Subtle ‘boom and bust’ response of *Macquaria ambigua* to flooding in an Australian dryland river

D. Sternberg^{*†}, S. R. Balcombe^{*}, J. C. Marshall[‡], J. S. Lobegeiger[‡], A. H. Arthington^{*}.

^{*} Australian Rivers Institute and eWater Cooperative Research Centre, Griffith University, Nathan, Queensland, 4111, Australia.

[‡] Department of Environment and Resource Management and eWater Cooperative Research Centre, 120 Meiers Road, Indooroopilly, Queensland, 4068, Australia.

[†] Corresponding Author. Email: d.sternberg@griffith.edu.au; Telephone: +61 07 37357361; Facsimile: +61 07 37357615

Abstract:

The ecology of dryland rivers is driven by their highly variable hydrology, particularly flooding regimes, whereby intermittent floods typically generate ‘booms’ of primary and secondary productivity, including massive fish production. We tested these concepts in the Moonie River, Australia, using the percichthyid, *Macquaria ambigua*, a dryland river species known to display pronounced ‘boom and bust’ abundance patterns in response to floodplain inundation followed by extended periods of low to no channel flow. We expected that body condition (as measured by whole body lipid content) and biomass of *M. ambigua* would be related to prey biomass, and that these factors would all ‘spike’ following widespread flooding. Instead we found more subtle responses. There were ‘booms’ in biomass of *Macrobrachium* and zooplankton, two important food items, whereas *M. ambigua* maintained relatively low but sustained lipid and biomass levels following flooding. It appears that instead of a ‘boom’ in fish biomass, abundant invertebrate food resources and sustained lipid levels contributed to high survivorship of this species during the ‘bust’ period over cool dry months.

Key words: Murray-Darling Basin, ‘boom and bust’, fish condition, lipid content, hydrology.

INTRODUCTION:

Dryland rivers present a unique environment in which to explore the influence of flow variability on ecological process. These river systems are typically characterised by low gradient landscapes, and a climatic regime dominated by isolated, but often intense, rainstorm events which produce less than 500 mm of mean annual rainfall (Kingsford and Thompson 2006). As a result, many dryland rivers show extreme variation in the timing, frequency, magnitude and duration of flow events (*sensu* Poff *et al.* 1997, Puckridge *et al.* 1998) and exist for much of the year as a series of unconnected waterholes (Arthington *et al.* 2005; Balcombe *et al.* 2005; Biggs *et al.* 2005; Bunn *et al.* 2003). Typically, these systems are dominated by long periods without flow, irregularly punctured by channel flow and flood events (Bunn *et al.* 2006a). Although the more frequent but smaller channel flows may be functionally important for recruitment processes (Humphries *et al.* 2002), it is thought that the much larger flood events, which inundate lateral floodplain areas and generate high rates of aquatic production, ultimately sustain biotic assemblages in these highly variable systems (Balcombe and Arthington 2009, Kingsford *et al.* 1999; Puckridge *et al.* 2000). This temporary 'boom' of aquatic production is inevitably followed by a period of 'bust' conditions owing to long periods without flow when production in isolated waterholes is limited to a thin, marginal band of algae (Bunn *et al.* 2003). This cycling of 'boom and bust' conditions has been well documented in recent times and is a widely accepted model of hydro-ecological processes for large dryland rivers (Balcombe *et al.* 2007; Balcombe and Arthington 2009; Bunn *et al.* 2006a; Kingsford *et al.* 1999; Sheldon *et al.* 2010). However, some challenges still remain surrounding our understanding of the ecological responses of obligate aquatic organisms to extreme fluctuations in wet and dry conditions.

Populations of dryland river fish are able to persist through the cycles of 'boom and bust' and the associated fluctuating availability of food resources due to their generalist ecological traits. Such traits include: high tolerance of harsh environmental conditions (Gehrke and Fielder 1988; Kingsford *et al.* 2006; Wager and Unmack 2000), opportunistic spawning strategies (Balcombe *et al.* 2007; King *et al.* 2003) and adaptive feeding strategies (Balcombe *et al.* 2005; Sternberg *et al.* 2008). Species with these attributes can often reach high levels of abundance and

biomass in large dryland rivers, where the productivity cycles of ‘boom and bust’ are mirrored by wide variations in fish abundance from ‘boom’ (high fish abundance) to ‘bust’ (low fish abundance). In dryland rivers, the combination of flooding and high seasonal temperatures associated with widespread floodplain inundation, have been shown to influence fish abundance (Balcombe and Arthington 2009), with most members of the fish assemblage in these rivers adapted to take advantage of the resource and growth opportunities associated with extensive floodplain inundation (the 'boom') (Balcombe *et al.* 2007). In comparison, when these same rivers dry to disconnected waterholes, with associated decreases in waterhole volume, habitat alterations and declining water quality, a 93% decrease in total fish abundance has been observed (Arthington *et al.* 2005). Given that inundated floodplain habitats represent areas of high resource potential, whereas drying river channels and waterholes do not generally provide resource rich habitats, it follows that the body condition of individual fish can be expected to vary with pronounced cycles of ‘boom and bust’.

Fish body condition relates to the amount of energy stored in the body fat of an individual under the assumption that more body fat equates to better condition (Hoque *et al.* 1998). Excess energy is typically stored as fat during periods of high prey availability and favourable biophysical conditions (‘boom’ periods) (Busacker *et al.* 1990; De Silva *et al.* 1998; Lloret *et al.* 2005). For example, Gomes and Agostinho (1997) reported that the mean condition factor (a measure of body condition) of curimatá, *Prochilodus scrofa* (Steindachner, 1881) from the upper Paraná River, Brazil, was significantly greater during a three month flood period than during baseflow conditions. In contrast, during periods of prolonged resource depletion and/or unfavorable physical and chemical conditions (‘bust’), fish recycle this stored energy, and may ultimately become lipid depleted (Paukert and Rogers 2004; Post and Parkinson 2001;). In a study of captive fish, Collins and Anderson (1995) showed that the body condition of yellowbelly, *Macquaria ambigua* (Richardson, 1845) significantly decreased after thirty days of food deprivation. Analysis of fish body condition may therefore provide a useful tool for understanding the importance of flooding and drying to fish production in dryland river settings.

Macquaria ambigua is a moderate to large percichthyid capable of growing to 760 mm and 23 kg; however more commonly grows to 400 – 500 mm LS and less than 5 kg (Llewellyn and MacDonald 1980; Pusey *et al.* 2004). This species is a

generalist carnivore feeding mainly on small fish and micro and macro crustaceans in dryland rivers (Pusey *et al.* 2004). Diet composition is spatially and temporally variable. Sternberg *et al.* (2008) found that predation on higher energy prey items (such as macrocrustaceans and fish) varied with season and resource availability in response to ‘boom and bust’ cycles. Given that this species typically sits at the highest trophic position in dryland rivers (Pusey *et al.* 2004), it is likely to be strongly dependant on the natural cycles of ‘boom and bust’ associated with flooding and drying.

In this paper we aim to expand our knowledge of ‘boom and bust’ ecology by investigating the physiological response of biota to flooding. Based on previous studies of dryland rivers, we hypothesised that fish biomass and body condition (measured using biochemical techniques) would show a delayed but significant increase following a major flow event, and eventually return to pre-flood levels by the end of the following dry season (*i.e.* through a full cycle of ‘boom and bust’). We also hypothesised that over the same hydrological cycle prey biomass/secondary production will display a similar trend, but with a more rapid response time. We tested these hypotheses in the Moonie River, Australia, using *M. ambigua*, a dryland river species known to display pronounced ‘boom and bust’ abundance patterns in response to floodplain inundation and extended periods of low to no channel flow.

METHODS

STUDY AREA AND SAMPLING DESIGN

Research was undertaken in the Moonie River, a dryland river situated east of St George in southern Queensland (Fig. 1). The river drains an approximate area of 14870 km² and runs for 525 km (Department of Environment and Resource Management, 1999) over the New South Wales – Queensland border, where it joins the Barwon River, eventually flowing into the Darling River system. The Moonie River catchment has a semi-arid climate, with average rainfall between 450 - 600 mm year⁻¹ and mean annual pan evaporation between 1800 - 2200 mm year⁻¹. As with most dryland rivers, there is considerable annual variation in temperature and inter-annual variation in rainfall which combine to generate irregular and infrequent flow events. The maximum recorded no-flow spell for the system was 13 months at Nindigully gauge in 1979 and 1980 (Biggs *et al.* 2005), whilst the 100 year modelled

maximum no flow spell is approximately two years (Department of Environment and Resource Management, unpublished data). Thus, for most of the year the river exists as a series of unconnected waterholes which act as refugia for obligate aquatic biota.

We conducted this research in ten waterholes sampled on four occasions between October 2007 and September 2008 (Fig. 1). Sampling occasions correlate with 1) spring pre-flood (October 2007); 2) late summer post-flood (March 2008); 3) autumn post-flood (April 2008); and 4) spring post-flood (September 2008) (Fig. 2). Owing to these large hydrological and seasonal differences across our four sampling occasions, we considered each occasion to be both biologically and hydrologically distinct from all others. Prior to commencement of fish sampling in October 2007, the last flow event to connect all waterholes within the main channel occurred in March 2007 ($\sim 5000 \text{ ML day}^{-1}$ at Nindigully Gauge [417201B]; Department of Environment and Resource Management, unpublished data; Fig. 2), and in the dry season months leading up to the first sampling occasion (spring pre-flood) there were no significant flow events through the system. Waterholes appeared typically still and turbid, and had contracted to a point of isolation from neighbouring waterholes. In the wet season months following the first sampling occasion there was a small waterhole connecting flow in December 2007 ($\sim 4000 \text{ ML day}^{-1}$), followed by a large ($\sim 18000 \text{ ML day}^{-1}$) flow event in February which inundated floodplain areas throughout the length of the river. This flood was the largest for 10 years and the sixth largest flow through the system since recording began in 1969 (Department of Environment and Resource Management, unpublished data). Environmental conditions following this event and during sampling (late summer post-flood) were noticeably different owing to an increase in waterhole depth and longitudinal connectivity among waterholes. Sampling during the autumn post-flood period and spring post-flood periods saw waterholes continue on a drying trajectory, becoming isolated and returning to pre-flood conditions. There were no other flows through the system during the 11 month study period (Fig. 2).

The average maximum length and width of waterholes was 2.06 km ($\pm \text{S.E. } 0.63$) and 38.1 m ($\pm \text{S.E. } 3.6$) respectively, while the average depth at the point waterholes became disconnected was 1.61 m ($\pm \text{S.E. } 0.18$) (Department of Environment and Resource Management, unpublished data). A number of waterholes were artificially enlarged by small weirs or road crossings, with several large weirs disrupting hydrological and biological connectivity throughout the system. Average

floodplain width surrounding study sites ranges from 3.01 km ($\pm$ 1.03 S.E.) in the upper catchment to 11.81 km ($\pm$ 0.42 S.E.) in the lower catchment (Biggs *et al.* 2005).

DATA COLLECTION

Fyke net capture methods were used to estimate *M. ambigua* biomass on all sampling occasions (*see* Arthington *et al.* 2005; Puckridge *et al.* 2000). Three fyke nets constructed of 25 mm mesh were set parallel to the bank in each waterhole no less than 50 m apart with two 8 m wings spanning 10 m, where possible. These fykes were set after mid-day and collected the following morning, giving an average set time of approximately 19 h. All captured fish were weighed on-site using Sartorius digital scales. A maximum of ten randomly selected *M. ambigua* individuals between 80 and 180 mm SL were retained in each waterhole and euthanized in an ice slurry (Blessing *et al.* 2010) and frozen on-site for laboratory analysis (whole body lipid content) in accordance with animal ethics procedures.

The biomass of the freshwater prawn, *Macrobrachium australiense* [henceforth *Macrobrachium*] (Blogs, 1627), an important prey item for *M. ambigua* (Pusey *et al.* 2004), was assessed via five seine net samples, using a 5 m net dragged through a portion of the littoral margins in all ten waterholes; the total area seined was measured for standardisation of catch per unit effort. Due to time constraints in October 2007 (spring pre-flood); the biomass of *Macrobrachium* was estimated via one 5 and one 15 m beach seine sweep through littoral habitat. Wet *Macrobrachium* biomass for was calculated by weighing all individuals in each seine haul on-site using Sartorius digital scales.

Zooplankton biomass was not estimated during the October 2007 (spring pre-flood) sampling trip. However, on subsequent sampling occasions a zooplankton net constructed of 75 μ m mesh was towed a total of 10 m on three occasions in the pelagic zone of all ten waterholes. All zooplankton were then bottled and frozen on-site, subsequently defrosted in the laboratory and concentrated onto a pre-weighed Whatman GF/C 47 mm filter paper using a vacuum pump. All samples were placed in aluminium foil trays and heated in an oven at 105 °C for 16 h and then placed into a desiccator for 2 h and re-weighed to calculate the dry weight of zooplankton as described in APHA (1992).

LABRATORY PROCEDURES

We chose to evaluate the proximate body condition of *M. ambigua* using biochemical techniques. Frozen fish samples were defrosted and patted dry to remove surface water and the wet weight (W_{weight}) determined to the nearest 0.01 g. All fish gonads were removed and weighed (G_{weight}), however gonads were not included in the estimation of whole body lipid content, as variations in gonad stage and fish gender may distort comparisons between individuals. Stomach contents were also removed from the intestines of *M. ambigua* and weighed (S_{weight}). Gut contents were not included in the determination of fish condition as they have the potential to distort results (Lochman *et al.* 1996). Eviscerated fish were placed into a vacuum freeze drying unit (Virtis SLC) for a minimum of 10 days to ensure desiccation. Fish were then re-weighed (D_{weight}) to the nearest 0.01 g. These evisceration and drying techniques were employed to estimate the percent water content (WC) of individuals, which was calculated as: $100 - (D_{\text{weight}}) * ((W_{\text{weight}}) - (G_{\text{weight}}) - (S_{\text{weight}}))^{-1} * 100$. Dried fish were then placed into a blender and the homogenised product used to determine the whole body lipid content (a biochemical measure of proximate body condition measured as a percentage of the wet fish) of fish.

LIPID CONTENT

A known amount of dried fish sample (DF_{weight}) was placed into a Whatman 90 mm qualitative filter paper vessel and placed into an accelerated solvent extractor (ASE) (DIONEX ASE 200) cell containing a single Glass-fibre cellulose filter and approximately 50g of 2 mm glass beads. The ASE was operated with default settings, however we performed 2 static cycles of 5 min each with HPLC chloroform (CHCl_3) acting as the solvent. The resulting product was poured into an aluminium foil tray of known weight, placed into a fume cupboard for 2 days to evaporate the remaining chloroform, and reweighed to achieve the extracted lipid weight (L_{weight}). The percentage of lipid in the dried fish sample (LDF%) was calculated by: $(L_{\text{weight}})/(DF_{\text{weight}}) * 100$. Finally, this value was converted to a percentage of lipid in the wet fish (proximate body condition) by the calculation: $\text{LDF\%} * (1 - (\text{WC} * 100^{-1}))$.

DATA ANALYSIS

Macquaria ambigua wet biomass (kg) was calculated by standardising the total catch in each fyke net to 10 m wing width and 19 h set time, then pooling the

fyke catches at each site (as per Arthington *et al.* [2005]). These counts were $\log_{10}(x + 1)$ transformed to meet statistical assumptions. *Macrobrachium* wet biomass (kg) and Zooplankton biomass (kg) were calculated by standardising each replicate sample to 1 m² and taking the median value of the 5 and 3 samples (respectively) from each site. These median values were then $\log_{10}(x + 1)$ transformed where necessary to satisfy statistical assumptions. The whole body lipid content of *M. ambigua* (%) was converted to a median value at each site and $\log_{10}(x + 1)$ transformed to satisfy statistical assumptions.

One-way analysis of variance (ANOVA) was used to test for temporal differences in *M. ambigua* wet biomass (kg), *M. ambigua* whole body lipid content (%), *Macrobrachium* wet biomass (kg) and zooplankton biomass (kg) between sampling trips. ANOVAs were undertaken on the assumption of independence between each sampling occasion due to large differences in both antecedent hydrology (ranging from flooding to extreme drying) and seasonal water temperature. Post-hoc comparisons were performed with Tukey's HSD tests.

We used Least Squares Regressions to test for relationships between the dependant variables (*M. ambigua* whole body lipid (%) and *M. ambigua* wet biomass (kg)) and independent variables (*Macrobrachium* wet biomass (kg) and zooplankton biomass (kg)) for each sampling occasion using waterholes as replicates. All statistical analyses were performed with SYSTAT 11.00.01 for Windows.

RESULTS

In total, 448 *M. ambigua* were captured from 10 sites over four sampling trips, with 94 individuals retained for body condition analysis. Median lipid levels generally trended upward over the 11 month sampling period (Fig. 3a). ANOVA revealed significant differences in body lipids between sampling trips ($p < 0.05$) with Tukey's HSD *post-hoc* comparisons showing significant differences between the spring post-flood sample and the spring pre-flood ($p < 0.05$) and late summer post-flood ($p < 0.05$) (Table I). No such differences in the biomass of *M. ambigua* were observed between sampling trips as shown by the ANOVA results (Table I).

Macrobrachium biomass showed a significant temporal response to flow history during the study period. Following the February 2008 flow event, a +2000% increase in the mean *Macrobrachium* biomass was observed between spring pre-flood

and late summer post-flood sampling occasions. Thereafter, *Macrobrachium* biomass declined to around pre-flood levels by the final sampling occasion in September 2008 (spring post-flood) (Fig 3c). ANOVA results confirmed significant differences in *Macrobrachium* biomass between sampling trips ($p < 0.001$) with Tukey's HSD post-hoc tests indicating significant differences between all sampling trips (Table 1) except between late summer post-flood (March 2008) and autumn post-flood (April 2008) (Table I).

Zooplankton biomass was not estimated on the first sampling occasion, however following the large flood event in February 2008, a steady increase in zooplankton biomass was observed over the remaining sampling trips (Fig. 3d). This trend produced significant differences in zooplankton biomass between sampling trips (ANOVA, $p < 0.001$) with post-hoc tests showing a significant difference between the final sampling occasion (spring post-flood) and late summer post-flood ($p < 0.001$) and autumn post-flood ($p < 0.001$) samples (Table I).

Linear regression showed no relationships between percent lipid content (dependent variable) and *Macrobrachium* or zooplankton biomass (independent variables) for each of the four sampling trips (Fig. 4). This same analysis failed to confirm any relationships between *M. ambigua* biomass and the biomass of *Macrobrachium* and zooplankton on each sampling occasion, with one exception. A significant relationship ($r^2 = 0.51$; $p < 0.05$) between *M. ambigua* biomass and zooplankton biomass was detected in the spring post-flood sample (Fig. 5).

DISCUSSION

The pattern of hydrology observed prior to and during the course of this study provided an opportunity to test the significance of 'boom and bust' cycles to the production patterns of fish in a dryland river ecosystem. In February 2008, the Moonie River experienced the sixth largest flow through the system since recording began in 1969. This event peaked at $\sim 18000 \text{ ML day}^{-1}$ and inundated floodplain areas over the length of the river. It was expected that following this flood event high rates of primary and secondary production on inundated floodplains would lead to marked increases in food resources, fish biomass and body condition (Balcombe *et al.* 2007; Bunn *et al.* 2006). There were 'booms' in biomass of *Macrobrachium* and

zooplankton, two important food items, however *M. ambigua* showed a more subtle response to flooding.

The body condition (i.e. lipid content) of *M. ambigua* over the study period did not increase significantly in relation to the large flood in February 2008. This result was surprising given that Collins and Anderson (1995) found this species to be capable of restoring depleted lipid levels to their original state after 30 to 60 days of re-feeding. There are a number of possible explanations for this lack of response of *M. ambigua* to floodplain inundation in the Moonie River. Firstly, the system may not have realised full ‘bust’ conditions prior to the commencement of sampling in September 2007. This would account for the lack of evidence of marked recuperation among individuals during subsequent sampling trips. It suggests that *M. ambigua* may be able to maintain baseline lipid levels after a 7 month period without sizeable channel flow and 48 months without major floodplain inundation (Fig. 2).

Secondly, the percent lipid values observed in *M. ambigua* during this study ($2.1 \% \pm 1.07 \text{ SD}$), may be relatively low in comparison to other species. Barziza *et al.* 2000 reported a mean proximate lipid content of $6.8 \% (\pm 2.9 \text{ SD})$ for 85 Largemouth bass, *Micropterus salmoides* (Lacepède, 1802) captured over a 13 month period in Texas, USA. Furthermore, for saltwater reef fish, lipid levels comprising less than ten percent of the dry muscle mass are considered low (Lloret *et al.* 2005). Adding to this, Collins and Anderson (2005) concluded that *M. ambigua* was, in relative terms, a “non-fatty fish”. These observed low lipid levels may have masked any increases in body condition during the ‘boom’ period and may be an evolved trait in this species given the variability of food resources typical in these dryland systems (Balcombe *et al.* 2005; Sternberg *et al.* 2008).

Thirdly, the Moonie River system may not have responded to the large flow event of February 2008 with the same magnitude of ‘boom’ seen in other dryland rivers with more extensive floodplains, such as Cooper Creek in the Lake Eyre Basin. The Cooper Creek system can experience extremely high magnitude flow events which inundate expansive floodplain areas (35% of the catchment) and stimulate bursts of algal, invertebrate and fish production (Arthington *et al.* 2005; Balcombe *et al.* 2007). In contrast, inundation of the narrow, relatively homogeneous floodplains of the Moonie River may not generate comparable ‘booms’ of primary and secondary production which ultimately sustain higher trophic organisms in systems such as Cooper Creek and the Warrego River (Arthington *et al.* 2005; Balcombe *et al.* 2006;

Balcombe and Arthington 2009; Bunn *et al.* 2006b) and in many tropical floodplain rivers (Rodriguez and Lewis 1997; Welcomme 2006).

The biomass of *M. ambigua* increased slightly following summer flooding and thereafter remained steady through autumn and winter months (dry season). This trend of sustained biomass is unusual for this species. In a larger study of fish assemblages in the Moonie catchment, *M. ambigua* biomass is generally more variable through time than recorded here, with biomass declining after autumn, through winter and increasing again after spring/summer flows. Fluctuations in *Macquaria* biomass have also been noted in the Cooper and Warrego catchments between dry and wet seasons (Arthington *et al.* 2005; Balcombe *et al.* 2006; Balcombe and Arthington 2009). We postulate that in the Moonie River, relatively brief inundation of the smaller floodplain areas reduces the capacity of the system to produce large scale ‘booms’ in fish production, instead, responding with more subtle increases in individual survivorship of *M. ambigua*, possibly supported by sustained lipid levels following summer flooding.

Notably, there was an apparent ‘boom’ in *Macrobrachium* biomass following flooding in the Moonie River. Given, that our first post flood sample occurred 4 weeks after flood recession, it seems likely that this increase in biomass was due to ‘boom’ processes driven by overland flooding. *M. ambigua* feeds opportunistically on *Macrobrachium* and zooplankton in the Moonie River (Sternberg *et al.* 2008) and elsewhere (Balcombe *et al.* 2005; Pusey *et al.* 2004) so it is interesting to note that high prey availability during the study period was not reflected in a corresponding marked increase in the proximate body condition or biomass of *M. ambigua*. The lack of strong relationships is unexpected and suggests that whole body lipid content may be a rather crude surrogate for the physiological response of this species to increased food availability. Collins and Anderson (1995) have shown that *M. ambigua* initially mobilise energy from hepatic tissue after 30 days of starvation (a worst case scenario). Analysing this active hepatic tissue (exclusively) may provide a more sensitive indication of fish body condition in situations where relatively short time scales and/or less severe ‘boom and bust’ cycles are present.

This study has shown that widespread flooding in the Moonie River had limited short-term influence on the lipid content (body condition) of *M. ambigua*. Similarly, the production levels of this species, measured in biomass, did not respond to flooding in the same pronounced manner as observed in other dryland rivers. This

occurred despite a significant increase in prey availability over the duration of sampling. Ultimately, the Moonie River system may be less dependent on the productivity cycles of the 'boom' associated with flooding than expected, and so presents new challenges in managing a dryland water resource which appears to function under a different set of opportunities and constraints. Nevertheless, this study suggests that flooding and a 'boom' in secondary production may contribute to high survivorship of *M. ambigua* during dryer months when this species usually exhibits high mortalities in drying habitats. The capacity to maintain relatively low but sustained lipid levels may contribute to survivorship of this species during dry times. In other words, the 'boom' response is not as spectacular as in other Australian dryland rivers (see Arthington *et al.* 2005; Balcombe and Arthington 2009) but neither is the 'bust'.

ACKNOWLEDGMENTS

We thank the Australian Rivers Institute, Griffith University, and the Department of Environment and Resource Management for supporting and supervising the Honours research programme of which this paper forms a part. The authors would like to thank Rene Diocares, Joel Huey, Leigh Bennett and Raymonde de Lathouder for their help with laboratory and field work. We also thank the landholders of the Moonie River Catchment for providing access to sites. Two anonymous reviewers are thanked for their helpful comments on the manuscript. This research was conducted under the Queensland Fisheries Permit PRM00157K and Griffith University Animal Experimentation Ethics Committee permit AES/14/05/AEC.

REFERENCES

- APHA (1992) Standardised methods for the examination of water and wastewater. American Public Health Association, Washington
- Arthington AH, Balcombe SR, Wilson GA, Thoms MC, Marshall J (2005) Spatial and temporal variation in fish assemblage structure in isolated waterholes during the 2001 dry season of an arid-zone river, Cooper Creek, Australia. *Mar Freshwater Res* 56:25-35

- Balcombe SR, Bunn SE, Davies PM, McKenzie-Smith FJ (2005) Variability of fish diets between dry and flood periods in an arid zone floodplain river. *J Fish Biol* 67:1552-1567
- Balcombe SR, Arthington AH, Foster ND, Thoms MC, Wilson GG, Bunn SE (2006) Fish assemblages of an Australian dryland river: abundance, assemblage structure & recruitment patterns in the Warrego River, Murray-Darling Basin. *Mar Freshwater Res* 57:619-633
- Balcombe SR, Bunn SE, Arthington AH, Fawcett JH, McKenzie-Smith FJ, Wright A (2007) Fish larvae, growth and biomass relationships in an Australian arid zone river: links between floodplains and waterholes. *Freshwater Biol* 52:2385-2398
- Balcombe SR, Arthington AH (2009) Temporal changes in fish abundance in response to hydrological variability in a dryland floodplain river. *Mar Freshwater Res* 60:146-159
- Barziza DE, Gatlin III DM (2000) An evaluation of total body electrical conductivity to estimate body composition of largemouth bass, *Micropterus salmoides*. *Aquat. Living Resour.* 13:439-447
- Biggs AJW, Power RE, Silburn DM, Owens JS, Burton, DWG, Hebbard CL (2005) Salinity audit – Border Rivers and Moonie catchments, 395 Queensland Murray-Darling Basin QNRM05462. Department of Natural Resources and Mines, Queensland
- Blessing JJ, Marshal JC, Balcombe SR (2010) Humane killing of fish for scientific research: a comparison of two methods. *J Fish Biol* 76:2571-2577
- Bunn SE, Davis PM, Winning M (2003) Sources of organic carbon supporting the food web of an arid zone floodplain river. *Freshwater Biol* 48:1-17
- Bunn SE, Thoms MC, Hamilton SK, Capon SJ (2006a) Flow variability and dryland rivers: ‘boom’, ‘bust’ and the bits in between. *River Res Appl* 22:179-186
- Bunn SE, Balcombe SR, Davies PM, Fellows CS, McKenzie-Smith FJ (2006b) Aquatic productivity and food webs of desert river ecosystems. In: Kingsford RT (ed) *Ecology of Desert Rivers*. Cambridge University Press, Cambridge, pp 76-99
- Busacker GP, Adelman IR, Goolish EM (1990) Growth. In: Schreck CB, Moyle PB (eds) *Methods for Fish Biology*. American Fisheries Society, Bethesda, pp 363-387

- Collins AL, Anderson TA (1995) The regulation of endogenous energy stores during starvation and refeeding in the somatic tissues of the golden perch. *J Fish Biol* 47:1004-1015
- Department of Environment and Resource Management (1999) Overview of Water Resources and Related Issues: The Moonie River Catchment. Department of Natural Resources, Brisbane, Australia
- De Silva SS, Gunasekera RM, Austin CM, Allinson G (1998) Habitat related variations in fatty acids of catadromous *Galaxias maculatus*. *Aquat Living Resour* 11:379-385
- Gehrke PC, Fielder DR (1988) Effects of temperature and dissolved oxygen on heart rate, ventilation rate and oxygen consumption of spangled perch, *Leiopotherapon unicolor* (Gunther 1859) (Percoidei, Teraponidae). *J Comp Physiol* 157:771-782
- Gomes LC, Agostinho AA (1997) Influence of the flooding regime on the nutritional state and juvenile recruitment of the Curimba, *Prochilodus scrofa*, Steindachner, in upper Paraná River, Brazil. *Fisheries Manag Ecol* 4:263-274
- Hoque MT, Yusoff FM, Law AT, Syed MA (1998) Effect of hydrogen sulphide on liver somatic index and Fulton's condition factor in *Mystus nemurus*. *J Fish Biol* 52:23-30
- Humphries P, Serafini L, King AJ (2002) River regulation and fish larvae: variations through space and time. *Freshwater Biol* 56:129-151
- King AJ, Humphries P, Lake PS (2003) Fish recruitment on floodplains: the roles of patterns of flooding and life history characteristics. *Can J Fish Aquat Sci* 60:773-786
- Kingsford RT, Curtin AL, Porter JL (1999) Water flows on Cooper Creek determine 'boom' and 'bust' periods for waterbirds. *Biol Conserv* 88:231-248
- Kingsford RT, Georges A, Unmack J (2006) Vertebrates of desert rivers: meeting the challenges of temporal and spatial unpredictability. In: Kingsford RT (ed) *Ecology of desert rivers*. Cambridge University Press, Cambridge, pp 3-16
- Kingsford RT, Thompson JR (2006) Desert or dryland rivers of the world: an introduction. In: Kingsford RT (ed) *Ecology of desert rivers*. Cambridge University Press, Cambridge, pp 3-16

- Llewellyn LC, MacDonald MC (1980) Family Percichthyidae – Australian freshwater basses and cods. In: McDowell R (ed) Freshwater fishes of South- eastern Australia. AH and AW Reed Pty Ltd, Sydney, pp 142-149
- Lloret J, Galzin R, Gil de Solas L, Souplet A, Demestre M (2005) Habitat related differences in lipid reserves of some exploited fish species in the north western Mediterranean continental shelf. *J Fish Biol* 67: 51-65
- Lochman SE, Maillet GL, Taggart CT, Frank KT (1996) Effect of gut contents and lipid degradation on condition measures in larval fish. *Mar Ecol-Prog Ser* 134:27-35
- Paukert C, Rogers RS (2004) Factors affecting condition of flannelmouth suckers in the Colorado River, Grand Canyon, Arizona. *N Am J Fish Manage* 24:648-653
- Poff NL, Allen JD, Bain MB, Karr JR, Prestegard KL, Richter BD, Sparks RE, Stromberg JC (1997) The natural flow regime: a paradigm for river conservation and restoration. *Bioscience* 47:769-784
- Post JR, Parkinson EA (2001) Energy allocation strategy in young fish: allometry and survival. *Ecology* 82:1040-1051
- Puckridge JT, Sheldon F, Walker KF, Boulton AJ (1998) Flow variability and the ecology of large rivers. *Mar Freshwater Res* 49:55-72
- Puckridge JT, Walker KF, Costelloe JF (2000) Hydrological persistence and the ecology of dryland rivers. *Regul River* 16:385-402
- Pusey BJ, Kennard MJ, Arthington AH (2004) Freshwater fishes of North-Eastern Australia. CSIRO Publishing, Collingwood
- Rodriguez MA, Lewis WMJr (1997) Structure of fish assemblages along environmental gradients in floodplain lakes of the Orinoco River. *Ecol Monogr* 67:109-128
- Sheldon F, Bunn SE, Hughes JM, Arthington AH, Balcombe SR, Fellows CS (2010) Ecological roles and threats to aquatic refugia in arid landscapes: dryland river waterholes. *Mar Freshwater Res* 61: 885–895
- Sternberg D, Balcombe SR, Marshall JC, Lobegeiger J (2008) Food resource variability in an Australian dryland river: evidence from the diet of two generalist native fish species. *Mar Freshwater Res* 59:137-144
- Wager RNE, Unmack PJ (2000) Fishes of the Lake Eyre Catchment of central Australia. Brisbane: Queensland Department of Primary Industries

Table I: ANOVA results for comparisons between sampling trips 1) spring pre-flood (October 2007); 2) late summer post-flood (March 2008); 3) autumn post-flood (April 2008); and 4) spring post-flood (September 2008). Post Hoc differences between sampling trips tested with Tukey's HSD. ^a indicates missing data (see methods for explanation).

	F Ratio	p Value	HSD
<i>M. ambigua</i> lipid (%)	4.273	0.007	1,2 vs. 4
<i>M. ambigua</i> biomass (kg)	1.193	0.326	-
<i>Macrobrachium</i> biomass (kg)	30.798	<0.001	1 vs. 2-4; 2,3 vs. 4
Zooplankton biomass (kg) ^a	21.102	<0.001	2,3 vs. 4

Figure 1: Moonie River catchment, its position in eastern Australia and the location of 10 study sites. Waterhole sites are Killawarra (KIL), Kurmala (KUR), Verena (VER), Kooroon (KOO), Altonvale (ALT), Carbeens (CAR), Appletree (APP), Nindigully (NIN), Nullera (NUL) and Fenton (FEN).

Figure 2: Hydrograph of mean daily discharge in ML day⁻¹ at Nindigully Gauge between October 2003 and October 2008. Dashed arrows indicate sampling trips: 1) spring pre-flood (October 2007); 2) late summer post-flood (March 2008); 3) autumn post-flood (April 2008); and 4) spring post-flood (September 2008).

Figure 3: Mean ($\pm$ S.E.) of a) *M. ambigua* % lipid; b) *M. ambigua* wet biomass (kg); c) *Macrobrachium* wet biomass (kg); and d) Zooplankton biomass (kg) between sampling trips 1) October 2007; 2) March 2008; 3) April 2008; and 4) September 2008.

Figure 4: Least squares regression plots of *M. ambigua* whole body lipid (%) (dependent variable) versus a) *Macrobrachium* wet biomass (kg); and b) Zooplankton biomass (kg); in all waterholes. See text regarding missing data.

Figure 5: Least squares regression plots of *M. ambigua* wet biomass (kg) (dependent) versus a) *Macrobrachium* wet biomass (kg); and b) Zooplankton biomass (kg); in all waterholes. See methods regarding missing data. The regression line indicates significant relationship.