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Granite outcrop pools in south-western Australia: foci of diversification and refugia for aquatic invertebrates

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Abstract

Pools and streams on granite outcrops in south-western Australia are reliably filled, but highly seasonal, freshwater habitats that support a diverse array of aquatic invertebrates. A recent biological survey of the wheatbelt has more than doubled the number of invertebrates, to at least 230 species, known from these habitats. Granite outcrops contribute significantly to endemism in the aquatic fauna of the inland south-west and have particular conservation value for about 50 species, mostly rotifers, microcrustaceans, phreodrilid oligochaetes and chironomid midges, restricted to them. Outcrops may also be important for the wider aquatic invertebrate fauna as a freshwater habitat, if salinity in the Western Australian wheatbelt continues to increase.

Keywords: Granite outcrops, aquatic invertebrates, wheatbelt, conservation.

Introduction

Granite rock outcrops are a conspicuous feature of the landscape in south-western Australia. Their weathered and fractured surfaces often hold water in small pools of different dimensions, varying from small deep holes to broad flat-bottomed depressions and elongate crevices (Bayly 1999). The pools are filled by rainfall, usually in winter, and persist for several weeks or sometimes for months, depending on their size, morphology and the time of year they fill. An additional aquatic habitat on granite outcrops is the ephemeral streams draining from pools, and from saturated moss beds, into marshy ground around the perimeter of the outcrop or into surrounding streams. These pool and stream habitats are inhabited by invertebrates that are able to deal with their temporary nature by having strong powers of dispersal (insects), adults that do not require water (most insects), a drought-resistant stage such as a resting egg (*e.g.* rotifers, copepods) or silk-encased larvae (some chironomid midges).

A number of publications have dealt with the ecology and systematics of particular aquatic invertebrates occurring on granite outcrops in south-western Australia (*e.g.* Linder 1941; Edward 1968, 1989; Jones 1971, 1974; Geddes 1981; Cranston & Edward 1987, 1999; Frey 1991, 1998; Liehne 1991; Smirnov & Bayly 1995; Benzie & Bayly 1996; Maly *et al.* 1997). At the community level, Bayly (1982, 1997) provided records of aquatic invertebrate assemblages from 26 outcrops in the south-west and discussed the strategies used by invertebrates to survive in such seasonal environments. More general accounts of granite outcrops, their fauna and conservation are given by Bayly (1992, 1999).

In this paper, we present the results of a survey of aquatic invertebrates from pools on 9 granite outcrops. These were sampled during a biological survey of Western Australian wheatbelt wetlands carried out as part of the State's Salinity Action Plan (Anon 1996) by the Department of Conservation and Land Management. The wheatbelt is a large area of dryland agriculture in south-western Australia, approximately bounded by the 600 mm average annual rainfall isohyet to the west and the extent of land clearing to the east (Fig 1). In this region a large proportion of wetlands are severely degraded by increasing salinity and other problems associated with rising water tables. The survey was designed to provide information on the distribution of biodiversity in the region to assist conservation planning. The survey results, together with previously published work, are used to compile an updated list of taxa from aquatic habitats on granite outcrops. The biodiversity, distribution and conservation of the aquatic invertebrate fauna of granite outcrop pools are discussed.

Materials and methods

A list of taxa previously recorded from granite outcrops was compiled from publications listed in the Introduction, with minor emendations resulting from taxonomic changes. For this list, records of the occurrence of taxa in individual pools sampled by Bayly (1982, 1997) were amalgamated to provide data on frequency of occurrence on whole outcrops. To this list were added data from 9 granite outcrops (Table 1, Fig 1) sampled during the Salinity Action Plan biological survey (henceforth referred to as the 'SAP survey'). All outcrops were within the wheatbelt, except Wannara Rock, which was located 10 km east of the line of land clearing. Codes for undescribed species in the list are those used in a voucher collection and database maintained by the Department of Conservation and Land Management, Woodvale. At each of the 9 outcrops, 2 samples were collected; 1 benthic sample using a 250 µm-mesh sweep-net and 1 plankton sample using a 50 µm-mesh net. Use of a plankton net with fine mesh allowed the first

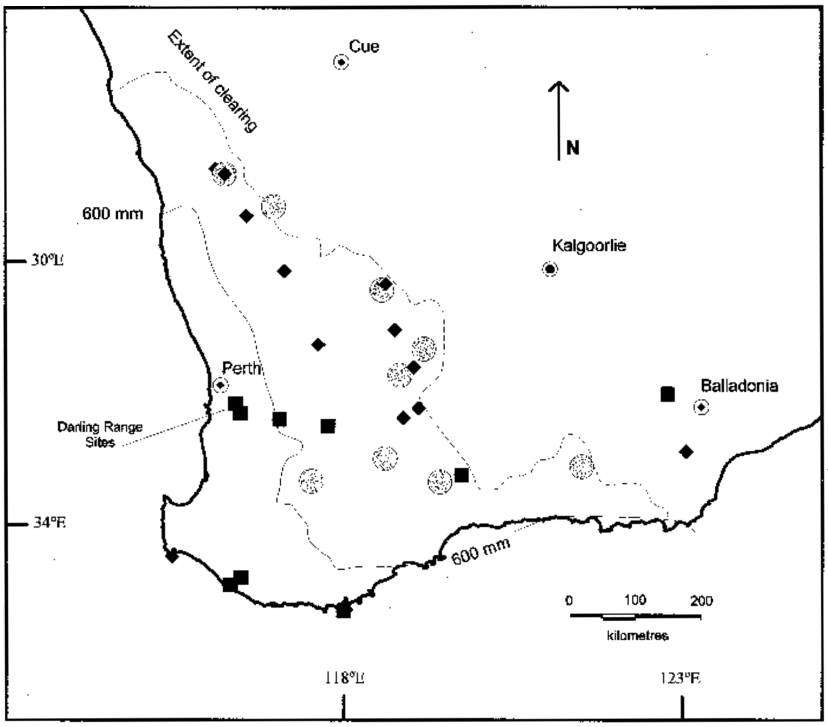

Figure 1. Map of south-western Australia showing granite outcrops sampled by Bayly (1982) (n), Bayly (1997) (u) and during the SAP survey ( ).

collections of rhizopods and rotifers from the region's granite outcrops. Where possible, sufficient pools (usually >10) were sampled to give a total sweep length of 50 m per sample. Material from separate pools was combined prior to preserving the benthic sample in 70 % alcohol and the plankton sample in 10 % formalin. Samples were sorted in the laboratory. The same methods were used to sample 140 other wetlands (including 40 fresh, <3 g L^{-1} TDS) in the central and southern parts of the wheatbelt during the SAP survey.

Water samples were taken from a single pool at each of the 9 outcrops in the SAP survey for analysis of nutrients (total persulphate nitrogen and phosphorus), chlorophyll (*a,b,c,* phaeophytin), total dissolved solids, turbidity, colour, alkalinity and ionic composition (Eaton *et al.* 1995). pH was measured in the field using a WTW Multiline P4 meter and probe.

The SAP survey outcrops were plotted on ordination axes (semi-strong-hybrid multi-dimensional scaling) on the basis of their invertebrate assemblages, for all taxa identified to species level and for just those species restricted to outcrops. This was performed using the PATN analysis package, presence/absence data with singletons masked and a β-value of –0.1 (Belbin, 1993).

Table 1

Granite outcrops sampled in the wheatbelt of south-western Australia during the Salinity Action Plan wetland survey.

Site	Date	Locality	Description and Tenure
1. Frog Rock	23 Sep 1997	31°29'49"S 119°13'57"E	Large domed outcrop. Jilbadgie Nature Reserve.
2. Cairn Rock	24 Sep 1997	31°51'31"S 118°50'39"E	Large domed outcrop. Cairn Nature Reserve
3. Dingo Rock	6 Aug 1998	33°00'34"S 118°36'08"E	Large domed outcrop. Walled to channel water to dam. Water Reserve within farmland.
4. Dunn Rock	8 Aug 1998	33°20'11"S 119°29'37"E	Large domed outcrop. Dunn Rock Nature Reserve.
5. Puntapin Rock	12 Aug 1998	33°19'31"S 117°24'02"E	Large domed outcrop. Shire Reserve.
6. Styles Rock	7 Sep 1998	33°07'35"S 121°48'02"E	Small flat outcrop, with few shallow pools. Shire Reserve.
7. Yanneymooning Rock	11 Sep 1999	30°40'50"S 118°33'10"E	Large domed outcrop. Yanneymooning Rock Nature Reserve.
8. Wannara Rock	8 Sep 1999	29°31'27"S 116°47'32"E	Large domed outcrop with artificially dammed (50cm deep) pool with macrophytes. Pastoral lease.
9. Pintha Rock (=War Rock)	28 Jul 1999	29°04'22"S 115°59'51"E	Small flat outcrop with few shallow pools. Shire Reserve.

Results

Chemical measurements at 1 pool from each of the 9 SAP outcrops are listed in Table 2. All pools were fresh and contained low concentrations of nutrients and phytoplankton (as indicated by chlorophyll concentration). Most had circum-neutral pH (5.81-7.53), though Styles Rock (site 6) was more alkaline. Sodium and chloride dominated ionic composition, except at Frog Rock (site 1) where calcium concentration was unusually high for a granite pool. This water sample was taken from the largest pool at Frog Rock, which was comparatively deep (about 40 cm) and had deeper than average sandy sediment.

Approximately 230 species of aquatic invertebrates have now been recorded from granite outcrop pools in south-western Australia (Appendix). This is a conservative figure because some groups, such as most bdelloid rotifers, nematodes, turbellarians, some annelids, and a few dipteran and beetle families, have not been resolved to species level. Inconsistencies between studies in degree of taxonomic resolution and in coding of species not formally identified also hindered an accurate estimate of regional richness. However, a plot of cumulative species richness versus number of outcrops sampled during the SAP survey (Fig 2) suggests additional sampling is unlikely to increase richness much beyond 250, unless additional groups are resolved to species level. Of the taxa in the Appendix, 190 were collected during the SAP survey. Previous studies recorded about 115 species, about two-thirds of which were also collected in the SAP survey. The Appendix includes the first records of rhizopod protozoans, rotifers, aquatic oligochaetes and numerous insects from granite outcrop pools in south-western Australia. Groups that lack active dispersal, lack ready passive dispersal, and/or do not have drought-resistant life-stages (such as oligochaetes other than a few granite-restricted phreodrilids and molluscs), are notably less diverse on granite outcrops than in other freshwater wetlands. Few species of water mites were collected even though their larvae parasitise the adults of actively dispersive insects such as beetles and flies.

Previous studies (listed in the Introduction) revealed a number of species restricted to granite outcrops in south-western Australia, including the fairy shrimp (*Branchinella longiristris*), cladocerans (*Plurispina chauliodis*, *Plurispina multituberculata*, *Daphnia jollyi*, *Macrothrix hardingi*), ostracod (*Ilyodromus candonites*), copepod (*Boeckella opaqua*), oribatid mite (*Chudalupia meridonialis*), mosquito (*Aedes occidentalis*), larvae of non-biting midges (*Botryocladius petrophilus*, *Allotrissocladius* spp, *Archaeochlus brundini*) and several undescribed microcrustacea listed by Bayly (1997). In addition to the above species, D Edward (The University of Western Australia) has recently collected 4 new phreodrilid oligochaetes and 2 more species of *Archaeochlus*, all from the same habitat as *Archaeochlus brundini* (seepages from moss beds at the headwaters of temporary streams), while the SAP survey recorded 34 possibly new species that are currently known only from granite rocks. Some of the latter species, listed in Appendix with a "*cf*" before the species name, are only tentatively separated from the nominate form and some, particularly chydorid cladocerans and ostracods, are likely to be synonymous with undescribed species listed by Bayly (1997). Nonetheless, existing information suggests about 50 granite outcrop species (see Appendix), representing about one-fifth of the total invertebrate fauna of outcrops, are currently known only from this habitat.

Table 2

Water chemistry of pools on 9 granite outcrops in the wheatbelt surveyed as part of the Salinity Action Plan survey of wheatbelt wetlands (see Table 1 for site details). Cation and anion concentrations given as % of total.

	Site								
	1	2	3	4	5	6	7	8	9
pH	7.15	6.73	5.81	7.12	6.77	8.81	6.33	7.53	7.30
TN (µg L^{-1})	400	570	390	640	810	600	630	550	750
TP (µg L^{-1})	10	10	<10	10	10	10	<10	20	40
chlorophyll (µg L^{-1})	0	1	3	1	15	1	3	6	33
Turbidity (NTU)	2.0	1.7	2.0	1.0	7.0	0.5	4.5	2.2	7.0
Colour (TCU)	<5	14	6	23	14	31	2.5	18	16
Total Dissolved Solids (g L^{-1})	0.03	0.11	0.04	0.03	0.03	0.08	0.08	0.09	0.04
Alkalinity as $CaCO_3$ (mg L^{-1})	3	10	3	3	3	8	3	15	10
Hardness as $CaCO_3$ (mg L^{-1})	19	<10	<10	<10	<10	13	13	11	<10
Silica (mg L^{-1})	1	4	<1	<1	<1	1	1	2	1
Sodium (% Meq)	39.04	78.15	78.15	76.76	59.95	70.57	65.85	85.82	71.24
Calcium (% Meq)	44.78	6.90	6.90	7.34	13.75	10.12	10.79	2.66	9.08
Magnesium (% Meq)	12.30	11.37	11.37	12.09	22.67	16.68	17.79	8.77	14.96
Potassium (% Meq)	3.83	3.54	3.54	3.76	3.53	2.59	5.53	2.73	4.65
Manganese (% Meq)	0.05	0.05	0.05	0.05	0.10	0.04	0.04	0.02	0.07
Total cations (Meq L^{-1})	0.669	0.724	0.724	0.680	0.363	0.986	0.925	1.875	0.550
Chloride (% Meq)	60.44	89.48	52.04	69.96	73.10	72.72	65.32	71.47	51.44
Bicarbonate+Carbonate (% Meq)	19.65	8.90	12.69	17.06	15.28	18.65	9.55	18.91	38.15
Nitrate and Nitrite (% Meq)	0.07	0.01	0.05	0.06	0.06	0.03	1.01	0.02	0.05
Sulphate (% Meq)	19.83	1.61	35.22	12.91	11.57	8.59	24.11	9.59	10.36
Total anions (Meq L^{-1})	0.420	2.585	0.650	0.484	0.540	0.969	0.863	1.736	0.603

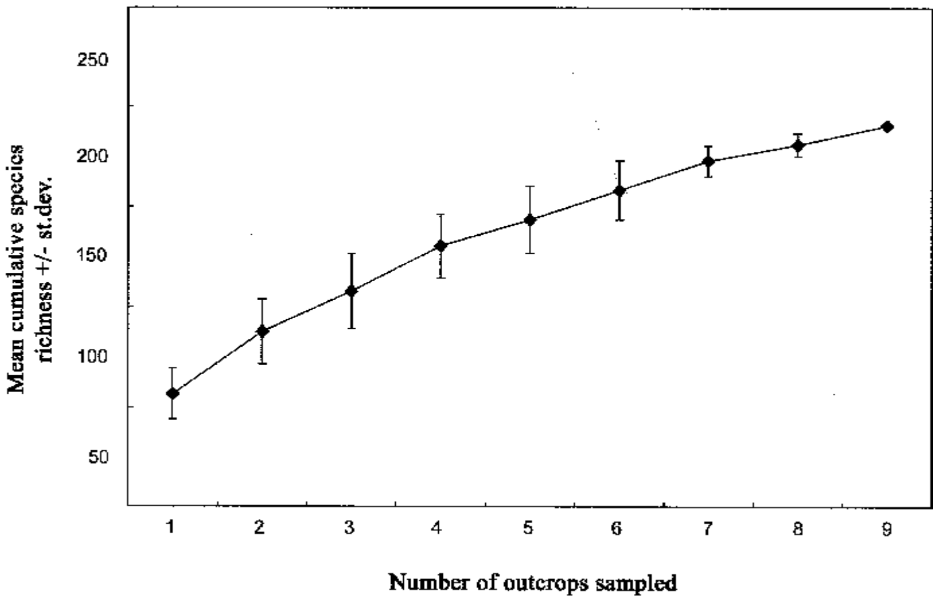

Figure 2. Mean cumulative species richness for the 9 granite outcrops sampled during the SAP survey, calculated from 10 randon re-orderings of outcrop sequence. Values are mean ± standard deviation.

Among the new species collected only from granite outcrops during the SAP survey are rotifers (*Asplanchnopus* and *Trichocerca*), chydorid cladocerans (*Alona*, *Celsinotum* and *Rak*), ostracods (*Limnocythere*, *Cypretta*, *Ilyodromus* and *Cypricercus*), copepods (*Boeckella*, harpacticoids) and oligochaetes (Phreodrilidae). Some chironomids (especially some of the Orthocladiinae) are probably also undescribed (D Edward, University of Western Australia, personal communication). The ostracod genera *Cypericercus* and *Ilyodromus*, in particular, appear to have undergone considerable radiation in granite outcrop pools (Appendix). The record of the rotifer *Taphrocampa selenura* from Pintha Rock (site 9) is the first time this cosmopolitan species has been recorded in Western Australia.

Some species in the Appendix that are not restricted to granite outcrop pools occurred in this habitat at a disproportionately high frequency during the SAP survey. Thus, for 32 species granite outcrops accounted for 50 to 100% of all wheatbelt records, despite outcrops representing only 14% of freshwater sites and 6% of all sites.

The most speciose invertebrate groups at the 9 SAP outcrops were dipterans (especially chironomids) and ostracods, although beetles and clacocerans were also well represented (Table 3). The proportions of different groups varied considerably among outcrops, with insects accounting for between 35 and 60 % of the fauna at any 1 outcrop. Like community composition, species richness varied widely (27-77 species), with some outcrops

Table 3

Species richness of major invertebrate groups for the 9 granite outcrops surveyed as part of the Salinity Action Plan (see Table 1 for sites).

	Site									
Invertebrate group	1	2	3	4	5	6	7	8	9	Mean
Protozoa	0	0	2	0	0	1	1	3	1	0.9
Rotifera	3	0	4	8	0	1	3	12	5	4.0
Cladocera	9	11	3	7	3	0	7	5	2	5.2
Ostracoda	4	5	7	11	8	3	11	12	7	7.6
Copepoda	2	1	2	2	3	1	1	5	0	1.9
Coleoptera	4	8	8	11	5	7	6	12	0	6.8
Diptera	16	12	9	12	6	7	7	10	9	9.8
Hemiptera	2	3	1	6	3	1	1	2	3	2.4
Odonata	6	4	1	1	5	0	0	4	3	2.7
Other Insects	3	3	1	2	0	0	2	3	2	1.8
Other non-insects	3	4	6	5	5	6	7	9	8	5.9
Total	52	51	44	65	38	27	46	77	40	48.9

Figure 3. Three-dimensional ordination of the 9 SAP survey granite outcrops based on the component of invertebrate assemblages restricted to granite outcrops, showing relative positions of outcrops in the northern (n), central (l) and southern wheatbelt(s). Stress = 0.12.

rivalling the more speciose wheatbelt lakes and swamps. The proportion of the overall fauna at the 9 SAP outcrops recorded from any 1 outcrop varied between 13 and 39 %, with a mean of 24.9 ± 7.6 %. Most taxa were rare, with 47 % occurring at only 1 outcrop and 83% at <4 outcrops. The species restricted to granite pools occurred at about the same frequency as the fauna overall, with 43 % occurring at only 1 outcrop and 82 % at <4 outcrops. This pattern of infrequent occurrence applied to insect as well as microinvertebrate groups, with individual beetle species occurring at an average of 2.2 outcrops, dipterans 2.1, rotifers 1.5, cladocerans 2.0 and ostracods 2.5. Even most of the granite outcrop obligates, such as *Daphnia jollyi*, *Macrothrix hardingi* and *Branchinella longirostris*, occurred at fewer than half the outcrops. The most frequently recorded species were *Rak* sp b, several *Ilyodromus*, *Cypretta baylyi* (the only species to occur at all sites), *Boeckella opaqua*, *Allodessus bistrigatus*, *Sternopriscus multimaculatus*, *Allotrissocladius* sp l, *Hemicordulia tau*, *Dasyhelea* sp, *Anisops thienemanni* and *Triplectides australis*. Most of these are opportunistic inhabitants of granite outcrops.

Ordination of SAP survey outcrops based on invertebrate assemblages showed little evidence of similarity according to geographic proximity when the full assemblage was included. However, an analysis restricted to species that are known only from granite outcrops showed some separation of outcrops by geographical location (Fig 3). In particular, the 4 southern outcrops (sites 3, 4, 5 and 6) separated from the rest in a plot of axis 1 *vs* 3, the 3 central outcrops (sites 1, 2 and 7) separated from the rest in a plot of axis 1 *vs* 2 and the 2 northern outcrops (sites 8 and 9) separated from the rest in a plot of axis 2 *vs* 3.

Discussion

New information from the SAP survey raises the number of species of aquatic invertebrate known to occur on granite outcrops in south-western Australia from about 115 to at least 230. Although Bayly (1982, 1997) sampled some outcrops near the coast in the south-western corner of the State and along the Darling Range (Fig 1), most of his sites and those of the SAP survey were located in the wheatbelt. Not surprisingly, therefore, more than 95% of species in the Appendix are known from the wheatbelt. The following discussion concentrates on the wheatbelt, because this is where most of the outcrops sampled were located and we have information about the fauna in surrounding wetlands of different types. The aquatic invertebrate fauna of wheatbelt outcrops represents about a quarter of the total wheatbelt aquatic invertebrate fauna, estimated to be at least 800 species (based on extrapolation from the 650 species from the two-thirds of the wheatbelt surveyed to date). The majority of the species recorded from granite outcrop pools seem to use this habitat opportunistically and are common in other types of wetlands, both in the wheatbelt and in south-western or southern Australia generally, or even farther north in the Carnarvon Basin (Halse *et al.* 2000). Data from the SAP survey to date, suggest that 32 widespread species, such as the ostracods *Gomphodella* cf *maia* and *Ilyodromus amplicolis*, cladocerans *Planicirclus alticarinatus* and *Rak* sp b and beetles *Paroster* spp, seem to be more likely to occur on granite outcrops than in other types of wetlands in the wheatbelt. Most of these are strictly freshwater species and granite outcrops may be important for their conservation in the wheatbelt, although they may be found to be common elsewhere as more non-granite wetlands are surveyed.

Previous studies noted about 12 described species restricted to granite aquatic habitats and Bayly (1997) listed numerous microcrustacea (particularly ostracods belonging to *Cypricercus*, *Cypretta*, *Limnocythere*, *Bennelongia* and chydorid cladocerans within *Alona* and *Rak*) that appeared to be new and known only from granite pools. With the results of the SAP survey, the number of species known only from granite outcrops is now about 50, assuming most of Bayly's undescribed species are synonymous with undescribed congeneric taxa recorded during the SAP survey. The richness of the granite rock pool fauna in inland south-western Australia reflects the generally high species richness in seasonal water bodies of this region, where there is increasing evidence of high diversity and endemism, particularly within some microinvertebrate groups (Frey 1991, 1998; Halse *et al.* 2000). Moreover, data from the SAP survey to date indicates that species known only from wheatbelt

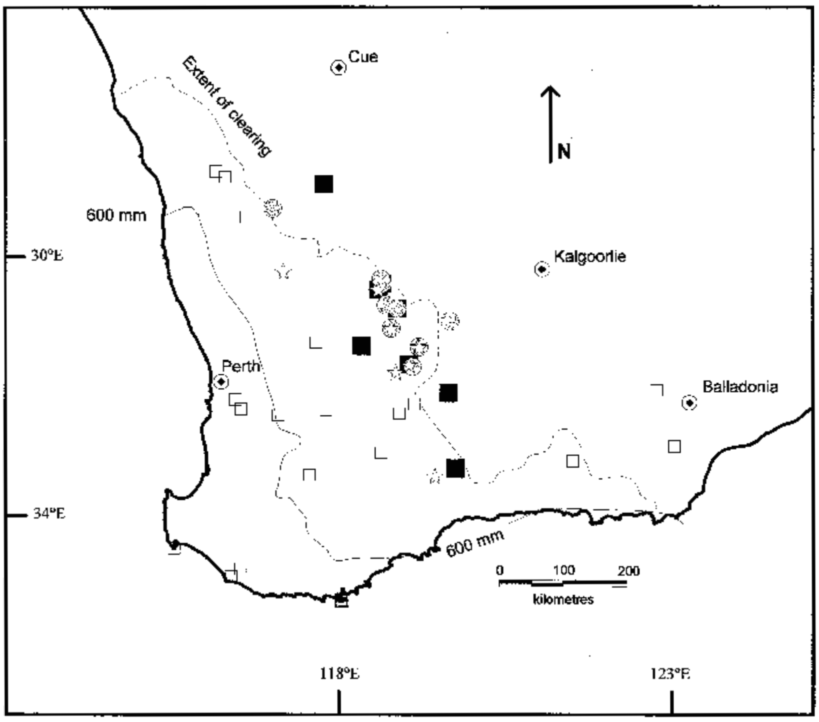

Figure 4. Known records of *Branchinella longirostris* (n), *Macrothrix hardingi* (◯) and *Daphnia jollyi* (I) on granite outcrops, with outcrops where these species not found (o) by Bayly (1982, 1997) or during the SAP survey.

granite outcrops are likely to represent at least a quarter of all aquatic invertebrates endemic to the region.

The isolated nature of granite outcrops, and the seasonally stressful environmental conditions experienced there, provide the kind of conditions under which genetic divergence and speciation might be expected (Hopper *et al.* 1997). The number of species apparently restricted to granite outcrops certainly suggests that speciation within some invertebrate groups has occurred in outcrop pools, but more definite comments about likely patterns of speciation are prevented by the absence of finer scale distribution data and an understanding of species relationships within these groups. About a third of species known only from granite outcrops have been collected from only a single locality but whether this reflects recent speciation events without subsequent dispersal or insufficient sampling remains to be determined. The remaining two-thirds are known from more than 1 locality, often 2 or 3 outcrops in the same region of the wheatbelt, although a few (such as *B. longirostris, M. hardingi, B. opaqua, D. jollyi, Limnocythere* sp 636 and *Bennelongia* sp 563) are more widespread, perhaps reflecting varying degrees of dispersal from their origin. The ordination analysis indicates that composition of the obligate granite fauna is more similar between outcrops in close proximity than between more distant outcrops, suggestive of local dispersal from a point of origin.

It seems likely that some species apparently restricted to granite outcrops in the wheatbelt also occur farther inland. Wannara Rock (site 8), which is located 10 km east of the northern wheatbelt, shared a number of new species with outcrops well within the wheatbelt, although 3 others (*Trichocerca* n sp, *Asplanchnopus* n sp and Harpacticoida sp 624) were found only at this site. Many of the species identified as granite outcrop obligates in previous studies are known only from along the eastern edge of the wheatbelt, and may represent the western extent of a more extensive inland range. This pattern is best illustrated by *Branchinella longirostris*, *Macrothrix hardingi* and *Daphnia jollyi* (Fig 4). *Boeckella opaqua* has a similar distribution but Bayly (1997) also recorded it further east, on Coragina Rock near Balladonia. Bayly (1997) recorded some undescribed species (*e.g. Cypricercus* n sp 2 and n sp 4 and *Limnocythere* n sp?) on outcrops in both the wheatbelt and in the south-western corner of the State, but found a larger number of species apparently restricted to the wheatbelt. Bayly (1982, 1997) found only 4 species (2 ostracods and 2 chydorid cladocerans) were restricted to sites along the south-west coast and none to the 2 Darling Range sites he sampled, although granite outcrops in these areas need to be more extensively surveyed before meaningful comparisons with other regions can be made.

There is general agreement between Bayly (1982, 1997) and the SAP survey data on which taxa tend towards ubiquity at granite outcrops, with *B. opaqua, C. baylyi, I. amplicolis, I. candonites, N.* cf *armata* and *Limnadia* consistently common. In the SAP survey *Rak* sp b, *Ilyodromus* sp 630, *Allotrissocladius* sp l and Dasyheleine ceratopogonid midges were also common. There is also agreement on the apparent rarity of most species. For the SAP survey, 47 % of species were collected from single outcrops (of the 9 sampled) while Bayly (1997) found even greater rarity, with 63 % of species present at only 1 or 2 outcrops (of the 17 sampled). There is thus a great deal of heterogeneity in the composition of outcrop assemblages. Similar heterogeneity was recorded for ephemeral pools on the River Murray floodplain, with 43% of 500 species restricted to single sites of the 112 sites sampled by Shiel *et al.* (1998). This heterogeneity is no doubt partly associated with processes of immigration and local extinction, which are usually held to determine the biota of islands (Lomolino 2000). Over longer time scales, speciation may contribute to the uniqueness of the fauna at single outcrops or regional outcrop faunas, but the data suggest this may be only a minor component of overall heterogeneity. Oftentimes, it is difficult to distinguish real differences between sites (caused by the above processes) from apparent heterogeneity in the data caused by limited sampling of sites in time (to account for succession) and space (to account for within site variability).

Succession in the highly seasonal pools of granite outcrops is likely to be a major cause of apparent heterogeneity. Bayly (1982) sampled pools on 2 outcrops on more than one occasion in the same season and noted a tendency for cumulative diversity to increase with time since flooding. Similarly, rapid changes in billabong microinvertebrate community composition after flooding were demonstrated by Tan & Shiel (1993) and Hillman & Shiel (in press). The outcrops sampled during the SAP survey and by Bayly (1997) were each sampled on only one occasion (over periods of 1 to 2 months in winter and spring) and so probably underestimated outcrop richness and exaggerated heterogeneity between outcrops by sampling different outcrops at different times since their pools flooded.

Outcrop pools are more heterogeneous in structure than might be imagined, varying in morphology, chemistry, substrate, presence of rocks providing habitat for insects such as caddis fly larvae, periphyton growth, organic litter and presence of mosses and higher plants. This variation in habitat between pools will also exaggerate heterogeneity between outcrops when few pools are sampled per outcrop. Bayly (1997) mostly sampled 1 or 2 pools per outcrop, but sampled 3 to 4 pools at three of his sites. Of these, Mount Madden pools had 7 to 15 species each but 29 species overall, War Rock had 3 to 14 species per pool and 21 overall, while Petruder Rock had 5 to 14 species per pool and 27 overall, indicating considerable heterogeneity between pools. This suggests that the greater number of pools sampled during the SAP survey (usually 10 per outcrop) would partly account for the higher species richness of 49 ± 15 per outcrop obtained by the SAP survey than the 14 ± 8 by Bayly (1997) and possibly for the lower frequency of species occurrence on outcrops recorded by Bayly (1997).

In summary, granite outcrops in the inland of south-western Australia support a rich and diverse aquatic invertebrate fauna that contributes to high biodiversity and endemism in the wheatbelt. Their fauna consists mostly of opportunistic species that are widespread in the south-west and inhabit a variety of wetland types. For this widespread component, granite outcrops may have an increasingly important conservation role as the wheatbelt becomes more saline over the next few decades (Anon 1996). The primary conservation value of the outcrops, however, is as habitat for the smaller number of species unique to the aquatic habitats the outcrops provide. The apparent heterogeneity between outcrop assemblages, even within this restricted element of the fauna, suggests there may be no such entity as a typical granite pool community. Results to date, showing that very few species occur frequently, with about half found at only a single outcrop, have important implications for conservation planning. They imply that a large proportion of granite outcrops in the wheatbelt will need to be protected to conserve all of the region's granite pool species. More intensive surveys of wheatbelt outcrops, examining seasonal succession at several sites, and of outcrops in the Darling Range and east of the wheatbelt, would show whether this intensity of protection is necessary or whether a subset of more widely distributed outcrops could achieve the same conservation goal.

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Appendix

List of taxa recorded from granite outcrops in south-western Australia. Records from 140 non-granite SAP survey sites are included to show how common species are in the wheatbelt of south-western Australia.

Major group	Family		Taxon	Occurrence in: 9 rock SAP sites	140 other SAP sites	Other studies, see below	9 rock sites of Bayly (1982)	17 rock sites of Bayly (1997)
PROTOZOA[†]								
	Arcellidae		*Arcella* sp	3				
	Centropyxidae		*Centropyxis* sp	1				
	Difflugiidae		*Difflugia graman* Penard	1				
		#	*Difflugia* sp a	1				
	Euglyphidae		*Euglyphia* sp a	1				
			Euglyphia sp b	1				
	Nebelidae		*Nebela lageniformis*	1				
MINOR GROUPS								
Flatworms			Unidentified Turbellaria	8				
	Typhloplanidae		*Bothromesostoma personatum*				2	+
Roundworms			Unidentified Nematoda	8			2	+
Tardigrades			Unidentified Tardigrada	2				
ROTIFERA								
	Philodinidae		*Rotaria* sp a	1	5			
			Macrotrachela sp	1	0			
			Unidentified bdelloids	3	0			
	Habrotrochidae		*Otostephanus auriculatus*? (Murray)	1	0			
	Testudinellidae		*Testudinella patina* (Hermann)	1	5			
	Asplanchnidae	#	*Asplanchnopus* sp a	1	0			
	Notommatidae	*	*Cephalodella forficula* (Ehrenberg)	1	0			
		*	*Cephalodella gibba* (Ehrenberg)	1	0			
		*	*Taphrocampa selenura* Gosse	1	0			
	Brachionidae	*	*Brachionus quadridentatus* Hermann	2	1			
			Keratella australis (Berzins)	1	5			
		*	*Keratella procurva* (Thorpe)	1	2			
	Colurellidae		*Lepadella ovalis* (Muller)	2	1			
		#	*Lepadella* cf *patella* (Muller)	3	0			
	Euchlanidae		*Euchlanis dilatata* Ehrenberg	2	5			
	Lecanidae	*	*Lecane flexilis* (Gosse)	2	0			
		*	*Lecane latissima* Yamamoto	2	0			
		*	*Lecane hamata* Stokes	1	0			
		*	*Lecane ludwigi* (Herrick)	5	4			
		*	*Lecane luna* (Muller)	1	1			
		*	*Lecane furcata* Murray	1	0			
	Synchaetidae		*Polyarthra dolichoptera* Idelson	3	1			
	Trichocercidae	#	*Trichocerca* sp a	1	0			
MOLLUSCA								
Snails	Planorbidae	*	*Glyptophysa* sp 3	4	2			
			Isidorella sp	1	9			
ANNELIDA								
Aphanoneurans	Aeolosomatidae		unidentified Aeolosomatidae	1	3			
Aquatic earthworms	Phreodrilidae	#	Astacopsidrilus WA09			3 a		
		#	Antarctodrilus WA21	1	0	3 a		
		#	Phreodrilidae WA10			1 a		
		#	Phreodrilidae WA22			1 a		
		#	Phreodrilidae WA23	1	0			
	Tubificidae		Tubificidae sp	1	59			
ACARINA								
oribatid mites			*Scapheremaeus* sp					1
			Trimaloconothrus sp					1
		#	*Chudalupia meridonialis* Wallwork			b	1	
			Oribatida spp	5	29		2	

Appendix (continued)

Major group	Family		Taxon	Occurrence in: 9 rock SAP sites	140 other SAP sites	Other studies, see below	9 rock sites of Bayly (1982)	17 rock sites of Bayly (1997)
Mesostigmatid mites			Unidentified Mesostigmata	3	38			
Trombidioid mites	Trombidiidae		Unidentified Trombidiidae	4	40			
Water mites	Eylaidae		*Eylais* sp	1	17			
CRUSTACEA								
Fairy shrimps	Thamnocephalidae	#	*Branchinella longirostris* Wolf	1	0	3 c, 5 d	1	4
		*	*Branchinella affinis* Linder	1	1			
		#	*Branchinella* cf *compacta*	1	0			
			Branchinella sp					1
Clam shrimps	Cyzicidae		*Cyzicus* sp	2	5			2
	Limnadiidae		*Limnadia* sp	5	0			6
	Lyncaeidae		*Lynceus* sp	2	4			2
Shield shrimps			*Lepidurus apus viridus* Baird			e		
Cladocerans	Chydoridae		*Alona rectangula novaezelandiae* Sars	1	3			
		#	*Alona* cf *affinis* Leydig	2	0			
			Alona rigidicaudis sl Smirnov	2	9		2	3
		*	*Alona macrocopa* (Sars)	4	1		4	
			Alona macrocopa group (4 spp)					1 to 8 each
			Alona intermedia (Sars)				1	
		*	*Alona* sp b	2	1			
			Alona sp n					1
			Alona setuloides? Smirnov & Timms					1
			Allonella excisa (Fischer) group					1
		#	*?Celsinotum* sp a	1	0			
		#	*Celsinotum* cf *hypsilophum* Frey	1	0			
		*	*Dunhevedia crassa* King	1	1			
		*	*Planicirclus alticarinatus* Frey	3	1			2
		#	*Plurispina chauliodis* Frey	2	0		3?	1
		#	*Plurispina multituberculata* Frey				1?	4
		*	*Rak* sp b	6	2			
			Rak sp c (see note f)					5
			Ephemeroporus barroisi sl (Richard)	1	3		3	3
			Monospilus diporus Smirnov & Timms					3
			Leberis aenigmatosa Smirnov			6 g		4d
	Daphniidae		*Ceriodaphnia quadrangula* sl (Mueller)	1	1			
		*	*Ceriodaphnia laticaudata* sl (Mueller)	1	1			
		#	*Ceriodaphnia* sp a	2	0			
			Ceriodaphnia sp				1	5
		#	*Daphnia jollyi* Petkovski	4	0			4
	Macrothricidae		*Macrothrix breviseta* Smirnov & Timms	1	6			2
		#	*Macrothrix hardingi* Petkovski	2	0	8 h		2
			Macrothrix indistincta Smirnov					2
			Macrothrix longiseta Smirnov					1
		#	*Macrothrix* sp a	2	0			
	Ilyocryptidae	#	*Ilyocryptus* cf *smirnovi* Kotov & Timms, 1998	1	0			
	Neothricidae	#	*Neothrix* cf *armata Gurney*	5	0		6	12
	Moinidae	*	*Moina micrura* ? Kurz	2	0			
			Moina sp					3
Ostracods	Limnocytheridae	*	*Gomphodella* cf *maia* DeDekker	1	1			
	Cytheridae		*Limnocythere mowbrayensis* Chapman		3			5
		#	*Limnocythere* sp 636	4	0			
		*	*Limnocythere* sp 557	1	0			
			Limnocythere spp (approx 3 spp)					1 each
	Cyprididae		*Bennelongia barangaroo* sl De Deckker	5	8		1	5
		#	*Bennelongia* sp 563	4	0			
			Bennelongia sp					2
			Candonocypris novaezelandiae (Baird)	1	11			1
			Alboa sp					1
		*	*Cypretta baylyi* McKenzie	9	8		6	11

Appendix (continued)

Major group	Family		Taxon	Occurrence in: 9 rock SAP sites	140 other SAP sites	Other studies, see below	9 rock sites of Bayly (1982)	17 rock sites of Bayly (1997)
		#	*Cypretta* cf *globosa*	2	0			
		#	*Cypretta* sp 647	2	0			
		#	*Cypretta* sp 648	2	0			
			Cypretta sp					9
			Kapcypridopsis asymmetra De Deckker				1	
		*	*Ilyodromus amplicolis* De Deckker	6	0		3	8
		#	*Ilyodromus candonites* De Dekker	7	0		4	3
		*	*Ilyodromus dikrus* De Deckker	1	0			
		*	*Ilyodromus* sp 566	3	0			
		#	*Ilyodromus* sp 573	1	0			
		#	*Ilyodromus* sp 630	7	0			
			Ilyodromus sp					6
			Heterocypris incongruens (Ramdohr)					1
		*	*Cypericercus unicornis* De Deckker	1	0			
			Cypericercus salinus De Deckker	2	1			
			Cypericercus sp 442	1	2			
		#	*Cypericercus* sp 634	2	0			
		#	*Cypericercus* sp 637	1	0			
		#	*Cypericercus* sp 643	2	0			
		#	*Cypericercus* sp 638	1	0			
			Cypericercus spp (approx 7 spp)					1 to 6
	Cypridopsidae		*Sarscypridopsis aculeata* (Costa)	1	30			2
		#	*Sarscypridopsis* sp 631	2	0			
		#	*Sarscypridopsis* sp 642 (nr aculeata)	1	0			
Copepods	Centropagidae	#	*Boeckella opaqua* Fairbridge	6	0		1	9
			Boeckella triarticulata (Thomson)	1	68			3
			Calamoecia ampulla (Searle)		15			1
	Cyclopoidae		*Microcyclops varicans* (Sars)	1	3			2
			Metacyclops arnaudi (Sars)		15		1	
			Metacyclops sp					2
			Mesocyclops australiensis (Sars)		8			1
		*	*Australocyclops similis* Morton	2	2			
			Mixocyclops sp				1	
	Harpacticoida	#	Harpacticoida sp 624	1	0			
		*	Harpacticoida sp 674	2	1			
			Harpacticoida sp				1	1
INSECTS								
Beetles	Dytiscidae		*Allodessus bistrigatus* (Clark)	8	36			3
			Liodessus inornatus (Sharp)	2	12			
			Paroster michaelseni Regimbart	3	0			
			Paroster niger Watts	3	4			1
		*	*Paroster couragei* Watts	1	0			
			Antiporus gilberti (Clark)	3	27			
			Sternopriscus multimaculatus (Clark)	6	26			2
			Necterosoma penicillatus (Clark)	3	49			
			Necterosoma darwini (Babington)	1	4			1
		*	*Necterosoma wollastoni* (Clark)	1	1			
			Megaporus howitti (Clark)	2	19			2
			Lancetes lanceolatus (Clark)	2	20			1
			Eretes australis (Erichson)	1	5			1
			Rhantus suturalis (MacLeay)	1	10		1	
			Platynectes sp (larvae only)	1				
	Hydrophilidae		*Berosus approximans* Fairmaire	2	18			1
			Berosus discolor Blackburn	1	29			
			Berosus macumbensis Blackburn	2	15			
			Berosus nutans (MacLeay)	3	4			
			Enochrus maculiceps (MacLeay)	1	4			
			Limnoxenus zeylandicus (Broun)		12			1
	Scirtidae		Scirtidae	2	13			
	Limnichidae		Limnichidae	1	3			
Fly larvae	Tipulidae		Tipulidae	1	23			

Appendix (continued)

Major group	Family		Taxon	Occurrence in: 9 rock SAP sites	140 other SAP sites	Other studies, see below	9 rock sites of Bayly (1982)	17 rock sites of Bayly (1997)
	Culicidae		*Aedes alboannulatus* (Macquart)	2	5	i		
		#	*Aedes (Finlaya) occidentalis* (Skuse)	2	0	i		
			Culicini sp	1	9			
	Ceratopogonidae		*Bezzia* sp 1	1	24			
			Bezzia sp 2	1	23			
			Other *Bezzia*	4	12			
			Culicoides sp	4	82			
			Monohelea sp 1	1	0			
			Atrichopogon sp a	1	2			
			Ceratopogonidae sp a	1	4			
			Dasyhelea sp	6	13		1	3
	Tabanidae		*Tabanidae*	1	48			
	Dolichopodidae		*Dolichopodidae*	2	49			
	Sciomyzidae		*Sciomyzidae*	1	6			
	Ephydridae		*Ephydridae*	3	64			
	Muscidae		*Muscidae*	1	35			
	Chironomidae	#	*Archaeochlus brundini* Cranston *et al*			a		
		#	*Archaeochlus* sp a			a		
		#	*Archaeochlus* sp b			a		
			Procladius paludicola Skuse	3	73			
			Procladius villosimanus Kieffer	1	29			
			Ablabesmyia notabilis Skuse	3	16			
			Ablebesmyia sp					1
			Paramerina levidensis (Skuse)	1	31			
		#	Tanypodinae sp a	1	0			
		*	Tanypodinae sp c	1	1			
			Parakiefferiella sp a	2	5			
		*	*Compterosmittia* sp a	1	1			
		#	*Botryocladius* sp h	1	0			
		#	*Gymnometriocnemus* sp f	3	0			
		#	*Allotrissocladius* sp m	2	0			
		#	*Allotrissocladius* sp l	6	0			
		#	*Allotrissocladius* spp			e	1	2
		#	*Botryocladius petrophilus* Cranston & Edward	1	0	j		
			Orthocladiinae spp					3
			Tanytarsus bispinosus Freeman	2	16			
			Tanytarsus sp a	2	59			
		*	*Tanytarsus* sp b	2	1			
			Chironomus tepperi Skuse	2	35		1	2
			Chironomus cf *alternans* Walker	4	56			
			Dicrotendipes cf "CA1" of Cranston	2	6			
			Dicrotendipes sp					1
			Kiefferulus martini Freeman	1	9			
			Polypedilum nubiferum (Skuse)	3	38			
			Polypedilum cf *watsoni* Freeman	1	4			
		#	*Paratendipes* sp a	4	0			?1
			Paraborniella tonnoiri Freeman	3	4	e		?1
			Cryptochironomus griseidorsum Kieffer	1	25			
			Cladopelma curtivalva (Kieffer)	2	36			
Mayflies	Baetidae		*Cloeon* sp	1	2			
True bugs	Veliidae		Veliidae	2	6			
	Corixidae		*Sigara mullaka* Lansbury		4		1	1
			Sigara sp	1	9			
			Agraptocorixa eurynome (Kirklady)	1	11			
			Agraptocorixa parvipunctata (Hale)	5	13			4
			Diaprepocoris personata (Hale)					1
			Micronecta robusta Hale	4	43			4
			Micronecta annae Kirkaldy					2
			Micronecta gracilis Hale	2	17			1
	Notonectidae		*Anisops thienemanni* Lundblad	6	36		1	5
			Anisops hyperion Kirkaldy	2	24		1	3

Appendix (continued)

Major group	Family	Taxon	Occurrence in				
			9 rock SAP sites	140 other SAP sites	Other studies, see below	9 rock sites of Bayly (1982)	17 rock sites of Bayly (1997)
		Anisops stali Kirkaldy		2			2
		Anisops baylii Lansbury		11			2
		Anisops gratus Hale		15			1
		Anisops cf *hackeri*				1	
Moth larvae	Pyralidae	*Pyralidae* sp	3	15			
Dragonfly nymphs	Coenagrionidae	*Ischnura heterosticta heterosticta* (Burmeister)	2	6			
		Xanthagrion erythroneurum Selys	1	22			
	Lestidae	*Austrolestes annulosus* (Selys)	1	40			
		Austrolestes aridus (Tillyard)	1	5			
		Austrolestes analis (Rambur)	1	14			
	Aeshnidae	*Aeshna brevistyla* (Rambur)	1	4			
		Hemianax papuensis (Burmeister)	2	30			
	Libellulidae	*Diplacodes bipunctata* (Brauer)	3	8			
		Diplacodes haematodes (Burmeister)	1	22			
		Orthetrum caledonicum (Brauer)	2	24			
	Hemicorduliidae	*Hemicordulia tau* Selys	7	43			
Caddisfly larvae	Leptoceridae	*Oecetis* sp	2	39			
		Triplectides australis Navas	6	35			

taxa known only from granite outcrops; * taxa for which granite outcrops represented >50% of SAP survey wheatbelt records; † protozoans not consistently picked for 140 other SAP survey wetlands; a, specimens and information provided by D Edward (The University of Western Australia), b, Wallwork (1981); c, Linder (1941); d, Geddes (1981); e, Jones (1971, 1974) and Edward (1964); f, equals *Rak stagnensis* nomen nudum of Bayly (1997); g, Frey (1998); h, Smirnov & Bayly (1995); i, Liehne (1991); j, Cranston & Edward (1999)