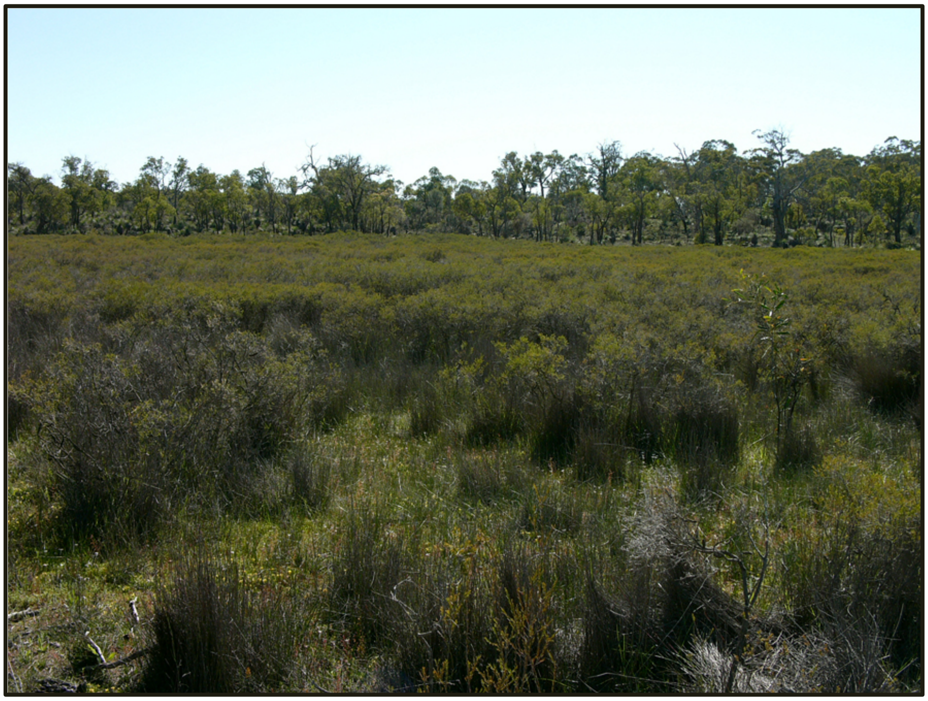
Invertebrate communities and hydrological persistence in seasonal claypans of Drummond Nature Reserve, Western Australia



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Summary

- This project aimed to determine the minimum hydroperiod required for invertebrates to reach stages that can tolerate or avoid drying.
- Aquatic invertebrate communities in the two Drummond claypans were sampled at regular intervals through a single filling event in 2011. An additional sample was taken in spring 2012 as part of the State Salinity Strategy monitoring program.
- The 2011/12 work increased the number of species recorded from these wetlands from 109 to 160. A notably high proportion of these are species with highly restricted distributions (including some possible local endemics) or which have otherwise been rarely collected. This project has further highlighted the very high conservation value of these wetlands.
- The data was also used to assess the wetlands against the single year and multi-year invertebrate biodiversity targets (as per Department of Environment and Conservation 2011). These targets were all met or exceeded.
- In 2011, almost all species, especially those that are resident rather than annual immigrants, reached a stage that could avoid or tolerate drought within 4.5 months after the wetland flooded. However, the 2011 hydroperiod was quite long (6 months) and shorter hydroperiods

are certainly a part of these wetland's historical hydrological variability. The wetlands were flooded for a much shorter time in 2010 but had a composition in 2011 not too dissimilar to that in 2004. There is a degree of flexibility in the life-cycles of many invertebrates inhabiting temporary waters, so that longer hydroperiods can be exploited and shorter hydroperiods survived, but this flexibility has limits. Results from studies of other wetlands suggest that if the Drummond wetlands were to have shorter hydroperiods more regularly then invertebrate diversity would decline. This would be due to depletion of resting egg banks for non-immigrating adults and less time for immigrants to reproduce. For the Drummond wetlands, 3.5 to 4.5 month hydroperiods in most years would be likely to maintain invertebrate communities within their current range of variation.

Introduction

The Drummond Natural Diversity Recovery Catchment, located 100 km north-east of Perth, was established in 2001 (Department of Environment and Conservation 2011). The conservation focus of the catchment is two seasonally inundated vegetated claypans, located within Drummond Nature Reserve. These support a Priority Ecological Community ('claypans with mid-dense shrublands of *Melaleuca lateritia* over herbs'), numerous rare flora and an invertebrate community with high diversity and a notably high number of rare or restricted species. These are herein referred to as the south-west (SW) and north-east (NE) wetlands.

Altered hydrology, through rising groundwater and/or climate change, is considered to be a major threat to these wetlands (Department of Environment and Conservation 2011). Rising groundwater has the potential to cause waterlogging, weed invasion, salinisation, nutrient enrichment and sedimentation in the south-west wetland. Reduced rainfall as a result of a drying climate may result in reduced frequency or duration of flooding but increased frequency of extreme events may also affect the claypans. The interaction between altered climate and rising groundwater on the wetlands' hydrology is unclear. Considering the potential impacts of altered hydrology and the possible need to manage water regimes, an action in the Drummond Natural Diversity Recovery Catchment Recovery Plan 2011–2031 (Department of Environment and Conservation 2011) was to "Determine tolerances and thresholds, that is EWRs, for the communities in the freshwater claypans …". As a contribution to this action, this project investigated the time taken for the aquatic invertebrate communities to develop during a winter/spring flood event, with an emphasis on determining the time between flooding and production of life-stages capable of tolerating or avoiding the dry summer/autumn period.

The composition and phenology of aquatic invertebrate communities in temporary waters is strongly influenced by hydrological regimes, as described by timing, predictability, duration and extent of flooding (Williams 2006). While all invertebrates that inhabit temporary waters have some drought tolerance mechanism(s), there is great variability in the duration of drought tolerated and the length of hydroperiod required. Some invertebrates, such as rotifers, can complete life-cycles within days whereas others require weeks to months. Some species can move in and out of dormancy without completing a life-cycle whereas others, once hatched or emerged, must produce a new generation before drying. In general, shorter hydroperiods and less frequent flooding result in lower species richness, largely through senescence and reduced replenishment of resting stages and reduced likelihood of colonisation (Wyngaard, Taylor & Mahoney 1991; Boulton & Lloyd 1992; Brooks 2000; De Block & Stoks 2004; Tavernini, Mura & Rossetti 2005; Waterkeyn *et al.* 2008; Siziba *et al.* 2013).

Methods

Field work

Conductivity, pH and water temperature were measured in the field with a calibrated meter (WTW 340i). Maximum depth of each wetland was estimated using a pole marked at 1cm intervals on each visit and depth of the north-east wetland was recorded twice daily by a depth logger. The logger doesn't register inundation until depth reaches 11.5 mm so very shallow water is not recorded. This is taken into account in the depths provided in Figure 1. Also, the beds of the wetland undulate so there can be small pools of water deeper than where the logger is situated. Rainfall was measured at 30 minute intervals by a rainfall station installed in the south-west wetland. Percentage areal cover of submerged macrophytes was estimated 'by eye'.

Invertebrates were sampled in both Drummond claypans on eight occasions between June 2011 and November 2011. Each sampling event consisted of two sweep net samples, each involving sweeping over about 10 metres of the wetland floor (for most dates) or 50 metres in late October (to provide one sample compatible with sampling in previous years). On each occasion, one 'benthic' sample was collected using a 250 µm mesh net to sample all habitats (e.g. open water, sediments, detritus, submerged vegetation), and a 'plankton' sample was collected using a 50 µm mesh net to sample the water column and submerged vegetation. These were preserved in the field and returned to the laboratory for processing. In 2012, the SW wetland was sampled once, in September, by using the standard 50 metre sweeps.

Laboratory work

The benthic samples were passed through 2000 µm, 500 µm and 250 µm sieves and the plankton samples were passed through 250 µm, 90 µm and 50 µm sieves. Each fraction (except the <90 µm fraction of the plankton sample) was sorted under a dissecting microscope. The <90 µm fraction contains only rotifers and protozoans (which were not identified in this project) and unidentifiable juvenile microcrustaceans.

Invertebrates were identified to species level where possible and notes made about maturity or reproductive state. Morphospecies names were assigned to undescribed species or to species that were represented only by immature stages that could not be associated with described adults. All identifications are consistent with previous DPaW projects.

The time taken to reach a drought-resistant life-stage could not be determined for all species. For some species, drought-resistant stages (such as ephippia in some cladocerans) were not observed (because it happened after we stopped sampling) or a transition from larvae to adult insects was not seen (e.g.

because it’s a terrestrial event). For some of these, proxies such as presence of late instar larvae or pupae were used because once adults are produced they leave the wetland. For some other insects only adults were observed. For cyclopoid copepods, the critical stage was deemed to be three weeks after first production of eggs, so that copepodites and/or adults from the following generation capable of aestivation would have developed (Maier 1989). Other species were only observed in very low numbers in one or two samples and timing of reproduction could not be determined. It is likely that some of the late arrivals didn’t successfully reproduce, but some of these may have already reproduced elsewhere and were dispersing. In a shorter hydroperiod they may never have colonised.

Data analysis

Non-metric multidimensional ordinations of invertebrate communities were produced using Primer v6.01 (Primer-E Ltd 2008) using presence absence data, including singletons and the Sorenson dissimilarity index.

Results and discussion

Water quantity and quality

Table 1 contains depth, conductivity, pH, temperature and macrophyte cover data for both wetlands during the 2011 study. Both wetlands were fresh for the duration of the study, but conductivity was generally higher early and late in the fill events. pH was about the same in both wetlands and showed little temporal pattern, other than being slightly lower in the NE wetland in June and July (<6). Water temperature was mostly 9 to 15°C but was higher in October and November (> 20 °C) which would have accelerated drying.

Figure 1 shows the timing of the 2011 flood event. The black line is data from the depth logger in the NE wetland and the circles are maximum depths measured during invertebrate sampling in the same wetland. In the NE wetland, a small amount of water was present in small depressions (≤ 140 mm deep) in early June (following 9 mm of rain a few days earlier), but those pools were semi-isolated and the water wasn’t detected by the depth logger. The depth logger registered some shallow inundation in early July (up to 50 mm depth), reflecting more widespread flooding in the basin, presumably from intermittent rain over the previous month (69 mm in June). Depth increased to just under 250 mm at the gauge on 11th July (after a further 44mm of rain between 1 and 10 July), but with the invertebrate sample taken over an area that included a slightly deeper area (300 mm). The depth of the north-east wetland remained between 350 and 400 mm between August and October and didn’t dry until mid- to late December. A short spike in depth in early December reflected the 19 mm of rain in the first week of that month, delaying drying for a week or so. The hydroperiod for the north-west wetland was thus about 6 months (early June to late-December). The flood event in the south-west wetland was similar, but with a slightly lower depth throughout (maximum 350 mm) and possibly an earlier drying. Data from 2004 to 2011 suggests that the north-east wetland tends to be deeper compared to the south-west wetland when sampled at the same time.

Table 1. Water chemistry and submerged macrophyte cover for the Drummond wetlands in 2011.

	South-west wetland							
Date	**7/06**	**12/07**	**30/07**	**16/08**	**13/09**	**11/10**	**25/10**	**22/11**
Depth (cm)	10	22	30	30	35	30	30	18
Field Conductivity (uS/cm)	400	109	104	122	134	139	148	202
pH	6.43	6.76	6.41	6.02	6.47	6.46	5.68	6.49
Temperature (^{o}C)	14.8	9.1	16.8	10.4	11.7	15.6	23.9	19.4
Submerged macrophyte cover	0	40	25	70	25	100	90	100

	North-east wetland							
Date	**7/06**	**12/07**	**30/07**	**16/08**	**13/09**	**11/10**	**25/10**	**22/11**
Depth (cm)	14	30	30	38	38	38	30	24
Field Conductivity (uS/cm)	123	201	142	122	337	220	255	477
pH	5.5	5.8	6.65	6.02	6.8	7.01	7.07	7.01
Temperature (^{o}C)	14.4	9.5	18.3	10.4	12.6	16.9	23.9	20.1
Submerged macrophyte cover	0	0	10	70	40	85	100	100

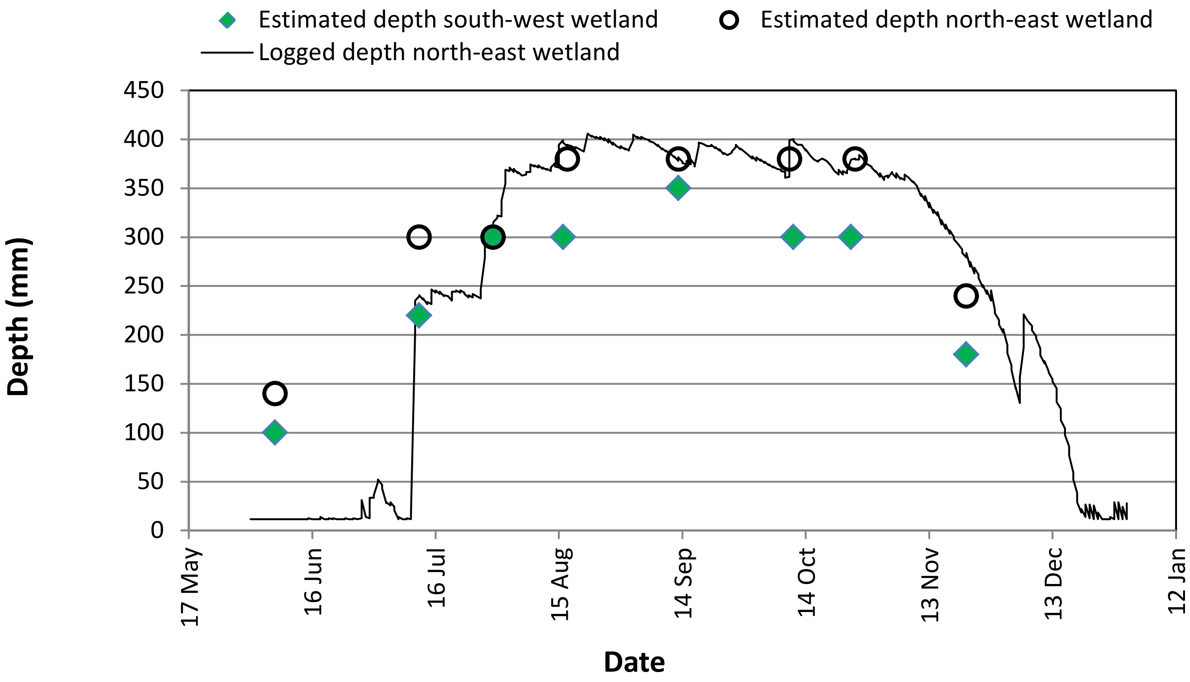

Figure 1. Estimated maximum depth within the south-west wetland (green diamonds) and the north-east wetland (black open circles) and depth from the depth logger in the north-east wetland (black line) during the 2011 fill event. Note that the baseline of 11.5mm is an artifact of the depth gauge setup.

Invertebrates

Diversity

Totals of 101 and 104 species of aquatic invertebrate were identified from the SW and NE wetlands respectively in 2011, with the combined total being 131. In October 2012, 46 species were recorded from the SW wetland, including three not recorded in either wetland previously. This brings the total number of species recorded from the SW and NE wetlands (from 2004 to 2012) to 119 and 129 respectively and the total from both Drummond wetlands to 160. These figures exclude rotifers and protozoans since they were not identified for the 2011 and 2012 samples, but 37 species of these have been identified from pre-2011 samples. These numbers also reveal considerable overlap in composition between wetlands and years.

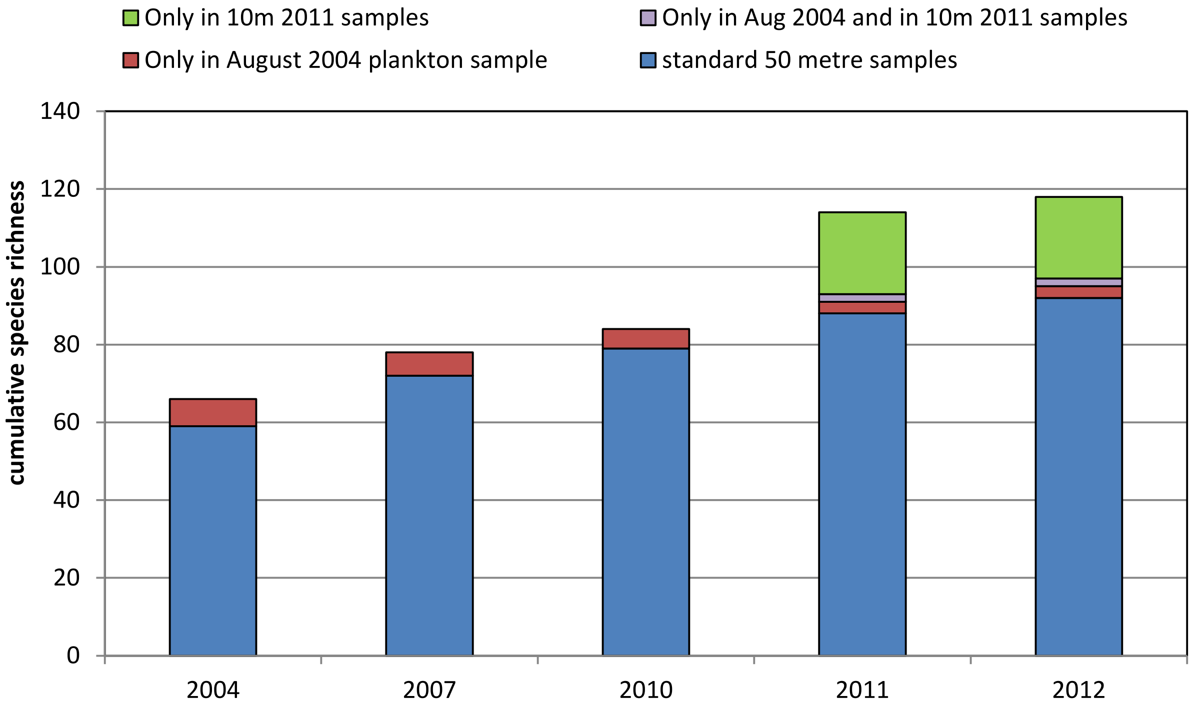

Figure 2. Cumulative species richness (excluding rotifers and protozoans) for the south-west Drummond wetland for collections between 2004 and 2012. Blue portions of columns are for standard State Salinity Strategy monitoring samples (one 50m benthic and one 50m plankton sample). Red portions are species collected only in a plankton sample collected in Aug 2004. Green portions are species collected only in the additional 10 metre samples collected in 2011 and purple portions are species collected both Aug 2004 and the additional 2011 samples.

Figures 2 and 3 show cumulative richness of invertebrates (other than rotifers and protozoans) in the SW and NE wetlands for sampling between 2004 and 2012. For samples collected as per standard State

Salinity Strategy invertebrate monitoring (50 metre benthic and plankton samples: blue portions of columns) there was a roughly linear trend of increasing cumulative richness between 2004 and 2011 in the SW wetland, but only four new species were collected in 2012. Fewer samples have been collected in the NE wetland but there was a similar trend between 2004 and 2011. The 10 metre samples collected in 2011 (green portions of columns) included an additional 22 and 33 species in the SW and NE wetlands respectively. Total cumulative richness was slightly higher in the north-east wetland, despite a lack of sampling in 2010 and 2012.

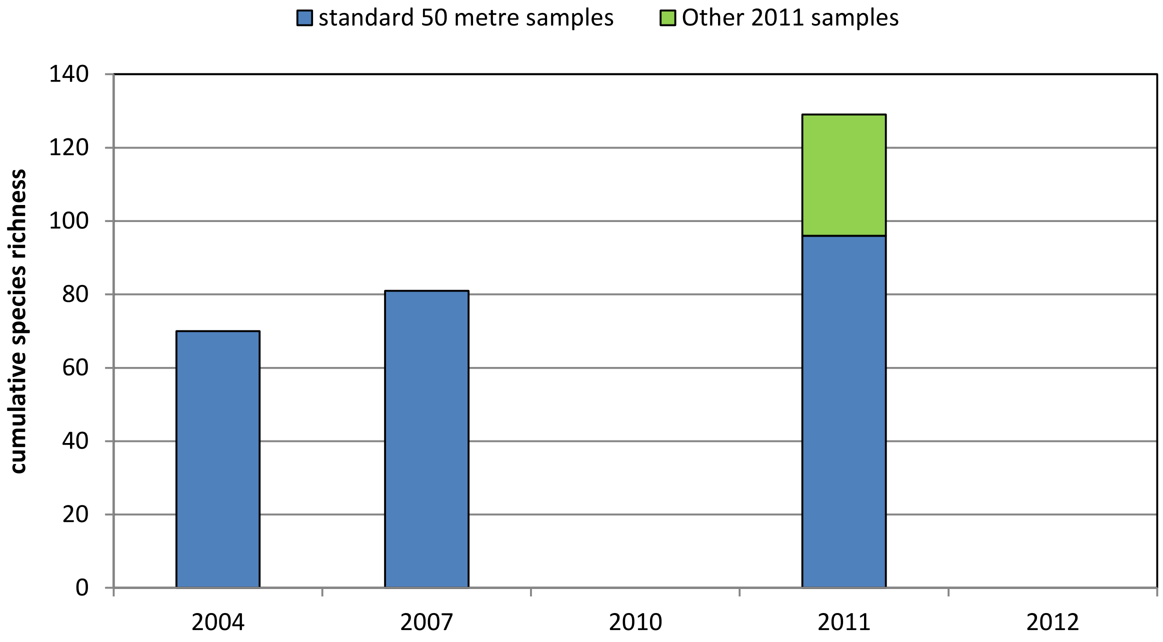

Figure 3. Cumulative species richness (excluding rotifers and protozoans) for the north-east Drummond wetland for collections between 2004 and 2011. Blue portions of columns are for standard State Salinity Strategy monitoring samples (one 50m benthic and one 50m plankton sample). Green portions are species collected only in the 10 metre samples collected in 2011. The north-east wetland was not sampled in 2010 and 2012.

In total, 52 species were collected in 2011 that had not been collected in either wetland previously. As might be expected, most (39 = 75%) of these were insects, which mostly immigrate to the wetland rather than remain as residents, so a different suite can arrive at the wetland each year. Furthermore, two of the twelve non-insects not recorded prior to 2011 were mites that may have arrived with the insects as parasitic larvae. Thus, the resident (non-immigrating) invertebrates have probably been well documented. It might be expected that the number of insects recorded using the wetlands would continue to rise with further sampling, although this was not the case in 2012, so it may be that the regional insect species pool capable of reaching the Drummond wetlands has also now been well documented.

Figure 4 shows the number of species in individual samples collected during late-winter and spring between 2004 and 2012, with samples coloured according to wetland and sample size and with depth indicated above the columns. There is no relationship with depth, but this would not be expected as richness is more likely to be associated with time since filling than with depth at time of sampling. Richness in 2004 was higher than for any individual sample collected subsequently. In August 2010 depth in the south-west wetland was only 60 mm and the sample was collected at that time because it was expected the wetland would be dry by the time of the usual spring sampling (the north-east wetland was already dry). The number of species present is much lower than for August samples collected in 2011 at a much greater depth (51 and 43 species for the SW and NE wetlands). In September 2007 depth was 200 mm in both wetlands, just over half the depth for the same period in 2011, but richness was not much higher than for 2010, suggesting the wetland had filled later than usual. These results highlight the value of knowing about the depth prior to the sampling event through use of depth loggers, which were not installed until 2010.

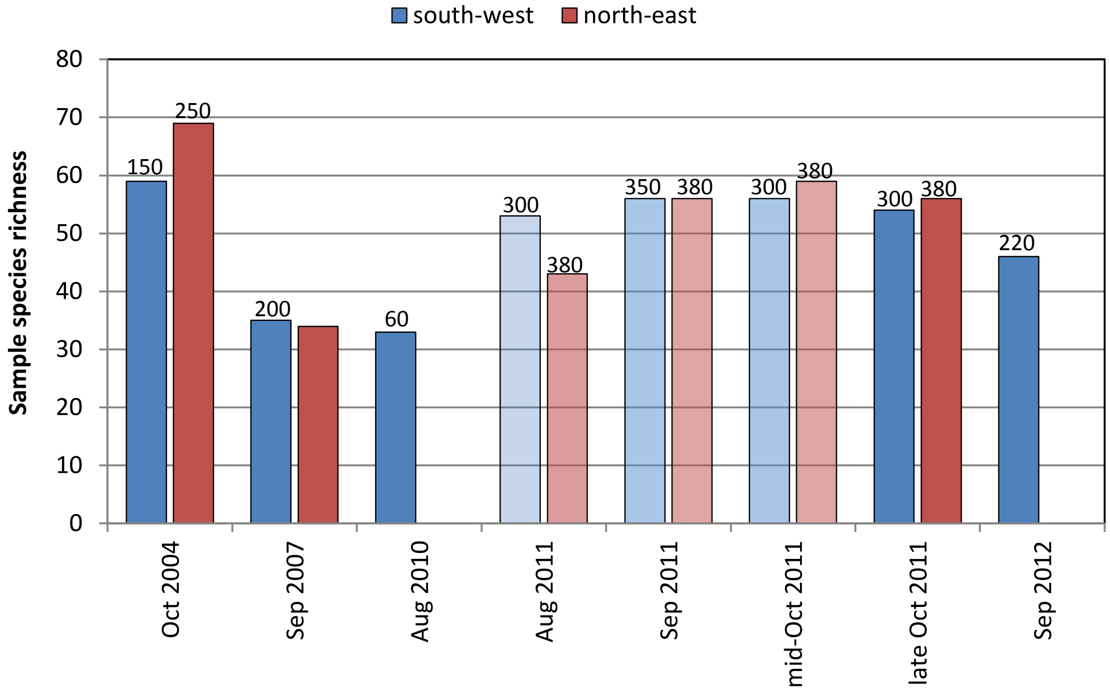

Figure 4. Species richness in samples (benthic plus plankton, excluding rotifers) collected from the south-west (blue columns) and north-east (red columns) wetlands during late winter and spring from 2004 to 2011. Numbers above columns are maximum depth (cm) for the same dates. Darker columns are for full sweep net samples collected over 50 metres and pale columns are for sweep net samples collected over 10 metres.

Figure 4 also shows that richness in the 10 metre sweep net samples collected in August to October 2011 (lighter columns) were comparable to most of the 50 metre sweep net samples collected in October 2004 and late October 2011 (darker columns). This suggests that invertebrate communities are sufficiently homogenous that the 50 metre samples may be a greater sampling effort than is required to document the aquatic invertebrate fauna of the small Drummond wetlands.

Community development in 2011

The pattern of species accumulation was about the same for the two wetlands, other than lower initial richness in June and July for the NE wetland (Figure 5 and 6). Cumulative richness increased throughout the season, but the rate of increase was higher early in the hydroperiod. While the rate of species accumulation declined during the season, there was no asymptote and in the NE wetland there was a jump in cumulative richness in November resulting from a late influx of insects. False negative records for species with very low abundance and inability to distinguish juveniles of closely related species may have resulted in an underestimation of the rate of increase in cumulative richness early in the study. Instantaneous species richness peaked at 56 and 59 (for the SW and NE wetlands) in September/October, 3 to 4 months after the wetlands filled. Instantaneous richness is higher than was reported for a temporary pond in Victoria sampled over 7 months by Lake *et al.* (1989): 33 to 45 species per sample but cumulative richness was lower (121 species in the Victorian pond).

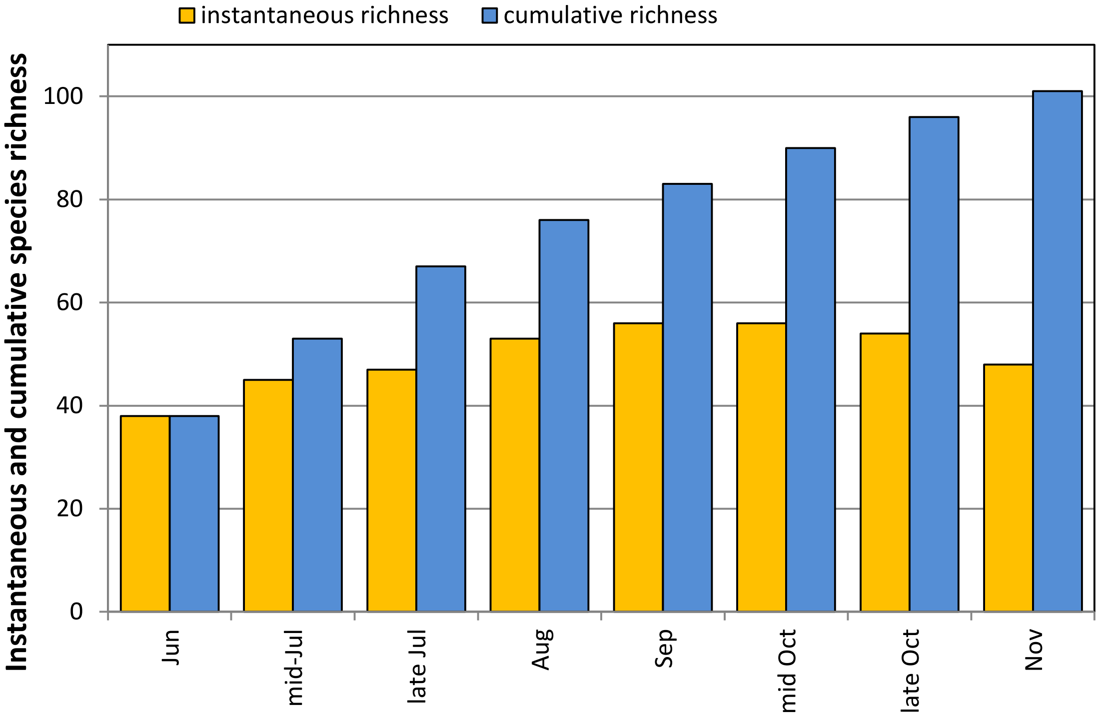

Figure 5. Instantaneous and cumulative richness of aquatic invertebrates in the south-west wetland of Drummond Nature Reserve June to November 2011.

One quarter of species occurred only once during the study (i.e. were singleton species). This is not unusual in aquatic invertebrate sampling. Hillman and Quinn (2002) sampled several permanent and temporary wetlands at weekly intervals and found 81 out of 289 taxa (28%) only in one of 72 samples. By contrast, only 17 out of 121 species (14%) occurred only in one sample in a temporary pond in Victoria sampled 12 times over 7 months by Lake *et al.* (1989), but sampling was more frequent and there was only a single small wetland.

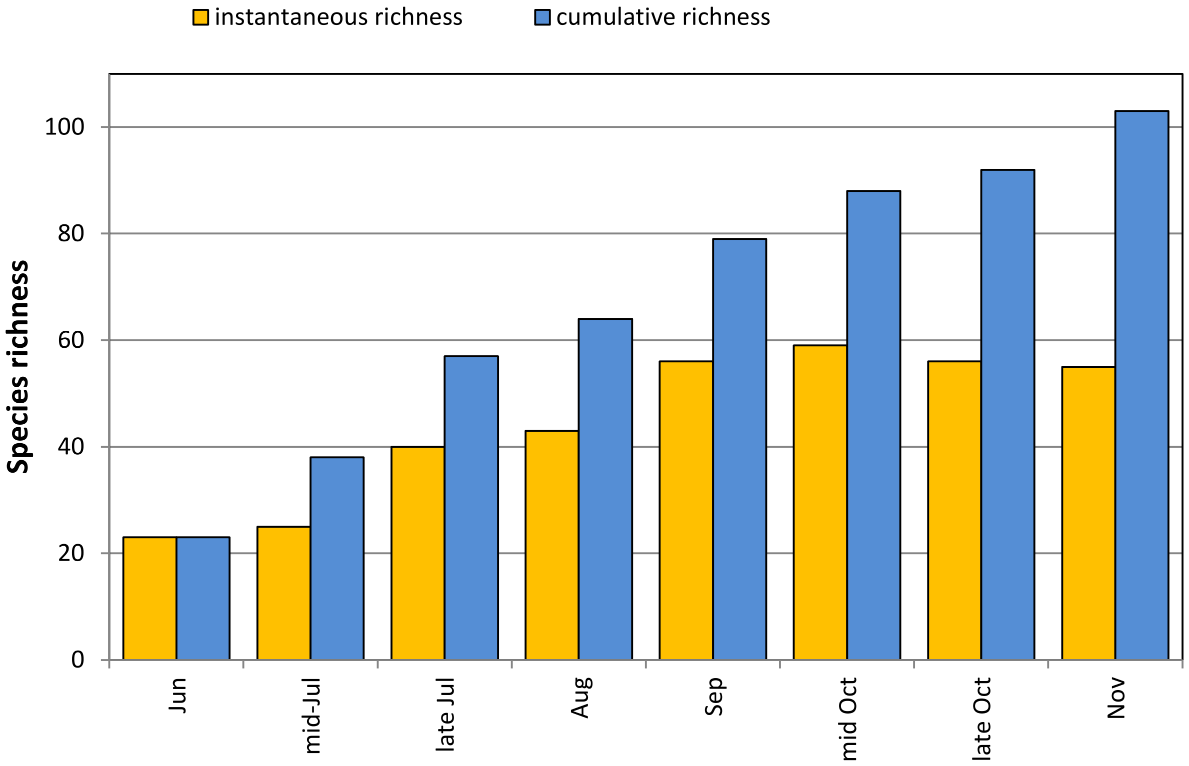

Figure 6. Instantaneous and cumulative richness of aquatic invertebrates in the north-east wetland of Drummond Nature Reserve June to November 2011.

A third of the singleton species were insects that seem to have arrived at the wetland late in the season, though many were collected as larvae indicating that the adults had arrived and laid eggs earlier. In a naturally shorter flooding event these late arrivals may not have been able to use the wetland at all (or at least not survived to maturity). Almost all of the 13 late-occurring species have either never been recorded at Drummond before or were previously only collected in 2004 when sampling occurred in October (not in 2010 and 2007 sampled in August and September respectively).

Only nine and five taxa were collected on all eight sampling occasions in the SW and NE wetlands respectively and this included nematodes and turbellarians which may have represented multiple species over time. Other species may have been present the whole time but missed on one or two occasions (e.g. *Acercella* n. sp. ‘absent’ only in September in the SW wetland). The proportion of species present in one or both of the first two sampling occasions and one or both of the last two sampling occasions was 18% for NE wetland and 23% for the SW wetland, indicating that these may have been present for most of the sampling period even when they were not collected.

Sampling artefacts aside, cumulative richness increased over the study period either through aerial colonisation or emergence from drought-resistant life stages. Of the newcomers in each sample, it might have been expected that insects would make up a larger proportion with each successive sample. This is because resident species that over-summered as a drought resistant stage would tend to emerge earlier in the flood event whereas there would continue to be an influx of insects. However, in both wetlands, the proportion of newcomers that were insects was initially high (53 and 64% for the SW and NE wetlands), then there was a decline to 22% and 13% in August, followed by increases to 100% by late October and a decline to 60% and 82% in November. Insects thus made up a substantial proportion of new species early in the flooding (before most resident species had emerged), but mid hydroperiod colonisers were being outnumbered by emerging residents. Later in the hydroperiod most residents had emerged and insects again dominated new species. There may also have been some limited colonisation by passively dispersing invertebrates, as was demonstrated by Jenkins & Buikema (1998) and Frisch and Green (2007) who recovered rotifers and microcrustacea from experimental ponds filled with rain or tap water. Colonisation in such cases would be by wind-blown propagules or transfer of resting stages by actively dispersing insects or waterbirds. However, very few of the non-insects had not been recorded previously so most of these would seem to be long-term residents that over summer in the dry wetland. Waterbirds have not been observed on the Drummond wetlands, but it would not be surprising if the occasional duck landed on the wetlands and brought in invertebrates (e.g. Green *et al.* 2008; van Leeuwen *et al.* 2012).

A non-metric multidimensional ordination (Figure 7) showed two main patterns in community composition. Firstly, the two wetlands had distinct communities, though community composition was more dissimilar earlier in the season. Secondly, there was a continuous and directional change in community composition, with greatest change happening early and, to a lesser extent, later in the study. At no point was a stable composition reached. Similar patterns were observed by Lake *et al.* (1989) for a temporary pond in Victoria and by Hancock & Timms (2001) for claypans in New South Wales. Hillman and Quinn (2002) also noted greater turnover in species composition in the first 6 weeks after temporary wetlands were artificially flooded. For those wetlands the water source was floodwaters coming from or through permanent wetlands, which brought in some of the initial colonizers, but the temporary wetlands always had a community composition that was different from the permanent ones.

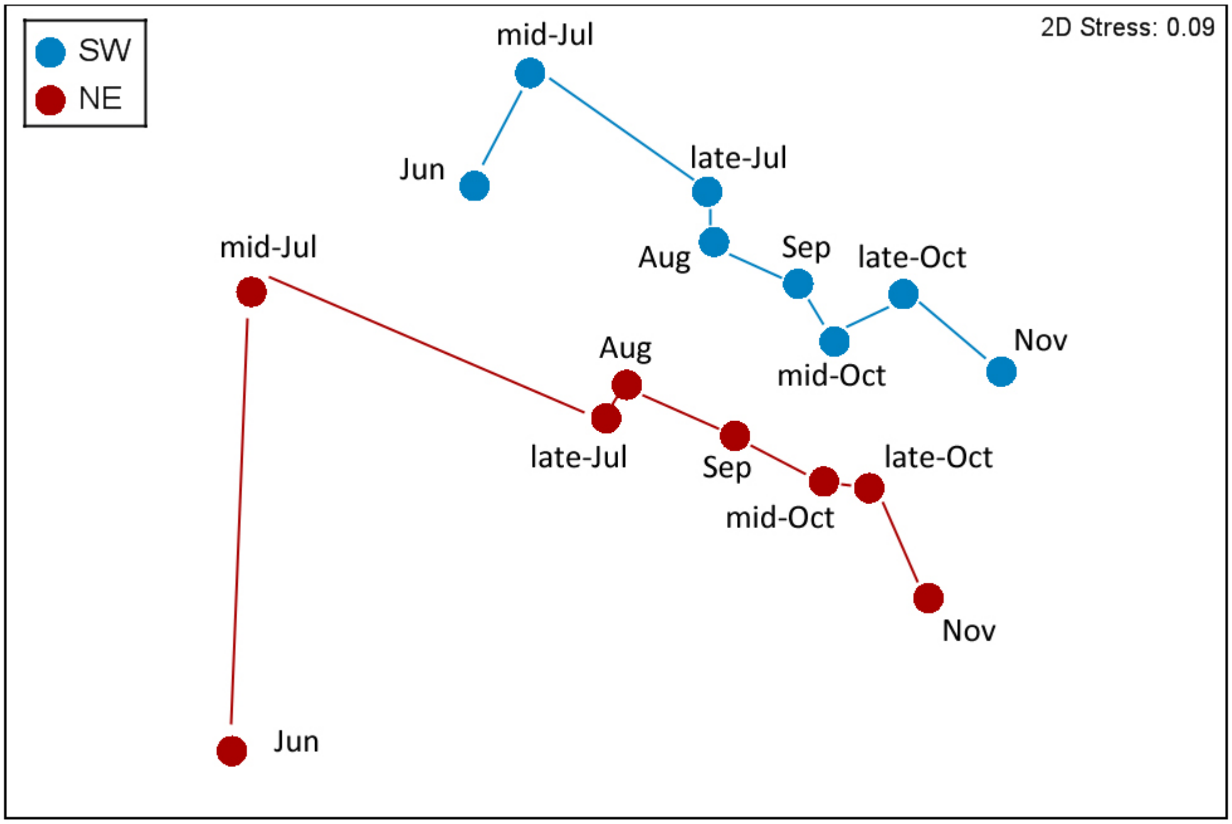

Figure 7. Two dimensional nMDS ordination of aquatic invertebrate samples from the south-west and north-east wetlands of Drummond Nature Reserve June to November 2011.

Figure 8 shows the results of a 2-dimensional ordination of all invertebrate data from October 2004 to September 2012. This plot shows the trajectories of change in community composition for the SW and NE wetland in 2011 (grey symbols), as in Figure 7, and samples from other years as coloured symbols. The 2011 trajectories roughly head from the top-left of the ordination (except for the June 2011 sample for the NE wetland) to the bottom right. There are clearly differences in composition between years, but if the 2011 trajectory is typical, then it suggests the 2007 and 2010 samples (green and blue symbols) were taken earlier in the hydroperiod whereas the 2004 samples (red symbols) were taken later. The September 2012 sample (yellow symbol) had a very similar composition to the September 2011 samples. In this figure, the symbols are scaled according to richness of the sample, which also suggests the 2007 and 2010 samples were collected earlier and the 2004 samples later in the hydroperiod.

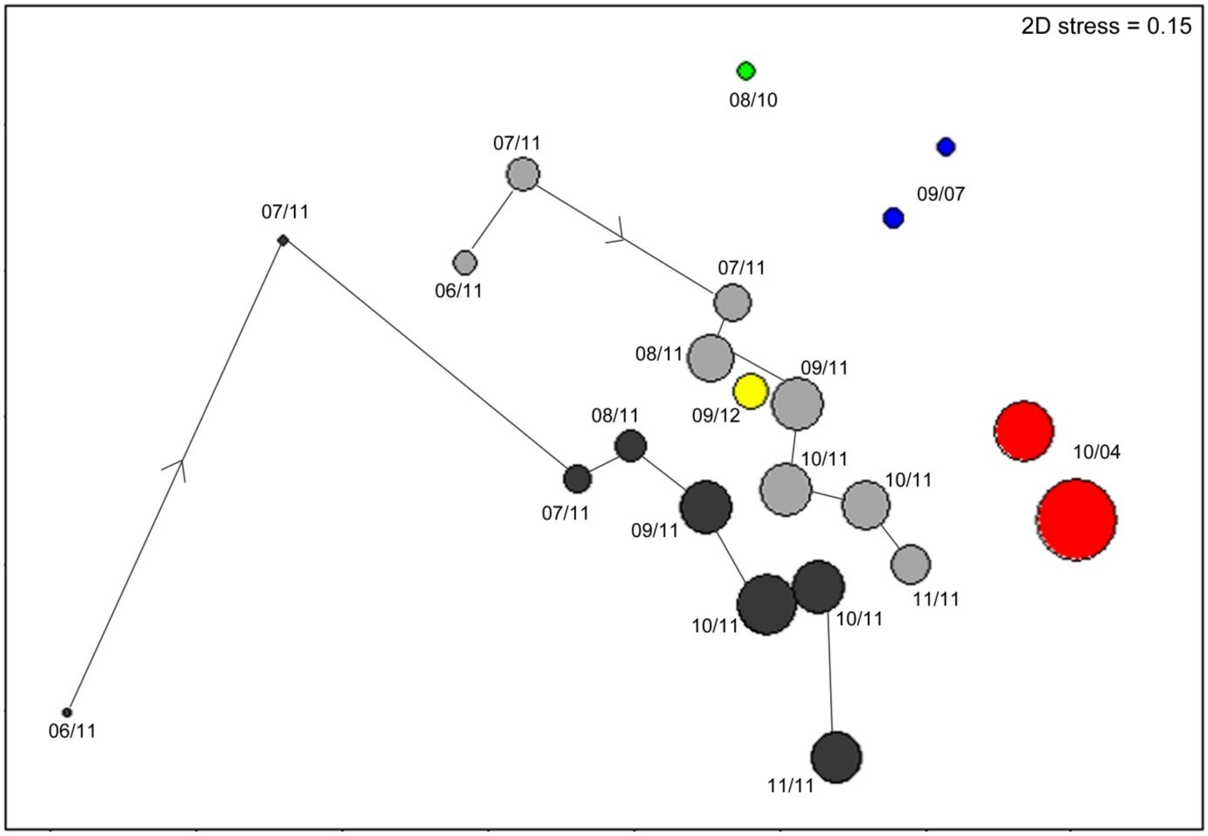

Figure 8. Two dimensional ordination of all invertebrate samples from October 2004 to September 2012. Samples collected in 2011 are in grey (light for the SW wetland and dark for the NE wetland) and samples collected in other years are in colour (red = 2004, blue = 2007, green = 2010, yellow = 2012). Symbols representing samples are proportional to the square of invertebrate richness.

Taxonomic notes

The *Arrenurus* water mite collected in 2004 and 2010 that had been called *Arrenurus* (*Micruracurus*) sp. 1 (a name otherwise applied to specimens from two sites near the south coast) is now thought to be a previously unrecognised species that we have called *Arrenurus* (*Micruracurus*) sp. 2. This was collected again in 2011 and 2012. It does not match any described species of Australian *Arrenurus* or other undescribed species in the DEC collection.

Another water mite, previously identified as *Acercella falcipes*, from both wetlands, is also a new species (Mark Harvey, WA Museum, pers. comm.). There are only two other species in this genus, one of which (*Acercella falcipes* Lundblad 1941) is widespread across southern Australia and is moderately salt-tolerant and the other (*Acercella poorginup* Harvey 1996) is known only from the Muir-Unicup wetlands.

The snails previously identified as *Gyraulus* (Planorbidae) have now been identified as *Glacidorbis* (Glacidorbidae). *Glacidorbis* is far less common than *Gyraulus* in south-western Australia. We have collected glacidorbids at only three other south-west wetlands (Nalyerin Lake in the Jarrah Forest, a wetland in Moore River Nature reserve and Lake Poorginup in the Muir-Unicup catchment), the latter of which was determined to be a new undescribed species by Winston Ponder (Australian Museum). The only species described from Western Australia is *G. occidentalis* Bunn and Stoddart 1985, but that was described from intermittent Darling Range streams and is smaller than the Drummond specimens. To date, this species has only been collected in the SW wetland.

Biodiversity target species

Pinder *et al.* (2011) identified a number of species, occurring in the Drummond wetlands, that typify communities of seasonal freshwater claypans in inland south-western Australia. Their sustained disappearance would therefore indicate a change in the character of the Drummond wetlands. These species are:

- *Lynceus tatei* (clam shrimp)
- *Bennelongia australis* (ostracod)
- *Paroster couragei* (beetle)
- *Berosus approximans* (beetle)
- *Calamoecia attenuata* (copepod)
- *Promochlonyx australiensis* (phantom midge)
- *Latonopsis brehmi* (cladoceran)

In the draft recovery plan for the Drummond Recovery Catchment (Department of Environment and Conservation 2011), these ‘indicator’ species formed the basis of one of the biodiversity targets, stated as:

> “No less than four indicator species should be present in any one wetland on any sampling occasion; no less than six indicator species should be present across both wetlands over a two year period; all seven indicator species should be present across both wetlands over a five year period.”

Table 2 shows the occurrence of these species in the Drummond wetlands between 2004 and 2012. Occurrence in 2011 is only for the late October 50 metre sweep net sample as this is the standard sampling effort in a normal year. On this date, all seven species were present in the north-east wetland and five were collected from the south-west wetland, meeting the target for a single wetland (≥ four species) for both wetlands. The beetles *Berosus approximans* and *Paroster couragei* were absent from the SW wetland but unidentifiable larvae of both of these species were present and adults of these species were collected on other dates in 2011. For both wetlands combined, the target of six species present over a two year period was met for two periods (2010-2011 and 2011-2012), as was the target of all seven species present over five years (2007-2011). In 2012, all seven species were present in the SW wetland (the NE wetland was not sampled).

Table 2. Occurrence of target invertebrate species in Drummond NDRC wetlands between 2004 and 2012. ? = immatures only so ID likely (since only 1 species ever recorded in these genera) but not confirmed. Totals reflect this uncertainty.

	2004 SW	2004 NE	2007 SW	2007 NE	2010 SW	2011 SW	2011 NE	2012 SW
Lynceus sp.	●	●	●	●		●	●	●
Bennelongia australis	●	●	●	●	●	●	●	●
Paroster couragei	●?	●?	●?	●?	●		●	●
Berosus approximans	●	●		●	●		●	●
Calamoecia attenuata	●	●	●?	●		●	●	●
Promochlonyx australiensis	●		●	●	●	●	●	●
Latonopsis brehmi	●	●	●			●	●	●
TOTAL	6-7	5-6	4-6	5-6	3-4	4	6	7

The Drummond wetland communities include an unusually high number of species that are presently known only from the Drummond claypans or otherwise from a few other similar wetlands, further highlighting the unique nature of these swamps. Some of these may also be claypan specialists.

Another biodiversity target could be based on the desire to protect these potentially rare and/or restricted species. These species are:

- ***Lecane* n. sp.?** (rotifer) – known only from Drummond wetlands.
- ***Cephalodella* n. sp.?** (rotifer) – known only from Drummond wetlands.
- ***Lacrymicypris* n. sp.** (ostracod) – known only from Drummond and one of only two species in the genus.
- ***Newnhamia* sp. DR4** (ostracod) – known only from Drummond.
- ***Macrothrix* n. sp.** (water flea) – known only from Drummond and one site in the Pilbara.
- ***Acercella* n. sp.** (water mite) – known only from Drummond, one of only three species in genus.
- ***Arrenurus* (*Micruracarus*) sp. 2** (water mite) – known only from Drummond.
- ***Aedes* (*Ochleratus*) sp. 5 ('dobaderry')** (mosquito) – otherwise known from Dobaderry Swamp.
- ***Glacidorbis* sp.** (snail) – potentially new and undescribed.
- ***Alona kendallensis*** (water flea) – known from very few other localities in WA.
- **Pentaneurini sp. A** (non-biting midge) – known from very few other localities in WA.
- **Pentaneurini nr genus V20** (non-biting midge) - known only from Drummond.
- **Orthocladiinae DEC sp. D** (non-biting midge) – from few other localities, including Goonapping.

The occurrence of these species in samples collected between 2004 and 2012 is shown in Table 3.

Table 3. Occurrence of rare/restricted invertebrate species in Drummond NDRC wetlands between 2004 and 2011. Dash indicates rotifers not identified.

	2004 SW	2004 NE	2007 SW	2007 NE	2010 SW	2011 SW	2011 NE	2012 SW
***Lecane* n. sp.?**	●		?			-	-	-
***Cephalodella* n. sp.?**	●					-	-	-
***Lacrymicypris* n. sp.**	●	●				●	●	●
***Newnhamia* sp. DR4**	●	●	●	●		●	●	●
***Macrothrix* n. sp.**		●						
***Acercella* n. sp.**					●	●	●	●
***Arrenurus* (*Micruracarus*) sp. 2**	●	●			●	●	●	●
***Aedes* (*Ochleratus*) sp. 5 ('dobaderry')**		●	●	●	●	●		
***Glacidorbis* sp.**	●		●		●	●		●
Alona kendallensis					●	●	●	●
Pentaneurini sp. A	●	●	●	●	●	●	●	●
Pentaneurini nr genus V20							●	
Orthocladiinae DEC sp. D								●

Notes on the occurrence of invertebrates by taxonomic group

Hydra (freshwater hydrozoids). Little is known about drought resistance of *Hydra* (Jankowski *et al.* 2008) but they are occasionally found in temporary wetlands that don't receive floodwaters, such as Pilbara claypans (Pinder *et al.* 2010) and seasonal wetlands in the south-west such as Fraser Lake (Cale, Halse & Walker 2004). In this study they were only recorded in November in the SW wetland, but since they are very small and easily overlooked they may have been present earlier. It is interesting to note, however, that they were not seen in samples collected in other years which were all taken in August to October.

Turbellaria (Flatworms). Both wetlands had two types of flatworms: a larger planarian (Tricladida) and a smaller microturbellarian. The former were most abundant and present on all sampling occasions and were egg-bearing in August (NE) or September (SW). Microturbellarians were present with eggs from mid-July in the SW wetland but not observed with eggs in the NE wetland. Both types would survive drying as eggs or cysts.

Nematoda (roundworms). These were present on all sampling occasions in both wetlands and survive drought as either eggs or as aestivating juveniles or adults, for many years in some cases. There may have been multiple species but they are particularly difficult to separate.

Gastropoda (snails). Two species of snail, *Glacidorbis* sp. (Glacidorbidae) and *Glyptophysa* sp. (Planorbidae), were present; the former from just the south-west wetland and the latter from both wetlands. *Glacidorbis occidentalis* Bunn and Stoddart 1983 is the only described species of that genus from Western Australia and occurs in intermittent streams in south-west forests (Bunn, Davies &

Edward 1989). Specimens from Nalyerin Swamp in the Jarrah Forest were also identified as this species but specimens from Lake Poorginup, in the Muir-Unicup catchment, may be an undescribed species (Pinder *et al.* 2004: id confirmed by Winston Ponder, Australian Museum). The Drummond specimens were slightly larger (1.5 mm) than reported for *G. occidentalis* (rarely > 1.2 mm). *Glacidorbis* have an operculum to seal the shell during drought and *G. occidentalis* survives summer drought by burrowing into the bed of intermittent streams of the Darling Range (Bunn *et al.* 1989). Female *G. occidentalis* brood the larval (veliger) stage in the body over summer and these are released after the snails emerge following the commencement of stream flow. In the SW Drummond wetland *Glacidorbis* were present in low numbers in June but were much more abundant by July, suggesting they emerged from aestivation more slowly than the *Glyptophysa* (see below). These early specimens were large and some were bearing veligers (presumably carried while aestivating over summer). Juveniles began to appear by August but most specimens were still very small in October and November. It is not clear when these could have moved to an aestivating state but it is probably flexible.

Glyptophysa lack opercula but secrete a mucosal coating over the aperture while aestivating (Richards 1963) and can breathe humid air. *Glyptophysa* were present as large adults in June, so presumably over-summered as aestivating adults, with juveniles not present until mid-September.

Polychaeta. *Aeolosoma*, in low abundance, were detected only in July and only in the SW wetland. They lack drought resistant life-stages, but perhaps survive as encysted animals in moist sediments or they may have been washed in from the catchment and not survived.

Oligochaetes (aquatic earthworms). Little is known about survival of oligochaetes in seasonal wetlands. It is likely that some survive as encysted adults (Montalto & Marchese 2005) or as embryos within cocoons, provided there is sufficient sediment moisture. These, and possibly other invertebrates, may also over summer in frog burrows, as has been shown for invertebrates in crayfish burrows elsewhere (Horwitz 1989). The frogs *Helioporus psammophilus* and *Helioporus albopunctatus* (both burrowers) are commonly recorded at both wetlands. *Ainudrilus* nr *nharna* is a sediment dwelling worm present on all sampling occasions in 2011 other than in June in the NE wetland. It has also been collected on all other sampling occasions so appears to be a resident species. It is either conspecific with or very closely related to *Ainudrilus nharna* Pinder and Brinkhurst 2000 which is known from other temporary wetlands in the south-west. Some specimens collected in mid-July had already mated (sperm present in spermathecae) and would have shed cocoons (containing fertilized eggs) shortly thereafter. Mated specimens were present for the rest of the study period. Two other species, *Pristina leidyi* and *Dero furcata*, can reproduce either asexually by budding or sexually. *Pristina* were present from July or August to November in 2011 and were collected in 2004 and 2012. These are crawling worms and, while they can occur in the interstices of coarse sediments and aquifers, they are probably not burrowing into the clay sediment at Drummond. No sexually mature specimens were seen and it is assumed they could have survived drying of the wetland at any time. *Dero furcata*, a burrowing species, was collected from September onwards, in the SW wetland only, and was sexually mature in October. It was low in abundance so may have been present, but undetected, earlier. Immature enchytraeids, which are mostly sediment dwelling worms, were detected only in July in the SW wetland. These may have been a terrestrial or amphibious species and have not been recorded in Drummond wetlands before.

Hirudinea (leeches). Glossiphoniid leeches were present only in the NE wetland in October and November 2011 and were recorded in the same wetland in October 2004. Glossiphoniids produce cocoons with embryos that may be able survive in moist subsurface sediments or in frog burrows. In 2011 only 1 specimen was collected on each occasion, so they are evidently rare and may have been present earlier but not detected. These feed on invertebrates so juveniles may have been brought in by flying insects, which may explain their late and infrequent occurrence.

Tardigrada (water bears). These were present between June and August in the SW wetland but only seen in July in the NE wetland. They survive dry periods either as eggs or as semi-dessicated adults (Williams 1980).

Acarina (mites). Five species of water mites (Hydracarina) and four other types of mites were detected. As adults, most mites lack specific adaptations for drought tolerance but subadult/adult aestivation is known (Münchberg 1952) and some species produce drought tolerant eggs. The larvae of most species are parasitic on other invertebrates, especially aerially dispersing insects, so can colonise wetlands via their hosts. *Arrenurus* (*Micruracurus*) sp. 2 were present from June (SW) or mid-July (NE) and were carrying eggs by late July. *Piona murleyi* was collected only once in each wetland, as immatures in June in the SW wetland and as egg bearing adults in August in the NE wetland. This species occurs in other temporary wetlands in south-western Australia. *Limnesia dentifera* were present from June (SW) or mid-July (NE), in both cases already with eggs. In the south-west wetland *Acercella* were juvenile in mid-June and not present as adults (albeit then also with eggs) until mid-July, whereas in the NE wetland this species did not appear until late July and did not have eggs until September. *Limnochares australica* was not detected until July and persisted until at least August (SW) or October (NE), although they were not abundant and none were observed with eggs. Of the non-hydacarines, the trombidioids (velvet mites), oribatids and mesostigmatids were detected from June or July to October (SW) or November (NE), but none of these was observed with eggs. Halacarids were collected only in July in the SW wetland. We have assumed that egg production is the critical stage for persistence of these species.

Calanoid copepods. Two species of calanoids, which lay drought resistant eggs, were collected: *Calamoecia attenuata* and *Boeckella geniculata*, both typical of freshwater seasonal swamps in south-western Australia. Both species occurred in the SW wetland but the NE wetland has only ever had *C. attenuata*. In the SW wetland immature calanoids were first observed in June, with specimens, of both species, mature enough to identify in late July. In this wetland the *Boeckella* were gravid in late July and disappeared from samples by October whereas the *Calamoecia* did not have eggs until August but then persisted until November. The *Calamoecia* in the NE wetland were first observed in late July and were also gravid by August and persisted until November. A similar pattern was observed in 2004 when mature *B. geniculata* were present in August but not in October whereas *C. attenuata* were absent (or not identifiable as such) in August but present in October. Earlier disappearance of some calanoids (two *Boeckella*) than others (a *Boeckella* and *Calamoecia*) was also reported by Lake et al. (1989). Hancock and Timms (2001) also found *Boeckella* maturing earlier (within two weeks of filling) than *Calamoecia* in claypans.

Cyclopoid copepods. Cyclopoids survive as aestivating adults or juveniles (copepodites) rather than as drought resistant eggs, so can emerge from the sediments and reproduce very quickly. Wyngaard et al. (1991) reported cyclopoids emerging within 1 day of inundation and completing life-cycles in two weeks during a short filling event in a temporary pond. *Metacyclops* cf. *laurentiisae* was present in June in both wetlands, already bearing eggs, but disappeared after August/September. This species was also present in August 2004 but absent by October of the same year, so it appears to be a species that emerges early but does not persist. *Mesocyclops brooksi* was present (and also bearing eggs) from June in the SW wetland, but in the NE wetland it was only present from late July and was not egg bearing until August. *Microcyclops varicans* appeared in July in both wetlands but were not egg-bearing until September in the SW wetland and no *M. varicans* with eggs were seen in the NE wetland. It is sometimes difficult to tell when copepods are reproducing because egg sacs are easily dislodged from the body during sample processing. We have assumed that each species was capable of diapause by the sampling occasion after eggs were first observed.

Harpacticoid copepods. *Canthocamptus* nr *australicus* was present on all sampling occasions in both wetlands and gravid females were present from July. This species would be resident and lays drought tolerant eggs. It was also recorded in 2004, 2010 and 2012.

Cladocerans (water fleas). This was the most diverse of the non-insects orders, with 18 species. To build up populations, cladocerans produce parthenogenetic eggs, that are not drought resistant. These hatch within the female's brood pouches. As conditions deteriorate, males are produced and mating results in drought tolerant embryos encapsulated within 'ephippia' that form a part of the female body and become bound in the sediment after the adult female dies. Patterns in species occurrence were quite different between the wetlands. Both wetlands had four species present in June, but with only *Diaphanosoma* cf *unguiculatum* common to both wetlands. Most of these early species then persisted for most of the season. Between late July and mid-October, an additional 1 to 5 species were added to the list per sampling event. A couple of species were not recorded until late in the season (*Neothrix armata* with asexual eggs and *Moina* cf. *micrura* without eggs, each only recorded once in the SW and NE wetlands respectively). These may have been present but undetected earlier. Most species had ovigerous individuals at, or shortly after, their first appearance and then persisted until October or November. Between the two wetlands only seven species were seen with ephippia, with four of these producing ephippia in both wetlands at the same time. Ephippia were first produced during September (2 species), October (1 species) and November, (four species). A male of an eighth species was found in October suggesting sexual reproduction had commenced. The rest presumably produced ephippia after sampling ceased in November as the wetland dried.

Ostracoda (seed shrimps). Most, if not all, of the ostracods occurring in the Drummond wetlands would be capable of producing drought resistant eggs, although adult diapause is a possibility where subsurface sediments remain moist. At least 12 species were present. In June, only unidentifiable immature animals were collected. In mid-July, *Candonopsis tenuis* was the only recognizable ostracod in both wetlands and in the SW wetland this already had mature gonads (testes and eggs clearly developing). By late July numerous other species were present but not mature, with composition differing between the two wetlands (with only *Ilyodromus* and *Cypretta* in common). In the SW wetland many were mature by August and most of the rest were mature by September, except for the largest species, *Lacrymicypris*, which matured in October. In the NE wetland, most species were also present by August, but did not mature until September or October. Most species were found in both wetlands, with the exception of *Paralimnocythere*, *Plesiocyprodopsis* sp. and *Candonocypris novaezelandiae* (NE wetland only) and *Cypricercus* (SW wetland only).

Conchostracans (clam shrimp). *Lynceus tatei* was present as small juveniles in both wetlands in June (which would have hatched from drought resistant eggs). These grew over the next 2 months, started developing eggs in August and these eggs were mature by September. *Lynceus* disappeared in late October in the NE wetland and in November in the SW wetland.

Lynceus clam shrimp with eggs collected in October

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Ceratopogonidae (biting midges). Some ceratopogonids can survive as larvae in moist refugia (Wiggins & Mackay 1980) or are able to withstand partial desiccation (Dodson 1987). Early instar *Culicoides* larvae were the only species present in June in the SW wetland and these persisted until September, although no mature larvae were ever observed. In the NE wetland, this species was observed only once as very early instars in July. In the SW wetland early instar *Bezzia* appeared in mid-July and some were at least 3rd instar by August and earlier instars were then again present throughout the rest of the study. *Bezzia* were present only as early instars in the NE wetland and only late in the season. *Dasyhelea* were observed only as early instars and then only in the SW wetland, but their absence between mid-September and mid-October might indicate emergence in late August/early September. In the NE wetland *Monohelea* were early instar in mid- July and late instar by late-July, with early instars present again (in both wetlands) by October (suggesting an intervening emergence as adults in August). *Atrichopogon* appeared late (and never as late instars) in both wetlands and *Forcypomyia* was observed only once as small larvae in both wetlands. Some of these patterns suggest initial colonization of one wetland, with emerging adults then colonizing the other wetland (e.g. for *Monohelea* and *Bezzia*).

Culicidae (mosquitoes). In the SW wetland, a few early instar *Anopheles* larvae, too immature to identify, were present in June and September, but larvae present in October and November were *Anopheles annulipes* and *Anopheles atratipes* respectively. In the NE wetland *A. atratipes* only occurred in mid-October, with unidentifiable very small larvae then present through to November. None of these specimens were late instar but mosquitoes can mature and emerge very rapidly so mature stages could have been missed. The only previous records of anopheline mosquitoes in the Drummond wetlands are of *Anopheles annulipes* in October 2004 and the genus was not recorded in 2012.

Some *Aedes* mosquitoes lay desiccation resistant eggs on the dry beds of temporary wetlands, which hatch upon flooding (Liehne 1991). Early instar larvae of *Aedes* were present in June in both wetlands, with most in the NE wetland identifiable as *Aedes ratcliffei*. By late July the latter had been replaced by *Aedes nigrithorax* and *Aedes alboannulatus* and those in the SW wetland were identifiable as *Aedes nigrithorax* and an undescribed *Aedes* otherwise known from Dobaderry Swamp (*Aedes* sp. 5). In the SW wetland the *A. nigrithorax* larvae were 4th instar in late July and this species, which is normally univoltine (Dobrotworsky 1965; Liehne 1991), was not seen in later samples. Pupae present in the same sample were probably this species as none of the *Aedes* sp. 5 were as developed. Fourth instar *Aedes* sp. 5 were present in September in the SW wetland, after which this species also disappeared. No mature Aedes were seen in the NE wetland but since all three species had disappeared by August it is presumed that they matured and emerged as adults between sampling events.

Chaoboridae (phantom midges). Small larvae of *Promochlonyx australiensis* were detected in very low numbers in June (SW wetland) or July (NE wetland). By mid-August to mid-September these had matured into 4th instar larvae and pupae. Both pupae and larvae continued to be present for the rest of the study suggesting continuous reproduction.

Ephydridae (brine flies). In the SW wetland ephydrid pupae were present in June indicating either over summer survival of larvae or pupae or rapid development from eggs (which may have survived over summer or been laid by immigrating adults shortly before or after flooding). A pupa of a second species (possibly dead before it was collected) was present in mid-July. In the NE wetland early instar larvae of this second type was present in September and October but no later instar larvae were seen.

Tabanidae (march flies). A large larva was present in the SW wetland in the June sample and smaller ones present from mid-July through to October, suggesting an early breeding and egg-laying. In the NE wetland, tabanids were present intermittently, but without any obvious pattern of synchronous development.

Stratiomyidae (soldier flies). Medium sized larvae were present from June to September but only in the SW wetland.

Tipulidae (crane flies). An early instar tipulid larva was present in June and another one in late July, but only in the SW wetland.

Sciomyzidae (Marsh flies). Larval sciomyzids, which feed on molluscs (Berg 1978), were collected only in October and November and only in the SW wetland. It is unclear how mature these larvae were. These also occurred late (November and February) in the study of a temporary Victorian pond by Lake et al. (1989).

Chironomidae (Non-biting midges).

Orthocladiinae. Orthoclad communities differed greatly in composition and development between the two wetlands. In June the NE wetland had three orthoclad species while the SW wetland had only an unidentifiable early instar. Commonalities between the wetlands include species V52 being present only in mid-July and Corynoneura V49 being present only from September to November. In the SW wetland sp. S03A/C was present from July and some were early 4th instar by August. In September no S03A/C fourth instar larvae were present, but they were present again in October, suggesting a bi- or multivoltine life-cycle. In 2004 orthoclad sp. SO3A/C were also present in August but not October. *Gymnometriocnemus* sp. was mature in mid-July (NE) to mid-August (SW) and present through most of the season. In the NE wetland *Paralimnophyes pullulus* were present in July and starting to mature by August whereas in the SW wetland they were present as early instars in October, were more mature (3rd instar?) in November and may have emerged as adults before the wetland dried in December.

Tanypodinae. Small larvae of Pentaneurini sp. A were present from June, some were early 4th instar by mid-July and 4th instar by late July. The other two tanypods didn't appear until later. *Ablabesmia notabilis* appeared in September and matured to 4th instar by October whereas *Paramerina levidensis* appeared in October and some were 4th instar by November.

Chironomini. Early instar *Paraborniella tonnoiri* were present in late July and were more mature by August (probably 3rd instar to judge from head capsule sizes provided by Jones (1974)), but then absent again until October. Jones (1974) found that desiccation resistant *Paraborniella* larvae became active in rock pools the day after rains, pupated the next day and adults emerged by day four. Similarly, Hillman and Quinn (2002) found this species in temporary wetlands within a week of flooding. Its absence at James Pool until July could mean that we missed its initial emergence from sediments and maturity in the days after flooding. In this case, the larvae collected in late July may have hatched from eggs laid by the first generation and these may have emerged and laid eggs which produce the larvae seen in October. This species was not collected from Drummond wetlands in previous years, despite collections being made at different times of year (August to October), so it is possible that it is not a persistent resident in the Drummond wetlands.

Tanytarsini. A mature *Tanytarsus fuscithorax* larva was present in the November sample and a different species (possibly morphospecies *Tanytarsus* sp. C) was present in the August sample, but this was early instar and not seen again.

Coleoptera (beetles). Several groups of beetles have aquatic larvae but almost all pupate on land. Adults emerge and find water to lay their eggs, either by entering the waterbody or laying eggs along the shore. Some families (e.g. dytiscids and hydrophilids) have primarily aquatic adults but even these can emerge from the water and seek other wetlands when conditions become unsuitable. Hydraenids are unusual in having aquatic or terrestrial adults but larvae that live on land near the waters edge. Beetles generally don't have drought resistant life-stages so adults would normally seek alternative wetlands when a wetland dries, although some aestivation of adults or larvae in moist refugia is likely (McKaige 1980; cited in Lake *et al.* 1989). Many of the beetle species were collected in a nearby farm dam by one of the authors (D. Cale) in 1998.

Seventeen species of beetles were collected; nine in the SW wetland and 12 in the NE wetland, with only six species in common. This strong difference no doubt reflects the fact that most, if not all, beetles would be annual immigrants. This means there can be multiple colonization events and so multiple asynchronous generations. *Berosus approximans* was present as adults from June or July but larvae were only seen from October. In the SW wetland, *Paroster* larvae were present in June and adult *P. couragei* were present in August, September and November. Larvae were present again from mid-September. In the NE wetland this species was present as adults on almost all sampling occasions and as larvae from August to mid-October. *Paroster* are strongly associated with temporary wetlands so probably mature from larvae to adults quite quickly. *Hyderodes crassus* were also present most of the time in both wetlands (from July) but never as adults. In the SW wetland these were not fully grown in September but had disappeared by October (presumably to pupate on the margins). This species matured to full size larvae in November in the NE wetland. In 2004, *Hyderodes* larvae were also present in the SW wetland in August but absent by October. *Limnoxenus zelandicus* was present only as larvae and for only a few weeks in each wetland. Both of these species presumably left the water to pupate. Larvae of scirtids, which have terrestrial adults, were present from July to November in the SW wetland and from September to October in the NE wetland. A few species were present only for very short periods and may not have reproduced at all. Some of these, *Megaporus* larvae were present in October and November in both wetlands indicating late arrival of adults that laid eggs but were not detected. *Enochrus* were present as adults in both wetlands but only in November so probably didn't reproduce. The *Hydraena* were present only as adults and only in June-July in the SW wetland, but their larvae live on the moist margins of wetlands so are unlikely to have been collected. Similarly, *Uvarus* were collected only as adults in the SW wetland between June and August, but *Uvarus* larvae are rarely collected (Watts 2002) and they may be using a habitat not sampled by sweep nets.

Odonata (damselflies and dragonflies). Seven odonate species were collected: the damselflies *Austrolestes analis* (Lestidae), *Austroagrion cyane* and Ischnura aurora (all Coenagrionidae) and the dragonflies *Hemianax papuensis* and *Adversaeschna brevistyla* (both Aeshnidae), Diplacodes (Libellulidae) and hemicorduliids that were always too immature to identify. Most odonates lay eggs in flooded wetlands, often in plant stems, and survive dry periods as adults or as nymphs in nearby permanent wetlands. A few species, including some *Austrolestes*, lay their eggs on dry sediment or in plant stems of dry wetlands (Watson, Theischinger & Abbey 1991), which then hatch upon flooding. However, there were very few nymphs present within two months of flooding, which suggests that egg laying mostly occurred after flooding. Early instar damselfly nymphs were present in late July, mid-instar *A. analis* were identifiable in September and by October mature nymphs of *A. analis* and *A. cyane* were present. In the NE wetland all three damselflies were seen but only in October and November and only *I. aurora* had reached full size by November.

A few very early instar dragonfly nymphs were collected in June, July and October, but these were not Aeshnidae (to which the later collected *H. papuensis* and *A. brevistyla* belong) and were not collected as mature nymphs. They may have been *Hemicordulia tau* which was recorded in this wetland in 2004. These may be the result of multiple or continuous egg laying events by aerial adults without successful maturation of nymphs (perhaps due to predation). Even nymphs recognizable as Aeshnidae in

September (SW wetland) were only 1st instar (2.5 mm long), with late instar *H. papuensis* nymphs then present in October and November. In the NE wetland, *A. brevistyla* were present from mid-October and late instar by late October.

Hemiptera (true aquatic bugs). Many bugs alternate between winged and wingless forms. Foregoing wing development can increase growth rates and fecundity in some species. Wingless adults plus a juvenile of *Microvelia oceanica* were present in June, suggesting that they hatched from eggs (perhaps laid in the previous year) very early. Juveniles (but not adults) were present in late-July. *Microvelia* were not seen again until they were collected as wingless adults and juveniles in October and winged adults and nymphs in November. That winged forms were produced only in November suggests they were preparing to leave the wetland (Anderson & Weir 2004). It is possible that winged forms could have been produced in October if the wetland had dried earlier.

Trichoptera (caddisflies). In the SW wetland a single early instar *Lectrides* larva was collected in October 2011. They were collected more frequently in the NE wetland from late July but no mature larvae were seen. Late instar *Lectrides* larvae were collected in October 2004 by Cale (2005) but no other caddisflies were collected in other years. In the NE wetland mature *Triplectides australis* larvae were collected in low numbers in September 2011 (and would have emerged as adults soon afterwards) and early instars were present in November.

Ecological water requirements

The composition of an intermittent wetland's invertebrate community is partly a function of current and recent past hydrological regimes and the landscape setting. The current hydroperiod influences survival of individuals that have emerged from dormant stages or colonised from elsewhere and recent past conditions have determined the composition of the store of dormant life-stages. The number, type and proximity of other wetlands in the landscape influence the mix of colonising species. For invertebrates, critical aspects of a temporary wetland's hydrological regime are that it is of sufficient duration on sufficient occasions to maintain the store of drought resistant propagules and to contribute to continued regional persistence of non-resident (migrating) species.

Temporary wetlands, especially in arid and semi-arid environments, tend to have highly variable hydrological regimes, to which aquatic invertebrates inhabiting them are strongly adapted. Drought resistant life-stages of some species can remain viable for consecutive dry years; decades in some instances (Hairston Jr. 1996; Brock *et al.* 2003), although viability declines over time. Some species employ bet-hedging strategies whereby only a proportion of dormant propagules will respond to any particular flood event or where hatching is staggered to preserve the propagule bank in case of premature drying (e.g. Angell & Hancock 1989; Vanoverbeke & De Meester 2009). For some species, life-history parameters (such as development times and number of generations) are sufficiently flexible to cope with variable hydroperiods (e.g. Ripley, Holtz & Simovich 2004; De Block & Stoks 2004). Other strategies include laying eggs at the water's edge to ensure that hatching will only occur during a similarly significant fill event. For many species, production of drought tolerant life-stages is triggered by conditions in the wetland rather than a fixed time interval. For example cladocerans will reproduce parthenogenetically while conditions indicate that water will persist for some time, but as changes in the wetland (such as increasing conductivity) indicate that the wetland is drying, males are rapidly produced and mating produces embryos encysted within hardened drought-tolerant ephippia. Factors such as temperature, photoperiod and food resources (which can themselves be affected by water quantity and quality) can also affect development times (Sarvala 1979; Vijverberg 1980; Abdullahi & Laybourn-Parry 1985; Johansson & Rowe 1999), so if temperatures are higher during a shorter flood event (due to shallower depth or a generally warmer season), then development time could be significantly shortened (albeit sometimes at the expense of fecundity).

However, while considerable variability can be coped with, persistent changes in hydrology, such as more frequent occurrence of shorter hydroperiods or altered timing of flooding, are likely to result in altered invertebrate communities over the long-term (Boulton & Lloyd 1992; Brooks 2000; Brock *et al.* 2003; Siziba *et al.* 2013).

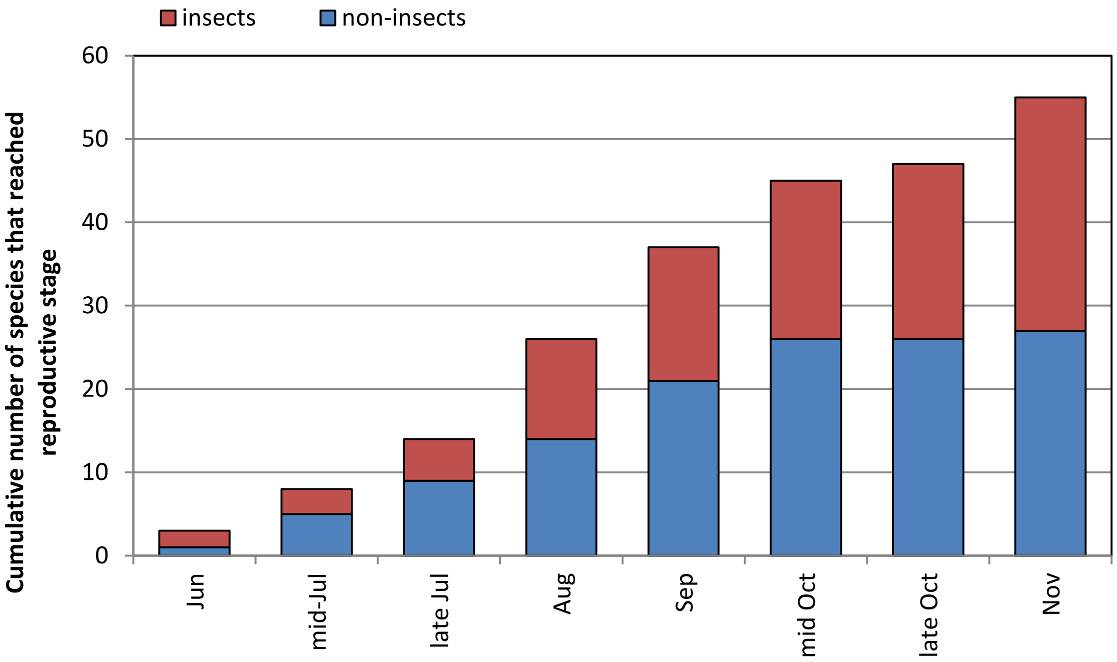

Figure 9. Cumulative number of species that had reached a reproductive stage over time in the SW wetland.

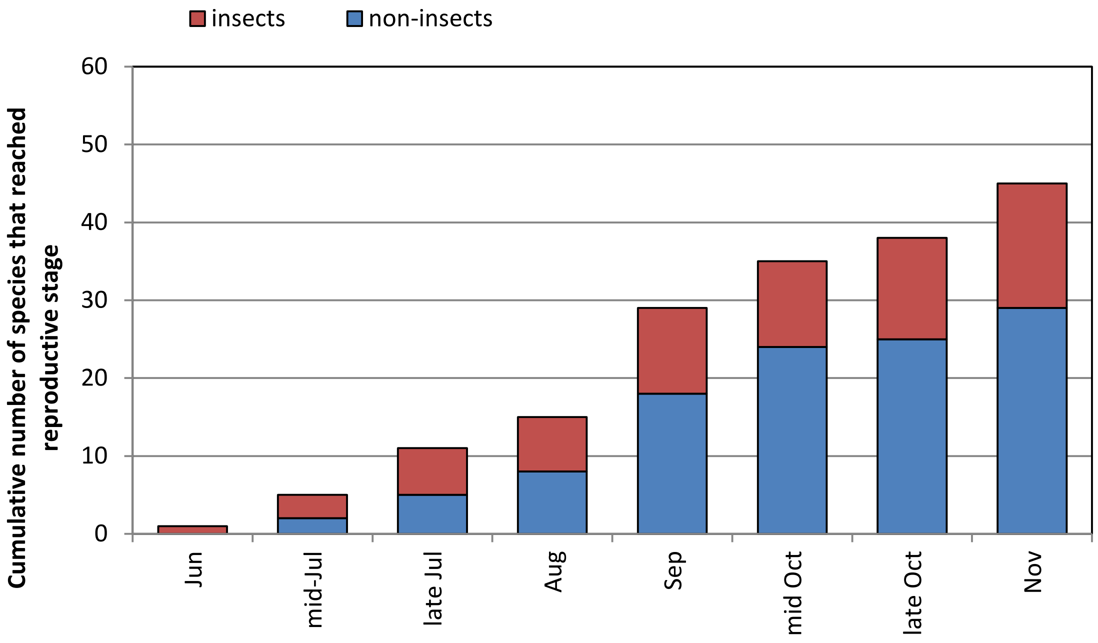

Figure 10. Cumulative number of species that had reached a reproductive stage over time in the NE wetland.

Figures 9 and 10 show the cumulative number of species that had reached a stage that could avoid or tolerate drying, where this could be known or assumed (which was for about half of the species recorded). About 85% and 84% (SW and NE wetlands) of those species whose drought-resistant stage could be identified or inferred had reached such stages by mid-October (about 4.5 months after filling commenced). For the non-insect species, those proportions were 96% and 83%. Very few additional non-insect species were observed to reach a drought resistant/avoidance stage after mid-October and most of those that did, were cladocerans producing ephippia (especially in the NE wetland, despite this wetland drying later). Of the late maturing insects most were late arrivals such as the *Megaporus* beetles and the dragonfly *Hemianax papuensis*.

This period of 4.5 months is the time between flooding and when almost all species had reached a drought resistant stage or were capable of leaving the wetland in 2011. However, as indicated above, life-history flexibility means that observed time to production of drought tolerant life-stages during a long flood event is not a good indicator of minimum hydroperiod requirement for many species. In particular, while some of the cladocerans produced drought tolerant ephippia in late October or November, even more would have produced them after the last sampling event as the wetland dried. Since production of these is a response to cues associated with drying, they would most likely have been produced earlier if the wetland had not persisted for so long. Considering this plasticity in development and life-histories, a somewhat shorter filling event (3.5 to 4 months) is probably adequate in most years. Furthermore, it is clear from the data that occasional much shorter filling events (such as in 2010) do not affect long-term community composition. Short hydroperiods or even non-filling in some years would certainly have been a component of past hydrological variability in these wetlands. Nonetheless, if these dry events were to become more frequent then community composition would change due to reduced immigration and reduced replenishment and viability of dormant drought resistant life-stages.

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