders, since more-accurate targeting of floodplain-inundation flows could potentially liberate water for other needs.

The purpose of this report is to investigate an enduring paradigm among freshwater fisheries scientists that floodplain inundation, necessarily involving large volumes of water, is an essential requirement for successful recruitment and long-term survival of at least some native fish species. Evidence to support this paradigm is limited and sometimes unclear. Some aspects have recently been debated.

The project's primary objective has been to review knowledge on the relationships between floodplain inundation and the responses of Murray-Darling Basin fish species. Topics investigated included:

- fish-population movement in response to the various phases of flooding,
- dependence of native fish on inundated floodplain habitats for breeding,
- dependence of fish species on flooding as a cue to initiate breeding,
- the role of fish-food production on inundated floodplains in pre-spawning conditioning,
- variations in fish-breeding responses with varying spatial and temporal scales of flooding,
- classification of floodplain habitats used by fish,

and related subjects. The report identifies knowledge gaps that currently hinder efficiencies in the allocation of water for environmental purposes and it proposes research designed to address these information requirements.

As expected, the literature does not cover each of the above areas equally, and the knowledge base on which management decisions must rely is uneven and incomplete. The area that has attracted the most attention is the dependence of native fish on inundated floodplain habitats for breeding. The least work has been devoted to the role of inundated floodplains in providing energy inputs to spawning and also to classifying rivers' habitats with respect to inundation patterns. Many questions remain and some of the work is contradictory.

There is some evidence of direct utilisation of inundated floodplains by native MDB fish, by only a small number of species. There is compelling evidence that the status of a wide range of fish depends on the effects of flooding and that reduced flooding through regulation has had adverse impacts. The nature of the mechanisms for these fish–ecology / river–flow interactions, and their relative significance for particular species and communities of fishes, is not yet clear.

Summary of research that could address the identified gaps

Area of interest	Recommended research
Movements of fish in response to flooding	<p>Radio tracking or radio telemetry.</p> <p>Fishways studies.</p> <p>Extend knowledge on movements of the various life-history phases of MDB fish in response to floods.</p>
The control of carp	<p>Investigate large-scale trends in carp abundance through Sustainable Rivers Audit.</p> <p>Test value of strategic carp removal work at key Barmah-Millewa locations.</p> <p>Assess carp control in regulated floodplain lakes using manipulation of water levels.</p>
Dependence of fish species on flooding as a cue to initiate breeding	<p>Small-to-medium-scale experiments on reproduction and larval/juvenile behaviour in response to water level changes, temperature, photoperiod and nutrition.</p>
Dependence of native fish on inundated floodplain habitats for spawning and nursery areas.	<p>Survey inundated floodplains for fish larvae and prey, using habitat stratification.</p> <p>Assess trophic relationships of larval and juvenile fish on floodplains.</p> <p>Carbon-isotope analysis of young fish and food web to find sources and locations of their growth.</p> <p>Use controlled-pond mesocosms to stimulate breeding and investigate distribution of young fish.</p>
The role of fish-food production on inundated floodplains in conditioning fish for spawning	<p>Continue evaluating the roles of materials and energy input from floodplains, including prey and snags.</p> <p>Extend laboratory experiments with various MDB species to detect requirements for surges in nutrition to promote fecundity.</p>
Variations in fish-breeding responses with varying spatial and temporal scales of flooding	<p>Reach-scale mapping to chart locations and sizes of floodplain habitats and to identify commence-to-flow levels in river channels.</p> <p>Fish-population modelling using inputs from maps plus knowledge of species' dependence on inundation of floodplain habitats</p> <p>Large-scale adaptive management based on environmental rehabilitation involving environmental flows and floodplains, and using data from the Sustainable Rivers Audit and other research.</p>

1. Introduction

1.1. Floodplain productivity and biodiversity

Floodplains and the rivers that serve them have been referred to as the most dynamic (Power *et al.* 1995) and valuable (Ward 1995) of all the habitats on Earth. They are capable of primary production that ‘far exceeds’ that of other natural environments (Bayley 1995) and their soils are among the richest agricultural soils anywhere (Cullen 2001). Unregulated floodplain rivers host a rich and complex variety of ecological communities (Junk *et al.* 1989; Welcomme 1985), made possible by the spatial heterogeneity and temporal fluctuation that naturally variable flow regimes impose on the system (Cummins 1993; Power *et al.* 1995; Shiel *et al.* 1998; see also the discussion of Connell’s intermediate disturbance hypothesis in understanding the heterogeneity of the Murray-Darling Basin in Young *et al.* 2001, p. 23). Floodplain rivers are also, however, among the most abused resources on the planet (Johnson *et al.* 1995; Ward 1995).

The productivity and biodiversity of the floodplains of unregulated rivers extend to the terrestrial, semi-aquatic and aquatic components of the system. A variety of agricultural and fisheries activities is made possible, even extremely profitable, by this productivity. The billabongs and other wetlands associated with floodplain rivers are particularly productive and diverse (Hillman 1989, 2001; Boon *et al.* 1990; Shiel *et al.* 1998; Bunn 1998; Kingsford 2000; Hillman and Quinn 2002). The macroinvertebrate and zooplankton communities of the main channel are also thought to benefit from inputs of energy from the floodplain, especially as high flows recede (Bennison and Suter 1990; Shiel 1990; Lake 1994). Fish production in floodplain rivers is greater than that which could be expected merely from the increase in water area that floods provide (Bayley 1991, 1995; Bayley and Li 1996).

1.2. River regulation

The variability of flow responsible for the productivity that makes floodplains so attractive for agriculture and fisheries, however, provokes the construction of dams, weirs and other structures designed to ensure continuity of the domestic, industrial and agricultural water supply (Walker *et al.* 1995; Cottingham *et al.* 1999; National Land and Water Resources Audit 2001). As well as regulating flows, such structures are also used for electricity generation, flood mitigation or to maintain stable water levels for navigation. The resulting controlled water level is quite different from that in the unregulated system, in which variable flow conditions are a prerequisite for ecological health and persistence (Figure 1). Levee banks designed to protect human communities, infrastructure, crops and livestock from floodwaters (Mussared 1997) further alienate the river from its floodplain. A large and growing part of the worldwide scientific literature devoted to the biology of rivers and floodplains is now concerned with the impacts of human activities on riverine productivity and biodiversity. The enormous scope of large dams and other hydrologic modifications has resulted in distinct regional trends of biotic impoverishment (Pringle *et al.* 2000).

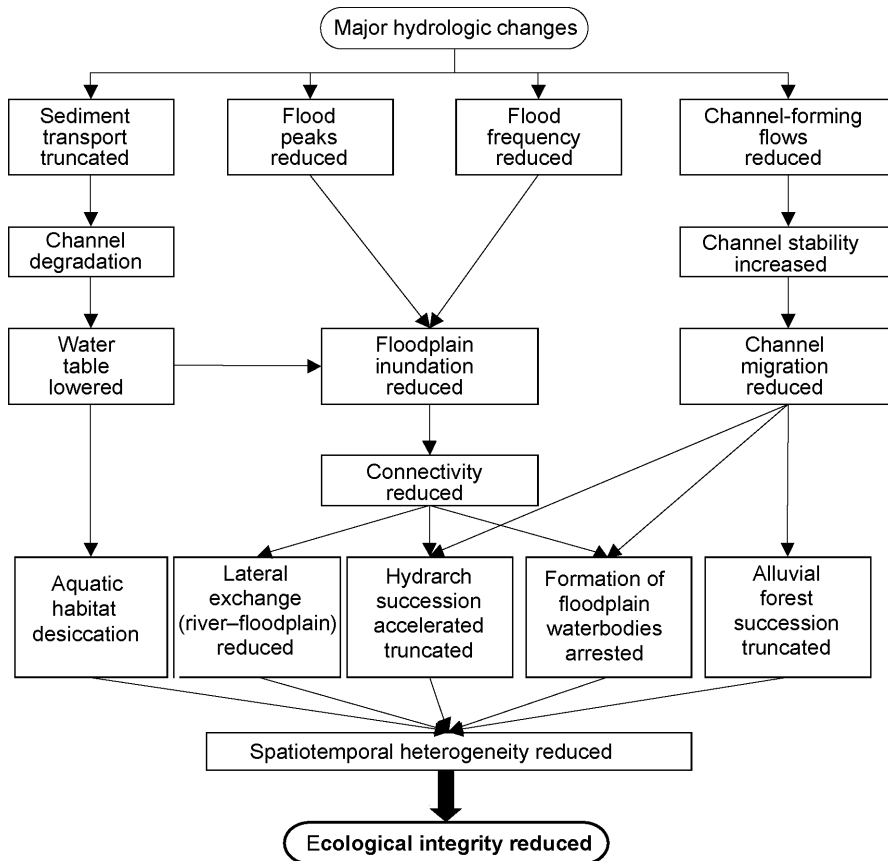


Figure 1. Some implications of major hydrological changes induced by flow regulation on downstream river–floodplain systems (Ward and Stanford 1995, reproduced with permission, John Wiley and Sons).

Current management approaches, the world over, often do not recognise that the integrity of flowing water systems depends largely on their natural dynamic character (Poff *et al.* 1997).

Processes responsible for deterioration in the condition of rivers are often complex and can span spatial and temporal scales at several orders of magnitude (Humphries *et al.* 1999). River regulation is only one of many causes of adverse effects on riverine fish fauna. Untangling the various impacts is difficult given the variability of flow and the scarcity of unregulated rivers with which to make comparisons. Kearney *et al.* (1999) grouped threats to the sustainability of Australia’s freshwater fisheries into six major headings. In addition to the effects of altered flows, they found habitat degradation, contamination, fishing, barriers to migration and introduced species to be the major problems faced by inland fisheries. The fish faunas of most of the world’s river systems suffer similar problems (Humphries 1999).

Rutherford *et al.* (1998) listed changed water regimes as the main problem facing Australian freshwater wetlands. Altering wetlands has had negative consequences for river systems, the River Murray especially. Modified flow regimes have resulted in many wetlands being more-or-less permanently

inundated. Others have had their connections to river flows modified so they are less frequently inundated. Together with reduced frequency and duration of small and medium-sized floods through impoundment and regulation, these changes have profoundly altered floodplain watering, with associated changes to the nutrient-cycling and succession processes driven by the natural cycle of wetting and drying (Pressey 1985; Lake 1994; Burns and Walker 2000).

The Murray-Darling Basin is seen as a prime example of a river system under stress, and quotes to demonstrate this abound. For example:

... many of the methods used to gain the economic rewards that flow from the Murray-Darling Basin are now seen as unsustainable (Blackmore and Connell 1997)

Floodplain billabongs ... are critical to maintenance of floodplain biodiversity, yet with isolation of floodplains from the parent rivers, billabongs are being lost or severely degraded (Shiel 1996).

Flow regimes in the Murray-Darling Basin have changed markedly over the past century, and especially the past 50 years. Average monthly and annual flows are now considerably lower than those that prevailed under natural conditions (Maheshwari *et al.* 1995). Storages in the Murray-Darling Basin are capable of holding 103% of the annual runoff, and 80% (Humphries and Lake 2000) to 87% (Kingsford 2000) of the available water is extracted for consumption. The seasonal distribution of flows has been changed, flood frequency has decreased and the amplitude, timing and duration of flooding have been altered (McKinnon 1997a). In particular, the occurrence of small and medium floods has been reduced (Thoms *et al.* 2000) and this has had impacts on population recruitment (Harris 1988) and other aspects of fish ecology.

A reduced amount of water available to the floodplain reduces the linkages (Walker *et al.* 1995; Thoms *et al.* 2000) or connectivity (Ward and Stanford 1995; Young *et al.* 2001) among floodplain elements and this is thought to prevent the periodic 'resetting' of ecosystem processes (Walker and Thoms 1993; Bayley 1995). The complexities of these linkages between inland waters and their catchment elements are not often addressed by current management systems (Environment Australia 2001).

1.3. Concepts in river ecology

Several models have been proposed to explain how lotic (i.e. running water) systems function. The 'flood-pulse concept' (FPC) and its variants are applicable to floodplain rivers (Johnson *et al.* 1995). The FPC states that annual inundation is 'the principal driving force responsible for the existence, productivity and interactions of the major biota in river-floodplain systems' (Junk *et al.* 1989). It emphasises the lateral exchange of materials between channel and floodplain during overbank flows (Thoms *et al.* 2000). It requires that the flood pulse be annual and of long duration, and that the flood always overflows the river channel — features that do not routinely characterise Murray-Darling Basin rivers.

The FPC has been called a 'unifying concept for ecological function of large flood-plain rivers' (Gutreuter *et al.* 1999) and although it is too general to be tested in its entirety, it has served as a useful source of testable hypotheses

about biological responses to floods (e.g. Bayley 1995; Gutreuter *et al.* 1999). Many river ecologists have sought to understand the effects of flow regulation in terms of this model. Its usefulness as a general explanatory and predictive framework applicable to a wide range of rivers may, however, be questionable because of the site-specific natural history needed to tailor models to specific ecosystems (Power *et al.* 1995) and the great variation in flow regime within and among rivers (Hynes 1970; Poff *et al.* 1997). This latter consideration can give rise to different ecological consequences for the same human activity in different locations (Poff *et al.* 1997) so the model may be of little help in understanding some of the effects of change relative to the natural condition. Eggleton and Schramm (1999) found application of the FPC may be misguided without modification for the different physical characteristics of temperate rivers. The FPC also requires modification if it is applied to semi-arid rivers such as those of the Murray-Darling Basin (Puckridge *et al.* 2000), which do not always meet its assumptions.

Another major conceptual model of river function is the 'river-continuum concept' (RCC) (Vannote *et al.* 1980), which emphasises longitudinal, instead of lateral, transport of organic material. Johnson *et al.* (1995) found, paradoxically, that the FPC, the RCC or both may apply, even within a single river. This situation can exist because of the geomorphology of the system and the temporal and spatial scales of analysis. Unsurprisingly perhaps, they saw the need for a new conceptual framework.

Thorp and Delong (1994) also questioned the ability of the models then current to explain adequately the function of riverine ecosystems. They postulated the 'riverine productivity model' (RPM) as an alternative to both the FPC and RCC. In this view, autochthonous (i.e. in-channel) production and direct organic inputs from the riparian zone are of greater importance in determining the food web structure and productivity of large rivers than 'direct, floodplain subsidies', because they can be assimilated more easily and are readily available. Further work led Thorp and Delong to revise the RPM to accommodate a decrease in the importance of input from riparian zones (Thorp *et al.* 1998). The authors of the RPM made the point that it does not obviate other important roles for a flood pulse. Dettmers *et al.* (2001) suggested that it might be more 'realistic' to view energy flow in large rivers as a combination of the RCC, the FPC *and* the RPM.

1.4. Fisheries

The Murray-Darling river system is the mainstay of Australian freshwater fisheries (Walker 1983). The Murray-Darling Basin is popular with recreational anglers and its commercial fisheries provide most of Australia's inland fish production, yet a perception exists that 'over-regulation of flows is driving our native fish stocks to extinction' (Dr S. Blanch, Australian Conservation Foundation, quoted in Woodford 2001). The declining productivity of the Murray-Darling Basin's fisheries has coincided with increased regulation of the water resource and reduced structural complexity of the ecosystem (Lake 1994; Reid *et al.* 1997). Ye *et al.* (2000) found that recruitment and productivity in the South Australian fishery for Murray cod was associated with spring flows. Many researchers have therefore postulated that a causal relationship exists, i.e. that flow regulation has caused profound changes in the river environment that in turn have caused

the range and abundance of native fish species to decline (e.g. Walker 1983; Pierce 1989; Brown 1992; Gehrke *et al.* 1995; McKinnon 1997; MDBC 2002a, among many others). Mallen-Cooper (1993), however, pointed out that the evidence for a causal relationship was usually anecdotal and difficult to separate from other changes in the habitat. For example, regulation has also obstructed fish passage in the Murray Darling Basin. Isolating the biological effects of changes in the magnitude, frequency, duration and timing of inundation from other possible causes of the decline of fish populations is impossible from studies of correlation alone.

Fish are thought to use floodplains for a variety of purposes: shelter (Saint-Paul *et al.* 2000), to survive catastrophic events, feeding (Merron 1993; Pusey and Bradshaw 1996), spawning and recruitment (see below), or a mixture of these (e.g. Reimer 1991). Pringle *et al.* (2000), in comparing the macrobiota of tropical and temperate floodplains in the New World, said it was 'unquestionable that many — if not most — fishes living in the main channel of floodplain rivers use naturally flooded habitats to some degree for feeding and reproduction'. Penaz *et al.* (1991) declared 'the great significance of the floodplain for the reproduction, nursery and recruitment of fish has been well documented'. Early experimental studies by Lake (1967) emphasised the role of flooding in the breeding ecology of inland fish. Concerning the fish of the MDB, Cadwallader and Lawrence (1990) said that 'flooding is essential for successful recruitment of most native fish in the system' and this conviction has been evident in the papers of many Australian freshwater fisheries ecologists (e.g. Gehrke *et al.* 1995; Humphries 1995). The body of opinion was so great that it assumed the status of a paradigm for many, if not most, of those interested in recruitment processes of freshwater fisheries. The evidence for some aspects of the paradigm has, however, been found to be limited and/or ambiguous and it has recently come to be invoked with greater caution (e.g. Schiller and Harris 2001).

The paradigm that fish need floods (the 'flood-recruitment model' of Harris and Gehrke 1994, Figure 5) is based on studies performed under hatchery conditions and on a limited number of recreationally important species, but also on evidence from studies that have found a correlation between river regulation and fish catches (e.g. Walker and Thoms 1993; Reid *et al.* 1997). It is derived from observations that increases in water level in aquaculture ponds initiate spawning in some species (Lake 1967), from limited studies of wild fishes, from the seminal studies of Welcomme (1985) and Junk *et al.* (1989) in overseas floodplain river systems, and from surges in Australian fish productivity following floods (Cadwallader 1978; Harris 1988; Cadwallader and Lawrence 1990; Gehrke *et al.* 1995; Reid *et al.* 1997). There is, however, little evidence that fish larvae, juveniles or adults actually use temporary floodplain habitats in the Murray-Darling Basin (Humphries *et al.* 1999; Schiller and Harris 2001; Meredith *et al.* 2002) and the benefits of floodplains may be indirect.

Restoring the pre-regulation flow regime for the sake of fish and fisheries is clearly difficult given the human demands currently placed on the system. The complexities of the MDBC's current *Living Murray* project (MDBC 2002b), which is examining the benefits and costs of allocating three different levels of flow for environmental purposes, provide a good example. Restoring full floodplain connectivity to the Lower Murray, for example,

would require the removal of all current delivery constraints and cessation of upstream consumptive uses, or that diversions across the entire basin are reduced by 30% (MDBC 2001). This could be achieved by greater efficiencies in the use of water and a change in the methods of its delivery. Of the water diverted for use only 77%, on average, actually reaches the customer. The remainder is lost to seepage or evaporation. The percentage delivered varies between 41% and 100% and reflects delivery techniques ranging from open channels to fully piped reticulation systems (National Land and Water Resources Audit 2001). Reduction by 30% is therefore conceivable but whether those water savings would be used solely for environmental flows is open to question.

Environmental flows — that is, residual flows deliberately left for a river to maintain its ecological integrity (Humphries 1995) — are seen as a means of ameliorating some of regulation's effects on the productivity and biodiversity of the river-floodplain system. A definitive, scientifically based conclusion about how much water is enough to prevent particular levels of environmental degradation in the MDB remains elusive, however. This is mainly because of the lack of sufficient information about the intricate relationships between flows and ecology (Pusey 1998; Thoms *et al.* 2000; MDBC 2001) and partly because of the complex factors interacting with flow changes in rivers. Restoring a flow pattern proportional to the natural hydrograph may be of little value, because many ecological processes show a nonlinear response to flow, evidenced by thresholds rather than continual gradients of change (Poff *et al.* 1997). Some researchers take the view that the declining health of river ecosystems can only be halted by returning 'substantial' amounts of water to the environment (e.g. Cullen *et al.* 1996; Walker *et al.* 1995). In the current situation, where water resources are already overcommitted and most surface waters are approaching or have exceeded their extraction limits (Shiel 1996; EPA 1997; Prime Minister's Science, Engineering and Innovation Council 2002) substantial amounts of water are difficult to provide. Water for environmental flows must therefore be targeted to those areas where it will be of most benefit.

The allocation of water to environmental flows has the potential to stem the decline of native fish that has occurred since regulation began (Phillips *et al.* 2002; MDBC 2002a). The substantial literature indicates that environmental flows can contribute strongly to fish conservation and to restoring sustainable fisheries in the Murray-Darling Basin. But, unless there is a detailed understanding of the relationships between floodplain inundation and the dynamics of native fish, maximum benefits may not be achieved from the allocation of valuable water. If, for example, some freshwater fishes require floodplain inundation to initiate spawning, allocating only 20% of that flow is unlikely to initiate spawning in 20% of fishes (Poff *et al.* 1997) and this water may have been more usefully employed elsewhere. Much research remains to be done to provide the knowledge required for precise targeting of environmental flows to benefit native fish in the MDB.

1.5. Project aims

The purpose of this report is to review current knowledge on the relationships between floodplain inundation and the responses of MDB fish. Research topics we have investigated include:

- fish-population movement in response to the various phases of flooding,
- dependence of native fish on inundated floodplain habitats for breeding,
- dependence of fish species on flooding as a cue to initiate breeding,
- the role of fish-food production on inundated floodplains in pre-spawning conditioning and larval and juvenile development,
- variations in fish-breeding responses with varying spatial and temporal scales of flooding,
- classification of floodplain habitats used by fish.

The report reviews the literature on these and related topics. It identifies knowledge gaps that currently hinder improved efficiencies in water allocation for environmental purposes and suggests research designed to address these information requirements.

2. Literature review

2.1. Movement of fish populations in response to flooding

There are few records of fish behaviour or habitat use during floods for the life-history intervals of any fish species (Harris *et al.* 1992; Jowett and Richardson 1994; McKinnon 1997b, cited in Humphries *et al.* 1999). Nevertheless, some observations have been made and Bayley (1995) has modelled the movement of fish populations in response to flooding (Figure 2).

In field studies, fish populations have been observed to make use of floodplain resources in New Zealand (Jowett and Richardson 1994) North America, Africa and the Amazon (Dudgeon 1983). Fish in these studies were observed feeding on terrestrial plants during flood events. The contributions of these plants to the diets of fish varied from slightly over half to almost the entire diet (Dudgeon 1983). In the Current River, Missouri, Matheney and Rabeni (1995) radio-tracked 25 northern hog suckers, *Hypentelium nigricans*, for a year and were able to determine their daily and seasonal patterns of habitat use. They demonstrated that these fish remained in their home area during high-flow events but used flooded riparian areas where current velocities were lower. Snedden *et al.* (1999), in a similar long-term study of spotted gar (*Lepisosteus oculatus*) in the Atchafalaya River basin, Louisiana, found that fish established home ranges that included large areas of inundated floodplain during flood events. They surmised that this area provided suitable spawning and nursery habitat. Bunn and Balcombe (2001) documented fish feeding on algae in the Cooper Creek floodplain of central Australia.

Evidence is emerging that fish populations use the floodplains of the Murray-Darling Basin (Humphries *et al.* 1999; Humphries 1999). Radio-tagging studies (Koehn 2000) have shown that Murray cod, *Maccullochella peelii*, make extensive use of inundated floodplain channels and anabranches. This activity may be driven by the availability of prey, particularly shrimp, crayfish and terrestrial invertebrates, produced abundantly after flooding of leaf-litter accumulations in these areas.

A number of native fish species (notably golden perch, *Macquaria ambigua*, spangled perch, *Therapon unicolor*, bony herring, *Nematalosa erebi*, and silver perch, *Bidyanus bidyanus*) in the Murray-Darling Basin make long migrations upstream, travelling up to thousands of kilometres, and this is often in response to rising flow (Reynolds 1983; Harris *et al.* 1992; Humphries *et al.* 1999; Mallen-Cooper *et al.* 1997; Harris 2001). After these migrations, fish have been thought to move laterally onto the floodplain to spawn, or else to spawn in the channel with the embryos and larvae later being swept on to inundated nursery areas (Lake 1967). Little evidence has emerged to support these ideas. McKinnon (1997a), when interpreting the results of fish tagging during experimental and natural floods of the Barmah Forest, concluded that the local migrations of Murray cod, golden perch and silver perch were 'somewhat' restricted to permanent creeks and floodplain gullies. He found only limited movement on the floodplain proper but fish

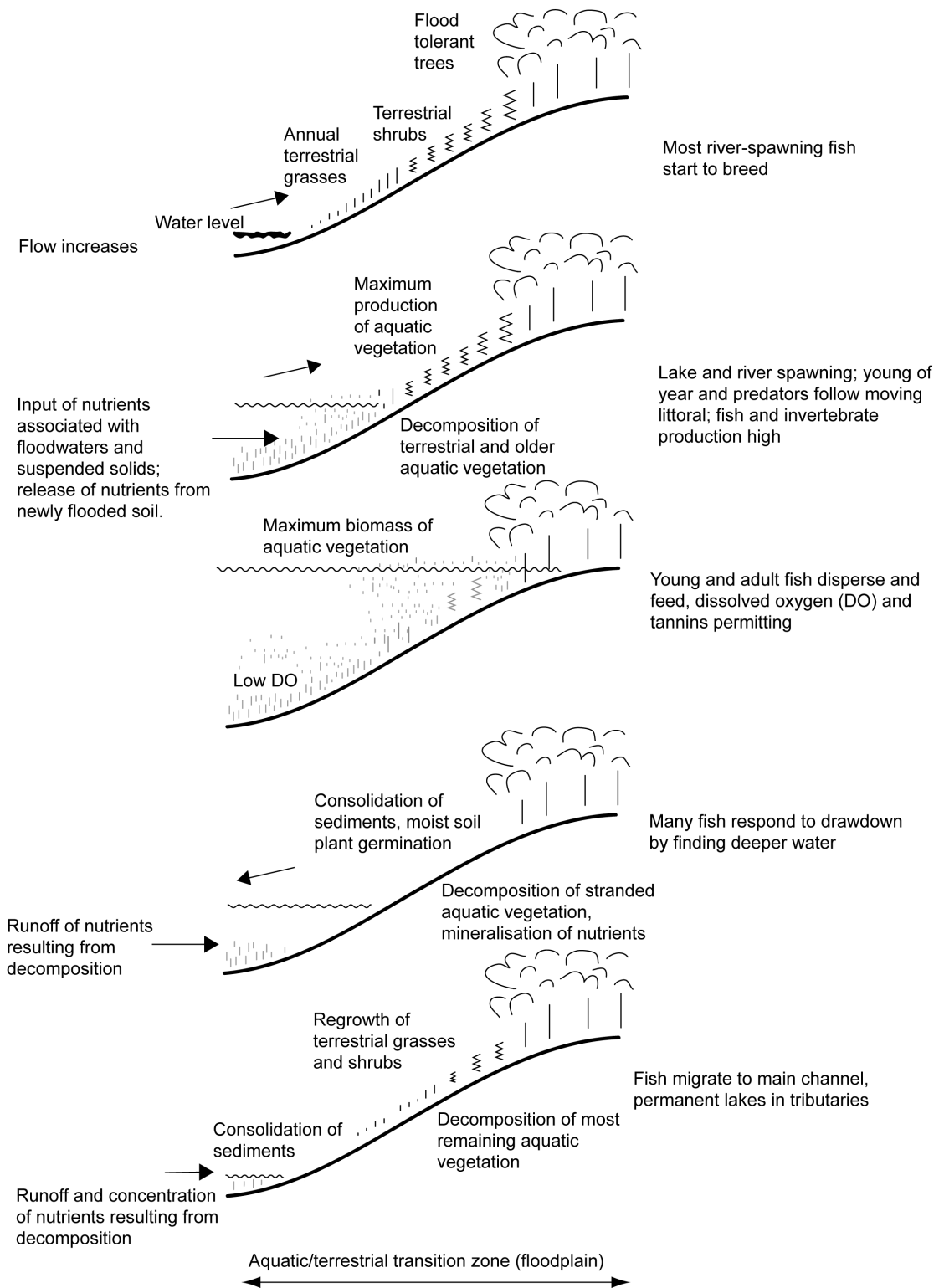


Figure 2. Schematic diagram of the flood-pulse concept (derived from Junk *et al.* 1989) showing a vertically exaggerated section of a floodplain in five snapshots of an annual hydrological cycle. Right hand column indicates typical life history traits of fish. Reproduced from Bayley (1995).

appeared to use the floodplain gullies for transit between creeks and other, more permanent waterbodies. Little information has yet been published about the movements of smaller species in floodplain channels. But current research to evaluate the effectiveness of various fishway designs, at sites such as Torrumbarry on the River Murray (Dr Lindsay White, MDBC, personal communication) or Balranald on the Murrumbidgee (Lee Baumgartner, NSW Fisheries, personal communication), is showing large-scale movements of small fish.

Flood occurrence and seasonality in Australian rivers are highly irregular and unpredictable by comparison with the great river systems in other continents (McMahon 1986). This unpredictability may reduce the opportunity for fish to evolve with specific adaptations for exploiting the resources of periodically inundated floodplains and helps explain the preponderance of opportunistic, generalist species in the Australian fish fauna.

The importance of flooding events for fish does not rely solely on whether or not the fish are actually present on floodplains during inundation. Fish may not have to use floodplains directly to benefit from them. Flooding releases nutrient inputs through the wetting-drying cycle and influences various less-direct responses, including migration. There is compelling, but indirect, evidence that increasing regulation of rivers and concomitant decrease in flow variation and volume in the MDB has caused the decline of fish stocks and/or reduced diversity (Reynolds 1976; Cadwallader 1978; Pollard *et al.* 1980; Cadwallader and Lawrence 1990; Harris and Gehrke 1997; Reid *et al.* 1997). Gehrke *et al.* (1995), for example, found a relationship between degree of regulation of four rivers (measured by annual proportional flow deviation) and the decline of species diversity. Walker and Thoms (1993) found a 'clear correspondence' between the decline of Murray cod and golden perch populations in the River Murray and the growth of storages and diversions. They also demonstrated a close correlation between golden perch catches and river levels in the lower Murray over the period 1939–1979. Reid *et al.* (1997) examined commercial fisheries data and found a strong association between river flows and large-scale cycles in fish recruitment and production. Large numbers of carp larvae were found drifting off floodplain habitats into the River Murray channel after floods (Stuart and Jones 2002). Harris (1988) demonstrated a direct correlation between annual population recruitment in Australian bass, *Macquaria novemaculeata*, and river level in the preceding spawning season. Conversely, Puckridge and Walker (1990) interpreted data on bony herring to show they do not depend on flooding for food production, indicating how the trophic dynamics of this herbivorous species differs from the numerous microphagic and macrophagic predators in the MDB fish community.

McKinnon (1997a) found no correlation between catch rates of native fish and flood stage. He strongly suggested that a combination of environmental factors was important in stimulating spawning-related migrations, rather than flooding or flood stage alone, and thought it 'entirely likely that spawning-related migration in native fish will occur in years when lower level flooding, or perhaps no flooding at all, occurs'. However, substantial lag times have been observed between spawning and the appearance of a cohort in catches, and species' catchability in fishing gear (e.g. Cadwallader 1978) can confound correlations between catch and flow.

Rather than being absolutely necessary for recruitment, large floods may provide migration and spawning cues and enhance population growth and survivorship across a wide area and for a relatively long time and so result in widespread, synchronous reproduction that later becomes evident as a large cohort.

Apart from effects on fish recruitment, periodic inundation also functions to maintain the diversity of habitats and organisms within the floodplain itself and, through disturbance effects, to prevent the occurrence of climax communities characterised by their uniformity.

2.2. The control of carp

Pest species, particularly common carp (*Cyprinus carpio*) are a threat to native fish and fisheries and may possibly be remedied by environmental flows. (An overview of the other alien fish in the MDB and their ecological impacts can be found in Schiller and Harris 2001.) Carp is the dominant fish species in rivers of the MDB (ASL 2002) where it now constitutes the overwhelming bulk of fish biomass (Grew 1996; Harris and Gehrke 1997; Brown *et al.* 2003), often around 90 per cent in some river reaches. There is debate about whether carp are a primary cause of degradation of river systems or whether their success is merely one of the consequences of declining river condition (Driver *et al.* 2005; ASL 2002). Carp are highly adaptable and tolerate broad ranges of environmental variables including temperature, depth, dissolved oxygen, turbidity and salinity. Their spawning requirements are less demanding than those of some native fish and they can often exploit habitats that may be unsuitable for many native species because of pollution (especially with cold water from thermally stratified dams) or other forms of habitat degradation (Harris 1997). They succeed in disturbed habitats such as highly regulated rivers (Driver *et al.* 2005).

Flow regulation is unlikely to be the sole reason for carp's dominance (Harris 1997; MDBC 2002a). Physical barriers to fish migration, and agricultural effects on habitat structure and water quality are just two of many other factors associated with high carp densities (Driver *et al.* 2005). With regard to the effects of flow, however, increasing departure from natural flow conditions caused by river regulation may reduce the reproductive success and subsequent recruitment of native species (Welcomme 1995) and tend to favour more-generalist, alien species such as carp, whose reproductive cycles are not so strongly cued to seasonal flow regimes (Li *et al.* 1987, cited in Gehrke *et al.* 1995).

The duration of a specific flow event is thought to affect its ecological significance (Poff *et al.* 1997). Fishes tolerant of low flow can persist in locations from which they might otherwise be displaced by dominant but less tolerant species or *vice versa*, depending on the flow regime. *Gambusia holbrooki*, for example, has been shown to recruit only weakly in the unregulated Cooper Creek during serial floods, and native fish have an apparent advantage in these conditions, although the mechanisms responsible for that advantage are unclear (Puckridge *et al.* 2000). Flood persistence presents conditions in which *Gambusia* could be expected to thrive but which instead have favoured the recruitment of native fish. Conversely, McKinnon (1997a) found that flooding was correlated with low catches of alien species but that large numbers of juvenile carp were present

after floods. He speculated that flooding might provide increased spawning and recruitment opportunities for carp, particularly if the flood was of unusually long duration. Research by Stuart and Jones (2002) supported and extended these conclusions.

Variable environmental flows designed to rehabilitate native fish present an opportunity to strengthen indirect control over carp by promoting competition and predation (Harris 1997; Phillips *et al.* 2002; MDBC 2002a; Lapidge 2003). Restoring a semblance of the natural hydrograph would, however, be unlikely to exert much control over carp numbers by itself, since carp are generalists with relatively few specific requirements (Phillips *et al.* 2002). Both direct and indirect methods are needed.

The Australian Society for Limnology considers environmental rehabilitation to be the method most likely to produce significant, widespread reductions in carp numbers (ASL 2002), based on the observation that carp are successful in damaged habitats. Rehabilitation is predicted to increase the resilience and resistance of damaged freshwater ecosystems to invasion by alien species like carp. There is anecdotal evidence that carp do not thrive in undisturbed natural systems but this has not been tested.

Other methods suggested for controlling carp populations include harvesting (Thresher 1997), poisoning (Sanger & Koehn 1997; Bonneau and Scarnecchia 2001), biological control (Roberts and Tilzey 1997), genetic manipulation (Lapidge 2003), viral diseases (Grew 1996) and hydrologic manipulation (Wilson 2000; Wilson *et al.* unpubl.). Reducing carp numbers by direct removal is likely to be only a short-to-medium term solution. If adult numbers are reduced, the survival of young carp may be greatly enhanced because density-dependent population-feedback mechanisms will have been removed, so that the total number of carp actually increases and a strong new cohort emerges (ASL 2002). The possible ecological consequences for the aquatic environment of replacing a number of large carp mouths with, potentially, a far greater number of smaller ones are also not yet fully understood (Gehrke 2002).

Hydrologic manipulation for the control of carp populations is not a new idea, mooted since at least 1957 (Shields 1957), but it has the potential to become an important tool. In 1994, an experimental 30 cm drawdown of Bowman-Haley Reservoir, North Dakota USA, during carp spawning left many shoreline areas covered with mats of dry carp eggs (Bonneau *et al.* 1995). The potential use of hydrological manipulation as a strategy for the control of carp has been investigated by the Cooperative Research Centre for Freshwater Ecology (CRCFE) (CRCFE 1999; Wilson 2000; Wilson *et al.*, unpubl.). Carp tend to lay their eggs around the shallow edges of lakes and billabongs. An understanding of when eggs are laid could allow the managers of small to medium size, regulated water bodies to eradicate a large proportion of the carp population's annual production of eggs by desiccation. Wilson (2002, and unpubl.) was able to manipulate water levels in replicate ponds and he succeeded in initiating spawning among the experimental populations of carp. Subsequent drawdown of the ponds left eggs stranded and desiccated.

The tendency of carp to spawn in shallow water during flooding can, in regulated river reaches, be used to direct them into an area where they can be netted (Wilson 2000) and their eggs can be stranded by subsequent lowering of the water level. Advantage can similarly be taken of their propensity to gather in relatively warm tributaries prior to and during spawning. Bonneau *et al.* (1995) used this behaviour to remove approximately half the estimated 680 tonnes of adult carp in the Bowman-Haley Reservoir. The identification by Stuart and Jones (2002) of focal areas of intense carp reproduction in the Barmah-Millewa Forest floodplains suggests that hydrological manipulation may potentially be a successful, large-scale technique for controlling carp in such areas of the MDB.

Because carp are likely to reproduce more successfully following reductions in population density, stocking with predator species after removal of the older fish may be necessary to control numbers of young carp (Bonneau *et al.* 1995). Stocking with predatory fish without first removing the larger fish is a strategy that generally fails because predation of adult carp is minimal (Crivelli 1981).

Environmental flows, provided as part of a general rehabilitation of river systems, particularly need to be integrated with a comprehensive program of direct and indirect methods (Harris 1997; CCCG 2000; Phillips *et al.* 2002; MDBC 2002a). Thus plans for rehabilitating ecosystems must also include restoring fish passage past dams and weirs, rehabilitating riparian vegetation and re-establishing more-natural water temperature regimes below dams (MDBC 2002a).

2.3. Dependence of fish species on flooding as a cue to initiate breeding

Agreement on this aspect of the relationship between fish and floods has not been reached in the literature. Several studies have shown that a flooding flow is necessary to initiate the migration and/or spawning of silver perch (Mallen-Cooper 1992; Walker and Thoms 1993; Rowland 1994), golden perch (Mackay 1973), and multiple species (Cadwallader and Lawrence 1990; Harris and Gehrke 1994; Gehrke *et al.* 1995). In coastal rivers, Australian bass, *Macquaria novemaculeata*, failed to recruit in drought years but recruited abundantly in proportion to peak flows when floods occurred during the spawning season (Harris 1988). Schiller and Harris (2001) grouped the native fish of the MDB into reproductive guilds based on the importance of floods to their spawning. Of 23 species of fish, three are believed to have a strong requirement for flooding (Figure 3; group 1) and eight to have a weaker requirement (Figure 3; groups 2 and 3). Of these latter species, flooding flows are thought to enhance the spawning success and recruitment of these fish but are not essential for it to begin.

Species that are thought to have their spawning enhanced by floods lay sticky eggs on either vegetation (Figure 4, group 1) or hard substrates (Figure 4, group 2) that will not be transported by floods. The sticky eggs of quite a few of these species (those shown in italics in Figure 4) hatch within three days or less, which allows larvae to benefit from floods by being transported to nursery areas. The three species thought to be strongly flood-cued spawners (Figure 3, group 1) have non-sticky eggs that are available

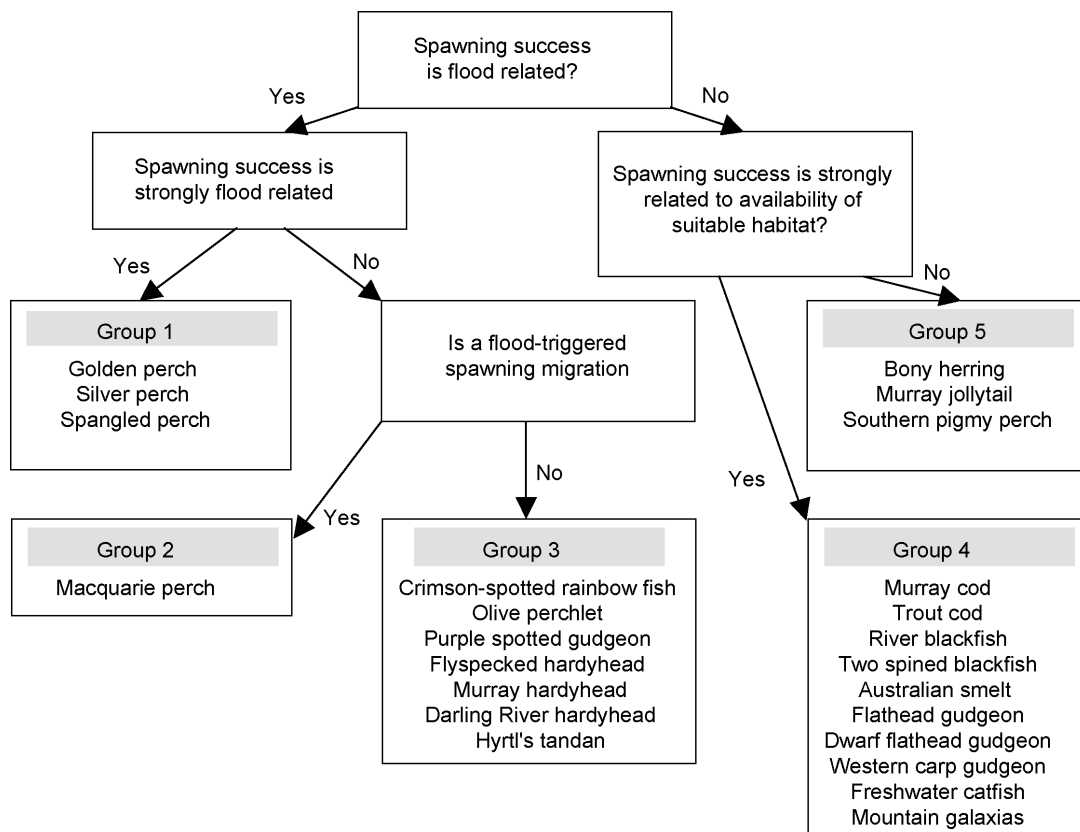


Figure 3. Reproductive guilds of the native freshwater species of the Murray-Darling Basin based on the associations between floods and spawning. Taken from Schiller and Harris (2001) with permission.

for transport by floods. This availability may be high, as in golden perch and silver perch, which produce semi-buoyant eggs, or less high in the case of spangled perch, with eggs that do not float. The association between flooding and spawning in these species seems clear but factors other than flooding have recently been implicated as cues for spawning. Humphries and Lake (2000) found that that for species present in the Campaspe and Broken Rivers, the hydrology during the winter and spring preceding breeding was unlikely to be a cue for final maturation and spawning. Humphries *et al.* (1999) stated that evidence from 'studies to date' had emphasised temperature more than flows in the likely cues for spawning of native Murray-Darling fishes. Few MDB literature reports consider changing photoperiod as a cue controlling fish reproduction, although there are many examples in fish biology. As stated earlier, McKinnon (1997a) found no correlation between catch rates of native fish and flood stage except for golden perch in two years. Instead he considered a combination of environmental factors to be important in stimulating spawning related migrations, rather than flooding or flood stage alone, and saw it 'entirely likely that spawning-related migration in native fish will occur in years when lower level flooding, or perhaps no flooding at all, occurs'. Mallen Cooper *et al.* (1997) found strong year classes of golden perch and silver perch in one section of the River Murray that were associated with spring flows contained

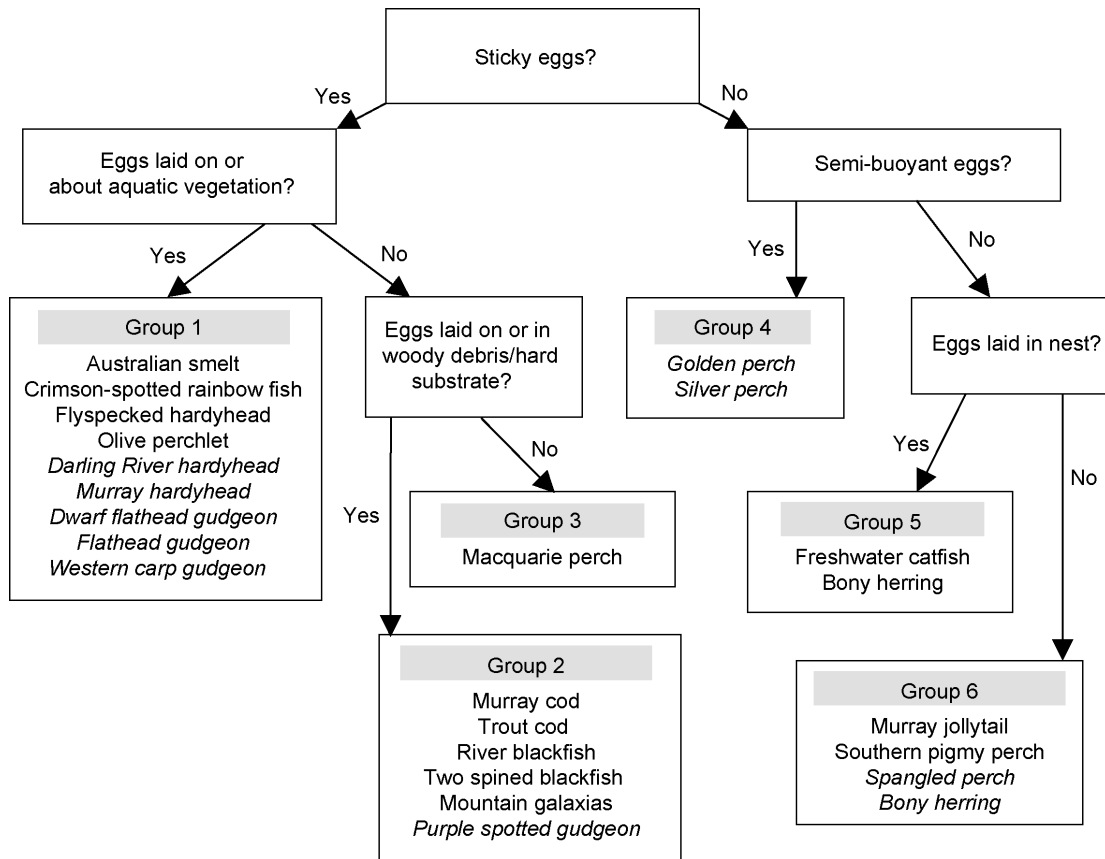


Figure 4. Reproductive guilds of the native freshwater fishes of the Murray-Darling Basin based on the physical properties of the eggs. Species in italics have a hatching time of three days or less. Taken from Schiller and Harris (2001) with permission.

within the river channel, and poor year classes associated with high spring flows that inundated floodplains. Humphries *et al.* (1999) saw this as evidence for different cues for spawning across the Murray-Darling Basin because of its mixture of climates and times of peak flow.

Collins and Anderson (1999) found no effect of temperature or flooding in the initiation of egg formation in golden perch. Instead, they saw rapid growth of oocytes and the achievement of near-mature eggs in fish that had been starved for 150 days and then fed. Flooding was not implicated because the egg development occurred in the absence of environmental stimuli such as temperature, water level and photoperiod. They postulated that such a strategy would allow fish to rapidly take advantage of sudden increases in food availability during floods.

If water level rises are not important in the initiation of spawning, or not as important as was once thought, then regulation may have had more of an impact on the post-spawning stages of recruitment than on prevention of spawning (Humphries and Lake 2000; Schiller and Harris 2001).

2.4. Dependence of native fish on inundated floodplain habitats for spawning and nursery areas

No native MDB fish species have been shown to depend on floodplain habitats for spawning. Given the unpredictability of inundation, such adaptations are unlikely. But international studies (e.g. Welcomme 1985) have demonstrated how abundant food, ample habitat and low predation rates create favourable nursery habitats for young fish on inundated floodplains. Availability of abundant suitable food at the ‘critical’ period of development is a major determinant of larval survival (May 1974). Opportunistic use of floodplain productivity for larval and juvenile growth and survival has often been reported as a reason for occasional strong cohorts that boost MDB fish populations (e.g. Llewellyn 1973; Cadwallader and Lawrence 1990; Schiller and Harris 2001). Data are relatively sparse on the ecology of most species of Australian native fish, especially information on larval ecology (Boulton and Brock 1999), although many field-identification guides and biological summaries have been produced (e.g. Merrick and Schmida 1984; McDowall 1996; Allen *et al.* 2002). The assumption that freshwater fish use, and in many instances require, flooding and inundated floodplains for spawning and/or nursery habitat has, however, formed the basis of, or been implicit in, many studies both in Australia and overseas (e.g. Grubaugh and Anderson 1988; Cadwallader and Lawrence 1990; Merron *et al.* 1993; Humphries 1995; DeAngelis *et al.* 1997; Snedden *et al.* 1999; Pringle *et al.* 2000) and a sequence of stages in the flood-recruitment model has been presented by Harris and Gehrke (1994, Figure 5). Walker and Thoms (1993) stated that at least 20 of the 30 native species found in the Murray-Darling Basin depend on floods for successful recruitment and that all had a ‘general reliance’ on flooding of the river–floodplain ecosystem.

Schiller and Harris (2001) grouped 11 species of fish in three reproductive guilds for which spawning success is flood related (Figure 3). As mentioned earlier, the reliance of fish in other continents on the regular inundation of floodplains for their reproduction has been referred to as ‘unquestionable’ (Pringle *et al.* 2000) and ‘well documented’ (Penaz *et al.* 1991). As recently as 1999, however, Humphries *et al.* (1999) could say that that no Murray-Darling fishes have been observed spawning on the floodplain proper and no larvae had ever been collected from seasonally inundated floodplain habitats. They categorised MDB fishes into four life-history ‘modes’, and placed only two species (instead of 11) in the mode for which the spawning cue was rising water level. They emphasised the uncertainty of this cue for the two species, golden perch and silver perch, with a question mark. Furthermore, Gehrke *et al.* (1993) showed that accumulated litter under river red gums, *Eucalyptus camaldulensis*, in the MDB produces polyphenols associated with ‘blackwater’ when inundated, and these compounds are highly toxic to fish if the floodplain is not well flushed.

Few studies of wild MDB populations have found evidence that adult fish and larvae use non-permanent floodplain habitats (McKinnon 1997b cited in Humphries *et al.* 1999). As Humphries *et al.* (1999) pointed out, this may be due to a lack of the right kind of study. However, Meredith *et al.* (2002) have since reported on larval and adult fish distributions in three contrasting habitats (fast creek, shallow pond and weir pool) in the lower River Murray. They found that large-bodied fish including Murray cod, golden perch and

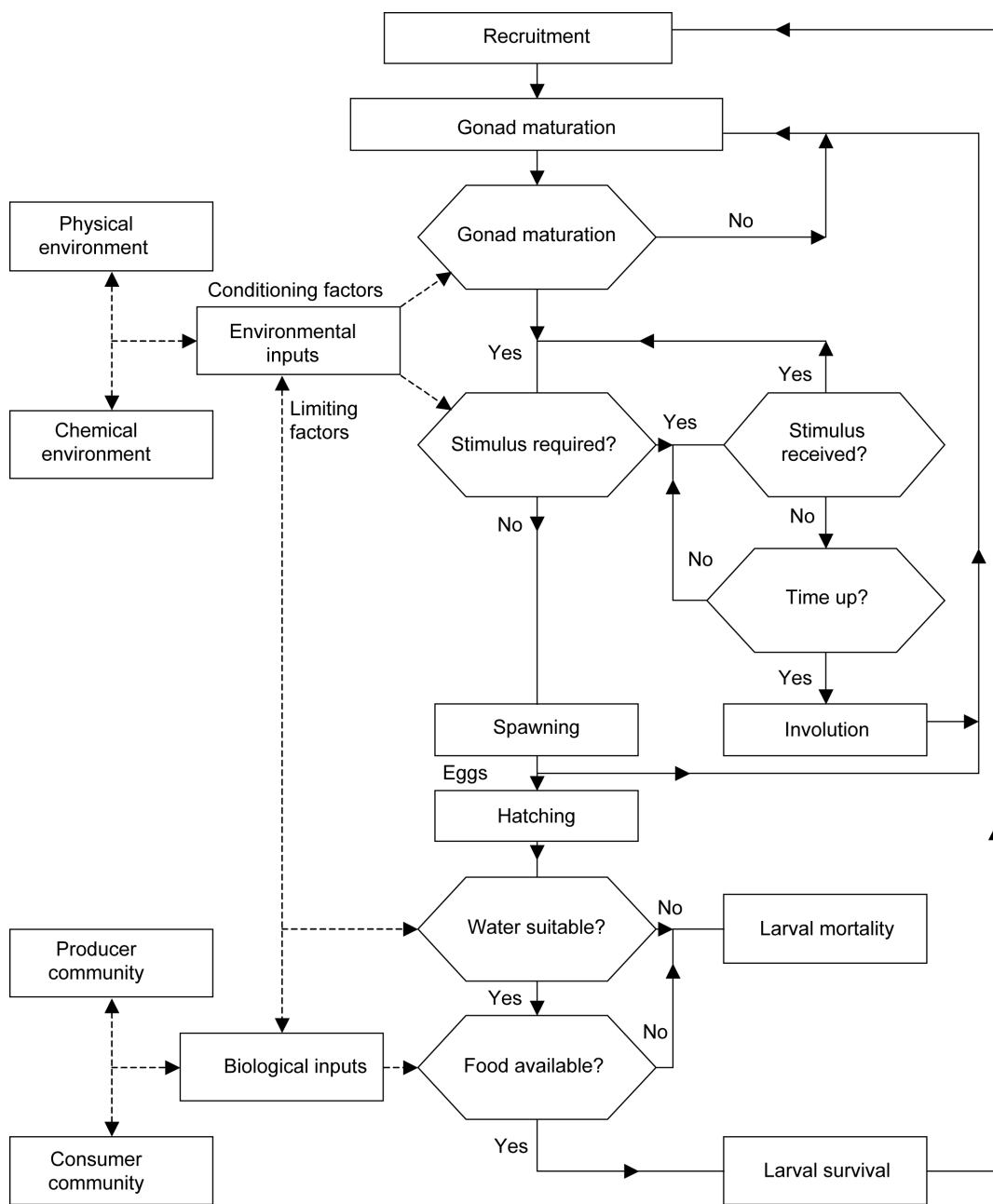


Figure 5. Flood-recruitment model for Australian native fish, with the adult (upper portion) and larval phases of the recruitment process. Taken from Harris and Gehrke (1994).

carp were most abundant in fast creek habitats, less abundant in shallow pond habitats, and least abundant in weir pool habitats. Smaller-bodied fish including gudgeons, *Hypseleotris* spp., hardyhead, *Craterocephalus* spp., and Australian smelt, *Retropinna semoni*, were most abundant in shallow ponds, followed by weir pools then fast creek habitats. Meredith *et al.* (2002) found that although the three habitat types had similar species diversity each tended to be characterised by a different group of species. Of

the total 13 species caught, only flathead gudgeon, *Philypnodon grandiceps*, Australian smelt and Murray rainbowfish, *Melanotaenia fluviatilis*, larvae were collected from all three habitats. Fish larvae of several species, as well as juveniles and adults, have been found in the floodwaters of Cooper Creek in anabranching systems of the Channel Country in western Queensland (Bunn and Balcombe 2001). Humphries and Lake (2000), citing the presence of fish larvae in the highly regulated Campaspe River and the less-regulated Broken River as evidence, inferred that most MDB species of fish spawn annually 'irrespective of the antecedent flow conditions'. Humphries *et al.* (1999) proposed a 'low-flow recruitment hypothesis' to explain why some species spawn and recruit at times of low flow and high temperatures. Meredith *et al.* (2002) concluded that their results supported this hypothesis, with production of larvae being timed to take advantage of warm, slower flows and summer peaks in the availability of zooplankton prey. They argued that, in their study, the diversity of flow conditions relevant to the low-flow recruitment hypothesis was provided spatially rather than temporally.

No studies have found that specific discharge levels are required for egg development or hatching (Koehn and O'Connor 1990), and studies of larval fish on floodplains are rare. Killgore and Baker (1996) collected larval fishes with light traps and plankton nets for two consecutive years in the channel and forested floodplain of the Cache River, Arkansas, USA. They found that mean catch of total individuals was greater in floodplain habitats than in the river channel and concluded that late winter and spring floods that inundate the adjoining forest appeared to be a major factor in regulating abundance of larval fishes.

2.5. The role of fish-food production on inundated floodplains in conditioning fish for spawning

Results from fish hatcheries for MDB native species indicate that nutrition in the months preceding the spawning season determines breeding success (e.g. Thurstan 1992; Rowland 1994). The literature contains much to indicate that inundated floodplains are very productive and that fish make use of this production. Hillman (2001) referred to floodplain billabongs as 'cauldrons of food' and Cullen (2001) noted that floodplain waters have 100–1000 times the number of organisms found in the river channel. Most of this food production is presumed to benefit only the larvae of fish (Gehrke 1992; Humphries *et al.* 1999), though it has not been demonstrated conclusively (Thoms *et al.* 2000). Scholz *et al.* (2002) showed the effects of drying and re-flooding in boosting nutrient availability in ephemeral deflation basin lakes in the MDB. It is likely that the blooms of zooplankton produced over a floodplain in the early stages of inundation are of little value to adults of most medium–large-bodied fish species preparing to spawn because the newly emergent plankton are very small and suited to the gapes, filtering ability and behaviour of fish larvae at the time of their first feeding.

Very little work appears to have been done on the role, if any, that floodplain food sources may play in conditioning fish for spawning. Bayley (1995) stated that most fish species anticipate flood conditions by spawning before or during the water rise but failed to mention where they get the energy required to do this. Collins and Anderson (1999) studied the role of food supply in preparing golden perch for spawning and found that they could be

cued to spawn by being fed after 150 days of starvation. This occurred in the absence of the stimuli normally associated with spawning and at a time of year when they are not normally reproductive. Fish that had been fed to satiety over the same period did not show any reproductive development.

The timing of floodplain inundation may be important in determining whether fish can use floodplain resources. Schramm *et al.* (2000) found that floodplain inundation provided little energetic benefit to fishes when water temperatures were below that required for active feeding. Flooding and warm temperatures do not regularly coincide in the 'southern Mediterranean' region of the MDB (Humphries *et al.* 1999). Rutherford *et al.* (1995) found that four species of fish from the lower Mississippi River exhibited their highest growth during years of limited floodplain inundation.

There is little evidence to indicate that changes in the spatial or temporal patterns of floodplain inundation have affected the way fish gain spawning condition, but few MDB studies have considered the condition of fish in the wild. Larvae of some native fish species have been observed in the highly regulated Campaspe River (Humphries 1999), indicating that spawning of at least some species occurs despite a lack of floods and that regulation may not prevent breeding in these species.

2.6. Variations in fish-breeding responses with varying spatial and temporal scales of flooding

Regulation has done much to change the spatial and temporal scales of flooding, mainly by decreasing the amplitudes of the rises and falls, changing the shape of hydrographs, reducing the frequency of small-to-medium floods and prolonging periods of stability. The scope of these changes has been detailed by Maheshwari *et al.* (1995), Thoms *et al.* (1996, 2000), Kingsford (2000) and MDBC (2002a). The ecologically important elements of a flood pulse are shown in Figure 6 and explained in Walker *et al.* (1995) and Boulton and Brock (1999). Flow variability at a number of spatial and temporal scales elicits major biological responses in fishes (Hjort 1926) and the duration, extent and time of occurrence of a specific flow event can determine its ecological significance (Ward 1989; Poff *et al.* 1997). These relationships between fish-community ecology and flow variability support the intermediate-disturbance hypothesis (Connell 1978), which indicates that species diversity is greatest when ecological disturbance occurs with intermediate frequency, rather than very often or very rarely.

Scheidegger and Bain (1995) recorded differences in the distribution of larval fish and their use of microhabitat in free-flowing and regulated rivers. Fontenot *et al.* (2001) found patterns of larval abundance of two species of fish were related to timing and duration of inundation. In that study, a longer-than-average flood resulted in a greater abundance of larval sunfish but a shorter and slightly later flood gave rise to a large population of larval shad. Damping of the natural flow fluctuations to meet the requirements of hydroelectricity generation on the Roanoke River in the USA increased juvenile abundances of native striped bass, but regulation of the Pecos River in New Mexico in such a way that its flow mimicked short duration peaks caused by summer thunderstorms resulted in greater reproductive success of the Pecos bluntnose shiner (Poff *et al.* 1997). Weisberg and Burton (1995) recorded increases in feeding and growth of fish in response to increased

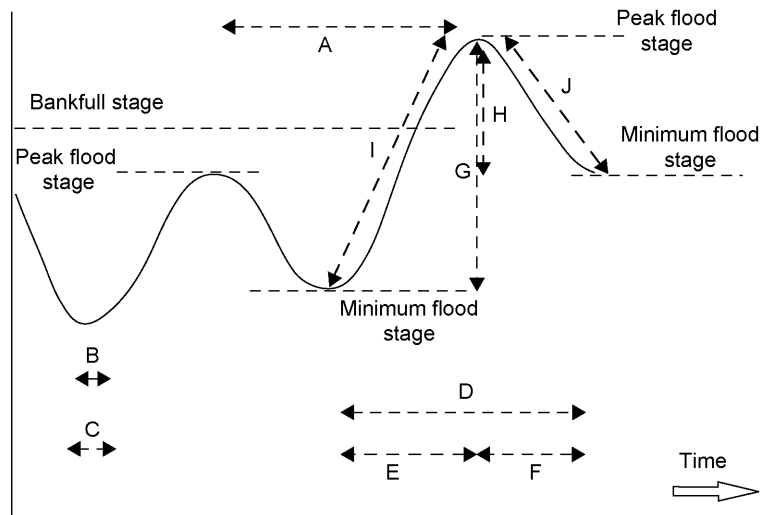


Figure 6. Spatial and temporal characteristics of a flood pulse that may have ecological significance. A, interval since last flood peak; B, duration of discontinuity of channel water bodies; C, duration of zero flows; D, interval since last flood minimum; E, duration of rising limb; F, duration of falling limb; G, amplitude of rising limb; H, amplitude of falling limb (aka drawdown, recession); I, slope of rising limb; J, slope of falling limb.

environmental flows below a dam. McKinnon (1997a) recorded an instance of increased carp reproduction during an unusually long-lasting flood. He saw this as evidence of the need to know when manipulated floods should stop, i.e. after the native species have spawned and recruited but before opportunistic pest species can spawn repeatedly. Puckridge *et al.* (2000) documented the cumulative effects of serial floods including increased recruitment and corresponding increases in adult populations.

An ecosystem's capacity to resist and recover from disturbance is thought to be a function of the biota's experience with natural spatio-temporal variation (Poff and Ward 1990). Poff and Ward argued that, since the ecosystems of dryland rivers are accustomed to great variation in flow, the effects of regulation should be comparatively minor. Conversely, Walker (1992) argued that the effect of regulation may be greater for dryland and arid rivers than for those that flood frequently because the difference between the natural and imposed flow regimes is so great.

The spatial and temporal scales of a flood have implications not only for the fish populations that result from that flood but also for those that may result from a subsequent flood. Duration of inundation affects the number and type of organisms that will emerge from the soil when an area is next inundated (Boulton and Lloyd 1992). The scale of past floods can thereby affect the quality of the resources available to larvae and juvenile fish during a subsequent flood. Bayley (1991) suggested that manipulated flows that aim to maximise fish production should follow a natural progression where flooding commences with a low to moderate rate of increase to a peak, followed by a slow retreat of floodwaters to enable increased plant production, thus benefiting aquatic production in subsequent years. These

principles have been promoted for the design of environmental flows in the MDB (Thoms *et al.* 1996, 2000; MDBC 2002a).

Changes to the spatial and temporal scales of flooding have been extensive in the MDB. Small to medium floods have been reduced or eliminated from regulated rivers. Although regulation has not been able to control the rare large floods, even these may be of little benefit to fish populations because their duration has been severely curtailed. In 1885 for example, the drawdown, or recession time, of a 3 m flood in the River Murray at Overland Corner in South Australia was 59 days. The recession of a 2 m flood in 1986 took only four days (Walker and Thoms 1993). This change may have been a factor in the decline of native fish populations, along with restricted access to floodplains because of levee banks (Grubaugh and Anderson 1988). It is risky for a fish to move on to a floodplain to spawn if the high flows are of only short duration (Humphries *et al.* 1999). Spawn may desiccate, larvae may have insufficient time for growth and development and adult fish risk becoming stranded by receding waters.

2.7. Summary

- There is some evidence of direct utilisation of inundated floodplains by native MDB fish, by only a small number of species.
- There is compelling evidence that the status of a wide range of fish depends on the effects of flooding and that reduced flooding through regulation has had adverse impacts.
- The nature of the mechanisms for these fish–ecology/river–flow interactions, and their relative significance for particular species and communities of fishes, is not yet clear.

3. Classification of floodplain habitats used by fish

Classification of river types would allow a river's attributes to be predicted from its appearance and would provide a consistent, reproducible frame of reference for communication among those working on river systems. Site-specific data collected on a given stream reach might be extrapolated to those with a similar character.

There have been various attempts to classify rivers. The majority of these have been concerned with characterising morphology and hydrology (e.g. Rosgen 1994; MDBC 1995; Eekhout *et al.* 1997). Some have focused on biology — there are river classifications based on vegetation (Holmes *et al.* 1998), annelid worms (Ferdinand 1998) and invertebrates generally (Wright *et al.* 1998).

As noted earlier, ecological processes in large rivers are controlled by their flow variability. However, it is difficult to find measures of hydrological variability that characterise groups of rivers and that can also be used to generate hypotheses about their ecology (Puckridge *et al.* 2000). Classification of the diverse range of habitats that are made available to fish and ecological processes and that are initiated by increasing levels of floodplain inundation would assist the sophisticated design of flooding flows targeted at fish ecology. No such classification scheme has yet been generally accepted.

The simplest classifications attempt to characterise rivers only on the basis of their water quality: good, bad or indifferent (e.g. SEPA 2002). But methods that integrate and analyse large volumes of data to provide practical outputs for use by managers and others with an interest in catchment management are also used (Raven *et al.* 1998). Table 1 summarises information from a number of sources in a descriptive classification of various floodplain elements on the basis of their spatial variability, permanence of inundation, connectivity to other floodplain elements and the ways they are used by fish. The scheme shows these characteristics of the floodplain elements in generally descending order.

Table 1. A classification of floodplain elements and their roles in fish ecology

Floodplain element	Fish habitat	Connectivity	Permanence	Spatial variability
Channel	G/M/S/N/I	P	P	H
Tributary	G/M/S/N/I	P	P	H
Distributary	G/M/S/N/I	S	P/T	M/H
Anabranh	G/M/S/N/I	S	P/T	M/H
Swamps/marshes	G/S/N/I	S	S/T	M
Billabong	G/S/N/I	O	S/T	M
Flood-runner	G/I	O	T/E	M
Swales/shallow depressions	I	O	T/E	L/M
Flat lands	I	R	E	L
Terrace benches	I	R	E	L

Key:

Column 2: G = Growth, M = Migration, S = Spawning, N = Nursery, I = Input (to trophic structure)

Column 3: P = Permanent, S = Semi-permanent, O = Occasional, R = Rare

Column 4: P = Permanent (if only as residual pools), T = Temporary E = Ephemeral

Column 5: H = High, M = Moderate, L = Low

4. General knowledge gaps and research opportunities

A common result of human-induced change is the decline in the structural complexity of ecosystems and, in turn, a decrease in diversity and productivity. Native freshwater fishes in the MDB have to contend in various areas with reduced flooding, reduced flow, modified hydrographs, barriers to longitudinal and lateral passage, increased turbidity, degraded habitat structure, increased salinity, pollution (especially by cold water), invasion by alien species and other challenges. Seven species of fish have so far been classified as threatened by the International Union for the Conservation of Nature and carp now comprise 70–90% of total fish biomass in MDB rivers. The links between some human activities (e.g. the restriction of fish passage by dams), habitat change and the decline of fish populations in the Murray-Darling Basin are well established. How much of the decline is due to the effects of reduced inundation of floodplains on the cues for the initiation of spawning, spawning itself and/or the survival and subsequent recruitment of offspring is, however, poorly understood. Whether flow-regime changes in the MDB have caused native fish declines through impacts on adult growth, production and survivorship seems never to have been considered, although such impacts are likely.

There is general agreement that the ecological knowledge needed for sound management still needs to be augmented (e.g. Pusey 1998; Thoms *et al.* 2000). That this has been an issue for some time can be seen in Table 2, which summarises the knowledge requirements as perceived by a variety of researchers over the period 1993–2000 (the unabridged version of this table is in the Appendix).

Environmental flow allocations in the early 1990s were ‘effectively *ad hoc*’ (Walker *et al.* 1995) because of this lack of information. In 2000, management of environmental flows was still based on ‘best informed guesses’ (Thoms *et al.* 2000) rather than hard data. One reason for this is the difficulty of applying rigorous experimental controls and statistical replication to a system that is spatially and temporally large and heterogeneous. Rivers do not make good replicates and the same environmental intervention may result in different ecological effects in different places, or even in the same river (Poff *et al.* 1997). The relevance of this to knowledge generation in the MDB is considered further in the next section. Apart from inherent difficulty, some useful lines of research may have suffered from lack of funds, the existence of other areas of research with higher perceived priority or because the value of the knowledge to be gained is not balanced by the cost of gaining it. In some cases the models to be examined or refined may not have been sufficiently well articulated in the first instance, making it hard for other workers to pin down appropriate hypotheses. For example, no river-valley-scale model of fish population and community dynamics for the MDB has yet been published.

Table 2. Summary of knowledge requirements identified in Australian and overseas studies of the ecology of freshwater fish.

Knowledge requirement	Mallen-Coope 1993	Swales and Harris 1994	Walker and Thoms 1993	Lake 1994*	Harris and Gehrke 1994	Johnson <i>et al.</i> 1995‡	Power <i>et al.</i> 1995‡	Walker <i>et al.</i> 1995	DIST 1996*	Freshwater Fisheries MAC 1996*	Petts 1996‡	EPA NSW 1997*	McKinnon 1997a	LWRRDC 1998	Pusey 1998	Humphries <i>et al.</i> 1999	Humphries and Lake 2000	Thoms <i>et al.</i> 2000	Davis <i>et al.</i> 2000
Determining adequate flows	✓	✓	✓	✓						✓	✓				✓			✓	✓
Hydrology-driven processes that influence ecology	✓				✓	✓		✓				✓			✓	✓	✓		✓
Effect of flow variability				✓												✓		✓	✓
Quantifying degree of change from natural condition								✓										✓	
Trophic relationships				✓		✓	✓								✓				
Understanding natural flow regimes and hydrology			✓						✓			✓							✓

*Taken from Kearney *et al.* 1999, which was not included because their knowledge requirements are in Davis *et al.* 2000

‡Overseas study

4.1. Movement of fish populations in response to flooding

There is little doubt amongst freshwater ecologists that freshwater fishes benefit from inundated floodplains in the MDB. Exactly what the fish are doing during floods and when they are doing it is still, however, something of a mystery. Although knowledge of the movement patterns and pathways of fish over floodplains during inundation is scanty, there is increasing understanding of movements by adult and sub-adult fish within channels, mostly through fishways assessments and radio-tracking studies. Koehn (1997), Crook *et al.* (2001) and Stuart and Jones (2002) have used radio tracking on various MDB fish. Snedden *et al.* (1999), in the USA, demonstrated the use of inundated floodplains by spotted gar in this way and Matheney and Rabeni (1995) did the same for the northern hog sucker, *Hypentelium nigricans*. Harris *et al.* (1992) used population-density measurements during a rising flood to assess fish movements over a weir in the Darling River. The longitudinal and lateral movements in MDB rivers of a number of the smaller fish species are especially poorly known. As Humphries *et al.* (1999) pointed out, the lack of evidence that adult fish and larvae use non-permanent floodplain habitats may simply be due to a lack of the right kind of study.

Further studies are needed of movements by the early life-history phases of MDB fishes in response to flow. An international workshop to assess knowledge and implications of downstream movement by fish was hosted by MDBC in June 2003 and proceedings are in preparation (B. Phillips, MainStream Environmental Consulting, personal communication). A better knowledge of the movements of carp during various flows would improve the ability of managers to control this species (Stuart and Jones 2002).

4.2. The control of carp

Greater knowledge of the breeding cycle of carp and the factors that affect it, including the role of flow, is required if effective control is to be established (Roberts and Tilzey 1997; Lapidge 2003). In view of the fact that they represent the greatest biomass of fish in the MDB and that there is some likelihood of their range continuing to increase, the need for this knowledge about carp is at least as important as it is for native fish (Gehrke *et al.* 1995). A novel genetic approach to carp control is being developed in a major collaborative project based in the MDB, using genetic manipulation to control populations by reducing the proportion of female carp among recruits (Lapidge 2003). Such techniques, if they reach practical application, would probably need to be combined with flow management that is guided by the results of such research, and other environmental rehabilitation works.

Flow regulation could be used to alter the hydrodynamic regime to at least partially restore natural conditions and improve ecosystem health, to the detriment of carp (Harris 1997; Phillips *et al.* 2002; MDBC 2002a). Stuart and Jones (2002) suggested that flow-management strategies could be used to control carp coming from areas of intense recruitment in the Barmah-Millewa floodplain. Wilson (2002) and Wilson *et al.* (in preparation) have shown how stranding can be used to prevent carp recruitment in waterbodies that have water-level controls and there is a need to test the value of this approach at larger scales. Greater knowledge about the effect of rate of rehabilitation is required; Poff *et al.* (1997) recommended incremental repair because the damage had usually been done in small stages. The validity of this view is unknown.

4.3. Dependence of fish species on flooding as a cue to initiate breeding

Further experimental work on the spawning cues of insufficiently studied species is required. There is a need to decouple the two components of recruitment — reproduction and survival — and to develop knowledge about the ways by which their separate constituents (i.e. gametogenesis, spawning, hatching, larval feeding, movement to nursery areas, predator–prey dynamics and so on) respond to environmental variables.

Much of our current knowledge of the breeding of native fish is based on aquaculture studies using populations of a single species of economically valued fish under controlled hatchery conditions (Thurstan 1992; Rowland 1994). These studies often avoid dependence on little-understood environmental cues by using artificial hormone dosage; a kind of ‘pharmacological rape’. Species that have so far been ignored because they

are small and/or not commercially valuable should be studied because they may provide fundamental ecological insights.

Relationships between gametogenesis, final stages of maturation, ovulation and release of eggs and environmental variables such as temperature, water level rises, food availability and photoperiod remain unclear. This is because controlled spawning-cue experiments that manipulate one variable while controlling for others have not been done until recently, as noted by Humphries *et al.* (1999), with the notable exception of the early studies in hatchery ponds at Narrandera (Lake 1967). But Wilson (2000) and Wilson *et al.* (in preparation) reported such experiments on carp spawning behaviour, showing rapid responses by suitably conditioned fish to flooding during the spawning season. Without such information, the management of environmental flows to benefit fish and fisheries will depend on subjective judgements or be derived from overseas data or general ecosystem models that may be of uncertain detail and applicability. If certain flows correlate with recruitment, the reasons for success will not be known.

4.4. Dependence of native fish on inundated floodplain habitats for spawning and nursery areas

There appears to be little evidence for the long-held view that spawning on floodplains is important for MDB species. Data on in-channel patterns of occurrence of larval and juvenile fish are emerging from River Murray studies (Meredith *et al.* 2002; Gilligan and Schiller 2003), but there are few observations on Australian floodplains, other than by Geddes and Puckridge (1989) and Puckridge *et al.* (2000). More knowledge is needed about larval and juvenile growth and survival on floodplains.

Again, as Humphries *et al.* (1999) pointed out, the lack of evidence that fish larvae use non-permanent floodplain habitats may simply be due to a lack of the right kind of study. The possibility exists that the huge increase in recruitment of fish that follows floodplain inundation results from post-hatching processes rather than alternative explanations: namely, pre-conditioning of adults on floodplains or flood-spawning cues. Sampling of floodplain habitats for fish larvae and emerging zooplankton and zoobenthos over large spatial scales is needed. The trophic relationships of larval and juvenile fish on floodplains and in flood channels should be examined, as should the extent of carbon cycling and primary and secondary productivity of various floodplain elements.

Stable-isotope analyses are providing powerful new tools in the study of aquatic ecosystems, especially in identifying the sources of organic carbon that ultimately support food webs (Robertson *et al.* 1996; Thorp *et al.* 1998; Smith and Storey 2001). Carbon-isotope analysis of tissues from young fish could add substantially to knowledge of the sources and locations of their growth.

4.5. The role of fish-food production on inundated floodplains in conditioning fish for spawning

The long-standing assumption that food production on inundated floodplains primarily benefits survivorship and growth among larval and post-larval fish needs to be tested. An alternative explanation for the productive surge that

follows flooding is that fecundity is boosted as a result of high nutritional status, as is well known among hatchery managers (Thurstan 1992; Rowland 1994). Spawning need not occur on floodplains for this nutritional boost to be important in population dynamics.

The role of energy inputs from floodplains should be investigated further. Carnivory is the rule for native fish in the MDB, and overseas observations of fish eating terrestrial plant matter as floodwaters rise are irrelevant here. An investigation of the food resources of flood plains should consider food that exists on floodplains prior to flooding, as well as concentrating on the emergence of zooplankton and macrobenthos — especially chironomids - from their resting stages. The assumptions that food items produced are small and only of benefit to larval and post-larval fish because food production on floodplains begins when the floodplains are first inundated need to be tested. Flooded terrestrial invertebrates, and crayfish migrating or emerging from burrows, may contribute significantly to these food resources.

Murray cod, golden perch and silver perch use floodplain gullies creeks and anabranches and other more permanent waterbodies (McKinnon 1997a; Koehn 2000), apparently to feed on prey produced abundantly as the result of nutrients from inundated leaf-litter accumulations in these areas. The roles played by these semi-permanent and intermittent floodplain habitats need further study. Sites where nutrient-rich detritus and snags accumulate probably promote production during floods. Being among the first sites to be wetted by a rising flood, low-lying secondary channels are likely to be the first sites of emergence of dormant zoobenthos and macrobenthos and then to be ahead of the rest of the floodplain in the successional stages of prey production. Studies at the Mildura Lower Basin Laboratory are investigating carbon cycling processes, including fluxes and storages and should provide useful insights (CRCFE 2003).

The key knowledge gaps are quantitative ones, concerning the level of dependence of pre-spawning fish on a rising nutritional plane for fecund breeding, and on the relative contribution of the various floodplain habitats in producing that food.

4.6. Variations in fish-breeding responses with varying spatial and temporal scales of flooding

The ecological roles of the various parts of the flow regime are poorly understood and deciding between the different hydrological components (timing, amplitude, duration, rates of change, frequency, antecedent conditions and degree of drawdown) to get the best effect in the Murray-Darling Basin is complex and difficult because of this lack of knowledge. Some guidance about the length of growth cycles of larvae and juveniles is available from hatchery studies (Thurstan 1992; Arumugam and Geddes 1987, 1992; Rowland 1994) and this suggests the need for attenuated drawdown from flood peaks. Thoms *et al.* (2000) recommended increasing flood peak height rather than increasing duration on the basis that flood frequency and the wetted area need to increase but this recommendation is based on untested assumptions and educated guesses. Welcomme (1979) showed that strong year classes of fish tend to result from gradually increasing water levels and flooding that combines high amplitude and long

duration. It seems unlikely that these conditions will apply again frequently in much of the Murray-Darling Basin. Bayley (1991) suggested that an as-yet-unknown optimum rate of increase in water level exists that would maximise fish production. But the alternative hypothesis, whereby the period of inundation is the more-important variable, is equally tenable.

Maximising fish production requires that a certain threshold in the length of the 'hydroperiod' must be exceeded (DeAngelis *et al.* 1997). It is reasonable to expect that if the rates of increase and (especially) decrease in water level were too fast, biological processes would not be able to keep up with the advance or retreat of the water level. But what these rates may be, or the threshold levels, are unknown. Arguing against this, perhaps, is the finding by McKinney *et al.* (1999) that, at least for rainbow trout, *Oncorhynchus mykiss*, sudden reduction in flows of moderate duration and magnitude had little apparent negative short-term consequences. But there are fundamental differences between habitats for trout and lowland MDB fishes. Conversely, if the period of inundation is too long, oxygen depletion might inhibit biological processes (Bayley 1991 1995) or blackwater toxicity might occur (Gehrke 1991; Gehrke *et al.* 1993). Fontenot *et al.* (2001) recommended a water management plan for an American river that was designed to increase the exchange of water between the main channel and backwater areas because widespread hypoxia limited the nursery potential of large areas of the inundated floodplain. Likewise, McKinnon (1997a) found that dissolved oxygen declined in floods of long duration and he also recommended manipulating floods so as to maintain flow and therefore oxygen levels. An ideal period of inundation has yet to be defined and must vary with the river reach in question.

The amplitude of a flood determines which of the potential floodplain habitats for fish will be inundated (Table 1). River discharge increases exponentially with flood stage, especially in over-bank stages, so that knowledge of the kinds and elevations of habitats that are most important can play a crucial role in determining priorities for flow allocation. If a particular high-elevation habitat provides only modest responses to flooding but requires large volumes for inundation, then its priority for watering is reduced. These considerations emphasise the importance of classifying floodplain habitats, charting commence-to-flow elevations for particular river reaches, and elucidating specific ecological roles of each class of habitat.

The ecologically important elements of a flood pulse (Figure 6) are highly variable. Australian river systems, particularly, experience great fluctuation in the various components of a flow, unlike overseas systems which are more seasonal and less drought-prone (e.g. Oldani 1990; Welcomme 1995). Further work is needed on the ecological effects on fish of spatial and temporal variation of flow. Regulation has the potential to provide that variation, both for experiments and for remedial management.

Elucidating the respective roles of the various phases of the flood cycle and how different species respond to them, plus any seasonal interactions, is a big task, even without considering the enormous complexity of flow paths and fish habitats on floodplains. Yet an understanding of the scope and significance of this variability is critical to the design of managed flow events to promote native fish rehabilitation in regulated systems (Phillips *et al.* 2002; MDBC 2002a). To succeed with such a prescriptive approach will

require not only the development of detailed models of fish ecology, but also a strong adaptive-management framework (Bearlin *et al.* 2002) to ensure that results of management intervention can be used to refine the knowledge base and continually improve ecological outcomes from the allocation of water for environmental purposes.

5. Recommended research

Research should aim to fill the major knowledge gaps identified in the preceding sections to do with the effects of human modifications of MDB flow regimes on the ecology, production and conservation of native fish. It is also needed to provide a basis for setting priorities among available flow-management strategies to conserve fish.

The mechanisms by which river regulation and reduced floodplain inundation are linked with the decline of fisheries are in need of clarification. Increases in regulation have been accompanied by a range of other impacts that may act in concert to the detriment of fish populations and this is an area that needs substantial further work. As the complexities of the system become more apparent and evidence emerges that factors other than floods (e.g. photoperiod, temperature, release from starvation and slight increases in river height) may initiate spawning, and in ways that can differ among species, the link between reduced floodplain inundation and the declines of fish and fisheries continues to demand investigation. This is not to say that over-bank flows and other high-flow features of the water regime are unimportant; their role as a source of energy is probably extremely significant to the post-spawning stages of recruitment. But the data required to show this are largely lacking.

Regulation of flow threatens the stability of the relationships between river and floodplain but also represents the most effective tool by which managers may reduce or redress the negative effects of human water-use (CRCFE 1996).

Regulation of flow also represents opportunities for research beyond those offered by unpredictable and uncontrollable large floods. All intrusive management or environmental intervention is a form of experiment and greater advantage should be taken of the opportunities presented by regulation. At the least we would learn from our previous mistakes, because the experimental perturbations of the environment resulting from management interventions would be in a framework in which their outcomes could be used to evaluate the models that underpin the policies and practices (Underwood 1990).

Stream flow in freshwater systems is one of the environmental conditions amenable to large-scale management (Harris and Gehrke 1994) and therefore large-scale experimental manipulation. This facility has been under-exploited by freshwater ecologists (Sparks *et al.*, cited in Power *et al.* 1995). Large-scale studies were once out of the realm of possibility but their use in studying the importance of flow regimes for river and riparian ecosystems is increasing. In 1993 experimental manipulations of flow and the use of artificial enclosures were beginning to be seen as viable possibilities. Experimental flooding trials in the Barmah-Millewa forest had begun. Walker *et al.* (1995) noted, however, that an experimental approach, involving ecosystem-level manipulations of key variables, was still 'scarcely represented' in the literature of big rivers, and recommended controlled floods to remedy this situation. Johnson *et al.* (1995), recognising that the pressing questions in lotic ecology were unlikely to be solved by laboratory or small-scale experiments, saw the need for 'natural experiments' (i.e. designing management interventions to permit rigorous interpretation of the

results), and large-scale manipulations that provide informative comparisons between rivers or river reaches.

The use of natural experiments is appealing because the circumstances required by the hypothesis are found pre-existing rather than having to be created, which is usually expensive and time-consuming. They are, however, prone to misinterpretation (Underwood 1990). Gutreuter *et al.* (1999), for example, designed a natural experiment to test a hypothesis derived from the flood-pulse concept but their study was confounded by temperature and other variables and an unambiguous interpretation of the results was therefore not possible, despite their stated conclusions. Manipulative experiments based on a clear understanding of the models from which hypotheses have been derived are the only way to remove this uncertainty.

Specific areas for future investigation are suggested below.

(a) Movement of fish populations in response to flooding

Radio tracking has the potential to solve many of the mysteries of fish movements. Using radio tracking or radio telemetry technology could remove doubts about the way fish move (or do not move) laterally and longitudinally during the various phases of flooding. Before the results from these experiments can be interpreted with any confidence, however, it is essential to satisfy the fundamental assumption (which is usually unrecognised, unfortunately) that tagging does not alter behaviour. Studies like that of Crook *et al.* (2001), in which golden perch and carp were tracked by radio telemetry for ten days and nights during non-flood conditions, should be extended to longer periods and to other species. Radio tracking should be used during experimental or natural flood events that drown out weirs and other small barriers to fish movement. Koehn (2000) discussed the kinds of tags available and their application to studies of this type.

There is considerable value in using fishways in recording fish movements (e.g. Mallen-Cooper *et al.* 1997; Harris 2001), especially those in floodplain tributaries and anabranches. Fishways sampling complements sampling in more-natural floodplain habitats, at least in low-to-moderate flows, because they constrain flow into a manageable channel and also because they are increasingly equipped with traps and cages for this purpose. At larger dams and weirs, resident staff may be available to join sampling studies.

The movement of fish larvae during flood events needs to be investigated, even though sampling design and methods can be challenging in the face of large-scale spatial and temporal variations in habitat conditions.

(b) The control of carp

Trends in carp abundance at the scale of valleys or valley zones will be apparent in data collected in the MDBC's Sustainable Rivers Audit (see MDBC 2003). Any changes over time should be assessed in relation to river-flow patterns.

The value of the approach by Wilson (2002) and Wilson *et al.* (in preparation), using stranding to prevent carp recruitment in waterbodies that have water-level controls, should be tested at larger spatial scales in floodplain lakes and over substantial periods of time. Recommendations by Stuart and Jones (2002) for strategic carp removal from key locations in the

Barmah-Millewa floodplain system should be adopted, as they offer potential opportunities for significant reductions in regional pest fish numbers.

(c) Dependence of fish species on flooding as a cue to initiate breeding

The cues that control gonad development, initiate spawning and determine hatching and larval survival are unclear and probably intertwined and species-specific. Using manipulative experiments to untangle them and determine the relative importance of each potential cue would be impossibly difficult in a large-scale natural system of floods and droughts in which the creation of controls and replication is extremely difficult. Replicated experimental facilities, at the scale of laboratory tanks or mesocosms, should continue to be used to test key hypotheses about gametogenesis, spawning, larval and juvenile behaviour in response to manipulation of water-level changes, water quality (especially temperature), photoperiod and nutritional status.

(d) Dependence of native fish on inundated floodplain habitats for spawning and nursery areas

Sampling of floodplain habitats for fish larvae and emerging zooplankton and zoobenthos over large spatial scales is needed. The trophic relationships of larval and juvenile fish on floodplains and in flood channels should also be examined, as should the extent of primary and secondary productivity of various floodplain elements. Carbon-isotope analysis of tissues from young fish could add substantially to knowledge of the sources and locations of their growth and help with targeting flow allocations for particular habitats.

While experimental approaches are often preferable because they can yield rapid, cost-effective answers to many such questions, some complex ecological interactions require field observations. For establishing distribution patterns of larvae and juveniles on floodplains, as well as trophic studies, field surveys seem necessary. These surveys need to be opportunistic, planned and equipped in advance of flooding, and scheduled through weather-forecasting and flood-warning services. They should follow a replicated design stratified to account for the floodplain habitat classes outlined in Table 1 and the well-known seining, light-trap and plankton-hauling techniques would be suitable for sampling.

Furthermore, the long-ago pioneering work of John Lake at Narrandera (Lake 1967), using mesocosm experiments to elucidate fish breeding, provides a useful model for studying young fish also. The greater ease of building and operating pond mesocosms, plus the accumulated knowledge now available to refine experimental hypotheses, indicates the possibility of rapid progress.

(e) The role of fish-food production on inundated floodplains in conditioning fish for spawning

The role of energy input from floodplains should be investigated further. An investigation of the food resources of floodplains should consider terrestrial fauna that exists prior to flooding, as well as concentrating on the emergence of zooplankton and macrobenthos — especially chironomids — from their resting stages. The assumptions that food items produced are small and only

of benefit to larval and post-larval fish need to be tested experimentally. Flooded terrestrial invertebrates, and crayfish migrating or emerging from burrows, may contribute significantly to food resources for adult fish. Laboratory experiments should be done on more species to assess whether, as a general rule, surges in nutritional status are important to promote fecundity during gonadal development.

(f) Variations in fish-breeding responses with varying spatial and temporal scales of flooding

With one exception, research based on traditional small-to-medium-scale manipulative experiments and surveys has limited potential value for studying fish-breeding responses to spatial and temporal variations in flooding. More-promising approaches include reach-scale mapping, fish-population modelling and adaptive management informed by large-scale studies such as the Sustainable Rivers Audit. The one exception identified concerns the need, discussed earlier, to use opportunistic, small-scale surveys to clarify the dependence of larval and juvenile native fish on inundated floodplain habitats.

Reach-scale mapping is needed to identify the locations and sizes of floodplain habitats and to find the commence-to-flow levels in the river channel that determine the discharge volumes needed to inundate them. Fish-population modelling using inputs from these maps plus knowledge about the dependence of particular species on inundation of the various floodplain habitats can then provide benefit–cost assessments that will enable objective, rational decision-making about water allocations.

As noted earlier, adaptive management at large scales is currently feasible (Bearlin *et al.* 2002). Major environmental rehabilitation works in MDB river valleys, often involving environmental flows and floodplains, are under way or planned (MDBC 2002b) and data from the Sustainable Rivers Audit and other MDB research can provide the knowledge feedback loops inherent in adaptive management.

5.1. Problems

Several common problems need to be overcome for successful research in the field of fish ecology and floodplain inundation. They relate especially to the individual character of rivers, the difficulty of supplying sufficient good-quality water for experiments, scale issues and methodological problems in sampling and generating data on fish movements.

Puckridge *et al.* (2000) illustrated yet again (e.g. see Hynes 1970) how individual rivers have distinctive patterns of variability that play an important part in their ecology and these idiosyncrasies may make management strategies developed for one river irrelevant to other locations, or even counterproductive. Australian rivers are probably much more idiosyncratic than those in other continents because flood occurrence and seasonality in Australia are highly irregular and unpredictable (McMahon 1986). The MDB encompasses a range of climatic zones and a variety of lifestyle and recruitment strategies have evolved among fishes (Humphries *et al.* 1999). Flow provisions must suit the individual needs of each river system or catchment (EPA 1997), and factors that have been identified as benefiting fish in one location or season may not have that effect in another.

Most of the water currently available for release from dams is cold, anoxic and nutrient-rich because it must be drawn from depth in thermally stratified storages (Phillips 2001). Research that uses experimental releases of water is likely to be hampered by this fact, since few dams can release surface water. Until such time as dams in the Murray-Darling Basin are able to release water at temperatures close to those that occur naturally in the streams they impound, low-flow experiments are probably going to be more useful than high-flow experiments because the results of the latter are likely to be confounded by the effects of cold water discharge and the alien fish species that tolerate them. There are also problems for the delivery of variable experimental flows because of infrastructure problems in supplying adequate releases. In real-world settings, experimental controls and statistical replication are often impossible (Poff *et al.* 1997).

There have been problems associated with the scale at which research has been done in the past, and knowledge of scale-dependent patterns and processes is generally undeveloped and non-quantitative (Cooper *et al.* 1998, quoted in Crook *et al.* 2001). Whittington (2000) noted that the appropriate scale for research is probably defined by the biological, physical and chemical characteristics of the particular region. Crook *et al.* (2001) recommended research at scales relevant to the fish rather than at those convenient for the researchers. Humphries *et al.* (1999) pointed out the potential for different conclusions to be drawn from the same type of study, depending on the scale at which the work was done.

Telemetry has potential as a method to examine the longitudinal and lateral movements of fish, but it also faces various difficulties (Harris 2001). The biggest of these, apart from actually applying the hardware to fish, is the untested and unlikely assumption that the equipment has no effect on subsequent behaviour or movement. Trapping of fish or using records from fishways rather than using telemetry, or at least to verify the telemetry assumptions, are other ways to deal with the problem. Very little is known about the migrations of small fish species but the use of telemetry in filling this knowledge gap is limited by the size of the hardware.

Summary of research that would address the identified gaps

Area of interest	Recommended research
Movements of fish in response to flooding	Radio tracking or radio telemetry. Fishways studies. Extend knowledge on movements of the various life-history phases of MDB fish in response to floods.
The control of carp	Investigate large-scale trends in carp abundance through Sustainable Rivers Audit. Test value of strategic carp removal work at key Barmah-Millewa locations. Assess carp control in regulated floodplain lakes using manipulation of water levels.
Dependence of fish species on flooding as a cue to initiate breeding	Small-to-medium-scale experiments on reproduction and larval/juvenile behaviour in response to water level changes, temperature, photoperiod and nutrition.
Dependence of native fish on inundated floodplain habitats for spawning and nursery areas.	Survey inundated floodplains for fish larvae and prey, using habitat stratification. Assess trophic relationships of larval and juvenile fish on floodplains. Carbon-isotope analysis of young fish and food web to find sources and locations of their growth. Use controlled-pond mesocosms to stimulate breeding and investigate distribution of young fish.
The role of fish-food production on inundated floodplains in conditioning fish for spawning	Continue evaluating the roles of materials and energy input from floodplains, including prey and snags. Extend laboratory experiments with various MDB species to detect requirements for surges in nutrition to promote fecundity.
Variations in fish-breeding responses with varying spatial and temporal scales of flooding	Reach-scale mapping to chart locations and sizes of floodplain habitats and to identify commence-to-flow levels in river channels. Fish-population modelling using inputs from maps plus knowledge of species' dependence on inundation of floodplain habitats. Large-scale adaptive management based on environmental rehabilitation involving environmental flows and floodplains, and using data from the Sustainable Rivers Audit and other research.

5.2. Conclusion

To find out the level of flow required to maintain or improve the health of river systems has been a goal for quite some time in Australia. Australian efforts in flow maintenance and riverine ecosystem restoration research have been praised in the international literature (Tarlock 2000). Yet Davis *et al.*, as recently as 2000, identified only the following flow-related knowledge requirements for Australia's freshwater fisheries:

- methods for indicative assessment of flow requirements
- the response of the ecosystem to environmental releases

- responses of fish and fisheries as indicators of the effects of environmental flow management
- information on the biology of fish species relevant to environmental flows
- understanding of natural variability and its impacts, and
- understanding of flow-related interactions within the ecosystem.

Nearly all these problems of determining the flow requirements of Australian river systems stem from an incomplete understanding of their ecology (Pusey 1998), particularly the ecology of their fish. The dominant paradigm has long been that floodplain inundation, necessarily involving large volumes of water, is an essential requirement for successful recruitment and long-term survival of at least some native fish species. Evidence that can be seen to throw doubt on aspects of the paradigm has been accumulating. The means of resolving this apparent conflict has been limited but manipulative experiments at larger scales are becoming increasingly feasible.

Experimental work suggested by Humphries *et al.* (1999), i.e. investigation of the recruitment patterns of fishes in the different life history modes under a variety of experimental flow releases, would help to decide between competing models of the dynamics of fish in the MDB, i.e. the 'low-flow recruitment hypothesis' and the 'flood-recruitment model'. Those species that recruit during low flow times should 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 flow period (Humphries *et al.* 1999). Refinements of both models, and tests of those refinements, can be envisaged should one of them prevail. Moreover, both may be valid, operating in sequence or in separate locations. Further testing of the flood recruitment model, for example, is required to elucidate the mechanisms behind observed interactions between river flow and ecology and to find the specific flow requirements of the various life-history stages of fish in the MDB.

It is necessary to know the level of flow required to initiate spawning, the level of flow required to get more spawn, the level of flow required for the survival and growth of larval fish, the level of survival required to get recruitment and the level of recruitment required to see a reversal of the decline of native fish. It is important to note that fish growth and production (i.e. the total elaboration of fish flesh in a given period) and adult survivorship (affected by fisheries exploitation, predation, disease, food supply and competition) are also critically relevant. Together with population recruitment, these fundamental dynamic attributes determine the viability of the species. Continued ignorance of these parameters and flow conditions will result in a failure to arrest the declines in native fish or inefficiencies in the use of water, or both. When the knowledge gaps that currently exist are filled, it will be possible to make efficient use of water resources to give the greatest possible benefit to native fish and other positive environmental outcomes in a context of competing requirements.

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7. Appendix: Unabridged list of knowledge requirements as seen by Australian and overseas freshwater ecologists

Research need	Source
Immigration, emigration, fecundity and mortality data	Schlosser 1991
Determination of habitat utilisation by fish and derivation of key habitat requirements, such as in-stream cover, substrates, role of aquatic and riparian vegetation and use of floodplains Flow needs of fish — for breeding, movement, dispersal and recruitment; Experimental evidence is needed on the levels of silt and sediment tolerated by fish at all life stages, and their response to key water quality variables; and Fish passage requirements. In addition, a broader knowledge of the swimming ability of native fishes is needed to design access into floodplains.	Mallen-Cooper 1993
There is a need for the development of a reliable and simple method for recommending minimum in-stream flows to protect aquatic life in Australian streams and rivers which is inexpensive, easy to perform and requires little or no field investigation.	Swales and Harris 1994
‘there is no standard method for describing a flow regime in ecologically relevant terms’	Walker and Thoms 1993
Long term ecological research; Protocols for rigorous surveys, experimentation and environmental monitoring and assessment; ecology of floodplain rivers; trophic structure; ecological roles of natural disturbances on streams, rivers and their floodplains; nutrient dynamics; patterns and maintenance of biotic diversity; ecological impacts of introduced biota; patterns and levels of biotic production in rivers; assessment of the nature and strengths of biotic interactions; the role of riparian vegetation in in-stream ecological processes; and stream classification	Lake 1994
Successful development of a predictive model for golden perch would permit a test of the value of manipulating recruitment using realistic water allocations.	Harris and Gehrke 1994
Which are the key taxa or functional groups that are linked in the chains of strong interactions. Second, how do their performances and impacts in food webs vary under changing environmental conditions, such as the dramatic fluctuations in area, depth, and velocities of river habitats	Power <i>et al.</i> 1995
Studies of the effects of habitat diversity on biological production and studies determining the energy sources and flows through trophic webs	Johnson <i>et al.</i> 1995
What are the relationships between flow regime, habitat diversity and productivity? Which habitat features are most important in determining riverine productivity? Are some life-history strategies more successful under certain flow regimes? What measures are good descriptors of the critical features of flow regimes and habitat diversity. In addition, efficient methods are needed for determining production at various trophic levels over large spatial scales.	Johnson <i>et al.</i> 1995

Research need	Source
Establishment of ongoing programmes to monitor environmental change requires design and review, surveys and monitoring driven by concepts, such as the ecosystem concept, that might provide for an understanding of processes and for inter-system comparisons.	Walker <i>et al.</i> 1995
Further research is required to improve our capability for modelling the roles of different flows and patterns of flows in sustaining river ecosystems	Petts 1996
There is little specific available information on tolerance limits of native Australian fish to many water quality variables, with the exception perhaps of salinity.	McKinnon 1997a
Document requirements of native vertebrate and invertebrate fauna; document natural condition of Australian streams; and elucidate relationship between floodplains and channels.	LWRRDC (1998)
There are seven distinct areas in which insufficient knowledge hampers ability to manage environmental flows in a sustainable manner as they relate to freshwater fishes. An understanding of the habitat requirements of many species of fishes. An understanding of basic life history and its relationship to hydrology for many species. An understanding of patterns of fish movement and their relationship to hydrology. An understanding of the processes that govern inter-specific interactions between freshwater fishes and understanding of the links between landscape, hydrology and community metabolism. The absence of clear guidelines available to water managers on the day to day management of in-stream flows and ability to include variability in such a process. An almost complete absence of validation of the sustainability of prescribed environmental flow allocations	Pusey 1998
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	Humphries <i>et al.</i> 1999
Properly controlled and rigorously designed experiments investigating spawning cues, preferably with long-term intensive studies of fish breeding in the wild; further studies into the movement of free embryos, larvae, juveniles and 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 Basin fishes.	Humphries <i>et al.</i> 1999
Our knowledge of (fish) movement is generally poor...The smaller species have been largely ignored in movement studies and this is clearly a major gap in our knowledge	Humphries <i>et al.</i> 1999
Future investigations should focus first on determining how environmental conditions correlate with recruitment and then on determining mortality schedules for the early life stages of fishes. Then we can identify when fish are most at risk.	Humphries and Lake 2000

Research need	Source
<p>Need to identify the changes to hydrology brought about by flow management and to produce generalisable descriptions of these changes. Such descriptions should be aimed at estimating the degree of change relative to the 'pre-regulation' state and thereby provide a means of ranking or comparing various sites within and between river systems. This approach would provide an index of modification. Alternatively, the aim might be to emphasise the hydrological change resulting from flow management by grouping and classifying sites using multivariate techniques.</p> <p>Suggests a trial experiment as a means of determining both the operational feasibility and ecological benefits of drawing down water levels in weir pools on a regular versus irregular or not at all basis prior to spring floods. Research into the relative merits of favouring certain components of the flow regime over others; specifically, flood peak versus duration, monitoring fish passage, investigating fish disease outbreaks from lake Victoria, determining adequate baseflows for the River Murray to protect fish, macrophytes and habitat; and ascertaining appropriate snag densities.</p>	Thoms <i>et al.</i> 2000
Quantifying biotic impoverishment on landscape and regional scales is an important step in evaluating the costs and benefits associated with massive hydrologic modifications	Pringle <i>et al.</i> 2000
<p>Methodologies for indicative assessment of flow requirements</p> <p>The response of the ecosystem to environmental releases</p> <p>Responses of fish and fisheries as indicators of the effects of environmental flow management</p> <p>Information on the biology of fish species relevant to environmental flows</p> <p>Understanding of natural variability and its impacts</p> <p>Understanding of flow related interactions within the ecosystem</p>	<p>Davis <i>et al.</i> 2000</p> <p>Kearney <i>et al.</i> 1999</p>
Although multi-scale analyses provide important information regarding spatial associations, manipulative experiments are still required to resolve the behavioural processes underlying observed patterns.	Crook <i>et al.</i> (2001)