Physical and ecological associations in dryland refugia: waterholes of the Cooper Creek, Australia

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Abstract Waterholes are a significant morphological feature of the Cooper Creek system in central Australia. Many of these waterholes contain water over extended no flow periods and are recognized as important refugia for aquatic biota. This paper explores how morphological features may influence ecosystem processes within waterholes. Each waterhole was characterized via a suite of morphological variables and it was found that the maximum fetch length was an important variable that separated waterholes into two groups. Water turbidity of these two groups of waterholes was different, as were rates of benthic production and respiration. Benthic production and therefore energy available to support the food webs of these waterholes was greater in the group of waterholes with shorter fetch lengths and lower turbidity. The possible associations between morphology, turbidity, and primary production highlight the importance of understanding the physical template of these dryland river ecosystems.

Key words Cooper Creek; refugia; primary production; turbidity; Australia

INTRODUCTION

The dryland river systems of the Lake Eyre basin in central Australia are characterized by extensive flood plains, a network of multiple channels and waterholes (Rust & Nanson, 1986). These rivers convey large volumes of water during flood periods but exist as a network of ephemeral channels and waterholes for most of the time. The abundance of waterholes is a distinctive geomorphological feature of the Cooper Creek system and Knighton & Nanson (1994) recorded over 300 permanent waterholes in the lower reaches of Cooper Creek between Windorah and Nappa Merrie. Waterholes are thought to be self-maintaining scour features that form at points of flow convergence (Knighton & Nanson, 2000) and can attain a degree of permanency once scour has breached the underlying mud–sand boundary. Flow variability and unpredictability are also features of Cooper Creek (Puckridge *et al.*, 2000), where the flow regime is characterized by extended periods of no flow and infrequent-high magnitude flood events. Hence, the waterholes of Cooper Creek are important refugia representing the only permanent habitat for the much of the aquatic biota during these periods of extended no flow.

The role of waterholes as physical refugia is two fold. First, they support populations not able to live elsewhere in this arid landscape (Nekola, 1999). Second,

they have a role in times of adversity, where refugia are defined as places (or times) where the negative effects of disturbance are lower than in the surrounding area (or time) (e.g. Lancaster & Belyea, 1997). During adverse conditions, organisms in refugia have a higher probability of survival. Organisms that survive play a very important role in re-establishing populations when conditions become more favourable.

The biological productivity of waterholes in the Cooper Creek system is among the highest recorded for streams and rivers (Bunn *et al.*, submitted). Primary production in these waterholes, as determined by the rate of benthic primary production, is heavily influenced by light and is generally restricted to a narrow littoral band. Given their size, shape and the limited presence of riparian vegetation, turbidity is likely to be the major influence on light availability and therefore benthic primary production (Bunn *et al.*, submitted). Waterhole morphology in Cooper Creek is diverse, so we may expect associated differences in the turbidity and hence primary production of these aquatic ecosystems.

In this paper we use preliminary data obtained from a larger study on the ecology of Cooper Creek waterholes to examine potential physical impacts (bottom-up controls) on river ecosystem functioning in a dryland setting. Interactions between physical, chemical and biological components are likely to be important to the ecology of each waterhole and we suggest that biological productivity is likely to be influenced by the physical structure of habitats. Furthermore, waterholes with different morphologies may also differ in terms of their primary productivity and ultimately the types of organisms using them as refugia in dry times.

STUDY AREA

The Cooper Creek catchment has its headwaters in southwestern Queensland and flows in a southerly direction terminating in Lake Eyre in central South Australia (Fig. 1). It has a semiarid to arid climate with mean annual rainfall varying from 400 to 500 mm in the headwaters to less than 100 mm at its entry to Lake Eyre. At Windorah mean maximum and minimum temperatures vary from 21 to 38° C and 7 to 24° C respectively. Annual evaporation rates are mostly in excess of 3000 mm. The majority of the streamflow is generated by seasonal monsoon rainfall in the headwaters and periodic local outbursts, hence flows are highly variable (Knighton & Nanson, 1994). Cooper Creek experienced 21 consecutive months of zero flow at Currareva during 1951/52, and the 1999 floods inundated adjacent flood plain areas in excess of the land area of England and Wales. During this flood the main flow path was wider than the English Channel. The prevailing wind direction is from the east and southeast with annual average speeds of approximately 15 km h⁻¹ at Windorah.

A dominant feature of the Cooper Creek system is its large flood plain and network of low gradient (S < 0.0002) multiple channels (Gibling *et al.*, 1998). The majority of the individual channels have a series of waterholes along their length. Waterholes are typically two to five times wider and two to three times deeper than the associated channels and have a distinctive linear appearance that range in length from a few hundred metres to over 20 km. Many have well-developed levees (Knighton &



Fig. 1 The Cooper Creek study area.

Nanson, 1994). The waterholes range in persistence from those that dry up every few years to those which, according to local and landholder knowledge, have not been dry since Europeans settled the area in the late 1800s.

METHODS

Fourteen waterholes from the Thomson River, Cooper Creek and Kyabra Creek were selected for investigation (Fig. 1). The morphological character of each waterhole was measured in the field and using a series of remotely sensed imagery. The plan form character (e.g. surface area, length, maximum fetch length, perimeter) of each waterhole were obtained from Landsat 7 1997 satellite imagery. A maximum of six cross-sections and a thalweg profile were surveyed in each waterhole and used to obtain further morphological data. Visual assessments of bank features and riparian vegetation were also conducted at each waterhole. Combined these data (Table 1) collected at a variety of scales (landscape, waterhole and within waterhole) were used to characterize the overall morphology of the 14 waterholes.

One-litre water samples collected in each waterhole were analysed in the laboratory by the Queensland Department of Natural Resources and Mines.

Landscape	Entire waterhole	Within waterhole
Total flood plain width	Area	Depth
Effective flood plain width	Perimeter	Width to depth ratio
Flood plain setting	Length	Wetted perimeter
Number of channels	Width	Hydraulic radius
Bifurcation ratio	Circularity index	Shape index
Channel distance from main	Horton's form factor	Irregularity
waterhole	Elongation ratio	Width
Lateral distance from main	Length to width ratio	Bed and bank complexity
waterhole	Volume	Offtake channels
channel distance from a main	Fetch length	Anabranches
Lateral distance from a main	Alignment of waterhole	Benches
channel		Bars
		Eroding banks
		Snags
		Overhanging vegetation
		Fringing vegetation
		Vegetative mats

Table 1 Waterhole morphology variables measured at the landscape, waterhole and within waterhole scales.

Benthic gross primary production (GPP) and respiration (*R*) were measured at each waterhole in April 2001 by monitoring dissolved oxygen within *in situ* Perspex chambers over 24 h (e.g. Bott *et al.*, 1978; Bunn & Davies, 1999). Four replicate dome-shaped chambers (diameter = 29 cm, height = 20 cm) were inserted into the sediment in the shallow edges of each waterhole to enclose a portion of the benthic algae. Dissolved oxygen concentrations were measured and recorded in each chamber every 10 min using a polarographic oxygen probe and meter. Respiration was calculated as the mean rate of change of oxygen concentration during the night and multiplied by 24 h to yield units of g $O_2 \text{ m}^{-2} \text{ day}^{-1}$. Gross primary production was calculated for each 10-min interval during the day as the difference between the rate of change of oxygen concentration during a polosynthetic quotient of one (1 mol O_2 produced = 1 mol CO_2 fixed; Lambert, 1984; Bender *et al.*, 1987).

RESULTS

The morphology of waterholes in the study area was diverse. The surface area of the waterholes ranged from 2.1 to 90.9 ha. Lengths of the bankfull channel varied between 0.5 and 8.7 km while average water depth ranged from 0.5 to 2.8 m at the time of sampling. There were two groups of waterholes in the Cooper Creek system as differentiated by maximum fetch length (Fig. 2). Group 1 contains waterholes with maximum fetch lengths over 1 km. Group 2 contains waterholes with maximum fetch lengths under 0.6 km.

When all waterholes were considered, it was found that the mean turbidity of waterholes with a longer fetch length was greater than that of waterholes with a shorter fetch length (Fig. 3).



Fig. 2 Maximum fetch lengths of waterholes in the Cooper Creek system.



Fig. 3 Turbidity averages for both groups of waterholes. Error bars show standard deviation.

Although mean respiration rates were nearly identical for the two waterhole groups, mean gross primary production of Group 2 waterholes was nearly twice that of Group 1 waterholes. As a result of these values, the ratio between production and respiration was also much greater for Group 2 than Group 1. The GPP/R ratio was greater than 1 for Group 2 (Fig. 4), indicating that the littoral zones of these waterholes are net producers of organic carbon (autotrophic). In contrast, the Group 1 mean was below 1, indicating net consumption of organic carbon in the littoral zones (heterotrophic).

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Fig. 4 The ratio between gross primary production and respiration for both groups of waterholes. Error bars show standard deviation.

DISCUSSION

Turbid water bodies are common in inland Australia (Kirk, 1985) because of the presence of high concentrations of fine suspended particles. In addition to sources of particles, turbidity can be influenced by many factors. In shallow water bodies, turbidity is largely influenced by turbulent re-suspension of bottom sediments caused by wave action. Physical characteristics such as size, shape and orientation to the prevailing wind direction largely influence wave action in water bodies (Hakanson & Jansson, 1983). Fetch was found to be an important factor related to waterhole turbidity in this study. All waterholes contained similar fine sediment, so it was unlikely to be the major contributing factor to differences between waterholes. Other factors that may have influenced turbidity differences among waterholes include disturbance by stock and other introduced species and protection from wind by riparian vegetation.

The results of this preliminary study support a physical (bottom up) influence on the biological productivity of dryland aquatic refugia. Waterhole morphology governs the fetch length, which in turn was shown to be closely linked with turbidity (Fig. 3). Turbidity affects primary production because it influences the amount of light available to benthic and water column algae for photosynthesis. Bunn & Davies (1999) and Bunn *et al.* (submitted) found that even with the high natural turbidity of the Cooper waterholes the major source of energy in these systems was benthic algae. It was often assumed that energy was derived from riparian and flood plain sources in rivers with such low light penetration. The preliminary work presented here suggests that benthic zones in waterholes which have short fetch lengths and relatively lower turbidity are net producers of organic carbon, while benthic zones in waterholes with longer fetch length and higher turbidity are net consumers of organic carbon. Since the energy base of the food webs of these waterholes is primarily algae, animals at higher trophic levels such as fish and turtles are dependent on within-waterhole primary production. Low turbidity waterholes might therefore provide more food resources and maintain larger animal populations than waterholes with higher turbidity.

The habitat templet has been proposed as a framework for considering abiotic influences on biota (*sensu* Southwood, 1977). In small streams combinations of flood frequency, flood predictability and overall flow variability have been suggested as the major axes of a flow habitat templet (Minshall, 1988; Poff & Ward, 1989). The situation may be more complex in large rivers (cf. Bayley & Li, 1992), particularly those in arid zones (Puckridge *et al.*, 1998) where the habitat templet may be multi-dimensional. This would consist of many components and the role of morphology would increase in prominence. This study has demonstrated that the length of a waterhole and its orientation to the prevailing wind direction are important because of their influence on turbidity. This highlights the link between morphology and ecological productivity in these important refugia.

Waterholes in the arid zone of Australia are essential to the persistence of populations of aquatic plants and animals. The findings of this study have implications for the management of these waterholes. In times of increasing pressure on water resources it is of great importance to preserve and identify the parts of the riverine ecosystems that are vital to maintaining its health. This study suggests one potential mechanism by which waterhole morphology may have an important influence on aquatic primary productivity and, ultimately, the populations of fish and crustaceans it supports. Determination of relationships between waterhole morphology and waterhole productivity may provide a mechanism for identifying key waterholes that are of great importance to the ecology of the Cooper Creek.

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