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COMPARATIVE ENDEMISM AND RICHNESS OF THE AQUATIC INVERTEBRATE FAUNA IN PEATLANDS AND SHRUBLANDS OF FAR SOUTH-WESTERN AUSTRALIA

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Abstract

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A study of the peatlands and shrublands in far south-western Australia was undertaken to examine patterns of endemism and richness in aquatic invertebrate faunas. Samples of surface water, interstitial water and crayfish burrow water were analysed from about 45 sites and in each season over a twelve month period in 1993. Six groups of aquatic invertebrates were chosen for more detailed analyses (mites, oligochactes, isopods, decapods, dipterans, and odonatans) and resolved to species level. For each species an assessment was made of its distributional status as either widespread and common, regionally endemic (to the south-west), or locally restricted to within the study region. Sites with high levels of local endemism were plotted geographically and their characteristics compared to other sites. The data are related to existing hypotheses concerning the depauperate nature of the freshwater fauna of the south-western part of the continent. It was found that such hypotheses need to be tempered by the role of salt in flowing systems, and the occurrence of hot spots of local endemism for freshwater fauna in the extreme south-west in non-flowing waters (and often subterranean habitats) where groups of non-insect invertebrate fauna show apparently elevated species richness.

Introduction

The inland aquatic biota of the south-western corner of Australia has been characterised as being one which displays a relatively high regional endemism, but a conspicuously depauperate richness. For instance the fish and invertebrate faunas of streams are said to be depauperate compared to the freshwater fauna of other temperate regions (Bunn and Davies, 1990). Bunn and Davies based their conclusions on comparisons of family or order level species richness of insects in south-western Australian streams, with those of south- eastern Australia. They proposed that three factors contributed to this reduced richness: the insular nature of the south-west, a previous history of aridity, and an extremely low level of primary productivity, and that these threc factors overrode a tendency for higher species richness in areas with a highly predictable climate.

The limnology of the extreme south-west is dominated by an ancient inland platcau which is topographically ill-defined with sluggish watercourses. Closer to the coast there is an area which is still relatively well vegetated, where higher rainfalls produce a steeper topography and more well-defined water courses. In fact the climatic gradients are steep in the far south-west, with rainfall of 1400 mm per annum near the coast diminishing to 400–500 mm on the inland plateau over 100 km away. Superimposed on these characteristics are trends in the ionic concentrations of the water. Inland in semi-arid areas salt has accumulated in the soil profile from millions of years of aerial deposition. In some places natural salt lakes have formed on old drainage lines. Elsewhere the salt has remained below the ground in the soil profile, and only recently become mobilised by rising water tables resulting from land clearance. All these features combine to give the south-west its unique riverine characteristics, first described by Morrissy (1974) for the Blackwood River. In general, the closer to the coast, the cooler the temperatures, the more rainfall it receives, the steeper thc countryside, and the fresher the water. In other words, the river systems in the south-wcst have reverse longitudinal profiles for temperature, geology, rainfall, topography and salinity.

Despite this conspicuous profile, the macroinvertcbrates from the Blackwood River in the south-west display little longitudinality in the fauna composition (Williams et al., 1991). The authors concluded that either the macrofauna might be a good deal more resistant and resilient

to salinity change than currently thought, or the present fauna represents the halotolerant vestiges of a previously more diverse fauna, most of which has been eliminated by rising salinities.

The findings of Williams et al. (1991), along with an understanding of the reverse longitudinal nature of rivers in the south-west, give reason to refine the hypotheses of Bunn and Davies (1990). Given that the latter authors dealt with the insects of flowing waters in their assessment of the depauperate nature of freshwater faunas:

- What role has salt in the landscape played to remove salt intolerant groups of species? Have salt flushes in riverine systems helped to eliminate (over geological time) such faunas? If so, one might expect vestiges of salt-intolerant biota closer to the coast, and possibly in non-flowing waters.
- Accordingly, is the fauna of non-flowing waters also depauperate? Bunn and Davies (1990) make no implication with respect to non-flowing waters. But would an examination of another group of habitats uphold the notions of high endemicity and low richness? If aridity was important then faunas that are able to evade aridity by retreating underground with the water should still contain evidence of past richness.
- Does the hypothesis apply to aquatic fauna other than insects? Bunn and Davies examined insect data, then equated these to invertebrates as a whole, as well as to fish.
- Does the hypothesis apply equally to all parts of the south-west? The theory implies that the south-west has been equally affected by aridity and low levels of primary productivity. If the south-west is homogeneous with respect to the effects of primary productivity, insularity and aridity on inland aquatic faunas then there should be no local endemic "hot spots" for aquatic fauna.

This paper aims to examine the above questions, by looking at the invertebrate composition (not just insects) in non-flowing surface and subterranean waters, and in an area which goes from high to relatively low rainfall.

Methods

The study was part of a survey requested by the Australian Heritage Commission to document the heritage values of peatlands and shrublands of the "Southern Forest Region" (SFR) of south-western Australia. The SFR is the administrative region of the Western Australian Department of Conservation and Land Management, approximately 170 × 130 km, which formed the boundary of the study (Figure 1). The region is dominated by karri forests, but many other forest associations and vegetation communities are found within it, including a diverse array of wetland types which occur extensively throughout the region (Wardell-Johnson and Horwitz, 1996 in press).

Forty-five wetland sites were sampled (Figure 1), being chosen if they conformed to one or more of the following characteristics: shrubland vegetation (where there was an impeded drainage), representativeness of geomorphological types (an attempt was made to sample the geographic range of geomorphologically variable wetlands), and wetlands with organically rich soils. In general non-flowing waters were sampled, although at wet times of the year some water flow occurred.

Three habitats types were selected for sampling wherever and whenever they occurred in wetlands: surface water, subterranean water in interstitial spaces (accessed through auger holes) and subterranean water in crayfish burrows.

For surface water habitats, samples were taken by a 125 µm mesh sweep net to include littoral emergent and submergent vegetation, benthos and the water column. Subterranean fauna was sampled entirely by siphon, then filtered through a 50 µm mesh. All samples were preserved in the field with addition of formalin to make up a solution of 5%. The volume of material collected by these sampling methods prohibited widespread sampling of microhabitats. Physicochemical attributes of water were measured prior to sampling each habitat, and environmental variables including nutrients, basic floristics, soils structure etc. were also taken (Horwitz, 1994).

All samples were washed and filtered through a sieve of mesh pore size of 125 µm, sorted under the dissecting microscope, specimens removed and stored in 75% alcohol and later identified to species level wherever possible (Horwitz, 1994).

The methods used resulted in an under sampling of freshwater fauna at all scales: regional variability was under sampled because many wetlands were inaccessible or unknown at the time of choosing sites; local habitat variability was under sampled because some wetlands had a diversity of wetland types (ie. swamp, pool, creek, lake), which were not all sampled; and microhabitat variability was under sampled because only one sample was taken for each type

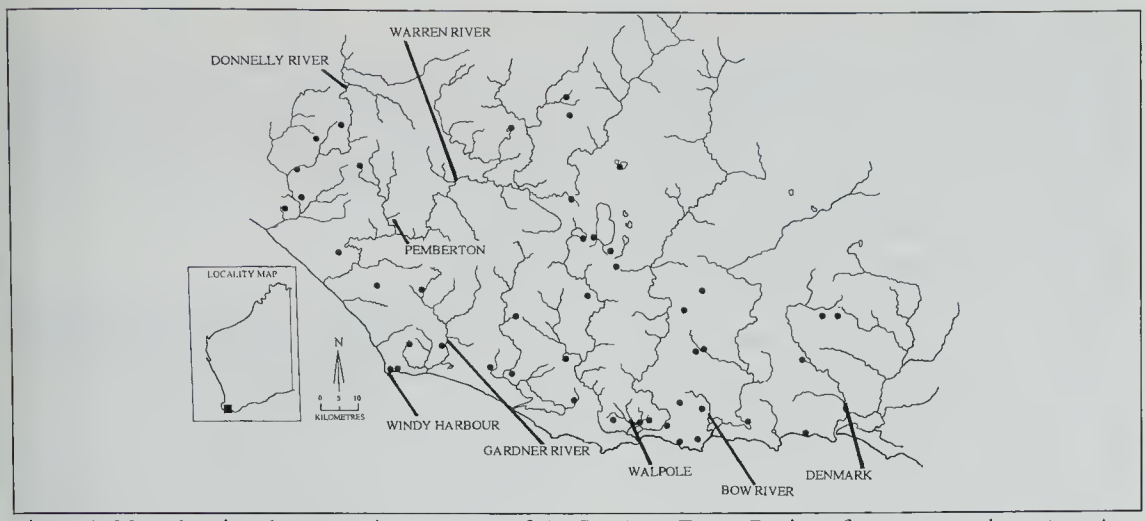

Figure 1. Map showing the approximate extent of the Southern Forest Region of extreme south-western Australia, with wetland sites sampled in this study, and locations of place names used in the text.

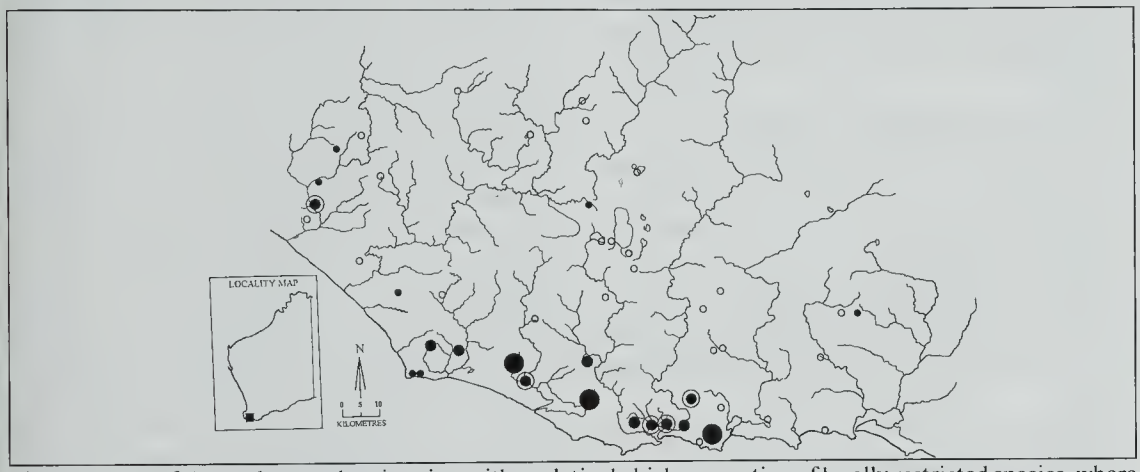

Figure 2. Map of the study area showing sites with a relatively high proportion of locally restricted species, where small dot = 1–5%, medium dot = 5–10%, medium dot ringed = 10–15%, and large dot = >15%.

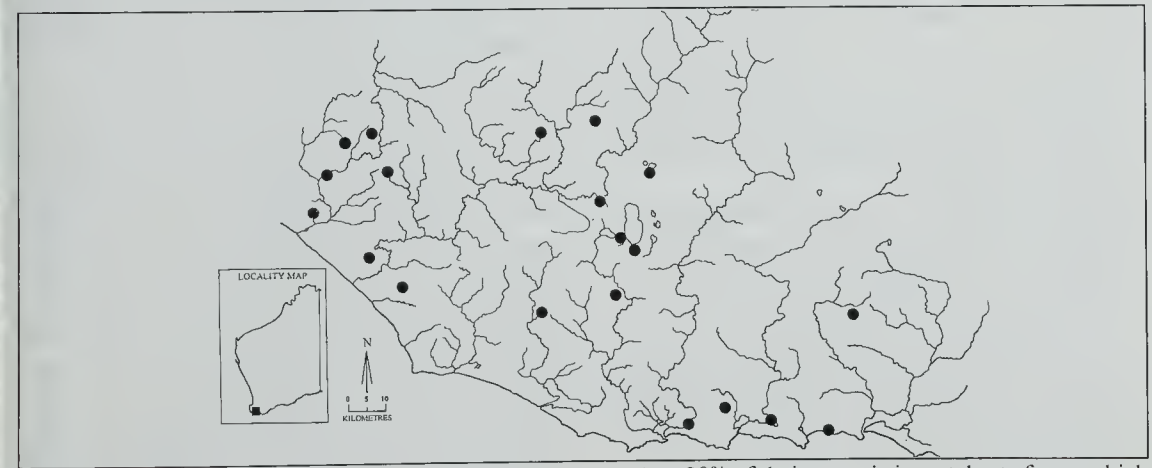

Figure 3. Study sites showing sites (solid circle) with greater than 20% of their aquatic invertebrate fauna which could be classified as common and widespread.

at each visit where possible (replicated sampling showed that one sample might result in somewhere between 40–70% of fauna present at that time (see Horwitz 1994)). In addition, the sampling methods were designed to capture very small animals since these were identified as potentially interstitial; therefore the methods selected for slower swimming fauna because the fine meshed nets clogged very quickly and faster swimming species could escape. For these reasons it can be assumed that the methods resulted in an underestimation of the local fauna at a site, so that an absence of a taxon at a site may not be real. Nevertheless, these limitations are common in regional surveys of this type, and such methods should be sufficient to indicate patterns in the relevant biota.

The faunal suite collected included all the known freshwater forms expected in a study of this sort, but in order to reduce the data set to a manageable form, several taxonomic groups were examined in detail to represent the fauna as a whole:

- a highly vagile group (Odonata);
- a group that is dominant in terms of biomass, with both vagile and restricted elements (Decapoda);
- the most diverse group (Diptera, in particular the Chironomidae);
- a group likely to contain taxa which show restricted distributions (Isopoda);
- a group whose larval stage is parasitic on other elements of the aquatic fauna (Acarina); and
- a group mostly wedded to the benthos (Oligochaeta).

With the assistance of taxonomic experts each species or taxon was categorised as belonging to one of the following status groups (where possible):

- Common — species or species groups which are known to occur across southern Australia (in both SW and SE Australia) and/or species which are known to occur outside the south-western Australia.
- Regional endemics — species proposed to be endemic to south-western Australia, either distributed throughout the south-west, or more restricted in distribution but not found exclusively within the study area
- Local endemics — species which are hypothesised to occur only within the study area. Taxa in this category are subject to the limitations given above.

Results

Table 1 shows the richness of each group and the number of taxa which could be apportioned to one of the three categories. Notes on the occurrence of taxa in each major group are given below; more details are available in Horwitz (1994).

Oligochaeta

Twenty three taxa belonging to five families were represented in the freshwater worm collections (Table 1). Enchytraeid worms were found at about two-thirds of the sites, but were unresolved beyond the family level. The Capilloventridae is monogeneric but the other three freshwater congenerics are restricted to south-eastern Australia (Pinder and Brinkhurst, 1994), so this represents the first find in the western part of the continent. It was found in sandy sediments of low shrublands. Eight phreodrilid species were found in the collections, none of them previously known from Western Australia. The phreodrilid fauna included two common and widespread species (*Insulodrilus nudus* and *I. lacustris*). Two species. *Insulodrilus* sp., and *Antarctodrilus* sp., occurred across the study region. Two further undescribed phreodrilids were relatively rare in the collections, being found only close to the coast between Gardner River and Walpole, and two more undescribed species (including an *Antarctodrilus* sp.) have similar distributions to the latter species but with one or more distributional outliers. Three distinctive species in the family Tubificidae were found (each from only one site), along with two forms of immature tubificid taxa. A new species in the genus *Ainudrilus* is the second freshwater species of this small genus, the other is known only from billabongs in the Northern Territory (Pinder and Brinkhurst, 1994). *Limnodrilus hoffmeisteri* is a very common species (and also known from one site in the Perth region; A. Pinder, pers. comm.), and was found once in the study area. *Telmatodrilus* ?sp. is morphologically similar to a Tasmanian species, and was found at only one site in interstitial water. In the family Naididae, three forms of the cosmopolitan genus *Pristinella* were recognisable, two of them relatively widespread, and one found at one site only. Five (otherwise geographically widespread; Pinder and Brinkhurst 1994) species were also recorded: *Pristina longiseta* from across the study area, *P. aequiseta* from one site only, *Dero furcatus* from four sites across the study region,

Table 1. Six groups of aquatic invertebrates which were examined in detail, showing the total number of taxa in each family. Where possible, each taxon was given a status category (see text; Common = common and widespread taxon, known to occur elsewhere in Australia, Regional E = taxon known to be endemic to the south-west but not restricted to the study area, Local E = taxon thought to be restricted to the study area). In most cases there were taxa which could not be assigned to one or other of the categories. For more details see text.

		Total No. Taxa	STATUS OF SPECIES		
			Common	Regional E	Local E
Oligochaeta	Capilloventridae	1			1
	Phreodrilidae	8	2	3	3
	Tubificidae	5		2	
	Naididae	8	5		
	Enchytraeidae	?			
	Total No.	23	7	5	4
Acarina	Arrenuridae	2	1	1	
	Aturidae	2		2	
	Eylaidae	1	1		
	Halacaridae	?	?		
	Hydrachnidae	1	1		
	Hydrodomidae	1	1		
	Hydryphantidae	2	1		1
	Hygrobatidae	2	1	1	
	Limnesiidae	1		1	
	Limnocharidae	1	1		
	Mideopsidae	1		1	
	Momoniidae	1		1	
	Oxidae	2	1	1	
	Pezidae	2		1	1
	Unionicolidae	3	3		
	Total No.	23	11	9	2
Isopoda	Janiridae	(2)		(1)	(1)
	Phreatoicoidea	?		?	?
Decapoda	Parastacidae	7		5	2
	Palaemonidae	1		1	
	Grapsidae	1	1		
	Total No.	9	1	6	2
Diptera	Orthocladiinae	24	8	2	1
	Chironominae	29	18	4	
	Tanypodinae	8	4	3	
	Aphroteniinae	2	2		
	Total No.	63	32	9	1
Odonata	Coenagrionidae	2	1		
	Megapodagrionidae	2		1	
	Lestidae	3	2		
	Gomphidae	1		1	
	Aeshnidae	3	1	1	
	Cordulidae	6	1	2	
	Libellulidae	5	3	1	
	Total No.	22	8	6	
	Totals	142	59	36	11

and *Dero digitata* from three sites with permanent water, and these species have also been found in wetlands on the Swan Coastal Plain. The fifth, *Chaetogaster diastrophus*, a globally widespread predatory worm, was previously known only from LaTrobe River in Australia, and found at one site. The most species rich site in the study contained 10 oligochaete taxa. The capilloventrid, and three of the undescribed phreodrilids were hypothesised to be restricted to the study area.

Acarina

The acarine fauna collected in the study area represented four suborders; of these only the known aquatic forms from the suborder Prostigmata were resolved taxonomically to genus or species. Twenty-three taxa were recorded, including:

- those endemic to south-western Australia: two new species in the family Pezidae (one of which is a new genus); *Wheenyoides cooki* (previously only known from two other locations); *Pseudohydryphantes doegi* found from one site, previously thought to have been extinct; and *Arrenurus* sp. near *tasmanicus* which is endemic but widespread in the south-west. Of these the new pezid genus, and *Pseudohydryphantes*, were regarded as locally restricted endemics.
- species in Gondwanan genera which are almost certainly endemic and restricted in their distributions, but not necessarily to within the study region (*Corticacarus*, *Axonopsella*, *Momoniella*, *Gretacarus*).
- species widespread in southern Australia (*Limnochares australica*) or species in a widespread genus in Australia (*Coaustraliobates*).
- species in cosmopolitan genera (*Hydrachna*, *Eylais*, *Hydrodoma*, *Diplodontus*, *Oxus*, *Frontipoda*, *Unionicola*, *Koenikea*, *Arrenurus*).

The most common taxon found in the collection was the halacarid mite, forms of which have also been found in cave material and on the Swan Coastal Plain (M. Harvey, pers. comm.). The richest site for water mites contained 11 of the 24 taxa.

Isopoda

Three main types of isopod were collected. Those belonging to the Oniscoidea are traditionally thought to be terrestrial rather than aquatic, but are regular components in some aquatic situations. Oniscoids collected in this study which came from crayfish burrows or auger holes are likely to have been fall-ins, but those from surface waters may be truly aquatic.

Phreatoicoidea were collected from wetland sites close to the coast between Bow Bridge and the Donnelly River, belonging to endemic species in the genus *Amphisopus*. Four taxa were found, including one described species (*A. annectens*) and three undescribed morphological forms (which may all be separate species, B. Knott pers. comm.). One of the forms was restricted to interstitial or crayfish burrow habitats in the Windy Harbour/Walpole region. For the purposes of determining their distribution status, *A. annectens* was deemed regionally endemic since it also occurred outside the study area, and the undescribed forms were collectively (and conservatively) considered to be one taxon which occurred only within the study area (ie. locally endemic).

Janirid isopods had not previously been recorded from south of Yanchep caves near Perth, although being widespread in south-eastern Australia. They were collected from 12 sites between Bow Bridge and Donnelly River in mainly coastal locations where their occurrence is thought to be associated with burrows of the crayfish genus *Engaewa* (at 11 out of 12 sites). A preliminary investigation of janirid isozyme electrophoresis using two populations in the study area, and two from outside the study are (one near Margaret River, and one near Yanchep), revealed that all four populations displayed large amounts of fixed isozymic differences in allopatry. A similar situation has been found in south-eastern Australia for these crustaceans (Horwitz, Andrew and Knott, unpubl.). Thus, two genotypes are recognised in this study, one from western sites near the Donnelly River; this taxon is deemed regionally endemic since it is likely to be found west (outside) of the study area (albeit still restricted). The second is regarded as locally endemic, and is located centrally.

Decapoda

The freshwater decapod fauna is represented by shrimps, crabs and crayfish. The shrimp "*Palaemonetes australis*" was collected from both coastal and inland sites with surface water. It is a widespread endemic species in the south-west. The crab *Leptograpsodes octodentatus* occurs in fresh or brackish areas on the southern coastline of Australia, particularly at contact zones between limestone and granite where freshwater seepages are established. Freshwater crayfish include the genera *Cherax* and *Engaewa*. Four species of the Australia-wide genus *Cherax* were collected: *C. tenuimanus*

(marron) from two permanent water sites, *C. preissii* (koonac) from most sites, and *C. quinquecarinatus* (gilgie) from eight sites. The fourth species, *C. crassimanus* is more restricted to the extreme south-western corner of the state, and was located at seven sites, principally those with organic rich soils. These species are all regional endemics.

The genus *Engaewa* is also restricted to the extreme south-western part of Australia. Three species were found in this study: *E. similis* was found in the western part of the region, around the Donnelly River; *E. subcoerulea* occurred at 8 sites between Gardner River and Bow River; and an undescribed species was located from two sites between Walpole and Bow River. The latter two species can be regarded as being locally endemic.

Diptera

One hundred and fifteen dipteran taxa were collected and identified, representing 12 commonly occurring families. Sixty three chironomid taxa were found. In distributional terms the taxa tended to fall into one of three groups:

- taxa generally widespread and common in the study region and beyond, including for instance *Lymnophyes pullulus*, *Chironomus* aff.*alternans*, *Cladopelma curtivalva*, *Dicrotendipes* sp. V47, *Tanytarsus* sp., *Procladius paludicola*, *Paramerina levidensis*, *Alotanypus dalyupensis*, Tanypodinae ?gen.?sp., Pentaneurini Genus C (previously only known from northeastern Tasmania);
- rare taxa from one, two or three sites, including: *?Limnophyes* sp.; *Stictocladius* spp. V35 and near V70, Orthocladiinae spp. VND1 and V15, *Cladopelma* sp., *Dicrotendipes ?conjunctus*, *Paratanytarsus grimmi*, *Polypedilum* nr. V33, *Stenochironomus* V27, *Aspectrotanypus* V9, *Aphroteniella tenuicornis* ; some of these taxa are common and widespread (like *P. grimmi*), while one could be regarded as truly rare and restricted, and Gondwanan in origin (*Stictocladius* sp. near V70) (Edward, pers. comm.); and
- taxa with disjunct, generally coastal distributions; for instance *Paratendipes* V12, *Polypedilum* spp. V3, near V3, and V33, *Riethia* spp. V4 and V5, and *Stempellina ?australiensis*.

Several of the taxa mentioned in the first two groups are common elements of the chironomid fauna found in eutrophic wetlands on the Swan Coastal plain (see Pinder et al., 1991).

Odonata

Twenty two taxa, including seven unidentifiable immature odonates, representing seven families and one subfamily, were collected. The most frequently collected species were *Austrolestes analis* (13 sites) and *Orthetrum caledonicum* (eight sites); most other taxa were collected at five sites or less. Odonate rich sites were invariably permanent water sites where sampling occurred amongst emergent or submergent vegetation. Synthemistinae were rarely found in crayfish burrows. No locally restricted taxa, and only five regionally endemic species were found (*Argiolestes minimus*, *Austrogomphus ?collaris*, *Austroaeschna anacantha*, *Procordulia affinis*, and *Synthemis cyanitincta*).

Discussion

Endemism, freshwater fauna and salinity

The category of locally endemic should be taken as an hypothesis which can be tested by detailed surveys for distributional points in subsequent studies, but should also serve as a focus for the regional importance of, and immediate conservation value of, freshwater fauna in the far southern wetlands. As described above, eleven taxa were regarded as being included in this category. It is therefore plausible to assume that approximately 8% at least of the freshwater fauna in the southern wetlands are locally restricted in distribution, and high in conservation value. These local endemics were not shared equally across all groups. Highly vagile groups of taxa (Odonata and Diptera) demonstrated low levels of local endemism, and groups with a perceived low vagility, which were apparently wedded to sandy, or organic-rich, saturated soils (ie. Oligochaeta, Isopoda and Decapoda) contained taxa which were hypothesised to be restricted in their distributions.

By geographically plotting the proportion of locally restricted taxa at any one site, Figure 2 shows that the highest proportions are found in the central, more coastal, sites of the study area. Inland, the potential for such species to occur still exists although less frequently in the data set. A high proportion of common species occur more at inland sites (Figure 3).

Although environmental predictors for the occurrence of endemic or common species are yet to be fully determined, it would appear that a site proximal to the coast, in the Walpole — Windy Harbour part of the study area is likely to harbour locally restricted endemics if those species exhibit an interstitial mode of existence.

This area corresponds to the highest rainfall part of the study region, and of the south-west in general. Wetlands here are influenced by all year round rainfall, with less seasonal water levels fluctuating near the surface in peatlands and shrublands, where such wetlands are frequently dystrophic. Fauna which require freshwater are more likely to be found in habitats which allow contraction to sediments to avoid less frequent and unpredictable aridity.

Further inland rainfall decreases, its seasonality increases, and the occurrence of saline wetlands increases. Indeed, the proportion of common species found at a site is significantly positively correlated with the (log of the) salinity of the surface water ($n=41$, $r=0.315$, $p<0.05$). These observations suggest that species which are common and widespread in the south-west are also those which are more likely to be able to tolerate seasonal rainfall and seasonal aridity, and saline waters of varying concentrations. Fauna requiring waters with a low ionic concentration of salts are unlikely to be found in inland wetland sites unless they are highly mobile and have other life history characteristics which enable them to capitalise on the sporadic occurrence of surface fresh waters.

Comparative richness

Seeking comparative information about the richness of groups in different areas is always fraught with methodological and taxonomic complications. An objective comparison can only be made where similar methods (particularly mesh size of nets), similar effort (with respect to seasonal sampling and habitats chosen), over a similar area with as many sites, are used. Taxonomic effort for each group must also equate. Realistically this is almost impossible to achieve. Perhaps the biggest obstacle for this study has been the absence of a similar-sized regional survey of these habitats from elsewhere in Australia, and the only recent emergence of a sound taxonomic basis for groups such as decapods, isopods, oligochaetes and acarines. Nevertheless, some comparisons are instructive.

For instance studies of the freshwater macroinvertebrate fauna of dune lakes of south-eastern Queensland and north-eastern New South Wales by Bayly et al. (1975), Bensink and Burton (1975), Arthington and Watson (1982) and Arthington et al. (1986) recorded only two oligochaete, six acarine, four decapod and no isopod species, yet 50 odonate species. Similarly, Timms' (1985) summary of species richness in the macrobenthic communities of a few maars and acid lakes in south-eastern Australia records low numbers of oligochaete and acarine species. The records of nine decapod species, 23 oligochaete and 23 acarine taxa in this survey from a temperate region of this size, cannot necessarily be regarded as "depauperate" for those taxa.

Conclusion

These data and speculations allow a refinement of the hypotheses of Bunn and Davies (1990), assuming that the component missing from the "depauperate" south-west is that which requires fresh water. Thus, periods of aridity and salinisation have contributed to a demise of taxa which live in waters with low ionic concentrations. Freshwater fauna in flowing waters will be vulnerable to extinction due to periodic flushes of saline waters from inland parts of catchments, increasing seasonality of rainfall and periodic aridity. Freshwater faunas of non- flowing waters have been forced to contract towards the coast where rainfall is less seasonal, where waters are more dystrophic, and where an interstitial habitat has been reliably available. In these areas, an endemism "hot spot", and indeed an apparently high richness in some non-insect groups, has been retained.

These notions are supported in part by the conclusions of Storey et al. (1993), who suggested that rotifers and microcrustaceans, with their drought resistant stages and poor dispersal characteristics, show high endemism and considerable radiation in coastal south-western Australian lakes, and that these coastal habitats probably provided refugia during arid periods.

In an unpublished report Main and Main (unpubl.) assessed and mapped the occurrence of fauna with Gondwanan affinity and therefore relictual status in south-western Australia. They argued that Gondwanan elements were likely to be found in, among others, high rainfall areas with short summer drought, areas adjacent to granite rocks from which water is shed, areas of impeded ground water flow so producing winter wet swamps, areas with southern or south-western aspect (thus sheltered from summer insolation), and sites with deep organic litter which gains moisture. While no evidence is presented here to demonstrate that the invertebrate species which characterise the southern "hot spot" are of Gondwanan origin, the concordance between the high levels of endemism, the dystrophic moist habitats, and the predictions of Main and Main, warrant both further research, and cau-

tious management activities which avoid enhancing seasonal aridity in the far south-west.

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