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Invertebrates of temporary waters in gnammas on granite outcrops in Western Australia

I A E Bayly

Department of Biological Sciences,
Monash University, Clayton VIC 3168

Abstract

Thirty-six flooded gnammas (rock pools), distributed between 17 different granite outcrops, were each sampled once only during the winter of 1990. The water of most pools was acidic (pH < 7.0) and of low conductivity (K_{25} < 200 µS cm^{-1}). A total of 88 invertebrate taxa were found with *Boeckella opaqua* (Copepoda; 19 occurrences), *Cypretta baylyi* (Ostracoda; 17) and *Neothrix armata* (Cladocera; 14) most common. A high proportion of the Crustacea consisted of species endemic to Western Australia. Six new species of *Cypricercus* (Ostracoda) were discovered. The mean number of taxa was 8.2 per pool. There was a highly significant positive correlation between species richness and the logarithm of both the pool volume and pool area. The nature of the fauna is reviewed within the framework of the type of adaptations employed by the animals for tolerating or avoiding the dry phase.

Introduction

The word "gnamma" is of Aboriginal origin and refers to a depression that has been weathered out of the surface of an outcrop of bare rock; some overseas workers (*e.g.* Smith 1941) have referred to these depressions as "weather pits". Gnammas, or weather pits, are commonly found on granite outcrops and especially on the top of domed inselbergs. Despite the widespread occurrence of gnammas in Australia, the aquatic biota of rain-filled gnammas has received remarkably little attention. This neglect might be partly explicable on the basis that, because gnammas are decidedly at the small end of the size spectrum of lentic waters (pool-pond-lake), they have been regarded as being of little interest or consequence to aquatic ecologists. In fact, small size confers on gnammas a number of methodological advantages, such as ease of sampling and experimental manipulation, as subjects for an ecologist. Sheldon (1984), for example, draws attention to the good potential of rock pools for comparative and experimental studies of the aerial colonization dynamics of adult aquatic insects. This claim for gnammas, along perhaps with phytotelmata (pockets of water held in plants such as the Albany Pitcher Plant; Bayly 1984), as being quintessential aquatic microcosms, is appealing. It may be claimed with some confidence, therefore, that the potential of studies of gnammas for illustrating ecological principles is just as great, if not greater, than that of large lakes.

Among the earliest written observations on the gnammas of Western Australian granite outcrops are those of the explorer Carnegie (1898). Interesting comments on the form, distribution and likely origin of granitic gnammas in this State were also recorded by the geologist Jutson (1934). Taxonomic work on invertebrates collected from Western Australian gnammas has been undertaken by Wolf (1911), Fairbridge (1945), Petkovski (1973), Wallwork (1981), De Deckker (1981), Frey (1991, 1998), Lansbury (1995), Smirnov & Bayly (1995) and Benzie & Bayly (1996). Studies of the ecology of these gnammas, or of specific animals living in them, have been made by Jones (1971, 1974) and Bayly (1982).

Thus far only a limited attempt has been made to deal with the fauna of these peculiar and distinctive aquatic habitats in a comprehensive manner. The aim of this paper is to provide a fairly complete account of the invertebrate inhabitants of gnammas located in the more southern regions of Western Australia. This is a necessary basis for the future realisation of the above-mentioned potential of gnammas for facilitating ecological studies. Ecological aspects of the present study include the documentation of some salient chemical features of gnamma waters and the examination of species richness in relation to pool size.

This account is based on collections made from 36 gnammas, distributed between 17 different granite outcrops, during the winter of 1990. Thirteen of the 17 outcrops were in the form of domical inselbergs while the remainder were small flat surfaces. With one exception, the gnammas were shallow, flat-bottomed pan-gnammas *sensu* Twidale & Corbin (1963). The exception was a deep pit-gnamma located on War Rock.

Materials and Methods

The maximum depth, length and width (the greatest width at right angles to the line of maximum length) were measured at each pool. Hydrogen ion concentration and conductivity of water samples collected in a polyethylene bottle were determined with a Metrohm E588 pH-meter and Radiometer CDM2e conductivity meter respectively. Invertebrates were collected with a rectangular-framed net conforming with that described by Bayly (1982), except that the mesh

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aperture was 150 µm, and preserved in either 10% formalin or 90% ethanol.

The product of the maximum length and maximum width of a pool was used to approximate (consistently overestimate) the true areas of the pools. Likewise, the product of the maximum length, maximum width and maximum depth was used to approximate (consistently overestimate) the true volumes of the pools. The approximated areas and volumes of the pools were log-transformed for correlation calculations.

Results

Data on the location and physical dimensions of the 36 pools as well as their water chemistry are presented in Table 1. With one exception, pH was within the range 4.6–7.9, but for 31 of the pools it was less than 7.0. With three exceptions, the conductivity (K_{25}) was less than 1000 µS cm^{-1}, and for the 33 pools whose conductivity was less than this value the mean was 147 µS cm^{-1}.

The results of taxonomic studies are summarized in Table 2. A total of 88 taxa were recorded and the mean number was 8.2 per gnamma. Branchiopod crustaceans were found in 18 pools, with *Limnadia* the most frequently occurring taxon. Cladocera occurred in 26 pools, with *Neothrix armata* the commonest species. Copepoda were found in 23 pools, with *Boeckella opaqua* occurring most frequently. Ostracods occurred in all but one gnamma and were the only animals collected from four gnammas. The commonest ostracod was *Cypretta baylyi*. At least six new species of *Cypricercus* were recorded. Insects were found in 19 pools, with *Anisops thienemanni* the commonest species. Pools 16 and 21 yielded a disporportionately high number of insect species. Oribatid mites were restricted to two small coastal pools.

There is a highly significant, positive correlation between species richness and the logarithm of approximated pool volume (Fig 1; Pearson r = 0.595, n = 36, P<0.001). If one outlier (two taxa from pool 19 with log volume 4.78) is removed from the data set, then the

Table 1

Physico-chemical features of Western Australian granite rock-pools sampled June-August 1990.

Locality number and name	Location (lat S, long E)	Sampling date	Maximum depth (cm)	Max. length x max. width (m^2)	pH	Conductivity (K_{25}; µS cm^{-1})
1. Coragina Rock (a)	32° 55', 123° 30'	24.vi.1990	25	16 x 7	8.7	91
2. Coragina Rock (b)	" "	"	6	3 x 2	6.4	59
3. Mt Madden (a)	33° 14', 119° 50'	26.vi.1990	30	30 x 10	6.3	74
4. Mt Madden (b)	" "	"	10	12 x 2.5	6.0	96
5. Mt Madden (c)	" "	"	15	5 x 2.5	6.1	38
6. Mt Madden (d)	" "	"	20	7 x 5	6.0	61
7. Cable Beach (a)	35° 07', 117° 54'	27.vi.1990	4	1 x 0.3	7.1	1480
8. Cable Beach (b)	" "	"	2	1 x 0.3	7.0	1490
9. Frenchman Bay Rd (a)	35° 06', 117° 57'	27.vi.1990	2	3 x 2	7.3	380
10. Frenchman Bay Rd (b)	" "	"	5	0.8 x 0.2	6.4	457
11. Muirillup Rock (a)	34° 39', 116°15'	2.vii.1990	12	3 x 1.5	4.6	93
12. Muirillup Rock (b)	34°39', 116°15'	"	6	2 x 1.5	5.5	101
13. Cape Leeuwin (a)	34°22', 115°08'	6.vii.1990	2	2.5 x 1.2	6.7	450
14. Cape Leeuwin (b)	" "	"	4	5 x 1.5	6.5	8040
15. Bilya Rock	29°00', 115°51'	12.vii.1990	11	3 x 2.5	6.1	90
16. War Rock (a)	29°05', 116°00'	13.vii.1990	22	25 x 9	5.2	55
17. War Rock (b)	" "	"	>100	6 x 2	7.9	798
18. War Rock (c)	" "	"	12	4 x 2	6.1	38
19. Bunjil Rock(a)	29°39', 116°21'	13.vii.1990	100	10 x 6	6.8	60
20. Bunjil Rock (b)	" "	"	9	8 x 5	6.1	34
21. Petrudor Rocks (a)	30°25', 116°58'	14.viii.1990	80	11 x 11	6.5	116
22. Petrudor Rocks (b)	" "	"	6	3 x 1.5	6.0	186
23. Petrudor Rocks (c)	" "	"	19	6 x 3	6.2	190
24. Elachbutting (a)	30°36', 118°37'	15.viii.1990	10	6 x 2	5.1	164
25. Elachbutting (b)	" "	"	19	6 x 5	5.7	162
26. Sanford Rock (a)	31°14', 118°46'	15.viii.1990	26	8 x 3	6.3	102
27. Sanford Rock (b)	" "	"	12	2 x 2	6.7	88
28. Jilbadgie Rocks (a)	31°29', 119°13'	16.viii.1990	18	6 x 4	6.2	34
29. Jilbadgie Rocks (b)	" "	"	20	13 x 6	6.3	42
30. Mt Hampton (a)	31°45', 119°04'	16.viii.1990	33	10 x 9	6.3	144
31. Mt Hampton (b)	" "	"	13	4 x 3	6.4	64
32. Yorkrakine Rock (a)	31°26', 117°31'	26.viii.1990	9	7 x 5	6.4	113
33. Yorkrakine Rock (b)	" "	"	12	4 x 3	6.2	146
34. King Rocks (a)	32°19', 119°09'	28.viii.1990	20	14 x 10	6.6	105
35. King Rocks (b)	" "	"	30	16 x 8	6.4	91
36. Wave Rock	32°27', 118°54'	28.viii.1990	12	9 x 3	6.3	113

Table 2

List of taxa and their occurrences.

Taxa	Pool (see Table 1)	Total number of occurrences
CRUSTACEA: ANOSTRACA		
Branchinella longirostris Wolf	5,24,25,26,27,31	6
B. sp	34	1
CRUSTACEA: CONCHOSTRACA		
Cyzicus sp	4,5,6,26	4
Limnadia sp or spp	15,22,25,27,28,29,30, 31,33,36	10
Lynceus sp	17,23	2
CRUSTACEA: CLADOCERA		
Chydoridae		
Alona cf *setuloides*	32,33	2
A. n sp	33	1
Alonella – excisa group	11	1
Biapertura – macropa group		
sp1	15	1
sp2	11,35	2
sp3	5,12,24,25,26,29,30,34,36	9
B. rigidicaudis Smirnov	6,27,28	3
B. n sp	9,11	2
Ephemeroporus-barroisi group		
sp1	6,34,35	4
sp2	11	1
Monospilus diporus Smirnov & Timms	4,23,26	3
Planicirculus alticarinatus Frey	26,31	2
Plurispina chauliodus Frey	12	1
P. multituberculata Frey	2,6,25,33	4
Rak stagnensis Frey	1,4,5,27,29,34	6
Leberis aenigmatosa Smirnov	27,29,31,34	4
Other families		
Daphnia jollyi Petkovski	23,26,29,31	4
Neothrix armata Gurney	1,3,6,12,15,18,21, 23,24,26,30,34,35,36	14
Macrothrix breviseta Smirnov	30,35	2
M. hardingi Petkovski	24,27	2
M. indistincta Smirnov	1,25	2
M. longiseta Smirnov	2	1
Ceriodaphnia sp	1,26,27,30,34,35,36	7
Moina sp	1,2,15,18	4
CRUSTACEA: COPEPODA		
Calanoida		
Boeckella opaqua Fairbridge	1,2,3,4,5,6,24,25,26,27,28, 29,30,31,32,33,34,35,36	19
B. triarticulata (Thomson)	17,19,21,23	4
Calamoecia ampulla (Searle)	21	1
Cyclopoida		
Mesocyclops australiensis (Sars)	21	1
Metacyclops sp	3,34	2
Microcyclops varicans (Sars)	1,21	2
Harpacticoida	11	1
CRUSTACEA: OSTRACODA		
Alboa n sp	16	1
Bennelongia barangaroo De Deckker	1,5,23,25,29	5
B. sp	3,21	2
Candonocypris novaezelandiae (Baird)	16	1
Cypretta baylyi McKenzie	3,4,6,11,12,16,18,20,22,23, 25,26,27,28,32,33,36	17
C. sp	2,10,15,22,25,28,31, 32,33,34,35	11
Cypricercus sp or spp	6,20,22,26,33,34	6
C. n sp 1	2,3	2
C. n sp 2	3,4,5,8,30	5
C. n sp 3	3,34	2
C. n sp 4	6,9,13,14,15,16	6
C. n sp 5	30	1
C. n sp 6	36	1
Heterocypris incongruens (Rahmdor)	2	1
Ilyodromus amplicolis De Deckker	2,10,18,20,23,29,31,32,33	9
I. candonites De Deckker	9,12,16,18	4
I. sp	4,15,21,24,27,36	6
Limnocythere mowbrayensis Chapman	2,3,7,34,35,36	6
L. sp	8	1
L. n sp?	13	1
L. n sp	32	1
Sarscypridopsis aculaeata (Costa)	17,21,23	3
ACARI: ORIBATEI		
Scapheremaeus sp	7,8	2
Trimalaconothrus sp	7,8	2
INSECTA: COLEOPTERA		
Dytiscidae		
Allodessus bistrigatus (Clark)	16,21,25	3
Eretes australis (Erichson)	21	1
Lancetes lanceolatus (Clark)	6	1
Megaporus howitti (Clark)	3,16	2
Necterosoma darwini (Babington)	11	1
Paroster niger Watts	7,8	2
Sternopriscus multimaculatus (Clark)	16,25	2
Hydrophilidae		
Berosus approximus Fairmaire	16	1
Limnoxenus zelandicus (Broun)	6	1
INSECTA: DIPTERA		
Ceratopogonidae		
Dasyhelea sp	2,22,25	3
Chironomidae		
Ablabesmyia sp	28	1
Allostrissocladius sp	28,30	2
Chironomus tepperi Skuse	2,23	2
Dicrotendipes sp	11	1
Paraborniella sp	16	1
?Paratendipes sp	33	1
Orthocladiinae	25,28,30	3
INSECTA: HEMIPTERA		
Corixidae		
Agraptocorixa parvipunctata (Hale)	3,6,16,21,23	5
Diaprepocoris personata Hale	11	1
Micronecta annae Kirkaldy	16,21	2
M. gracilis Hale	21	1
M. robusta Hale	4,6,25,26,36	5
Sigara mullaka Lansbury	26	1
Notonectidae		
Anisops baylii Lansbury	5,6,16	3
A. gratus Hale	21	1
A. hyperion Kirkaldy	3,6,17,21	4
A. stali Kirkaldy	17,21	2
A. thienemanni Lundblad	3,6,16,17,21,23,25,30	8

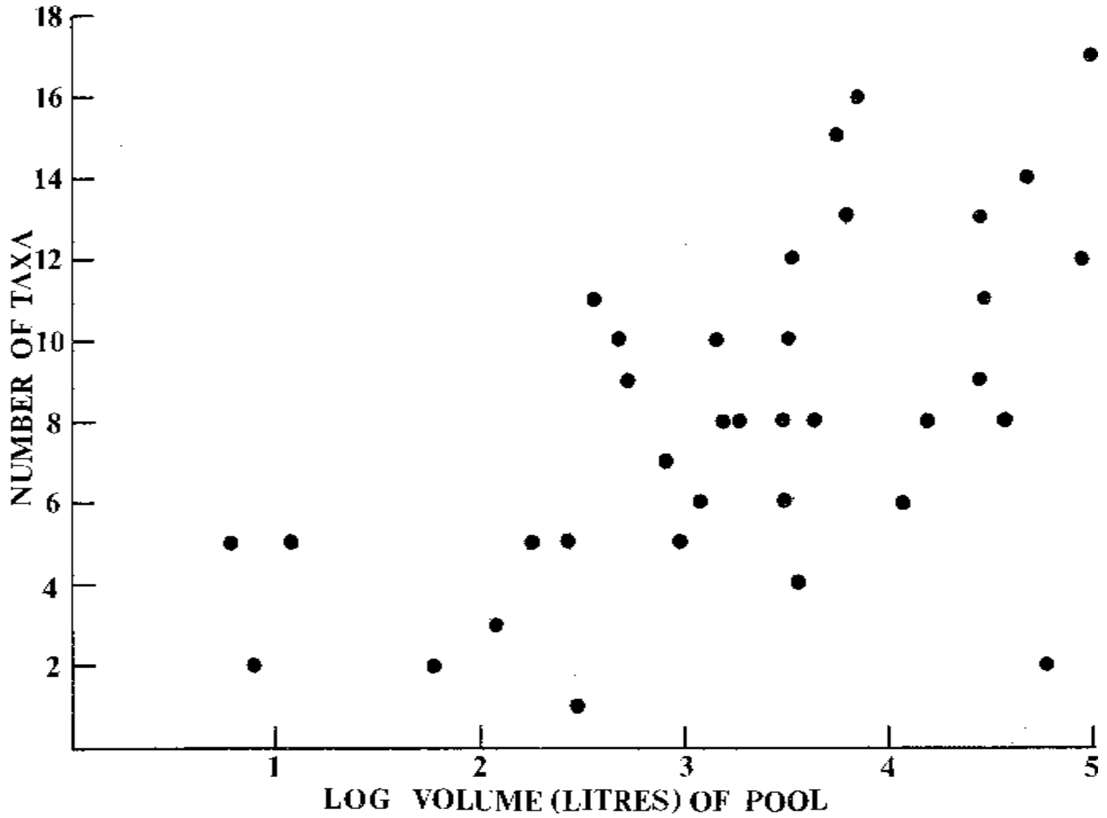

Figure 1. Plot of species richness against the logarithm (base 10) of the estimated volume (in litres) for all 36 gnammas. There is a highly significant positive correlation between these two variables (Pearson r = 0.595, n = 36, P<0.001). The outlier at two species and log volume 4.78 is pool number 19 in Table 1.

correlation is considerably improved (r = 0.696, n = 35, P<0.001). There is also a highly significant positive correlation between species richness (Pearson r = 0.577, n = 36, P<0.001) and the logarithm of approximated pool area (Pearson r = 0.641, n = 35, P<0.001).

Discussion

With seven exceptions, the conductivity (K_{25}) of the pools (Table 1) was less than 200 µS cm^{-1} – a finding broadly consistent with that of Bayly (1982) for a series of 19 granite rock pools in Western Australia. Six of the seven exceptions were pools with a maritime location (Cable Beach, Frenchman Bay and Cape Leeuwin) and whose high conductivities were clearly caused by the accession of ions from marine salt spray. The remaining exception was a deep pit-gnamma located on War Rock; this gnamma probably rarely loses accumulated ions by means of overflow.

The pH of almost all of the inland pools is acidic, as expected for a granite substratum. The exceptionally high pH recorded for Coragina Rock (a; Table 1) was discussed by Bayly (1992) who attributed it to the use of cement mortar between the exfoliated slabs of granite used to raise the level of the pool.

Although no quantitative data are available, it is noteworthy that granite rock-pools lack the high turbidity that is so characteristic of pools lying on the regolith, especially in arid regions.

The total number of taxa listed in Table 2 is 88. This, however, is an underestimate of the total number of metazoan invertebrate taxa because black planarians (*Bothromesostoma?*) and nematodes were present in several collections but were not identified and are omitted from Table 2. The total of 88 taxa greatly exceeds the 18 invertebrate taxa listed by Bishop (1974) as occurring in a series of shallow pools located on sandstone at Kanangra Walls in the Blue Mountains, New South Wales. The 88 taxa from all 36 pools and the 17 taxa from the richest pool (number 21) may also be compared with the 121 invertebrate taxa reported by Lake *et al.* (1989) from a single temporary pond (not located on a granitic substratum) in western Victoria that was repeatedly sampled over 7 months.

The animals listed in Table 2 may be classified into four groups according to their adaptations for tolerating or avoiding the dry phase following the system of Wiggins *et al.* (1980) as modified by Williams (1985).

• **Group A** (Group I of Wiggins *et al.* 1980) consists of permanent residents of the pools that are capable of only passive dispersal. These organisms are dormant during the dry season and typically avoid desiccation as a resistant stage (shelled egg or embryo). All of the Crustacea listed in Table 2 should be assigned to this group, a salient feature of which is the high proportion of species endemic to Western Australia. Such endemics include *Branchinella longirostris, Daphnia jollyi, Macrothrix hardingi, Boeckella opaqua, Ilyodromus amplicolis, I. candonites, Leberis aenigmatosa, Plurispina* *chauliodus* and *P. multituberculata.* This list does not include the new species of *Cypricercus* some of which are likely to prove endemic. A distinctive negative feature of this group is the absence of notostracans. Despite their possession of a suite of adaptations (including resistant eggs) for occupancy of small temporary waters, an unknown factor excluded notostracans from granite rock pools studied here. A possible reason is that the concentration of calcium in waters on granite is so low that it is physiologically impossible for *Lepidurus* or *Triops* to fabricate their relatively large carapace. The carapaces of *Ilyodromus* and other ostracod taxa living in granite rock-pools contain practically no calcium; instead their carapaces are strengthened by non-calcareous ridges to compensate for this deficiency P De Deckker (*pers comm*).

• **Group B** (Group II of Wiggins *et al.* 1980) comprises animals (typically insects) that are capable of active dispersal but which are typically still present during the dry season in a dormant form (quiescent larvae). *Allotrissocladius, Paraborniella* and *Dasyhelea* are assigned to this group. The ability of the larvae of these taxa to resist desiccation in gnammas was investigated by Jones (1971, 1975).

• **Group C** (Group IV of Wiggins *et al.* 1980) consists of animals (typically insects) capable of active dispersal and which have a discontinuous presence in the pools; they avoid the dry period altogether by emigrating to permanent waters before the pools dry up. To this group are assigned all the Dystiscidae, Hydrophilidae, Corixidae and Notonectidae listed in Table 2, some 20 species in all.

• **Group D** [Williams' (1985) replacement for Group III of Wiggins *et al.*] comprises animals which lack a resistant stage in their life cycle but possess exceptionally good dispersal ability thus allowing a discontinuous presence in the confines of a temporary water basin. A single species, *Chironomus tepperi*, may be assigned to this group. The ability of this species to rapidly colonize temporary waters has been demonstrated by Maher & Carpenter (1984).

The biology of the oribatid mites, *Chudalupia meridionalis* (see Bayly 1992), *Scapheremaeus* sp and *Trimalaconothrus* sp is insufficiently known to allow their assignment within the Wiggins-Williams system.

Wiggins *et al.* (1980) mentioned the habit of burrowing into bottom sediments as a behavioural adaptation for avoiding desiccation in temporary pools. While this pattern of behaviour may provide an escape for some animals in most pools, there is little scope for it in most pan-gnammas because of minimal amounts of sediment and the impossibility of burrowing into granite. Deep pit-gnammas left undisturbed for long periods may accumulate a significant amount of sediment and provide an exception.

Fryer (1985), on the basis of studies in England, concluded that chydorid cladocerans "show an unambiguous preference for large water bodies". However, this conclusion is of doubtful validity in the Australian context (Frey 1998). Although sampled once only, some gnammas contained four species of Chydoridae and there is presently no evidence that this number is significantly exceeded in large Australian lakes. Timms (1981), for example, sampled the littoral region of Lake Purrumbete, a large (552 ha) freshwater lake in Western Victoria, monthly for a year, but recorded only six chydorid species.

The finding of a significant positive correlation between species richness and the volume of the pools is consistent with earlier investigations. Ranta (1982) reported a significant correlation between the number of water beetle species and the logarithm of pool volume in a series of 20 coastal (marine supralittoral) rock pools located in the Baltic region. A similar finding for a greater diversity of taxa was made by March & Bass (1995) for a series of six temporary pools located in Oklahoma.

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