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Is fish biomass in dryland river waterholes fuelled by benthic primary production after major overland flooding?

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ABSTRACT

Dryland river foodwebs are thought to be largely driven by autochthonous production derived from littoral/benthic algae, particularly during extended periods of zero flow, with allochthonous production taking primacy after flooding as floodplain carbon is distributed into waterholes during flood recession. This study tested whether we could detect any influence of autochthonous production (littoral gross primary production) on fish biomass after flooding in Cooper Creek, a dryland river in the Lake Eyre Basin, Australia. It was found that the majority of fish biomass, mostly large carnivores, was not supported by benthic algal production. However, the biomass of juvenile bony bream *Nematalosa erebi*, the highly abundant benthivore of many Australian dryland rivers, was indeed driven by benthic algal productivity throughout the post-flood period, a finding also evident in post-flood waterholes in the nearby Warrego River (Murray-Darling Basin). With a consistently high abundance turnover of bony bream juveniles and their significant importance to dryland river food-webs this study demonstrates not only the need to protecting intact littoral zones for *N. erebi*, but by association, fish assemblages in general.

1. Introduction

A large proportion of Australian rivers flow through arid and semi-arid (dryland) regions (Thoms and Sheldon, 2000). Australia's Cooper Creek, a dryland river in the Lake Eyre Basin, has one of the world's most variable flow regimes for rivers of comparable size and discharge (Puckridge et al., 1998; Arthington and Balcombe, 2011). Largely termed 'boom and bust' ecosystems, dryland river systems are characterised by their extreme periods of productivity during periods of flooding, followed by severe decreases in species diversity and abundance in periods of drought (Puckridge et al., 2000; Arthington et al., 2010). More specifically, fish assemblages in Australian dryland river systems have been shown to exhibit high temporal variability in assemblage structure and biomass, often corresponding to the dramatic 'booms' of high productivity during/after floods and 'bust' conditions in periods of drought (Gehrke et al., 1995; Arthington et al., 2005; Balcombe et al., 2007; Sheldon et al., 2010).

Numerous studies suggest that fish production correlates with primary productivity (Melack, 1976; Downing et al., 1990; Lewis et al., 2001; Fellows et al., 2009). During periods of seasonal or longer-term drought when remnant waterbodies in dryland rivers have limited sources of external carbon input, a substantial portion of fish energy requirements is believed to be derived from autochthonous primary production (Thorp and Delong, 1994; Bunn et al., 2003, 2006; Turner and Edwards, 2012). Thus the relative importance of autochthonous primary production in supporting fish biomass can be expected to increase with time elapsed since flooding as benthic algae proliferate in drying waterbodies. This expectation was not supported by the work of Fellows et al. (2009) who found that the relationship between total fish abundance and gross primary production (GPP) was only significant for immediate post-flow sampling occasions in Cooper Creek waterholes, not for periods of extended zero-flows. This relationship was somewhat surprising and may potentially be an artefact of using total abundance as a surrogate for biomass (and ultimately secondary production). To Interestingly in the same river, Burford et al. (2008) found that floodplain energy subsidies were important for fuelling the food web in a single Cooper Creek waterhole immediately after flood recession, and floodplain subsidies (largely contained in fish tissues) continued to drive food web processes (via fish

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Abbreviations: CPUE, Catch per unit effort; DO, Dissolved oxygen; GPP, Gross primary production; *M. australiense*, *Macrobrachium australiense*; *N. erebi*, *Nematolosa erebi*; *N. hyrtlii*, *Neosilurus hyrtlii*; *P. argenteus*, *Porochilus argenteus*.

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mortality and subsequent consumption by resident fish) up to eight months post-flood. Furthermore, results from their waterhole Carbon budget revealed that the daily carbon requirements of resident fish were unlikely to be met by carbon inputs from autochthonous primary productivity within the 8 month post-flood period. These results do suggest that more generally, allochthonous, rather than autochthonous primary production has a greater influence on fish production in the short-term (months) after flooding in dryland river waterholes.

Nonetheless, in light of Fellows et al. (2009), we set out to further investigate the importance of gross autochthonous primary production (GPP) on fish production for both the higher level-trophic consumers (medium to large bodied carnivorous fish) and lower level trophic consumers such as benthivorous juvenile fish. Our primary hypothesis was that the majority of the fish biomass in post-flood waterholes would not be associated with GPP in the time period between initial disconnection after flood recession through to significant waterhole drying, some ten months later. A large component of fish biomass in disconnected waterholes after flooding can be attributed to higher trophic level fish species, such as Lake Eyre golden perch, *Macquaria* sp. B., and two species of plotosid catfish (Arthington et al., 2005; Balcombe and Arthington, 2009). As such, it was the dominance of these species that provided the majority of the evidence for short-medium term floodplain subsidies supporting fish biomass in one Cooper Creek waterhole (Burford et al., 2008). Our secondary hypothesis was that the biomass of lower-order trophic consumers that feed directly on algal biofilms such as some juvenile fish and benthic invertebrates will indeed be positively associated with littoral GPP in the short-term after significant overland flooding.

In dryland rivers, of the northern Murray Darling and Lake Eyre Basins, bony bream (*Nematalosa erebi*) and the freshwater prawn, *Macrobrachium australiense* constitute a large component of the biomass of lower trophic levels, and are significant consumers of algae. *N. erebi* is a detritivore/algivore, with a similar ecological role to *Macrobrachium* (Pusey et al., 2004), with detritus and algae contributing up to 86% of its total food consumption (Balcombe et al., 2005; Sternberg et al., 2008). Furthermore, juveniles are more likely to feed directly on algae rather than detritus compared to adults of the species (S. Balcombe, unpublished data). Given, our second hypothesis we also had the opportunity to examine the response of juvenile bony bream biomass to variation in GPP across 14 waterholes in the nearby Warrego River, northern Murray-Darling Basin that had been sampled using comparable methods to those in Cooper Creek in a period that was 3 months after on overland flood. This allowed us to examine whether such fish/GPP relationships could hold in different catchments.

2. Materials and methods

2.1. Hydrology

The Cooper Creek catchment has a semi-arid climate with mean annual rainfall varying from 400 to 500 mm in the headwaters. The timing and volume of rainfall events are highly variable, and there was only one major flood within the study period, occurring in January 2004 and peaking at 9000 $m^3\ s^{-1}$. Additionally, there was a small flow pulse in February 2004 (450 $m^3\ s^{-1}$), followed by a very small pulse in May 2004 (10 $m^3\ s^{-1}$). See Balcombe and Arthington (2009) for site details.

The Warrego River catchment is around 75 000 km^2 and is located in the north-west Murray-Darling Basin. It is characterised by extensive floodplains and numerous waterholes. Similar to Cooper Creek, this region experiences highly variable annual rainfall with headwaters receiving ~650 mm and lower reaches ~250 mm per annum. Prior to sampling in April 2002, there were two recent flow events. The first was a large overbank flood peaking at 6250 $m^3\ s^{-1}$ in January 2002 and a small in-channel pulse of 58 $m^3\ s^{-1}$ in March 2002. See Balcombe et al. (2006) for site details.

2.2. GPP

Benthic gross primary production (GPP) was measured during the day by monitoring changes in dissolved oxygen (DO) in enclosed transparent chambers as per Fellows et al. (2009). Changes in DO concentrations over time were used to calculate metabolic rates (mg $O_2\ m^{-2}\ h^{-1}$), which were then converted to units of carbon. Measures of GPP were obtained from the mean of four benthic metabolic chambers for each site in four waterholes in Cooper Creek, and additionally 14 waterholes in the Warrego River catchment.

2.3. Fish and Macrobrachium biomass

Fish assemblages were sampled using three set fyke nets and three seine net trawls that encircled the littoral margins of each waterhole. The duration (time of fyke set) and waterhole area sampled (wing width of fykes and area sampled by seines) were recorded and used to calculate a standard catch per unit effort (CPUE). Full details of sampling methods can be found in Arthington et al. (2005) and Burford et al. (2008). The biomass of fish and prawn standing stocks were calculated by summing the total biomass from the standardised seine and fyke net catches and data converting to kg ha^{-1}. Fish and prawns were collected from four Cooper Creek waterholes (Glenmurken, Mayfield, Murken and Shed) over four visits to the catchment (March, June, October and December 2004). Hence, sampling periods represent 1, 5, 8 and 10 months after disconnection of the channels and waterholes from the floodplain. The dominant fish species present included the Lake Eyre golden perch (*Macquaria* sp. B), bony bream (*N. erebi*) and two species of catfish, Hyrtl's tandan (*Neosilurus hyrtlii*) and silver tandan (*Porochilus argenteus*). We used a 60 mm standard length cut-off to quantify juvenile bony bream biomass as per Balcombe and Arthington (2009).

The Warrego River data was collected using similar methods to the Cooper Creek data, however only one seine haul was used at each site (Balcombe et al., 2006). This data was collected in April 2002, 3 months after the disconnection of floodwaters from the channel and waterhole network. Although there was some difference in the fish sampling methods we were not directly comparing the two datasets, rather looking for a consistent pattern between fish biomass and GPP across the two rivers.

2.4. Statistical analyses

Linear regression (Systat version 11) was used to identify significant relationships between GPP (independent variable) and species biomass (dependent variable). All data were Log_{10} transformed prior to analyses as these transformations improved normality and equalised variances.

3. Results

Mean values of time series data for the Cooper Creek catchment (Table 1) indicate several general trends through time. Total fish biomass and the biomass of *Maquaria* sp. B and catfishes decreased over time. There is a particularly strong decrease in total fish biomass and catfish biomass from sampling time one (March) to two (June). *Macrobrachium* and total *N. erebi* biomass show high variation through time with no general pattern evident. However,