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Extreme flow variability and the ‘boom and bust’ ecology of fish in arid zone floodplain rivers: a case history with implications for environmental flows, conservation and management

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ABSTRACT

Floodplain rivers in arid and semi-arid regions may be the most threatened of all river systems because water resource developments typically dampen their most distinctive characteristics – extreme flow variability and ‘boom and bust’ ecological dynamics. This paper shows how one of the world’s most variable arid-zone river systems – Cooper Creek in Australia’s Lake Eyre Basin – functions and how it supports its unique fish assemblage and productive fisheries. The ecological roles of drought refugia, channel flows and flooding are reviewed in relation to fish persistence and losses, life history strategies, movement potential, food web processes and production levels. Comparisons are drawn with other floodplain rivers and fisheries to draw out common understandings and universal principles for conservation and management of arid-zone rivers and their fish resources. Ecological implications of hydrologic alterations and land based activities are presented to highlight the importance of maintaining the hydrologic, geomorphic, sedimentary and biogeochemical processes of arid-zone river systems. Preservation or restoration of natural flow intermittency, sequential flood pulses, complex habitat mosaics, connectivity, and identification of the environmental flow requirements for highly valued species and processes are key scientific principles for the management of arid-zone floodplain rivers.

KEY WORDS: fish, flood pulse, connectivity, refugia, environmental flows, conservation

INTRODUCTION

Many of the world's rivers are increasingly affected by activities and pressures that disturb their hydrologic regimes and disrupt ecological processes dependent upon naturally dynamic wetting and drying cycles (Poff *et al.*, 1997; Nilsson *et al.*, 2005; Postel and Richter, 2003). Floodplain rivers are particularly vulnerable to flow regime alteration and other stresses associated with human occupancy and use of catchment resources (Tockner *et al.*, 2008, 2010). Floodplain rivers in arid and semi-arid regions (drylands, Tooth, 2000) with low annual rainfall (mean <500 mm) and high annual evaporation rates are perhaps the most threatened of all river systems. Their defining hydrological characteristic is extreme flow variability (Walker *et al.*, 1995; Young and Kingsford, 2006), and to dependent humans this presents many difficulties with respect to achieving reliable water supplies. Water resource developments (e.g. river capture, impoundment, flow diversion, interbasin transfers) are all designed to dampen or compensate for the natural dynamics of erratic hydrologic regimes (Wishart, 2006; Young and Kingsford, 2006). In so doing such developments can radically disrupt the delicate ecological dynamics of arid-zone floodplain rivers, in particular the pronounced 'boom and bust' phenomena associated with aquatic habitat expansion during floods and contraction during dry spells.

This paper is focused on how arid-zone river systems function in relation to their erratic hydrologic regimes, and how they support diverse fish assemblages and productive fisheries. It is timely because climate change is likely to further disrupt hydrologic processes in many floodplain rivers. Under drier conditions, aquatic habitats in arid-zone rivers are likely to become even more fragmented and stressful for aquatic life during extended dry periods, and patterns of flooding may also change (Bond *et al.*, 2008; Murphy *et al.*, 2008; Larned *et al.*, 2010). These changes are likely to threaten all obligate aquatic species.

Over 50% of the world's land area can be classed as 'dryland', including regions of hyper-arid, arid, semi-arid and dry-subhumid climate (Tooth, 2000). Rivers that flow through these landscapes are often termed 'dryland' or desert rivers, and they are generally very poorly studied compared to rivers in wetter regimes. Yet their persistence and ecological health are vital for millions of dependent people and communities in Africa, Asia, the Mediterranean region and

parts of the Americas (Jensen, 2001; Welcome *et al.*, 2006a). In Australia, 92% of the 3.5 million kilometres of river channels measured at the 1:250,000 scale are classified as lowland rivers (Thoms and Sheldon, 2000), and most of these lowland rivers can be characterized as dryland rivers (Sheldon *et al.*, 2010). Although their hydrographs are extremely variable within and between years, some of these rivers are the major sources for irrigation water and are also important sources for stock and domestic water supply (e.g. major tributaries and the main stem of the Murray-Darling river system, Walker *et al.*, 1995). Massive pastoral developments are dependent upon the pulsing of floods over vast areas, and these spectacularly biodiverse landscapes and seasonal events attract thousands of tourists.

Australian dryland rivers lie at the extremity of the flow variability spectrum for 52 of the world's large rivers identified by Puckridge *et al.*, (1998). Cooper Creek, one of the major rivers in the Lake Eyre Basin (Fig. 1), has the most variable hydrological regime of any of the world's large rivers of comparable discharge (Puckridge *et al.*, 1998), followed by the Diamantina, Burdekin, Limpopo, Fitzroy, Vaal and Darling rivers, with the Colorado, Mississippi and Mekong rivers far more predictable in their flows by comparison. As a largely undeveloped catchment with a near natural and very erratic flow regime, Cooper Creek may provide a model arid-zone floodplain river system for the study of natural ecohydrological processes captured in the 'natural flow regime paradigm' (Poff *et al.*, 1997), the 'flood pulse concept' (Junk *et al.*, 1989) and various flow-ecology principles (e.g. Bunn and Arthington, 2002).

This paper offers a review of these dynamic hydroecological processes with a focus on fish. Its objectives are: (1) to summarize current understanding of how the natural flow regime of Cooper Creek underpins the structure and dynamics of this floodplain river system and, in particular, the ecology of its fish assemblages; (2) to outline the potential ecological impacts of water resource development and landuse change on the river and its fish assemblages; and (3) to describe water planning and river conservation principles designed to protect the natural values of arid-zone rivers and their catchments in Australia's Lake Eyre basin. Throughout this review, comparisons are drawn with other floodplain rivers and fisheries, to identify common understandings and universal principles for conservation and management of arid-zone rivers and their fish resources.

CLIMATE AND HYDROLOGY OF COOPER CREEK

The Cooper Creek catchment (approximately 290 000 km², Fig. 1) receives a mean annual rainfall varying from 400-500 mm in the headwaters to <100 mm at its entry to Lake Eyre (Puckridge, 1999; Bunn *et al.*, 2003). The climate is classed as semi-arid to arid (category B in the Koppen and Geiger climate classification). Mean daily maximum air temperatures at Windorah range from 38.1 °C in January to 21.4 °C in July and mean daily minima from 24 °C in January to 7 °C in July. Mean annual evaporation exceeds 3 m and, together with evapotranspiration, drainage diffusion and infiltration, results in transmission losses below Windorah accounting for more than two-thirds of the discharge by the time it reaches the South Australian border (Knighton and Nanson, 1994a).

The hydrology of the Cooper catchment has been well described (Puckridge *et al.*, 1998; Knighton and Nanson, 2001; McMahon and Finlayson, 2003). Most stream flow is generated by summer monsoon rainfall in the headwaters of the Thomson and Barcoo rivers and by periodic local rainfall (Fig. 1). At Currareva near Windorah (Fig. 1) the mean annual discharge is 3.05 km³ yr⁻¹ (97 m³s⁻¹), with wide inter-annual variation, irregular flow pulses for a few months or less each year and periods of zero flow lasting up to 21 months based on 49 years of record (Bunn *et al.*, 2003). Cooper Creek experiences infrequent high-magnitude flow events (linked to ENSO phenomena) that can inundate extensive areas of floodplain, often for several months at a time (Knighton and Nanson, 1994b; Knighton and Nanson 2001). Episodic floods can inundate tens of thousands of square kilometres of floodplain, equivalent to 35% of the catchment (Figs 2 and 3). This expansive flooding serves to reconnect channels, anabranches, distributaries and isolated channel and floodplain waterholes (see Fig.3), turning a fragmented river network into a mighty river, occasionally flowing on to help fill Lake Eyre (Knighton and Nanson, 1994a,b; Magor, 2000).

More frequent but smaller flow pulses that remain within the river channels are also important (Figs 2 and 3). They refill aquatic habitats that would otherwise dry completely over time, and the larger pulses serve to reconnect waterholes within channels and wet up backwaters and

anabranches (Hamilton *et al.*, 2005). Hydrological ‘connectivity’ (Heiler *et al.*, 1995; Ward and Stanford 1995) varies spatially in degree, frequency and duration, contributing to the overall variability and unpredictable nature of the aquatic environment of Cooper Creek.

After flood recession, Cooper Creek between Windorah and Nappa Merrie dries down into a complex system of anastomosing channels (the ‘channel country’) and more than 300 relatively deep (6-10 m) channel segments known locally as ‘waterholes’ (Knighton and Nanson, 1994b; Unmack, 2001). Waterholes develop at points of flow convergence, typically at the confluence of several channels, or where a channel is constricted between the remnants of aeolian dunes or a floodplain edge or valley side (Knighton and Nanson, 1994a). Localised scour associated with the rising flood stage is sufficiently powerful to cut into the cohesive upper layer of clay, allowing the underlying sand sheet to be excavated into large pools. As floodwaters subside, the clay particles settle and seal the depressions to create relatively permanent waterbodies (Knighton and Nanson, 2000). Cooper Creek waterholes are typically 2-5 times wider and 2-3 times deeper than the associated distributary channels and have a distinctive linear morphology (hence the township named “Longreach”, see Fig. 1). Waterholes range in length from a few hundred metres to over 20 km (Knighton and Nanson, 1994b). Many have well-developed vegetated levees that also help to concentrate flow. The variability of aquatic habitats during the natural hydrological cycle is represented in Figure 3.

Evidence from major solute and stable isotopic tracers indicates that during the isolation phase, the hydrology of waterholes in the Cooper Creek system is dominated by evaporative water loss; very few waterholes receive local groundwater inputs (Hamilton *et al.*, 2005). Therefore, the interval between flows that fill the waterholes to bankfull level dictates whether they persist as habitat for aquatic biota, and in this respect they behave like other Australian dryland rivers (Costelloe *et al.*, 2004). Although they have an unusual mode of origin, the waterholes of Cooper Creek are the ecological equivalents of the isolated floodplain lakes and lagoons left in other floodplain river systems after floods recede (e.g. Rodriguez and Lewis, 1997; Tejerina-Garro *et al.*, 1998). This paper explores how this highly dynamic river system can offer lessons for the conservation and management of fish assemblages in other arid-zone rivers with highly variable flow regimes.

THE FISH FAUNA OF COOPER CREEK

The fish fauna of Cooper Creek is comprised of 12 indigenous fish species in eight families, and two alien species: the goldfish, *Carassius auratus* and the mosquitofish, *Gambusia holbrooki* (Table 1). Both alien species are relatively rare in most of this catchment (Kerezszy, 2010). Although the fish fauna of Cooper Creek is not rich compared to many of Queensland's coastal rivers (23-55 species, Pusey *et al.*, 2004), the native fishes recorded in this arid-zone river are of ecological and conservation significance, and several are valued socially and economically for recreational fishing (Wager and Unmack, 2000). Four of the native species - the endemic Cooper Creek tandan (*Neosiluroides cooperensis*), the Lake Eyre yellowbelly (*Macquaria* sp. B), the desert rainbowfish (*Melanotaenia splendida tatei*) and Welch's grunter (*Bidyanus welchi* - are confined to central Australia. Five species have a tropical and central Australian distribution - *Porochilus argenteus*, *Neosilurus hyrtlii*, *Leiopotherapon unicolor*, *Ambassis* sp. and the Barcoo grunter, *Scortum barcoo*. The Australian smelt, *Retropinna semoni*, has a subtropical and temperate distribution and the bony bream, *Nematolosa erebi*, is widespread in central, eastern and northern Australia (Pusey *et al.*, 2004). In 15 waterholes sampled in 2001 (Arthington *et al.*, 2005), five widespread indigenous species contributed 96% of the total catch based on standardised fyke net sampling - the silver tandan, *P. argenteus* (45.5%), northwest *Ambassis* (19.9%), spangled perch, *L. unicolor* (12.5%), bony bream, *N. erebi* (9.7%) and Hyrtl's tandan, *N. hyrtlii* (8.4%). Seven species contributed 4 % the catch, and most of these species were patchily distributed among waterholes (Table 1). The fauna spans a range of body sizes, physiological tolerances, habitat and dietary preferences and reproductive strategies (Arthington *et al.*, 2010; Pusey *et al.*, 2004).

DRY SPELLS AND THE 'BUST' PHASE

Aquatic refugia

During dry periods when there is little runoff or flow along stream channels, wetted habitat takes the form of a patchy and highly fragmented mosaic of disconnected waterholes and wetlands scattered along channels and across vast dry floodplains (Figs 1 and 3). Fragmentation of

aquatic habitat in Cooper Creek is likely to be extreme on a global scale because of the system's high flow variability (Walker *et al.*, 1995; Puckridge *et al.*, 1998; Thoms and Sheldon, 2000). During dry periods, the larger permanent and semi-permanent waterholes function as *refugia* for a wide variety of aquatic organisms requiring permanent water to survive (Morton *et al.*, 1995; Arthington *et al.*, 2005; Bunn *et al.*, 2003). A '*refuge*' may be regarded as a habitat that supports populations not able to live elsewhere in a landscape (Nekola, 1999), or as a place (or time) where the negative effects of disturbance are lower than in the surrounding area or time (Lancaster and Belyea, 1997). During adverse conditions, organisms living in refugia have a higher probability of survival and the survivors are subsequently available to recruit *in situ*, or may recolonise other areas of the landscape when more benign conditions are restored (Lancaster and Belyea, 1997).

Drivers of fish losses

Fish living in arid-zone rivers typically possess well-developed 'resistance' traits enabling them to cope with the harshness of life in drying waterholes, where physico-chemical conditions and predator-prey and competitive process can exact high mortality (Ruello, 1976; Wager and Unmack, 2000; Matthews and Marsh-Matthews, 2003). The Cooper Creek fauna is no exception. Yet even though all 12 species possess some resistance traits (e.g. habitat generalism, dietary flexibility, tolerance of abiotic extremes), fish abundances and assemblage composition in individual waterholes have been shown to change markedly over dry periods (Puckridge *et al.*, 2000; Arthington *et al.*, 2005; Balcombe and Arthington, 2009). The typical pattern is one of declining populations and the loss of up to 6 of 11 species from individual waterholes over periods of no flow and waterhole drying; complete disconnection inhibits any recolonization by fish movement from one waterhole to another (Table 1; see also Arthington *et al.*, 2010). Factors associated with fish losses include waterhole morphology (wetted perimeter, depth), habitat structure (bench development, off-take channels), waterhole quality (eroded banks, gross primary production), size of surrounding floodplains and the relative isolation of waterholes on their floodplains (Arthington *et al.*, 2010).

The main biological mechanisms underlying species losses are their particular habitat requirements, trophic ecology and physical/chemical tolerance characteristics. For example, for the desert

rainbowfish (*M. s. tatei*), low physical habitat diversity and susceptibility to decreasing water temperatures drove losses from 11 of 14 waterholes. The Lake Eyre yellowbelly (*Macquaria* sp. B), an important recreational fish in Australia's inland rivers (Wager and Unmack, 2000; Pusey *et al.*, 2004), was lost from six of 14 waterholes, particularly those with higher numbers of offtake channels and ones situated far out on the fringes of the floodplain which are rarely rewetted and reconnected. The Barcoo grunter (*S. barcoo*) was lost from 11 waterholes, especially those with low levels of bed and bank complexity, reduced habitat heterogeneity and less cover that could afford protection from predators (Kennard, 1995; Pusey *et al.*, 2004). This grunter was also less likely to persist in waterholes situated on narrow floodplains, possibly because fish coming off narrow floodplains may not have accumulated the body lipids that govern condition, and probably survival, in isolated, drying waterholes (Puckridge *et al.*, 2000).

The fate of the endemic Cooper Creek tandan (*N. cooperensis*) in drying waterholes is particularly interesting. Whilst deeper waterholes exhibited losses, waterholes that experienced increases in gross primary production over the dry season were able to sustain this catfish (Arthington *et al.*, 2010). During dry periods, a conspicuous, shallow "bath-tub ring" of benthic algae forms around the margins of isolated waterholes (Bunn *et al.*, 2003) and this sustains the entire fish assemblage; riparian sources of carbon make a very small contribution to the aquatic food web. Fellows *et al.* (2009) established that the marginal band of benthic algae achieves significantly greater biomass in the shallow sloping littoral zones of Cooper Creek waterholes than in the steeper, deeper waterholes of this system and the Warrego River (Murray-Darling Basin). This is perhaps especially important for larger species such as the Cooper Creek tandan (*N. cooperensis*) that feed on large-bodied invertebrates (crustaceans and gastropods), themselves sustained by high levels of littoral primary production (Bunn *et al.*, 2003). It is noteworthy that this catfish is the only species not yet found on the floodplains of Cooper Creek when they are inundated (Balcombe *et al.*, 2007). Without an energetic subsidy from the food-rich floodplain (Balcombe *et al.*, 2005), the Cooper Creek tandan would be totally reliant on the waterhole food web, and this is not very productive in steep-sided waterholes where the bath-tub ring of algae is usually less well-developed.

Individual species in Cooper Creek suffered moderate to very high changes in abundance per waterhole and total losses for each species varied from 50 -100% over a 6-month dry period (Table 1). Across the entire fauna 93% of individuals were lost from drying waterholes between April and September 2001.

Mechanisms of species losses in the drying waterbodies of Cooper Creek are generally consistent with previous studies that explain differences in fish assemblage structure in isolated floodplain waterbodies in terms of habitat structure and waterbody quality (Rodriguez and Lewis, 1997; Tejerina-Garro *et al.*, 1998; Welcomme *et al.*, 2006a). In Cooper Creek, with decline in waterhole depth and volume, exposure of habitat features would reduce the range of sheltered places where fish can rest and forage, take cover from predators, or launch ambush attacks on prey (Kennard, 1995; Crook and Robertson, 1999; Pusey *et al.*, 2004). Loss and change of aquatic habitat is also important in intermittent streams subject to natural periods of low flow or drought (Magoulick and Kobza, 2003; Matthews and Marsh-Matthews, 2003; Larned *et al.*, 2010). In rivers with altered flow regimes, habitat loss is typically the first process documented and addressed in the assessment and provision of water allocations for the environment (i.e. ‘environmental flows’) (Poff *et al.*, 1997; Bunn and Arthington, 2002; Tharme, 2003), and in species recovery plans in general (Bond and Lake, 2003).

Water quality effects

As well as habitat alteration and loss, many studies in floodplain rivers have found that deterioration of water quality (e.g. salinity, dissolved oxygen, turbidity, pH) is also a major factor in species losses from drying streams and aquatic habitats left on floodplains during dry periods (Rodriguez and Lewis, 1997; Magoulick and Kobza, 2003; Matthews and Marsh-Matthews, 2003). Yet in Cooper Creek, changes in prominent features of water chemistry (e.g. conductivity and nutrient concentrations) did not influence the persistence of Cooper Creek fishes over a 6-month dry period; this is because the fauna is generally very tolerant of changes in salinity (Pusey *et al.*, 2004). However, Balcombe and Arthington (2009) found strong correlations between declining numbers of Barcoo grunter (*S. barcoo*), spangled perch (*L. unicolor*) and silver tandan (*P. argenteus*) and increasing pH associated with waterhole drying in the Windorah reach of Cooper Creek.

Biotic processes

Across all species and waterholes in Cooper Creek, 26% of spatial variation in fish losses was unexplained by the 25 floodplain, waterhole and habitat factors studied. Biotic processes, such as predation, competition for food resources or space, or exposure to parasites and diseases, may also contribute to fish losses during dry periods (Ruello, 1976; Jackson *et al.*, 2001; Magoulick and Kobza, 2003; Balcombe *et al.*, 2005). Burford *et al.* (2008) suggested that high fish mortalities during dry periods (93% across 14 waterholes) may be related to declining food resources, lower fish lipid levels and possibly, fish starvation as water levels decline over time.

FLOODS AND THE ‘BOOM’ PHASE

The Flood Pulse Concept

In the Flood Pulse Concept the pulsing of river discharge from dry-season channels into fringing floodplain areas determines the degree of connectivity and the potential for exchanges of matter and organisms across river-floodplain gradients and *vice versa* (Junk *et al.*, 1989). The predictable annual flood pulse of long duration, and associated primary and secondary productivity on the floodplain, underpin massive ‘booms’ of fish biomass in some of the world’s most productive freshwater fisheries (Van Zalinge *et al.*, 2000; Craig *et al.*, 2004; Welcomme *et al.*, 2006a). The FPC has undoubtedly contributed to appreciation of the ecological roles of flooding in tropical floodplain-river systems but is it relevant and useful in systems that do not experience predictable annual flooding, regular hydrological connectivity and frequent river-floodplain linkages? Recent studies on the Cooper Creek floodplain around the township of Windorah (Fig. 1) have examined whether large floods do in fact drive fish production and other processes to the extent observed in tropical and sub-tropical river systems.

Fish production on floodplains

During the 2004 summer flood in Cooper Creek, shallow floodplain areas near Windorah (Fig. 1) supported high fish biomass in the range of 21–240 kg ha⁻¹, a figure reasonably comparable to data for some of the world’s key freshwater fisheries, such as fisheries in Bangladesh (50–400 kg ha⁻¹; Craig *et al.*, 2004), the Mekong (138–175 ha⁻¹; Van Zalinge *et al.*, 2000) and the Amazon

(24 kg ha⁻¹; Bayley, 1998). Sampling on the Windorah floodplain during a flood of similar magnitude in February 2000 revealed similar fish biomass (14–150 kg ha⁻¹). This similarity of response to floods four years apart, and the congruence with productivity estimates in monsoonal floodplain rivers, suggest that the fish fauna of Cooper Creek is adapted to take advantage of intermittent floods and the resources and growth opportunities associated with extensive floodplain inundation (Craig *et al.*, 2004; Balcombe *et al.*, 2007).

The global literature records strong relationships between the magnitude and/or duration of the annual flood pulse, floodplain area inundated and fish production in the same or subsequent years (Bayley, 1991; Welcomme *et al.*, 2006a). Similar relationships have been demonstrated in Cooper Creek. The February 2000 flood in Cooper Creek (Fig. 2) inundated nearly 14 000 km² of floodplain, and was followed by a massive increase in fish abundance that was still evident in waterholes sampled 14 months later (Arthington *et al.*, 2005). In April 2001, *Melanotaenia splendida tatei*, *P. argenteus*, *L. unicolor*, *Macquaria* sp. and *S. barcoo* were all more abundant in waterholes with large total and/or effective floodplain width (Arthington *et al.*, 2005). The strong influence of sequential antecedent floods on fish populations has also been observed in the Coongie Lakes along the lower Cooper Creek catchment (Puckridge *et al.*, 2000).

Fish life history and recruitment

In the flood pulse model, floods act as cues for the initiation of fish breeding and by opening up floodplain habitats and resources that are used by the larvae, juveniles and mature stages of many species for feeding and growth (Junk *et al.*, 1989). In Cooper Creek, 11 of the 12 native species most closely resemble the eupotamonic phytophilic fish guild of Welcomme *et al.*, (2006b): they are able to migrate laterally between waterholes, channels and floodplains and/or down the floodplain under flood conditions. Species in the eupotamonic phytophilic guild have flexible breeding strategies, and may spawn at floodplain margins, in flowing channels, or on the floodplain itself, and they use floodplains as nursery habitat, and for juvenile and adult feeding (Welcomme *et al.*, 2006b). Most Cooper Creek fishes share these reproductive traits, with two of three life stages of 11 species found on floodplains, while the six most common species use floodplains as larvae, juveniles and adults (Balcombe *et al.*, 2007).

Although most species in Cooper Creek use the floodplains during their growth and recruitment phase, spawning is not necessarily cued by flooding or rising channel flows. Several species spawn in isolated waterholes during no flow periods but typically show strong patterns of juvenile recruitment following extensive floodplain inundation (Arthington *et al.*, 2005; Balcombe and Arthington, 2009). The plotosid catfish (*N. hyrtlii*) may be the only obligate flood spawner, with recruitment restricted to the summer months after rising flows. Balcombe *et al.*, (2006) reported obligate flood spawning of this catfish in the dryland Warrego River (Murray-Darling Basin), and imilar recruitment patterns have been reported in populations of *N. hyrtlii* from northern Australia (Orr and Millward, 1984; Pusey *et al.*, 2004).

The only species not yet recorded from Cooper Creek floodplains is the endemic Plotosid catfish (*N. cooperensis*) related to the nest-building genus *Tandanus*. The biology of the Cooper Creek catfish is poorly known but in aquaria it has been reported to produce relatively few eggs (approximately 1000) of a very large size (3-4 mm: Unmack, 1996). Cooper catfish grow to a large size (up to 600 mm), suggesting that this species may be long-lived, and it appears to be relatively sedentary. For *N. cooperensis*, periodic release of relatively few large eggs over channel substrates (possibly in a nest) represents a far less risky strategy than dispersal of small numbers of larvae and juveniles onto floodplains. The Cooper catfish shares some traits with the eupotamonic pelagophilic guild - channel residents that do not enter the floodplain (Welcomme *et al.*, 2006b). Unlike most members of this guild, and given its patchy occurrence and relative rarity, *N. cooperensis* appears unlikely to undertake long-distance migrations, but local movements of < 10km have been recorded in far western rivers of the Lake Eyre Basin (Kerezszy, 2010).

In fish assemblages of the Lake Eyre Basin, there appear to be representatives of the three main life history strategies – opportunistic, periodic and equilibrium - arising from interrelationships among three basic demographic parameters, survival, fecundity, and the onset and duration of reproductive life (Winemiller and Rose, 1992). Assignments to these strategies are tentative, and do not necessarily imply full achievement of evolutionary “endpoints”; however they are consistent with groupings determined for congeneric freshwater species in coastal drainages of eastern Australia (Olden and Kennard, 2010). Opportunists in the Cooper Creek fish assemblage

include the small-bodied gudgeons, desert rainbowfish, smelt, *Ambassis* and the introduced *Gambusia holbrooki*, with early maturation, low fecundity per spawning event, and low juvenile survivorship (Pusey *et al.*, 2004). Such species tend to inhabit environments subjected to frequent and intense disturbances. All Cooper Creek opportunists extend the advantages of this strategy by moving into backwater habitats, flooded channels and intermittently inundated floodplains to feed and grow in shallow, food rich, warm-water habitats (Balcombe *et al.*, 2007).

Several species of moderate body size (golden perch, silver tandan, Hyrtl's tandan, bony bream, spangled perch and the grunters – Table 1) share features with periodic strategists. They are moderate-sized fishes with late maturation, high fecundity per spawning event, and low juvenile survivorship (i.e. no parental care), typically inhabiting patchy, seasonal, periodically suitable environments. Periodic fishes spread their reproductive effort over numerous reproductive events, and high reproductive success occurs only intermittently during particularly favourable environmental conditions between prolonged intervals of low reproductive success (Winemiller and Rose, 1992). Only one of the mooted periodic spawners, Hyrtl's tandan, has an obligate dependence on rising flows or flooding as a spawning cue in Cooper Creek and other river systems (Pusey *et al.*, 2004; Balcombe and Arthington, 2009). Other common species – bony bream and yellowbelly – can breed at any time of year, producing many small eggs, and colonising lateral and floodplain habitats mainly as juveniles, a strategy that would maintain at least some breeding-age fish in relatively stable channel waterholes.

The remaining species, the large-bodied Cooper tandan, has some of the traits of an equilibrium species – moderate to long generation time, low fecundity per spawning event and high energetic effort per offspring (Unmack, 1996; cf. Winemiller and Rose, 1992). If it spawns into a 'nest' like its close relative in the Murray-Darling Basin (*Tandanus tandanus*), it might be said to possess a primitive form of parental care. The 'equilibrium' conditions to which it is adapted are conceivably those found in the larger waterholes with long persistence times and a predictable seasonal thermal regime.

Fish movement

The movement behaviours of 11 native fishes in Cooper Creek and other floodplain rivers of the Lake Eyre Basin are consistent with those of species in the eupotamonic phytophilic guild (Welcomme *et al.*, 2006b). In Cooper Creek, fish species richness and total biomass were uniformly spread across the floodplain around Windorah on two occasions of flooding (2000, 2004). This even distribution of species and individuals suggests that the inundated floodplain provides a major conduit for movement and mixing of the fish species that are otherwise confined to isolated waterholes during the dry season (Balcombe *et al.*, 2007). Other studies have reported similar uniformity of fish catches during and shortly after flooding, implying significant movements and the development of well-mixed ('panmictic') populations that are still quite similar at the early stage of habitat fragmentation into separate lagoons on the floodplain (e.g. Rodriguez and Lewis, 1997). In the Cooper catchment, four species (*N. erebi*, *R. semoni*, *N. hyrtlui* and *P. argenteus*) repeatedly found in waterholes and on the Windorah floodplain show low levels of genetic variability at the catchment scale, suggesting that for these species there is high genetic and therefore biotic connectivity throughout this catchment (Huey *et al.*, 2006; Hughes and Hillyer 2006). Other evidence from floodplain-waterhole biomass budgets suggests that the yellowbelly (*Macquaria* sp. B) also makes extensive migrations on the Cooper Creek floodplain (Balcombe *et al.*, 2007), consistent with the long-distance migrations of its close relative, *Macquaria ambigua*, in the Murray-Darling River system.

CHANNEL FLOWS

Cooper Creek experiences relatively few very large floods, however in-channel flows or flow 'pulses', can occur before or after a large flood, or occur independently in association with localised rainfall (Bunn *et al.*, 2006a). These times between no flow periods and major floods (Bunn *et al.*, 2006b) reconnect, refill and replenish waterholes that have been disconnected during dry times and also serve to maintain connectivity for some time after flood recession (Fig. 3). Channel flows (and declining flood flows) may reset the physical and chemical template for benthic algal production by rapidly submerging the pre-existing littoral photic zone (Bunn *et al.*, 2006a) and by changing water turbidity and nutrient concentrations (Fellows *et al.*, 2009). Primary production in desert streams tends to show considerable temporal variability in response to flow events, but typically recovers very rapidly after flooding or drought (Fisher *et al.*, 1982).

For example, the biomass and production values of algae returned to pre-disturbance levels in less than one month after flooding in a semi-arid Spanish stream (Velasco *et al.*, 2003), and to 50% of maximum levels within 10 days after flooding in a Sonoran desert stream (Grimm, 1987).

While water is flowing and more turbid and water levels are fluctuating, benthic algal production is expected to decline (Bunn *et al.*, 2006a) and this may have implications for fish that become wholly dependent on the waterhole food web. Fellows *et al.*, (2009) found a significant relationship between Gross Primary Production (GPP) and fish abundance in Cooper Creek waterholes immediately after flood recession. This relationship did not persist into the no-flow 'bust' period while water levels became more stable, or were falling, because by then the food web was supported by benthic algae forming the littoral (bath-tub) band. During the drying phase, fish in isolated waterholes seem to be more strongly affected by abiotic habitat factors, water quality changes, and perhaps biotic processes, rather than by variations in waterhole productivity (Arthington *et al.*, 2010).

Channel flows are important to fish in several other ways. They can provide cues for movement and dispersal within channels and into backwater habitats or tributaries (Nunn *et al.*, 2010), a trait that should enhance opportunistic discovery of high quality habitats and richer food resources, or permit avoidance of predators. Most species in Cooper Creek are highly vagile, moving into backwaters, flood runners and out onto floodplains when they become inundated and using floods as a means for wider movements (Wager and Unmack, 2000; Balcombe *et al.*, 2007). In this arid environment, moving at every opportunity is evidently a more successful strategy than staying put, except possibly for the Cooper Creek tandan, *N. cooperensis*, which appears to be relatively sedentary. Hence it may have a similar ecology, and fill a similar ecological niche, to another large bodied, nest building plotosid catfish, *Tandanus tandanus*, in the Murray-Darling River system.

As well as opening up pathways for movement, channel flows may act as cues for spawning of another plotosid catfish, *N. hyrtlui*, the only species that appears to need rising flows or flooding to spawn and recruit in Cooper Creek and more northern river systems (Pusey *et al.*, 2004; Balcombe and Arthington, 2009; Kerezszy, 1010). For the entire fish assemblage, the capacity to

use periodically flooded habitats is an important life history trait enabling most species to build up sufficient numbers for at least some healthy individuals to persist through periods when channel flows are low or waterholes are drying down during the 'bust' period (Balcombe and Arthington 2009). These temporal population fluctuations and variable recruitment strategies have many parallels in fishes of the world's arid-zone rivers (Lowe-McConnell, 1985; Kingsford *et al.*, 2006a; Zeug and Winemiller, 2008).

IMPLICATIONS OF HYDROLOGICAL ALTERATIONS FOR A BOOM AND BUST SYSTEM

Implications of changing the natural flow regime

The role of the natural flow regime as an important driver of riverine ecology (Poff *et al.*, 1997; Bunn and Arthington, 2002; Naiman *et al.*, 2008) is spectacularly evident in the boom and bust ecology of fishes in arid-zone rivers such as Cooper Creek. Resistance to harsh physico-chemical conditions during the dry times, flexible feeding and reproductive strategies, high vagility and opportunistic responses to flow events or flooding, are vital traits of most fish species in Cooper Creek. These traits largely explain the prominent 'boom and bust' patterns of fish production in response to wetting and drying cycles. However, a pronounced capacity to swing between low and high population levels does not imply that there are no limits to the pressures that can be placed upon the hydrologic regime and fishes of arid-zone rivers (Arthington *et al.*, 2005; 2006). The fish assemblages of Cooper Creek and other desert rivers are likely to be extremely vulnerable to alteration of the flow regime and catchment characteristics in several important ways. These are presented below with associated implications and principles for conservation and management.

Vulnerability of refugia

First, the absolute necessity for all species of fish to be able to persist in 'refuge' habitats (waterholes) during dry periods renders them extremely vulnerable to any process that may accelerate rates of water loss and reduce the number of waterholes that could sustain aquatic biota over extended dry periods. Hamilton *et al.*, (2005) estimated that most Cooper Creek waterholes would dry up within 22 months if not replenished by channel flows or flooding; after

24 months of no flow, only four of the named waterholes along Cooper Creek would remain (Bunn *et al.*, 2006b). Under climate change scenarios for this part of Australia, increased air temperatures could enhance evaporation and rates of water loss in isolated waterholes, depending up situational factors such as position on the floodplain, exposure to wind and turbulence, and protection from riparian vegetation (Hamilton *et al.*, 2005). Furthermore, reduced frequency and volume of flow pulses and large floods that top up water levels would further threaten fish and other obligate aquatic biota (Leigh *et al.*, 2010).

A further vulnerability is that steep, highly eroded banks, decreasing water depths and low habitat diversity contribute to fish losses in drying waterholes, particularly those located far out on the floodplain (Arthington *et al.*, 2010). Several natural processes influence bank instability and erosion in alluvial rivers, and sedimentary processes can be exacerbated by disturbance of riparian vegetation. The free access of cattle to waterholes may contribute to bank erosion and instability at some waterholes, however, most of the time cattle take their drinking water from controlled watering points on the floodplains. The greatest threat to bank erosion would be any action that alters the natural hydraulic processes in the system. In regulated dryland rivers of the northern Murray-Darling Basin, massive losses of bank material are associated with rapid drawdown during water extraction (Thoms and Sheldon, 2000).

The identification and protection of refugia for obligate aquatic species is an essential component of river management during dry periods and drought (Dekar and Magoulick, 2007; Bond *et al.*, 2008; Larned *et al.*, 2010; Pires *et al.*, 2010). However, deciding upon the spatial configuration and number of discrete aquatic habitat patches required to sustain each species requires a capacity to model patterns of connectivity, fish movement, colonization and extinction rates at landscape scale (Gotelli and Taylor, 1999; Davey and Kelly, 2007; Pires *et al.*, 2010). Until these processes and the drivers of metapopulation structure are better understood, it would be risky to base the conservation of fish diversity in Cooper Creek on the protection of a few select waterholes.

Importance of connectivity

Many floodplain rivers across the globe have lost floodplain and river channel connections, and these losses of connectivity have compromised the movement of various aquatic species and their different life-stages (Heiler *et al.*, 1995; Welcomme *et al.*, 2006a,b; Barko *et al.*, 2006; Tockner *et al.*, 2008). Altered catchment configurations (e.g. levee banks, roads and infrastructure) can cut off or impede delivery of flows onto floodplains, reduce 'connectivity potential' (Heiler *et al.*, 1995) and inhibit fish movements from unfavourable to favourable waterholes, inundated floodplains and better opportunities for feeding and recruitment. The disruption to connectivity between waterholes and their floodplains has been clearly implicated in the upper Murray-Darling system, where the yellowbelly has shown recruitment failure in the waterholes affected by flow regulation compared with those where the water regime remains relatively unaltered (Balcombe *et al.*, 2011).

Importance of floods

The redeeming factor in the precarious ecological dynamics of arid zone floodplain rivers is the erratic flood pulse. Although flooding is unpredictable in frequency, extent and duration at any point in Cooper Creek, floods underpin similar processes to the predictable annual floods of tropical and sub-tropical floodplain rivers (Balcombe *et al.*, 2007; Balcombe and Arthington, 2009; Leigh *et al.*, 2010). During occasional large floods, waterholes become filled and reconnected, nutrients are replenished, fish reproduction and dispersal become possible on a grand scale, and fisheries productivity off inundated floodplains reaches 'boom' proportions (Bunn *et al.*, 2006a; Balcombe *et al.*, 2007; Burford *et al.*, 2008; Fellows *et al.*, 2009). These floodplain processes and fish behaviours maximize the chances of nearby waterholes starting the dry season with a diverse, abundant and healthy fish assemblage immediately after flood recession, and this would ultimately enhance the survival of fish through prolonged periods of adverse conditions – the 'bust' (Walker *et al.*, 1995; Balcombe *et al.*, 2007). Flooding can be considered essential for maintenance of the diversity and long-term health of the Cooper Creek fish assemblage and the resilience of the aquatic ecosystem (Walker *et al.*, 1995; Puckridge *et al.*, 2000; Balcombe *et al.*, 2007). Floods also enhance recruitment of frogs, turtles and waterbirds (Kingsford *et al.*, 2006a) and support the high levels of pasture production that underpin the vitality and viability of the pastoral industry in dryland catchments of western

Queensland (Morrish, 1998; Ogden *et al.*, 2002). Dampening or elimination of occasional large floods or smaller channel flows undermines the resilience of arid-zone ecosystems, both aquatic and terrestrial, and is inevitably disastrous for the fisheries, pastoral and flood recession industries dependent upon regeneration of floodplain resources (Kingsford *et al.*, 2006a; Welcomme *et al.*, 2006a, b).

Floodplain food webs

Perhaps the major difference between rivers like the Amazon and Mekong and arid Cooper Creek is the relatively low contribution of terrestrial vegetation and derived organic matter to the floodplain food web (Bunn *et al.*, 2006; Balcombe *et al.*, 2007; Burford *et al.*, 2008). Primary production by algae fuels the entire floodplain food web (Fellows *et al.*, 2009). Furthermore, a large amount of the fish biomass produced on the floodplain is returned to waterholes when floods recede (Balcombe *et al.*, 2007), fuelling short-term production in waterholes by the unusual pathway of fish mortality, with 50% of carbon in fish from Murken waterhole derived from floodplain sources (Burford *et al.*, 2008). Storage or diversion of flood waters or reducing their magnitude and the duration of floodplain inundation can have flow-on effects for the entire linked floodplain-waterhole food web (Wooton *et al.*, 1996; Burford *et al.*, 2008). The importance of productivity potential on floodplains must be recognised and maintained, by ensuring the uninterrupted delivery of flood waters, carbon and nutrients generated throughout the catchment. A catchment approach to river management is essential to ensure that these landscape and biogeochemical processes are not disrupted (Tockner *et al.*, 2000).

Waterhole food webs

Channel flows reset the physical and chemical template of waterholes by transporting nutrients and sediment, drowning the photic zone, altering the light environment and temporarily inhibiting primary production by benthic algae (Fellows *et al.*, 2009). Fish populations dependent upon the waterhole food web may decline until more stable conditions are restored and the littoral band of primary producers becomes well established and is able to track falling water levels (Bunn *et al.*, 2006b). With restoration of the food web, fish appear able to persist on a low diversity invertebrate diet, or algae/plants. In addition, most species in Cooper Creek gain energetic subsidies from their time spent foraging on inundated floodplains, where food

resources are more diverse and plentiful (Balcombe *et al.*, 2005; Burford *et al.*, 2008). Periodic phytoplankton blooms and zooplankton are also important sources of energy within the waterholes of dryland rivers (see Balcombe *et al.*, 2005; Medeiros and Arthington, 2008). Any activity or management strategy that interferes with the generation or stability of the waterhole food web has potential to threaten aquatic biota, including fish (Bunn *et al.*, (2006b; Leigh *et al.*, 2010).

CONSERVATION AND MANAGEMENT OF ARID-ZONE FISHES

Temporal variability in hydrological characteristics has been recognized as the driving force maintaining the ecosystems of semi-arid and arid-zone streams and intermittent rivers in many arid regions of the world (Walker *et al.*, 1995; Kingsford 2006; Maltchik and Medeiros, 2006; Dekar and Magoulick, 2007; Larned *et al.*, 2010; Leigh *et al.*, 2010). Long-term conservation of arid-zone rivers such as Cooper Creek requires recognition and protection of their special dynamic characteristics, embracing hydrologic, geomorphic, sedimentary, biogeochemical, ecological and evolutionary processes. Human disturbances of these regimes and processes by dam and weir construction, river regulation, diversions or groundwater pumping typically remove or dampen the dynamic hydro-geomorphic and ecological processes that define dryland rivers (Walker *et al.*, 1997; Kingsford, 2006; Wishart, 2006). Dramatic ecological impacts and fish losses have been observed in many regulated arid and semi-arid floodplain river systems, for example, the Aral Sea in Uzbekistan and Kazakhstan, the Mesopotamian Marshes, Lake Mono in California and the Macquarie Marshes in the Murray-Darling Basin, Australia (Kingsford *et al.*, 2006b).

Walker *et al.* (1995) proposed that sustainable water management in dryland rivers like Cooper Creek should adopt the “simple formula” of matching the pattern of water demand to that of supply. In this catchment, water use is confined to homesteads, townships, the pastoral industry, localised horticulture and mining operations. Protection of the hydrological regime from excessive extraction during dry times, limiting extraction to certain conservative threshold flows during times of channel flows, and maintaining unrestrained flooding during wet seasons (except where human lives, habitations and local supporting enterprises are threatened), would

simultaneously achieve conservation of biodiversity, ecological integrity, evolutionary processes and the economic benefits based upon the prevailing pastoral industry (Walker *et al.*, 1995; Welcomme *et al.*, 2006a,b).

The Queensland Government's proposal to extend wild rivers protection to rivers of the Lake Eyre Basin (DERM, 2010a) and to revise the Cooper Creek Water Resources Plan (DERM, 2010b) will protect the ecological integrity and natural values of the iconic Cooper Creek river system. The Queensland Government recognises that these arid-zone river systems are unique, have high natural values, and that preserving these values not only protects natural assets but is less costly and more effective than subsequent rehabilitation. These natural values include (but are not limited to) hydrologic processes and connectivity between the river system, aquifers, off-stream water bodies and adjacent floodplains, geomorphic processes, riparian functions, wildlife corridor functions, and water quality.

The Water Resource Plan (WRP) manages any interference with water resources, the take of water from watercourses and from overland flows (return flows from floodplains). The WRP also has the potential to allow for environmentally relevant activities to occur in ways that will prevent contaminated runoff from any source entering the watercourse, whereas water quality impacts of activities in the catchment (such as mining operations or urban developments) that could impair aquatic biogeochemistry are managed under the Environmental Protection Act.

Whilst the future of western Queensland's channel country river systems within the Lake Eyre Basin, including Cooper Creek and the Georgina and Diamantina rivers, seems likely to be secure under the Queensland Government's Wild River legislation and the revised Cooper Water Resources Plan, it is clear that water regimes can still be affected by various activities in their catchments, and by future climate change. Vigilance is required to ensure that the hydrological, sedimentary and biogeochemical processes supporting the ecosystems of these catchments are maintained (Davies *et al.*, 1994; Kingsford, 2006; Wishart, 2006). Preservation or restoration of natural flow intermittency, sequential flood pulses, complex habitat mosaics, connectivity, and identification of the environmental flow requirements for highly valued species and processes are key scientific principles for arid-zone rivers (Larned *et al.*, 2010; Sheldon *et al.*, 2010).

Conservation of Cooper Creek as a model arid-zone floodplain river system, and further study of its resistance and resilience to extreme forms of natural hydrologic disturbance, should offer insights to inform the management of this and other dryland rivers, as well as more mesic river systems, as climates become hotter and drier and river flows decline across much of the globe. Arid-zone rivers may yield vital lessons for biodiversity protection and water management in an increasingly dry future.

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TABLES

Table 1. Fish species found in waterholes of Cooper Creek in April and September 2001 (based on all sampling methods), showing % reduction in catch per unit effort (cpue) for fyke net data expressed as mean \pm standard error of change per waterhole, and total change in catch per unit effort across all waterholes. Note the absence of % change data for *Hypseleotris* spp. because this small species was caught more often in September 2001, when low waterhole volumes tended to increase its catch rate.

Family/species	Common name	No. of waterholes where present April 2001	No. of waterholes where present September 2001	Mean \pm s.e. of % change in fish cpue per waterhole April to September 2001	Total change (%) in cpue April to September 2001
Indigenous species					
Chandidae					
<i>Ambassis</i> sp.	Northwest ambassis	14	10	44 \pm 12	97
Clupeidae					
<i>Nematalosa erebi</i> (Günther, 1868)	bony bream	15	13	21 \pm 9	82
Eleotridae					
<i>Hypseleotris</i> spp.	carp gudgeons	2	9		
Melanotaeniidae					
<i>Melanotaenia splendida tatei</i> (Zietz, 1896)	desert rainbowfish	12	3	70 \pm 23	99
Percichthyidae					
<i>Macquaria</i> sp. B (after Musyl & Keenan, 1992)	Lake Eyre golden perch	14	8	45 \pm 13	69
Plotosidae					
<i>Neosiluroides cooperensis</i> (Allen & Feinberg, 1998)	Cooper Creek tandan	4	2	33 \pm 42	50

<i>Neosilurus hyrtlii</i> (Steindachner, 1867)	Hyrtl's tandan	15	13	36 ± 11	95
<i>Porochilus argenteus</i> (Zeitl, 1896)	silver tandan	15	14	19 ± 9	93
Retropinnidae					
<i>Retropinna semoni</i> (Weber, 1895)	Australian smelt	2	2	50 ± 50	50
Terapontidae					
<i>Bidyanus welchi</i> (McCulloch & Waite, 1917)	Welch's grunter	4	0	100 ± 0	100
<i>Leiopotherapon unicolor</i> (Günther, 1859)	spangled perch	15	13	36 ± 12	96
<i>Scortum barcoo</i> (McCulloch & Waite, 1917)	Barcoo grunter	15	4	86 ± 10	99
Alien species					
Cyprinidae					
<i>Carassius auratus</i> Linnaeus, 1758	goldfish	10	6	39 ± 20	68
Poeciliidae					
<i>Gambusia holbrooki</i> (Girard, 1859)	mosquitofish	3	1	100 ± 0	100

List of Figures

Figure 1: Lake Eyre Basin, Australia, showing Cooper Creek and other major rivers and locations mentioned in the text.

Figure 2: Daily discharge of the Thompson and Barcoo rivers (combined) between December 1999 and December 2004, and daily maximum and minimum air temperatures at Windorah between January 2001 and December 2004. Discharge data provided by the Bureau of Meteorology for stream gauges at Stonehenge (Thomson River) and Retreat (Barcoo River).

Figure 3: Aquatic habitat conditions associated with the natural hydrological cycle in Cooper Creek, Lake Eyre Basin, showing A: drying waterhole (bust) phase, B: rising channel flow, C: rising flood and breakout onto floodplain, D: very large flood in February 2000 (boom phase), E: falling flood and flood recession, F: falling channel flow, bare banks and exposure of habitat features such as fallen timber. Patterns of increasing and decreasing connectivity are also represented, with B – F representing the case when a rising channel flow becomes a falling channel flow rather than breaking out onto the floodplain, and C – E represents the case when a small flood recedes off an inundated floodplain. In both cases connectivity pathways are reduced compared to those achieved by a very large flood. All photographs by A H Arthington except photograph D taken by S E Bunn, Griffith University.





