

## Aquatic invertebrates of rockholes in the south-east of Western Australia

I A E Bayly<sup>1,2</sup>, S A Halse<sup>3</sup> & B V Timms<sup>4</sup>

<sup>1</sup>School of Biological Sciences, Monash University, Melbourne, Vic., 3800

<sup>2</sup>Address for correspondence: 501 Killiecrankie Road,  
Killiecrankie, Flinders Island, Tas., 7255  
✉ iaebayly@activ8.net.au

<sup>3</sup>Bennelongia Pty Ltd, 5 Bishop Street, Jolimont, WA, 6014  
✉ stuart.halse@bennelongia.com.au

<sup>4</sup>Australian Wetlands & Rivers Centre, University of NSW, Kensington, NSW, 2052  
✉ brian.timms@unsw.edu.au

Manuscript received March 2011; accepted October 2011

### Abstract

Twelve flooded rockholes located to the east of the Yilgarn Craton, in the Western Australian sector of the Great Victoria Desert, were sampled for aquatic invertebrates. The fauna was depauperate in comparison with that of pan gnammas on the Yilgarn Craton. Only three crustacean species (*Lynceus* sp. nov., *Moina australiensis* and *Sarscypridopsis* sp. nov.) and one insect family (Culicidae) occurred in more than half of the rockholes. Although deep rockholes like pit and pipe gnammas typically have a longer hydroperiod than pan gnammas they have few, mainly eurytopic, species.

**Keywords:** Great Victoria Desert, Officer Basin, rock pool, gnamma, *Lynceus*, *Moina australiensis*, *Sarscypridopsis*, Culicidae

### Introduction

If we consider that part of Western Australia south of latitude 26°S, it consists of two major geological regions: that to the west of longitude 123° 30'E (say west of Yamarna) is occupied mainly by the Yilgarn Craton consisting chiefly of Achaean granites, and that to the east of this line (the Eucla and Officer Basins) of largely non-granite rocks of lesser age (Fig. 1). Much of the latter region was subject to extensive marine inundation in the Early Cretaceous around 120–100 Ma BP and a lesser marine flooding in the Eocene from about 52–37 Ma BP (BMR Palaeo-geographic Group 1990), but most of the Yilgarn Craton escaped these floodings. The Yilgarn region is studded with hundreds of granite inselbergs on the surface of which chemical weathering has etched out thousands of gnammas or rockholes. Either intermittently or episodically these gnammas are filled with rainwater and provide habitat for a surprisingly diverse assemblage of aquatic invertebrates. The nature of this assemblage for the Yilgarn region has received considerable attention during the past two decades and is now relatively well known (see, e.g., Bayly 1997; Pinder *et al.* 2000; Timms 2006; Jocqué *et al.* 2007). In contrast, the aquatic fauna of rockholes in the south-east of Western Australia, those to the east of the Yamarna-Balladonia line, has been almost totally neglected.

The word “gnamma” comes from the Nyungar language and refers to a rockhole, especially one capable of holding water, and is now firmly established in the anthropological, biological and geological literature. Following the seminal paper of Twidale & Corbin (1963) a gnamma is a rockhole that has been produced

by chemical weathering. Despite the fact that chemical weathering is generally more potent than physical weathering (Twidale & Campbell 2005), some rockholes are formed wholly or mainly by physical processes such as thermal expansion, frost riving, growth of crystals or pressure release. Such processes commonly result in the shattering of rocks. Silcock (2009) treats rockholes in the sandstone ranges of the Lake Eyre Basin as the product of fracturing followed by the scouring out of rock fragments by running water. Rockholes produced by physical processes generally have sharp, angular surfaces in contrast to the more smoothly rounded features that are so characteristic of true gnammas. While most of the rockholes encountered in this study are gnammas in the sense of Twidale and Corbin, albeit of the non-granite variety, some are not because they were judged as being produced mainly by physical processes. In summary, all gnammas are rockholes but not all rockholes are gnammas. A further point is that most deep gnammas on non-granite substrata such as the laterites that dominate the so-called “breakaway” country in Western Australia are morphologically quite different from those on granite. Unlike the pit gnammas on granite, almost all of which are basin-shaped, many of the deep non-granite gnammas are tube-like or cylindrical with vertical sides and flat bottoms. Timms (in manuscript) has distinguished these by the new name “pipe gnammas”. This new term applies to a subset of what, in more general terms, may be called “cylindrical gnammas”.

Also included in this study are two rather squarish, rock-floored basins surrounded by rock on three sides but dammed by a ridge of soft sediments on the fourth. These may be plunge pools of systems that are intermittently lotic after occasional heavy rain (but this is not certain) and are referred to as “waterholes” rather than “rockholes” in Table 1, but the title and text of

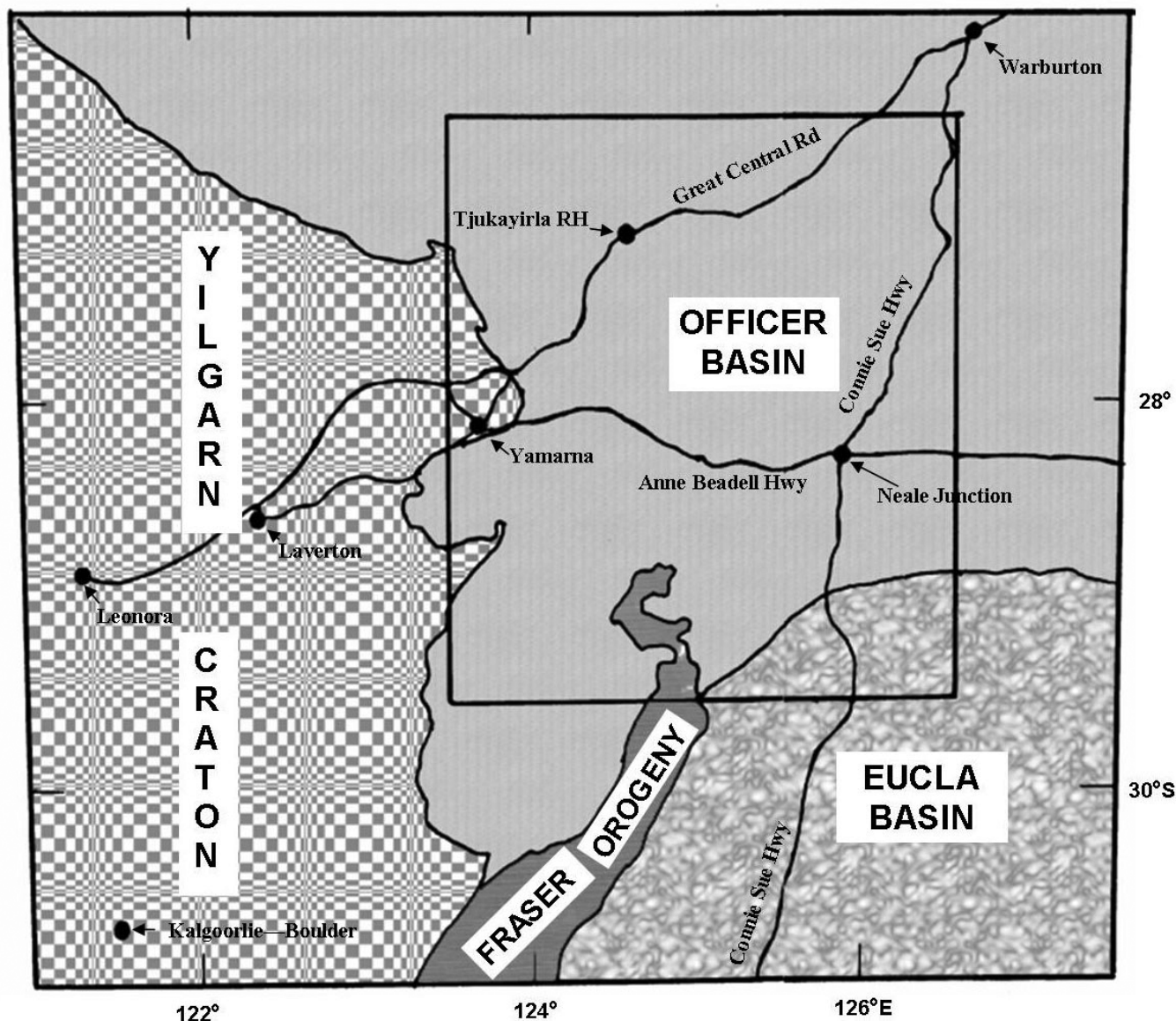


Figure 1. The study area (inset) in relation to the major geological elements surrounding it.

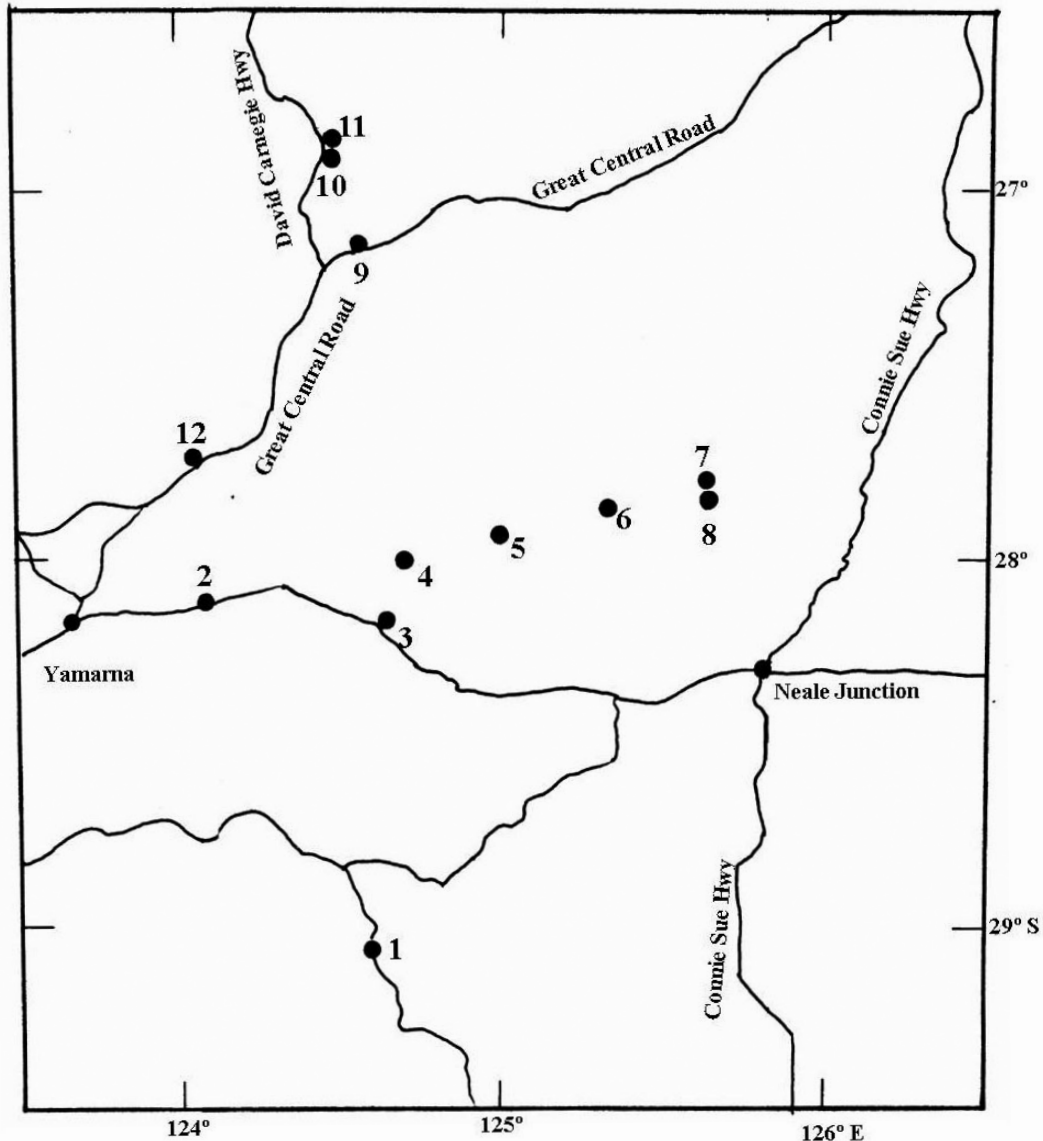
this paper has not been accordingly encumbered with dual terminology. The labelling of these two basins as waterholes is concordant with Silcock's (2009) contention that, in general, true rockholes are not located on major drainage lines (potholes gouged into hard bedrock forming the channel of major but ephemeral rivers would, of course, be an exception).

The aim of this paper is to provide inaugural data on the invertebrate assemblages of rockholes in the Officer Basin, and to make tentative comparisons with the better known Yilgarn region.

### Study Areas

All rockholes selected for study lie outside the Yilgarn Craton, to the east of longitude 124° E (Figs 1 & 2). One collection of zooplankton from a rockhole near Bartlett Bluff to the south-east of Lake Rason was made by Ian Elliot on 6 July 2010. All other collections and field measurements were carried out by one of us (IAEB)

during an expedition into the Great Victoria Desert, largely following the route taken by Frank Hann in 1903 (see Donaldson & Elliot 1998), between 24 August and 5 September 2010. All of the Hann Track localities lie easily within the Officer Basin which is dominated by Permian rocks (Myers & Hocking 1998). The Bartlett Bluff rockhole lies very close to the boundary between the Fraser Orogeny and a small pocket of the Officer Basin. Beard (2002) treats the Great Victoria Desert as being situated on the Gunbarrel Basin which overlies the Officer Basin, but the former basin is not recognized in South Australia, so the latter is adopted in this paper. Rainfall registrations (mm) at Laverton (nearest available station) for the seven months preceding sampling in 2010 were as follows (long term monthly means in parentheses): January 12.0 (24.0), February 8.4 (29.8), March 5.4 (30.1), April 38.0 (23.0), May 17.4 (23.5), June 8.8 (23.8), July 24.4 (16.5), January–July 114.4 (170.7). Only 2.0 mm fell in August as against the long term average of 13.3 mm.



**Figure 2.** Details of the study area showing the location of water-containing rockholes sampled for invertebrates. 1, Bartlett Bluff Rockhole; 2, Point Sunday Rockhole; 3, Knight Gnamma Holes; 4, Lily Rockhole; 5, Sunday Surprise Rocks; 6, Amy Waterhole; 7, Saunders Range North; 8, Point Saunders Waterhole; 9, Tugaila Rockhole; 10, Pikalu Rockholes; 11, Calcalli Rockhole; 12, Eurothurra Rockhole.

### Methods

Invertebrates were collected via a net with a rectangular frame measuring 20 x 30 cm to which was attached nylon mesh with an aperture size of 150  $\mu\text{m}$ . The net was operated so as to explore all major parts of the hydro-space without, however, deliberately taking up bottom sediment. The catch was preserved in 80% ethanol. At locality 4 (Lily Rockhole) only, a small phytoplankton net with mesh aperture of 30  $\mu\text{m}$  was deployed to collect phytoplankton, and invertebrates of rotifer or protozoan size. This catch was preserved in Lugols solution.

In the laboratory, initial sorting of specimens into major groups was carried out (by IAEB) under a stereomicroscope. Ostracods were identified by Halse, and large branchiopods and cladocerans by Timms. Other taxa were identified by Bayly.

At each rockhole sampled during the Hann Track expedition, the maximum length and maximum width (measured at right angles to the maximum length) at the water surface, and maximum water depth, were recorded using a flexible steel measuring tape. Water temperature and conductivity (K 25) were measured *in situ* with a YSI EC300 portable conductivity-temperature meter. Approximate total dissolved solid (TDS) values, as a colligative property of conductivity, were also recorded. No conductivity measurement was made at Bartlett Bluff rockhole.

### Results

Physical dimensions of the rockholes, and conductivity and TDS data for the water they contained, are presented in Table 1. Apart from Lily Rockhole and the two presumptive plunge pools, the rockholes were small, with

Table 1

Geographical, physical and chemical features of small aquatic habitats in the Great Victoria Desert sampled for invertebrates.

Locality no. & name	Date	Lat. & long.	Type of hole	Max. length X max. width or diameter (cm)	Max. water depth (cm)	Conductivity (K25) (mScm-1)	Putative TDS (mg L-1)
(1) Bartlett Bluff Rockhole	6.vii.2010	29°04.900'S 124°36.615'E	Non-gnamma rockhole	100 X 50	50		
(2) Point Sunday Rockhole	24.viii.2010	28°07.433'S 124°03.077'E	Pipe gnamma	80	30	165	107
(3) Knight Gnamma Holes	25.viii.2010	28°12.795'S 124°39.993'E	Pipe gnamma	54	28	1028	668
(4) Lily Rockhole	26.viii.2010	28°00.271'S 124°44.832'E	Non-gnamma rockhole	400 X 310	83	155	101
(5) Sunday Surprise Rocks	27.viii.2010	27°57.369'S 125°00.350'E	Pipe gnamma	20	13	214	139
(6) Amy Waterhole	27.viii.2010	27°52.097'S 125°18.553'E	Plunge-pool waterhole	400 X 300	52	45	29
(7) Saunders Range North	29.viii.2010	27°49.693'S 125°37.453'E	Pipe gnamma	83 X 56	42	179	117
(8) Pt Saunders Waterhole	30.viii.2010	27°50.865'S 125°38.356'E	Plunge-pool waterhole	255 X 220	37	69	45
(9) Tugaila Rockholes	3.ix.2010	27°09.355'S 124°34.378'E	Pipe gnamma	100	51	14	9
(10) Pikalu Rockholes	4.ix.2010	26°54.795'S 124°27.505'E	Pipe gnamma	80	96	86	56
(11) Calcalli Rockhole	4.ix.2010	26°54.007'S 124°28.070'E	Pipe gnamma	60	78	64	42
(12) Eurothurra Rockhole	5.ix.2010	27°44.786'S 124°03.016'E	Pipe gnamma	120 X 120	66	137	89

Table 2

Occurrence of invertebrate taxa in rockholes in the Great Victoria Desert

Locality	1	2	3	4	5	6	7	8	9	10	11	12
Taxa												
CRUSTACEA												
Laevicaudata												
<i>Lynceus</i> sp. nov.	X	X		X	X	X	X	X	X	X		X
<i>Lynceus macleayanus</i> (King)			X		X							
<i>Lynceus</i> sp.											X*	
Cladocera												
<i>Alona</i> sp				X								
<i>Ceriodaphnia dubia</i> Richard				X								
<i>Chydorus</i> sp				X								
<i>Moina australiensis</i> Sars	X			X	X	X	X	X	X	X		X
Ostracoda												
<i>Heterocypris tatei</i> Brady			X		X		X		X			
<i>Heterocypris</i> sp.	X											
<i>Ilyodromus</i> sp.				X								
<i>Sarscypridopsis</i> sp. nov.	X	X		X	X	X	X		X	X		X
INSECTA												
Chironomidae							X	X				
Culicidae	X	X		X			X	X	X		X	
Other Diptera	X				X		X	X	X		X	
Zygoptera						X						
Total no. taxa	6	3	2	8	5	4	7	5	6	3	3	3

\*Based on an abundance of distinctive metanauplii.

openings in the range 20–120 cm. All water depths were less than 1.0 m. Conductivities (K25) ranged from 14–1028  $\mu\text{S cm}^{-1}$ , and TDS values from 9–668  $\text{mg L}^{-1}$ , which data indicate fresh water in all cases.

The results of taxonomic studies are presented in Table 2. A total of 14 taxa were recorded, but if locality 4 is excluded, the total is reduced to only 10. It was a simple assemblage: the pea shrimp, *Lynceus*, occurred in all rockholes, and *Moina australiensis*, *Sarscypridopsis* sp. nov. and culicid larvae in most. Other important taxa were *Heterocypris tatei* and dipteran larvae other than those of Culicidae and Chironomidae.

Table 3 compares present findings with those for different types of depression on Yilgarn granite. It is convenient to restrict this comparison to Crustacea. The Officer Basin series aligns closely with granite

pit gnammas but not with data from Yilgarnia that includes pan gnammas. *Lynceus*, *Moina australiensis* and *Heterocypris* are distinctive taxa for rockholes that are not pans. Table 3 also shows that the shallow pans are considerably more speciose than deeper depressions whether they are granite pits or non-granite pipe gnammas.

### Discussion

A striking feature of this series of rockholes is the depauperate nature of the invertebrate fauna, with the total number of taxa per locality lying in the range 2–8 (mean 4.6) (Table 2). Further taxonomic resolution of insect taxa and repeated sampling at times other than late-winter/early-spring would doubtless elevate this

**Table 3**

Comparison of crustacean taxa from different types of rockholes and different regions. (The data sets were compiled on different bases with respect to sampling intensity, seasonal coverage and geographical coverage.)

Region and cavity type	Officer Basin non-granite rockholes	Yilgarn granite pit gnammas	Yilgarn granite pan gnammas	Yilgarn granite pan and pit gnammas	Yilgarn granite pan gnammas
Study	Present	Timms (unpublished)	Bayly (1997)a	Pinder <i>et al.</i> (2000)	Jocqué <i>et al.</i> (2007)
Some commonly found taxa					
LAEVICAUDATA					
<i>Lynceus macleayanus</i>	X	X		Xd	
<i>Lynceus</i> sp. nov.	X				
SPINICAUDATA					
<i>Caenestheriella mariae</i>			Xb	Xe	X
<i>Limnadia badia</i>			Xc	Xf	X
ANOSTRACA					
<i>Branchinella longirostris</i>			X	X	X
CLADOCERA					
<i>Daphnia carinata</i>		X			
<i>Daphnia jollyi</i>			X	X	
<i>Ephemeroporus</i>			X	X	X
<i>Macrothrix breviseta</i>			X	X	X
<i>Macrothrix hardingi</i>		X	X	X	X
<i>Moina australiensis</i>	X	X			
<i>Neothrix armata</i>			X	X	X
<i>Planicirculus alticarimatus</i>			X	X	X
OSTRACODA					
<i>Benmelongia barangaroo</i>			X	X	X
<i>Candonocypris</i>			X	X	X
<i>Cyprretta baylyi</i>			X	X	X
<i>Cypricercus</i>		X			
<i>Heterocypris tatei</i>	X	X			
<i>Heterocypris</i> sp.		X			
<i>Ilyodromus amplicolis</i>			X	X	X
<i>Limnocythere</i>			X	X	X
<i>Sarscypridopsis</i>			X	X	X
<i>Sarscypridopsis</i> sp. nov.	X				
COPEPODA					
<i>Boeckella opaquua</i>			X	X	X
<i>Boeckella triarticulata</i>		X			
<b>Total crustacean taxa</b>	<b>10</b>	<b>12+</b>	<b>60</b>	<b>90</b>	<b>29</b>

a, omitting data for one pit gnamma and one pan gnamma almost (intermittently) connected to a deep artificial impoundment; b, reported as *Cyzicus* sp.; c, as *Limnadia* sp.; d, present in one pit gnamma only; e, as *Cyzicus* sp.; f, as *Limnadia* sp.

number, but is judged unlikely to alter the interim assessment that the fauna is depauperate. In contrast, Jocqué *et al.* (2007), sampling in winter only, obtained a mean value of 18.7 invertebrate taxa per pool for a series of 57 pools on Hyden Rock which is located on the Yilgarn Craton and consists of granite. It is not possible to extract data on taxa per rockhole from the study of Pinder *et al.* (2000), but if Protozoa and Rotifera (not generally included in the present study) are excluded, they obtained a mean number of 44 species per granite outcrop on the Yilgarn Craton (approximately 10 pools per outcrop were sampled).

The fauna of locality 4, Lily Rockhole, was exceptional in including three species of Cladocera, and one of Ostracoda, that occurred at no other locality (they were all taken with the 150 µm net). This higher diversity of micro-crustaceans is almost certainly related to the abundance of macrophytes in this rockhole and the fact that it represents a semi-permanent aquatic habitat. A separate study of this rockhole and its plants (I. Bayly, unpublished) established that it experiences exceptionally long hydroperiods for a desert locality, and contains an abundance of *Ottelia ovalifolia* and *Potamogeton octandrus*. Collections from this locality with a phytoplankton net contained large numbers of the protozoan *Euglypha*. It is thought that this testate amoeba is associated with the undersurface of the floating leaves, and the submerged leaves and stems, of the two macrophyte species. The elevated species richness in Lily Rockhole suggests that lack of habitat heterogeneity in the remaining 11 rockholes may be a significant factor in their paucity of species.

Data presented in Table 3 suggest that the morphology of rockholes may have a major influence on their aquatic biology, with the deeper holes, containing water of greater permanency, being less speciose. At first sight this runs completely counter to current orthodoxy regarding the relationship between hydroperiod and the degree of complexity of community structure. Wellborn *et al.* (1996) explored the concept of what they called "permanency gradient" and "permanency transition", noting that "as hydroperiod increases, so does the potential species pool", and quoting several studies that observed positive correlations between degree of permanency and species richness. Concordantly, Therriault & Kolasa (2001) found that biotic diversity in coastal rock pools decreases with decreasing hydroperiod, and this general principle was endorsed by Jocqué *et al.* (2010). Finally, the data in Table 3 apparently run counter to Bayly's (1997) demonstration that in pan gnammas there is a significant positive correlation between species richness and water volume. Present findings are, therefore, difficult to explain without the realization that pit (or pipe) and pan gnammas are not as closely comparable as habitats as hitherto thought, and have few common species (Table 3). The two habitats present different levels of stress apart from hydroperiod. Pit gnammas are rather "generalized" habitats with relatively long hydroperiods and mainly eurytopic species, whereas pan gnammas are more "specialized" habitats which not only require a life cycle attuned to short hydroperiods, but also special adaptations to the short, highly transparent water column. Dark pigments to protect against strong UV radiation may be cited as an example of the latter.

Pans have been subject to prolific speciation, perhaps as a result of marked climate changes over long periods of geological time, resulting in multiple species in many genera, particularly of Cladocera and Ostracoda (Pinder *et al.* 2000). Their crustacean-dominated fauna is specialized and largely endemic. In both the shallow and deep pools there is increasing species richness with increasing water volume (*e.g.* Bayly 1997 for pans; B. Timms unpublished for pits) but it is not appropriate to amalgamate the two sets of data.

Two marine intrusions into what is now the Officer Basin would have caused mass annihilation of freshwater habitats. The first of these occurred in the Early Cretaceous about 120–110 Ma BP, and the second in the Eocene somewhere in the range 52–37 Ma BP (BMR Palaeogeographic Group 1990). Iasky (1990) confirmed that the last marine transgression into parts of the Officer Basin, as represented by the Lampe Formation, occurred in the Eocene. [The Eucla Basin was again flooded by marine waters in the Early Miocene.] With the final retreat of marine waters from the Officer Basin occurring early in the Tertiary much time has elapsed for dispersal from the Yilgarn region and elsewhere to the Officer Basin. The availability of long stretches of time is a key consideration because, after many decades of untested assumptions and myths to the contrary, it is now recognized that dispersal in passively dispersed freshwater invertebrates is a very infrequent event (see Bohanek & Jenkins 2003 for masterly review). Good direct and experimental evidence of poor powers of dispersal in freshwater zooplankton including micro-crustaceans is provided by Jenkins (1995) and Jenkins & Underwood (1998). As for macro-crustaceans, Hulsmans *et al.* (2007) reviewed the evidence from several studies on anostracans and concluded that there is "high genetic differentiation on a scale of more than 100 m". In their own study of *Branchipodopsis wolffi* they found that a distance of 50 m is already an effective barrier to gene flow and that such small distances are a constraint on effective dispersal. Jocqué *et al.* (2010) point out that rock pools are a repository for a remarkably high diversity of passive dispersers, and that the diversity of rock pool species in Australia apparently exceeds that of all other continents.

Green *et al.* (2008) considered the potential of water birds as dispersers of invertebrates in the desert regions of Australia. However, the rockholes of the present study have a small surface area, and in some cases cryptic entrances as a result of overarching vegetation, and, if an anthropocentricism is permissible, they appear unlikely to attract the attention of large water birds such as the four species (Grey Teal, Eurasian Coot, Black Swan and Australian Pelican) studied by Green *et al.* (2008).

The most widely distributed insect group in the present study, the Culicidae, is one of the very few actively dispersed taxa for which the extent of dispersal has been accurately quantified. Service (1997) emphasized that short distance dispersal is the norm in mosquito biology; using capture-mark-recapture methods he showed that the maximum distance flown is usually in the range 1–5 km, with almost half the records being less than 1 km. One overseas rock pool species, *Aedes vittatus*, is not only an active disperser but also has desiccation-resistant eggs (Roberts 2004).

Insects such as hemipterans and coleopterans, that are common in Yilgarn pit gnammas were entirely absent from the desert rockholes. There are few staging points in the desert for bugs and beetles whereas on the Yilgarn Craton there are many farm dams and some larger artificial water bodies that can serve as refuges during dry periods. Additionally, as with birds, the small opening size of such rockholes as pipe gnammas may militate against access by active invertebrate dispersers.

**Acknowledgements:** We thank Ian Elliot for the collection from the Bartlett Bluff rockhole, and for his skillful navigation along the Hann Track. Ian Elliot, Paul Kennedy and Diane Sullivan assisted with the field work during the August–September expedition and are thanked for so doing. We gratefully acknowledge Greg Dempster for his assistance in preparing Figures 1 and 2. Joan Powling is thanked for the identification of *Euglypha*. Patrick De Deckker kindly provided a copy of one geological reference.

## References

- Bayly I A E 1997 Invertebrates of temporary waters in gnammas on granite outcrops in Western Australia. *Journal of the Royal Society of Western Australia* 80: 167–172.
- Beard J S 2002 Palaeogeography and drainage evolution in the Gibson and Great Victoria Deserts, Western Australia. *Journal of the Royal Society of Western Australia* 85: 17–29.
- BMR Palaeogeographic Group 1990 Australia: Evolution of a Continent. Bureau of Mineral Resources, Canberra.
- Bohonak A J & Jenkins D G 2003 Ecological and evolutionary significance of dispersal by freshwater invertebrates. *Ecology Letters* 6: 783–796.
- Donaldson M & Elliot I (eds) 1998 Do Not Yield to Despair: Frank Hann's Exploration Diaries in the Arid Interior of Australia. Hesperian Press, Carlisle.
- Green A J, Jenkins K M, Bell D, Morris P J & Kingsford R T 2008. The potential role of waterbirds in dispersing invertebrates and plants in arid Australia. *Freshwater Biology* 53: 380–392.
- Hulsmans A, Moreau K, De Meester L, Riddoch B J & Brendonck L 2007 Direct and indirect measures of dispersal in the fairy shrimp *Brachipodopsis wolffi* indicate a small-scale isolation-by-distance pattern. *Limnology & Oceanography* 52: 676–684.
- Iasky R P 1990 Officer Basin. *In: Geology and Mineral Resources of Western Australia*. Geological Survey of Western Australia Memoir 3: 362–380.
- Jenkins D G 1995 Dispersal-limited zooplankton distribution and community composition in new ponds. *Hydrobiologia* 313/314: 15–20.
- Jenkins D G & Underwood M O 1998. Zooplankton may not disperse readily in wind, rain or waterfowl. *Hydrobiologia* 387/388: 15–21.
- Jocqué M, Timms B V & Brendonck L 2007 A contribution on the biodiversity and conservation of the freshwater fauna of rocky outcrops in the central Wheatbelt of Western Australia. *Journal of the Royal Society of Western Australia* 90: 137–142.
- Jocqué M, Vanschoenwinkel B & Brendonck L 2010 Freshwater rock pools: a review of habitat characteristics, faunal diversity and conservation value. *Freshwater Biology* 55: 1587–1602.
- Myers J S & Hocking R M 1998 Geological Map of Western Australia, 1: 2,500,000. Geological Survey of Western Australia, Perth.
- Pinder A M, Halse S A, Shiel R J & McRae J M 2000 Granite outcrop pools in south-western Australia: foci of diversification and refugia for aquatic invertebrates. *Journal of the Royal Society of Western Australia* 83: 149–161.
- Roberts D 2004 Prolonged survival of eggs of the rock pool mosquito, *Aedes vittatus*, in the extreme heat of the Arabian Peninsula. *Journal of Arid Environments* 57: 63–70.
- Service M W 1997 Mosquito (Diptera: Culicidae) dispersal: the long and short of it. *Journal of Medical Entomology* 34: 579–588.
- Silcock J 2009 Identification of Permanent Refuge Waterbodies in the Cooper Creek & Georgina-Diamantina River Catchments for Queensland and South Australia. South Australian Arid Lands Natural Resources Management Board, Port Augusta.
- Therriault T W & Kolasa J 2001 Desiccation frequency reduces species diversity and predictability of community structure in coastal rock pools. *Israel Journal of Zoology* 47: 477–489.
- Timms B V 2006 The large branchiopods of gnammas (rockholes) in Australia. *Journal of the Royal Society of Western Australia* 89: 163–173.
- Twidale C R & Campbell E M 2005 Australian Landforms. Rosenberg Publishing, Kenthurst.
- Twidale C R & Corbin E M 1963 Gnammas. *Revue de Géomorphologie Dynamique* 14: 1–20.
- Wellborn G A, Skelly D K & Werner E E 1996 Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology & Systematics* 27: 337–363.