

Fringing trees may provide a refuge from prolonged drying for urban wetland invertebrates

Scott R. Strachan¹ · Edwin T. Chester¹ ·
Belinda J. Robson¹

Published online: 27 February 2016
© Springer Science+Business Media New York 2016

Abstract Climate change is causing prolonged drying in many seasonal wetlands, including urban wetlands, potentially affecting aquatic invertebrates that take refuge in wetland sediment during dry periods and thereby threatening wetland biodiversity. We collected sediment from two habitats: open water (OW) and fringing trees (FT), in eight urban wetlands after seasonal inundation had ended. Both habitats are inundated during winter–spring and dry in summer–autumn. Each sediment sample was divided into subsamples. One set of subsamples were inundated in the laboratory to test the hypothesis that emerging invertebrate assemblages would differ between OW and FT sediments. Another set of subsamples was dried, stored for a year, and inundated to test the hypothesis that prolonged drying would reduce the abundance and taxa richness of emerging invertebrates. The composition of emerging invertebrate assemblages differed between habitats, with more amphibious species found in FT sediment. Invertebrate responses to prolonged drying and storage varied among species: for some, effects depended on habitat type, while others delayed emergence or showed no response. Microcrustacean abundance was unaffected by drying, suggesting that their productivity during refilling may resist drier water regimes. Surface temperatures of dry sediment are cooler beneath FT, and this sediment has higher organic matter, holds more water and is less dense than OW sediment; and FT sediment remained cooler than OW sediment in the laboratory, despite the absence of shading. Fringing trees may therefore provide a refuge for some freshwater invertebrates relying on dormant stages in the sediment to survive drying in urban wetlands.

Keywords Aestivation · Desiccation · Hydroperiod · Refugia · Riparian vegetation · Temperature

✉ Scott R. Strachan
s.strachan@murdoch.edu.au

¹ Environmental and Conservation Science, Murdoch University, South Street, Murdoch, WA 6150, Australia

Introduction

Seasonal wetlands are a common freshwater habitat globally. When inundated, they provide habitat for a diverse range of waterbird, amphibian, reptile, fish and invertebrate species (Waterkeyn et al. 2008). When dry, the absence of surface water means that animals must either leave the wetland (being resilient to drying, Sim et al. 2013) or must rely on resistance traits to take refuge in wetland sediments (Strachan et al. 2014). Dormancy may be used by some invertebrate species to survive in dry sediments, while others have desiccation-resistant eggs (Boulton et al. 2014; Strachan et al. 2015). Many factors are known to affect the emergence of aquatic invertebrates from sediments, including the frequency, duration and timing of reflooding (Lake 2000), temperature, sediment moisture content, organic matter content, sediment particle size, and duration of the dry period (Stubbington and Datry 2013). Declines in the diversity and abundance of invertebrates emerging from sediments as the duration of drying increases have been observed in several studies (e.g. Larned et al. 2007; Datry et al. 2012). Also, Jenkins and Boulton (2007) found that for microinvertebrate egg banks, drying for a period greater than 10–20 years resulted in marked declines in species richness. In contrast, inundation every 2–3 years produced species-rich invertebrate communities. These studies suggest that prolonged drying may negatively affect the diversity of invertebrate assemblages emerging from wetland sediments, potentially reducing food supply to higher trophic levels and affecting re-establishment of wetland food webs when wetlands re-fill.

In addition to increasing air temperatures, climate change may cause reduced annual precipitation in many places. In southwest Western Australia reduced precipitation has already caused a decline in annual stream flow of up to 60 % (CSIRO 2011). A decrease in rainfall and runoff is also lowering the groundwater table (Boulton et al. 2014), which is the principal supply of water to many wetlands. Along with regional groundwater extraction for water supply, these processes are reducing inundation periods in urban wetlands (Sim et al. 2013). Connectivity to groundwater may cause patches of wetland sediment to remain damp (Strachan et al. 2014). Conversely, declining groundwater tables and increased air temperatures may increase sediment water loss. Together with prolonged dry periods, these factors may lead to sediment becoming drier and less able to support invertebrate resting stages.

Although many wetland invertebrates are known to use sediments as a refuge from drying, little is known of the effects of other environmental factors on the occupancy of, and emergence from, wetland sediment. Wetland sediments may vary substantially in their physical and chemical qualities. For example, seasonal wetlands may form on granite outcrops where the bed is stony (Pinder et al. 2000), in claypans where the bed is clay (Sharitz 2003) and on sandplains where the bed may be a mixture of sand and peat (Davis and Froend 1999). Each of these substratum types will have different physical and chemical qualities, such as: texture, capacity to retain water, structure when dry, electrical conductivity (EC) and pH. Variations in these qualities are likely to provide different opportunities for species taking refuge in sediments. For example, sediments with high organic matter content shrink as they dry, creating cracks in the sediment that may allow access to groundwater as a refuge for species (Strachan et al. 2014). Furthermore, many wetlands have fringing trees (FT) that shade the sediment during dry periods, as well as contributing organic matter to the sediment, potentially increasing its capacity to retain moisture (Rawls et al. 2003). In a basin-shaped wetland, sediment beneath fringing trees around the wetland perimeter is at higher elevation than sediment beneath OW in the centre of the wetland (Boulton et al. 2014). Therefore, sediment

beneath FT has a shorter inundation period than sediment from beneath OW. Nevertheless, FT sediment potentially provides a refuge for desiccation-resistant life stages of wetland invertebrates because it may be cooler and could retain moisture (Strachan et al. 2016). Although sediment from open water at the centre of a wetland is expected to have a longer hydroperiod, it will be exposed to higher temperatures when dry (Strachan et al. 2014), potentially exceeding the tolerances of some invertebrates and reducing the diversity and abundance of assemblages emerging upon inundation.

In this study, we compared invertebrate emergence from sediment from beneath FT with emergence from sediment from OW areas from eight urban wetlands sampled during the dry season. We hypothesized that sediment characteristics would differ between habitat types because of the large contribution of leaf litter and bark to FT sediment. Secondly, we hypothesized that assemblage compositions of emerging invertebrates would differ between habitats, and, since sediment moisture facilitates dormancy (Stubington and Datry 2013), that diversities and abundances of invertebrates emerging from OW sediment would be lower than in FT sediment. Thirdly, we hypothesized that the assemblage emerging from sediment dried for an unusually long period would have lower richness and abundance of invertebrates, and therefore changed assemblage composition. This was examined by manipulating the moisture content, drying and period until re-wetting of sediment taken from the field.

Methods

Study area

The eight wetlands sampled are located on the Swan Coastal Plain in Perth, south-western Australia (Table 1). All are seasonal wetlands (they fill in winter and dry in summer-autumn) except for Lake Joondalup West and Chelodina Swamp, which dry down to small central pools in autumn. All eight wetlands have at least 70 % of their perimeter fringed by a mature canopy of swamp paperbark trees (*Melaleuca raphiophylla*, Table 1) that provide dense shade. Generally, Swan Coastal Plain wetlands are shallow, groundwater-fed and underlain by sandplain (Boulton et al. 2014). Most are inundated for 6 or 7 months in winter–spring and dry out for 5 to 6 months in summer–autumn (Table 1), with strong seasonality and marked inter-annual variability characteristic of mediterranean-climate regions (Waterkeyn et al. 2008). The wetlands lie within regional parks and nature reserves managed for recreation and conservation in the metropolitan area of Perth (which has a population of around 2 million). Four of the wetlands (Joondalup West, Lake Booragoon, North Lake, Bibra Lake) receive stormwater drainage. The least disturbed wetlands were Chelodina Swamp and South Lake, which are surrounded by remnant bushland. Additional detailed descriptions of these wetlands, their hydrology, ecology and biodiversity may be found in: Davis and Christidis (1999), Horwitz et al. (2009) and Sim et al. (2013).

Field sampling

Six randomly-located replicate sediment samples were taken from within each of the two different types of habitat (OW and FT) at each wetland when surface water was absent from the wetlands in autumn (March–May) 2011. We collected samples from the top 10 cm of sediment using a trowel (newly deposited organic matter lying on the sediment surface was not collected).

Table 1 Wetland locations, historical inundation pattern for previous 3 years and fringing tree cover. Inundation was recorded monthly except for Booragoon Lake where it was recorded every 6 months (Government of Western Australia, Department of Water & Water Authority data base)

Wetland name and area	Location	2009 dry period and duration	2010 dry period and duration	2011 dry period and duration	Fringing tree cover (percent of wetland perimeter)	Average width of tree fringe (m)
Joondalup West, 529 ha*	S31°45.716' E115°47.391'	No record	No record	No record	70	260
Joondalup South, 529 ha*	S31°46.623' E115°47.738'	No record	No record	No record	80	80
Booragoon Lake, 12.3 ha	S32°02.629' E115°50.602'	May, >4 weeks	January–April, 3 months	May, >4 weeks	100	95
North Lake, 24.6 ha	S32°04.652' E115°49.348'	February–June, 5 months	January–June, 5 months	November 2010–June, 7 months	70	80
Bibra Lake, 188.7 ha	S32°05.450' E115°49.278'	March–July, 5 month	February–July, 5 months	December 2010–July, 7 months	80	200
South Lake, 31.5 ha	S32°06.227' E115°49.125'	February–July, 6 months	January 2010–July 2011, 17 months	Dry until July 2011	100	245
Forrestdale Lake, 247 ha	S32°09.640' E115°56.055'	January–June, 6 months	December 2009–July, 7 months	December 2010–June, 6 months	100	140
Chelodina Swamp, 3.3 ha	S32°04.286' E115°50.096'	No record	No record	No record	100	130

* Joondalup West and Joondalup South are part of the same system but separated by Ocean Reef Road causeway

The top 10 cm of the sediment is considered to be the source of most emerging invertebrates in wetlands (Brendonck and De Meester 2003). To determine whether sediment surface temperatures differed between habitat types, three HOBO data loggers (HOBO pendant temp/light, 64 k UA-002-064; Onset Computer Corporation, Bourne, MA, USA) were placed in OW habitat and three in FT habitat at South Lake; temperatures were logged every hour for the period for which the lake was dry (March–May 2012) until surface water returned. South Lake was chosen because it was the least disturbed of the eight wetlands.

Study design

Although it has rarely been documented, there is likely to be patchiness in the spatial distribution of dormant invertebrates and their propagules in wetland sediments. As we did not have data on propagule distribution for these eight wetlands, each sediment sample was divided into three portions by volume, immediately after field collection: one portion was immediately inundated, the second portion was dried and stored for a year before inundation (see experiments, below), and the third portion of each sediment sample was analysed to

describe physical sediment properties (see below). The advantage of subdividing the samples before applying experimental treatments was that the effect of the drying treatment on the emerging assemblage could be determined through comparison with the assemblage emerging from the damp, freshly sampled sediment. Furthermore, the effect of drying on the assemblage could also be directly related to the sediment properties of each sample. If, for example, the drying treatment caused mortality of the eggs of a particular species within samples, we would know that mortality had occurred, because the eggs in the other third of the sample, which were not exposed to drying, would hatch. In contrast, if we had collected samples for each treatment independently, we could not be sure that the reason for the absence of a species from the dried samples was simply that no eggs had been present in the samples prior to drying. However, the non-independence of treatments inherent in this design does have some drawbacks. In particular, a crossed design analysing habitat (2 levels) by experimental treatment (2 levels) could not be used to analyse the data, because the assumption of independence between treatments was violated. Instead, analyses were used that assume non-independence between treatments, or the difference between each pair of subsamples was analysed.

Sediment physical properties

A portion of each sediment sample was dried in an oven for 12 h at 50 °C and placed in separate jars, then distilled water was added in increasing proportion by weight: EC (mS. cm^{-1} at 25 °C) was measured at 1, 2, 5, 10, 20, 50 % to determine the relationship between EC and moisture content. Salinity and pH were also measured to detect any dissolved ions released from the dried sediment into the distilled water. The bulk density relationship was determined by placing a known weight of dry sediment into a jar and measuring the occupied volume (Gordon et al. 1992). The ability of the sediment to retain water was also measured by adding water to the point of saturation and then slowly drying the sediment at 40 °C, measuring the water loss by weight every 6 h for 180 h. The organic content of the sediment was determined by loss on ignition (ten grams of sediment heated for 500 °C for 6 h). All sediment properties, except organic matter content, were calculated for each replicate sample individually. Organic matter measurements were repeated twice for each replicate sediment sample and the results averaged.

Laboratory experiments

To test the first hypothesis, that different invertebrate assemblages would emerge from the two habitats (OW, FT), a 500 mL subsample from each field sample was placed in a 900 mL wide-mouth jar and flooded with distilled water. Open water sediment was heavier than FT sediment because it had a higher sand content: 500 mL of OW sediment weighed ≈ 200 g whereas 500 mL of FT sediment weighed ≈ 100 g. Distilled water was used because it did not introduce biological (Boulton and Lloyd 1992) or chemical contaminants to the experiments. Jars were placed in random order on a laboratory bench beneath large windows that provided natural lighting, and left for 10 days, at which time water containing the emerged invertebrates was decanted from the sample and filtered (125 μm mesh). Fresh distilled water was replaced into each jar. The invertebrates were then live picked and preserved in ethanol for counting and identification to the lowest possible taxonomic level. Decanting was repeated at days 20 and 30. A 30 day duration was chosen as sufficient to stimulate hatching and emergence in most species, based on similar studies (Jenkins and Boulton 2007; Larned et al. 2007; Chester and

Robson 2011; Datry et al. 2012). These studies all used similar methods of inundation with non-chlorinated water, decanting and filtering with the exception that, as in Jenkins and Boulton (2007), samples were not aerated because the sediments were from lentic rather than lotic habitats. No turbidity or anoxia was observed in jars. Sediment temperatures were measured throughout the experiment using iBTag G data loggers (iBTag G, Thermodata Pty Ltd, Brisbane, QLD, Australia). Loggers were placed on the surface of six randomly chosen OW and six randomly chosen FT sediment samples and six loggers were also placed on the surface of the bench as a control. These logged temperature hourly throughout the experiment. Upon conclusion of the experiment, sediment was preserved so that any remaining invertebrates could be collected and identified. Sediments were filtered (125 μm mesh) and then examined under a microscope, but no additional invertebrates were found upon examination of the preserved sediment.

The third 500 mL portion of each sediment sample was dried under halogen lights (diurnal pattern of 12 h on/off) in foil trays until an EC of zero was reached in all samples; this took 14 days. Trays were randomly repositioned under the lights every 3 days to ensure similar exposure. Following drying, sediment samples were stored in the dark at 18 °C for 12 months and then were inundated and sampled using the same experimental methods described above. Although this treatment was intended to test the effect of prolonged drying on invertebrate emergence, (where drying was sufficient to remove all water content from the top 10 cm of lake bed sediments), the treatment was probably harsher than field conditions, because events such as dew-fall or summer rain were excluded. Furthermore, storage in the dark is an artificial condition as lake bed sediments would be exposed to UV light and heat. These effects thus make the experimental results a very conservative test of species abilities to survive drying, and application of the results to field conditions must be interpreted cautiously.

Data analysis

Mean maximum daily temperatures were calculated using logger data for the two habitat types (OW, FT) in South Lake. As a measure of daily variation in temperature, squared differences were calculated for 12 h lags (i.e. intervals with the highest negative correlation) for each logger, within each habitat type; the averages of these were then analysed using t-tests. For the laboratory temperatures, the average hourly temperature from each habitat was determined.

To test the hypothesis that sediment characteristics differed between habitat types, a two factor ANOSIM (habitat, 2 levels: OW, FT; wetland, 8 levels) was used based on a Euclidean distance matrix of the sediment variables (Table 2). A PCA ordination was carried out on the Euclidean distance matrix to identify the variables separating the habitats and wetlands.

Invertebrate assemblage data was pooled across the three sampling times to represent total emergence over 30 days. Using Primer vers 6.1.12 (Clarke and Warwick 2001), data were square-root transformed and Bray-Curtis similarity matrices calculated. Then, to test the first hypothesis, a two factor crossed ANOSIM (Factor 1, habitat, 2 levels: OW, FT sediment; Factor 2: wetland, 7 levels: all wetlands except North Lake) was carried out for both treatments, separately. A crossed design was used because both habitat types were present in all seven wetlands. By using this design, we assume that the effect of habitat is expressed independently of wetland, that is, we expect the effect of trees on sediment and other physical conditions to be large enough to overwhelm wetland-to-wetland differences. The use of wetland as a random factor (below) enables us to assess the effect of wetland-to-wetland variation on emerging assemblage. North Lake was omitted because so few individuals

Table 2 pH range and average sediment properties for each wetland and habitat type. Water retention potential was determined by the gradient from the line of best fit of these data, i.e. grams water lost per hour at 40 °C

Habitat	Wetland	pH	Conductivity (mS. cm ⁻¹ at 25 °C)	Water retention potential (g.h ⁻¹ @ 40 °C)	Density (g.cm ⁻³)	Organic content (%)	Water saturation (%)
Open water	Joondalup West	6.76–7.11	0.68	−0.011	3.65	3.6	40.74
	Joondalup South	5.50–6.98	3.35	−0.008	1.20	34.2	181.35
	Booragoon Lake	4.87–5.96	18.51	−0.007	1.25	58.0	153.33
	North Lake	4.18–4.66	12.94	−0.008	1.63	48.5	107.08
	Bibra Lake	6.46–8.00	16.25	−0.008	2.19	23.1	102.09
	South Lake	6.63–7.89	5.66	−0.006	1.16	62.9	216.64
	Forrestdale Lake	7.94–8.21	5.60	−0.008	1.80	29.5	135.77
	Chelodina Swamp	4.29–5.34	2.16	−0.009	1.88	25.8	111.13
Fringing vegetation	Joondalup West	6.89–7.62	1.10	−0.008	1.18	46.0	192.30
	Joondalup South	6.43–7.03	1.36	−0.022	1.02	54.9	193.88
	Booragoon Lake	4.43–6.00	2.79	−0.008	0.75	68.8	307.17
	North Lake	5.07–6.18	0.44	−0.007	1.52	24.4	167.64
	Bibra Lake	6.50–7.23	0.91	−0.006	1.66	29.3	144.52
	South Lake	5.67–6.58	2.73	−0.009	0.82	66.9	260.27
	Forrestdale Lake	6.71–7.78	0.62	−0.007	1.76	27.8	185.90
	Chelodina Swamp	4.14–5.77	0.91	−0.006	1.30	47.6	150.81

emerged that the dataset was predominantly zeroes, so it distorted the relationships between samples. SIMPER analyses were used to determine the taxa associated with each habitat type.

Using SPSS version 21, a two-factor crossed ANOVA (habitat, fixed factor, 2 levels: OW, FT; wetland, random factor, 6 levels: all wetlands except North Lake, Lake Booragoon), was carried out on taxa richness and invertebrate abundance, the latter was log₁₀ transformed to meet the assumptions of ANOVA. The large numbers of zeroes in the data from North Lake and Lake Booragoon, owing to comparatively few emerging invertebrates, violated the assumptions of ANOVA to such an extent that these two wetlands were excluded from the analysis.

To test the second hypothesis regarding the effect of drying and storage on emerging assemblages, we used Primer vers 6.1.12 (Clarke and Warwick 2001) Mantel tests were used to compare the Bray-Curtis similarity matrix of invertebrates emerging from the damp and dry treatment sediment samples. A non-metric multidimensional scaling (nMDS) ordination plot was constructed to display the trajectory and magnitude of change in assemblage composition between the damp and dried samples for each wetland (pooled) and habitat type. SIMPER analyses were used to determine the species associated with the differences between each combination of habitat type and treatment. To directly compare the effect of the drying and storage treatment on the abundance of emerging invertebrates, the number of invertebrates emerging from each dried sample was subtracted from its corresponding damp sample, and the difference analysed using the same mixed-model crossed ANOVA described above.

To relate sediment properties to the invertebrate assemblages emerging from damp OW and FT sediment in each wetland, invertebrate data was pooled across the three sampling times.

Primer was used to create a Bray-Curtis similarity matrix for the invertebrate assemblage. The BIOENV procedure in Primer was then used to relate the Bray-Curtis similarity matrix of invertebrate data to the Euclidean distance matrix of sediment characteristics to determine which sediment variables, if any, were associated with the variation in the invertebrate data.

Results

Temperature

In South Lake in autumn, the mean daily maximum temperature was significantly lower beneath the FT (30.9 ± 2.7 °C 1 S.E.) than in the OW habitat (36.8 ± 2.6 °C, $t_{86} = 3.92$, $P = 0.0001$), but the magnitude of mean diurnal change (FT 17.5 ± 1.1 °C; OW 23.4 ± 0.7 °C) did not differ ($t_{86} = 4.65$, $P = 0.09$). Interestingly, sediment temperatures measured in the laboratory were also substantially cooler on FT samples (21.5 °C ± 0.01) than on OW samples (27.6 °C ± 0.01), and bench control temperatures (21.5 °C ± 0.01) were similar to FT sediment.

Sediment properties

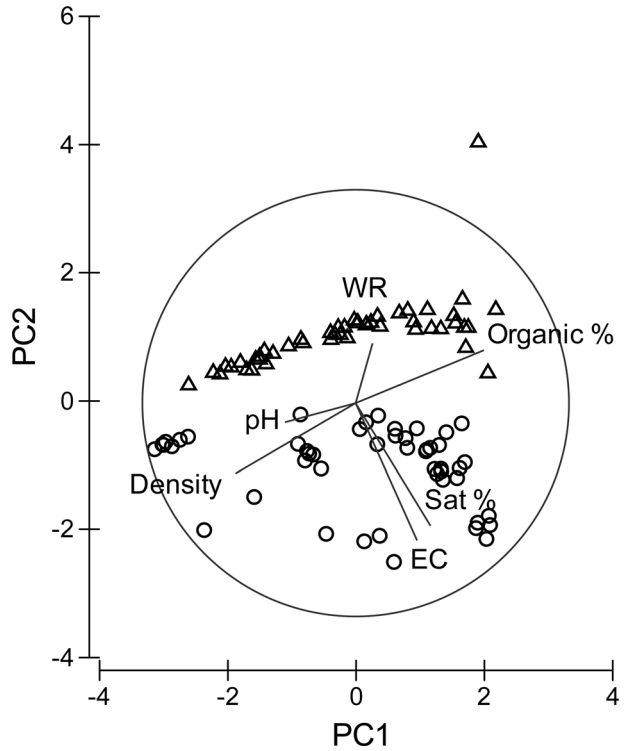
Sediment properties differed between habitats (Fig. 1) (Global $R = 0.437$, $P = 0.001$) and between wetlands (Global $R = 0.344$, $P = 0.001$, Table 2). Moisture content and organic matter content were higher in FT sediment than in OW sediment, which had higher EC and density (Table 2). Overall sediment pH range was similar for OW (4.18–8.21) and FT (4.14–7.78) habitats, but pH varied widely at all wetlands and in both habitats (Table 2). Electrical conductivity was higher in OW sediment (8.14 ± 2.40 mS.cm⁻¹) compared to FT sediment (1.36 ± 0.32 mS.cm⁻¹). Saturation percentage was significantly lower in OW sediment (131.02 ± 19.06 %) than in FT sediment (200.31 ± 19.80 %). Organic matter content was also lower in OW sediment (mean 35.7 ± 6.98 %) than FT sediment (mean 45.7 ± 6.13 %). Open water sediment (1.84 ± 0.29 g.cm⁻³) had much higher density than FT sediment (1.27 ± 0.13 g.cm⁻³) because of its lower organic content. The two habitats were distinguished by percent water saturation and EC (Fig. 1, Table 2). Therefore, the first hypothesis, that FT sediment would have higher moisture content than OW sediment was supported, but there were also other differences between sediment types.

Effects of habitat type and prolonged drying on invertebrate emergence

Species emerging from the sediment samples were dominated by Crustacea, with one common cladoceran species (*Ilyocryptus spinifer*), some less common Chydoridae, copepods (Harpactacoida, Cyclopoida) and three commonly occurring species of Cyprididae ostracod: *Bennelongia gwelupensis* (previously *Bennelongia australis*), *Cypretta* sp. and *Diacypriis spinosa* (Tables 3 and 4). Amphibious Collembola and Oribatida mites were also commonly present and insects were mainly Coleoptera (Hydrophilidae *Berosus* spp.), Diptera (Chironomidae) and Odonata (*Hemicordulia tau*). Although invertebrates were abundant in most samples, richness was relatively low (Tables 3 and 4).

In the damp sediment, emerging invertebrate assemblages differed greatly between habitats ($R = 0.476$, $P = 0.001$) and between wetlands ($R = 0.511$, $P = 0.001$), partially confirming the first hypothesis (Tables 3 and 4). Some taxa occurred in both habitat types, such as *I. spinifer*, *B. gwelupensis*, Chydoridae sp., *D. spinosa*, while others predominated in one habitat or the

Fig. 1 PCA ordination plot of the physical properties of wetland sediments. Overlaid vectors inside a unit circle show correlations with the physical variables. Open water = circles, fringing vegetation = triangles, EC = electrical conductivity (milliSiemens), Sat % = water saturation percentage, WR = water retention potential, Organic % = percentage organic matter, Density = sediment density $\text{g}\cdot\text{cm}^{-3}$. Principal component 1 explains 43 % of the variation in the data, principal component 2 explains 27 % of the variation in the data, totalling 71 % of the variation in the sediment data



other (e.g. Collembola in FT; Oribatidae and *Berosus* sp. 1 in OW, Table 3). Within damp sediment samples, Collembola, Chydoridae and *D. spinosa* always emerged more commonly from FT than from OW samples (Table 4), presumably because they are detritivores. Two common taxa, *Ilyocypris spinifer* and the ostracod *B. gwelupensis*, varied in their emergence pattern between habitat types and wetlands. *B. gwelupensis* emerged in higher abundances from OW samples from Joondalup West and South Lake, but only emerged from sediment

Table 3 Average abundances (per 500 mL sample) for taxa characterising habitats by treatment combinations from the SIMPER analysis of pooled invertebrate data. SIMPER results are pairwise comparisons between the treatments for open water (average dissimilarity 82.60) and fringing vegetation (average dissimilarity 90.18)

Species	Open water damp treatment	Open water dried treatment	Fringing vegetation damp treatment	Fringing vegetation dried treatment
<i>Ilyocypris spinifer</i>	1.51	2.30	1.20	0.54
<i>Bennelongia gwelupensis</i>	0.84	0.97	0.83	0.00
Chydoridae sp.	0.67	0.87	1.18	0.75
<i>Diacypriis spinosa</i>	0.39	0.32	1.24	0.30
<i>Cypretta</i> sp.	0.37	0.14	0.56	0.04
Cyclopoida sp.	0.18	0.08	0.57	0.00
Oribatidae sp. 1 (A)	0.04	0.16	Absent	Absent
Collembola	0.04	0.00	1.47	0.04
<i>Berosus</i> sp. 1 (A)	0.11	0.00	Absent	Absent

Table 4 SIMPER analysis of invertebrate data (total number of individuals in $n=6$ replicates pooled), comparing habitat within each wetland (damp treatment only)

Site	Taxa	Open water average abundance	Fringing trees average abundance	Contribution %
Joondalup West average dissimilarity 56 %	Cyclopoida sp.	0.19	23.82	37.53
	<i>Ilyocryptus spinifer</i>	23.26	38.06	34.13
	Harpacticoida sp.	0.00	4.17	6.90
	<i>Diacypriis spinosa</i>	0.38	3.69	6.78
	<i>Bennelongia gwelupensis</i>	5.12	3.45	6.65
Joondalup South average dissimilarity 82.5 %	Chydoridae sp.	11.73	27.19	40.10
	<i>I. spinifer</i>	9.84	5.00	21.29
	<i>D. spinosa</i>	0.77	17.02	16.70
	<i>B. gwelupensis</i>	6.24	0.00	13.01
Booragoon Lake average dissimilarity 91.4 %	<i>I. spinifer</i>	7.69	22.51	35.62
	<i>B. gwelupensis</i>	0.00	17.58	30.18
	Collembola	0.16	4.75	12.75
	<i>Cypretta</i> sp.	0.00	7.11	9.79
	Chydoridae sp.	0.00	2.26	5.33
North Lake average dissimilarity 100 %	Collembola	0.00	63.49	90.21
Bibra Lake average dissimilarity 95.4 %	<i>I. spinifer</i>	12.94	7.81	52.85
	Chydoridae sp.	0.04	9.36	17.95
	Collembola	0.00	4.66	14.64
	<i>D. spinosa</i>	0.23	3.67	8.06
South Lake average dissimilarity 65.5 %	<i>D. spinosa</i>	3.43	27.29	32.06
	Chydoridae sp.	10.58	24.41	21.66
	<i>B. gwelupensis</i>	18.33	7.97	19.75
	Collembola	0.00	5.52	8.85
	<i>I. spinifer</i>	3.02	3.35	5.78
	Oribatida sp.	0.95	4.09	5.43
Forrestdale Lake average dissimilarity 100 %	Collembola	0.00	95.32	88.57
	<i>Cypretta</i> sp.	3.72	0.00	3.06
Chelodina Swamp average dissimilarity 99.7 %	Collembola	0.00	68.39	63.98
	Chydoridae sp.	0.60	17.72	15.71
	Orthocladinae sp.	8.45	0.00	7.69
	<i>Berosus</i> sp.	2.40	0.00	2.44
	<i>Hemicordulia tau</i> larvae	1.67	0.00	1.92

beneath FT in Lake Booragoon samples. *I. spinifer* emerged in higher numbers from samples collected beneath FTC in Joondalup West and Lake Booragoon, but were more abundant emerging from OW sediment from Joondalup South and Bibra Lake; they emerged in similar numbers from both habitat types in South Lake (Table 4). Some taxa therefore showed flexible responses to habitat and drying.

The dried and stored samples showed smaller, but still significant differences between habitats ($R=0.303$, $P=0.001$) and among wetlands ($R=0.393$, $P=0.001$) (Tables 3 and 4).

Collembola and *Berosus* sp. 1 appeared to die when exposed to the drying and storage treatment, and other species showed reduced numbers emerging when exposed to this treatment (e.g. Cyclopoida sp., Table 3). The drying treatment also had positive effects, or no effect, on some species (Table 3). More *Ilyocryptus spinifer* (Cladocera) emerged from dried OW samples than from damp OW samples, although the effect was reversed in FT samples (Table 3). The drying treatment did not affect emergence by the ostracod *Bennelongia gwelupensis* in OW samples (Table 3), but prolonged drying led either to mortality or exceptionally delayed emergence (beyond the 30 days duration of this experiment) (Table 3). Thus, for most species, location in a particular habitat altered the effect of the drying treatment.

The Mantel tests showed a significant but modest overall correlation between assemblages emerging from dried and stored samples compared with assemblages emerging from damp samples ($\rho=0.308$, $P=0.001$). However, when the two habitat types were analysed separately, there was a stronger correlation between damp and dried OW samples ($\rho=0.447$, $P=0.001$), than between damp and dried FT samples ($\rho=0.307$, $P=0.002$). Furthermore except in Chelodina Swamp, the assemblages that emerged from OW sediment changed little in response to drying compared to assemblages that emerged from beneath FT, some of which changed substantially (Fig. 2). This was explained by the high abundances of amphibious collembolans in damp FT samples compared to the dried and stored FT samples, where they were rare. In OW samples Collembola were rare (Table 3), so the strongly negative effect of drying on collembolans was an effect that only occurred in FT samples. Damp FT sediment also had higher abundances of the ostracod *Diacypriis spinosa* and a species of Chydoridae cladoceran than did open water or dried FT sediment (Table 3). Another ostracod, *Cypretta* sp., was rare in the dried samples but of moderate abundance in the damp sediment samples (Table 3). Thus, the drying treatment reduced the abundance of some species in both habitats, but the effect was larger in FT sediment, reducing the correlation between pairs of damp and dried FT sediment samples.

Taxa richness of assemblages emerging from damp sediment differed between the two habitats, but this pattern differed among wetlands (habitat x wetland interaction: $F_{5,51}=3.34$, $P=0.011$). In Lake Joondalup South, Lake Forrestdale and Chelodina Swamp, more taxa

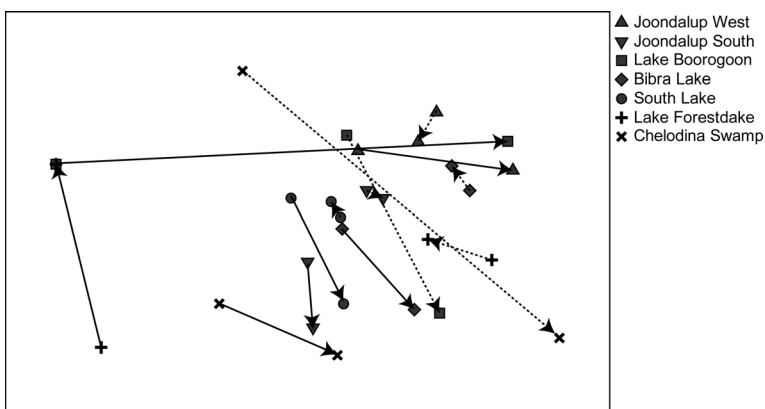


Fig. 2 Non-metric multidimensional scaling ordination plot for the two treatments (damp/dry) in the two habitats (open water, fringing vegetation) in each wetland (Stress: 0.12). Each symbol represents the pooled data from a single wetland by treatment combination. Solid lines show the change in the emergent invertebrate assemblage from fringing vegetation samples and dotted lines show change in open water sediment samples. Arrows connect from a damp sample to the dried sample in the same wetland

emerged from open water sediment, but in Lake Joondalup West, Bibra Lake and South Lake, more taxa emerged from FT sediment. Mean taxa richness per sample did not differ between habitat types (OW: 2.8 ± 0.23 ; FT: 2.7 ± 0.24) or wetlands (range of means 1.7–3.9 taxa per sample). A similar pattern was observed for taxa richness of invertebrates emerging from the dried and stored treatment (habitat \times wetland interaction: $F_{5,32} = 4.78$, $P = 0.002$). Taxa richness was highest emerging from dried OW samples in Lake Joondalup West, Lake Joondalup South, Lake Forrestdale and South Lake, higher in dried FT samples from Bibra Lake and did not differ between the habitats in Chelodina Swamp. The drying treatment altered the pattern of taxa richness between habitats, but not in any consistent way, and, overall, there was no consistent difference in the numbers of taxa per sample emerging from the two habitats. Log-transformed abundance of invertebrates emerging from either treatment did not differ between habitats, but did differ between wetlands (damp treatment $F_{5,51} = 3.6$, $P < 0.01$; dried and stored treatment $F_{5,32} = 4.42$, $P < 0.01$). This was due to the wetlands differing in average invertebrate abundance: in the damp samples Chelodina Swamp and Bibra Lake had particularly low abundances (range of mean abundance per sample 4.0–28.9); in the dry samples, Lake Forrestdale and Chelodina Swamp also had low abundances emerging (range of abundance per sample 1.8–15.7). The analysis of the difference in abundance of emerging invertebrates between the damp and dried samples showed that the change in abundance when samples were dried did not differ between habitat types or wetlands (habitat type $F_{1,2} = 0.17$, $P = 0.9$; wetlands $F_{5,28} = 1.7$, $P > 0.05$). There was no trend in invertebrate abundance associated with either habitat or treatment; so differences in assemblage composition described above were solely attributable to taxon composition rather than abundance.

Relationship between sediment properties and emerging invertebrates

Salinity, pH and percent water saturation were significantly associated with patterns in the invertebrate data (BIOENV routine, $\rho = 0.256$, $P = 0.01$), because salinity was significantly higher and saturation percentage was significantly lower in OW sediment than in FT sediment, and pH range within each wetland was often lower in FT sediment than OW sediment (Table 2). The correlation between sediment variables and invertebrate data suggests that sediment properties may influence the composition of the emerging assemblage.

Discussion

Habitat type, prolonged drying and invertebrate emergence

The first hypothesis was only partially confirmed because, although the assemblages emerging from the two habitat types differed consistently in composition, they did not differ in abundance and taxa richness was not consistently higher in either habitat. Similarly, the second hypothesis, that drying and storage would decrease taxa richness and abundance of emerging invertebrates and alter assemblage composition was also only partially confirmed, because drying only altered assemblage composition, it did not reduce taxa richness or abundance. This difference in assemblage composition may be attributable to factors such as past hydroperiod, sediment conditions and temperature. However, invertebrates that take refuge from wetland drying in OW sediment during the summer–autumn dry period have to be able to withstand higher temperatures ($\approx 35^\circ\text{C}$) caused by direct sunlight. In contrast, beneath fringing trees there

is continuous shade resulting in lower temperatures (≈ 30 °C), and FT sediment retains a higher moisture content and percentage of organic material which the laboratory results show also reduce sediment surface temperature even under direct light. The different surface temperatures on each sediment type in the laboratory (under identical lighting conditions) arise from the sediments having different albedo (i.e. the fraction of solar radiation reflected from a surface). Under dry conditions, sandy sediments have a higher albedo than sediments high in organic matter, resulting in higher maximum surface temperatures on sand (Zhang et al. 2012). Furthermore, factors such as sediment texture and moisture content also influence albedo (Zhang et al. 2012). Sediments such as those beneath fringing trees, that have a higher organic matter content and a rougher texture than OW sediment, retain moisture and dry more slowly, thereby remaining cooler even when unshaded (through both lower albedo and evaporative cooling). These factors, together with past hydroperiod, control sediment moisture levels. Sediment moisture is known to be important for the viability of invertebrate life stages taking refuge in sediments (Stubbington and Datry 2013). OW sediment may have a longer hydroperiod, but after drying, conditions are likely to be much harsher. Also, recent experiments show that invertebrates emerging from inundated FT sediment are then able to survive up to 30 days in damp conditions should surface water be lost to evaporation, whereas in OW sediment, loss of surface water causes abortive hatching (Strachan et al. 2016).

Some species emerged in higher abundances from FT sediment than from OW sediment, suggesting that while both sediment types provide a refuge from annual wetland drying, the cooler, moister conditions beneath FT provide a refuge for less desiccation-tolerant species. Indeed, several of the taxa that were present in high abundances in FT sediment showed the largest negative responses to the drying and storage treatment (e.g. *Cyprretta* sp., *Cyclopoida* sp.), suggesting that they were less tolerant of dry conditions than other taxa. Amphibious taxa (e.g. *Collembola*) were also found mostly in the cooler, moister FT sediment habitat. Collembolans usually require high humidity to survive and may absorb water from the air (Bayley and Holmstrup 1999), and many species live at the water's edge, feeding on organic detritus. It is therefore not surprising that they were found mainly in FT sediment. Their response to experimental drying was strongly negative, indicating that they are rarer in open water sediment because of the higher temperatures and lower moisture content there. There are few studies of wetland *Collembola*, but Tronstad et al. (2005) showed that they did not follow declining water levels across a floodplain, indicating that these taxa may remain in FT sediment in these wetlands.

Drying and storage for 12 months altered the composition of emerging assemblages, partially confirming the second hypothesis. Some fully-aquatic invertebrates, such as the ostracods *D. spinosa* and *Cyprretta* sp., were inhibited by experimental drying. *Diacypris* was most affected in FT sediment, but *Cyprretta* sp. abundances declined in both habitats in response to drying. Both species respond to drying by aestivating with their bivalve shell closed (Strachan et al. 2014) and it appears that the higher temperatures and prolonged dry conditions during experimental drying exceeded their capacity to withstand desiccation. The greatest survival rates following desiccation occur after slow drying that gives sufficient time for animals to adjust their metabolism (Ricci and Pagani 1997). In this experiment, drying was relatively slow, taking 14 days. Thus, it is likely that higher temperatures and longer dry periods (exceeding 12 months in some documented cases, Sim et al. (2013)), associated with climate change, groundwater extraction or loss of fringing trees, may also exceed these species' tolerances.

For two species, the effects of experimental drying were mediated by habitat type. The ostracod *B. gwelupensis* emerged in similar abundances from the damp treatment sediment in both habitats and from the dried OW sediment, but failed to emerge from FT sediment after

drying and storage. *B. gwelupensis* hatches from desiccation resistant eggs following dry periods (Strachan et al. 2014), so the eggs present in the FT sediment were either killed by the drying treatment, did not receive the correct hatching cue, or had delayed hatching beyond 30 days of inundation. Interestingly, this ostracod showed different patterns of distribution between the two habitat types in damp sediment in different wetlands, although the effect of the drying treatment was the same across all wetlands. Recent research shows that the genus *Bennelongia* has high levels of cryptic diversity in south-western Australia (Schon et al. 2015), so it is possible that the variable distribution patterns we observed among wetlands were caused by inadvertently pooling more than one *Bennelongia* species. Drying also affected hatching of *I. spinifer* from ephippia. Similar abundances hatched from inundated damp sediment in both habitats, but after drying, the number hatched from OW samples actually increased, whereas the number hatching from FT samples decreased. Flexibility in hatching or emergence timing within species has been observed in other studies of both crustaceans and insects (e.g. Brock et al. 2003; Wickson et al. 2012). Clearly, the effect of prolonged drying on some species will differ depending on the habitat where eggs or ephippia are deposited, or where individual invertebrates enter dormancy.

Although the drying and storage treatment applied here was almost certainly harsher than the conditions to which sediments are exposed during annual drying in these wetlands, many taxa survived and some were unaffected. For example, hatching of another cladoceran (*Chydoridae* sp.), was unaffected by prolonged drying. This species was absent from OW sediment in some wetlands, and in others it hatched in higher abundances from dried/stored FT sediment; but in all cases, dried or damp, it only hatched in substantial numbers towards the end of the 30 d experiment (authors unpublished data). This species, which hatches from ephippia, showed delayed emergence regardless of habitat or preceding environmental conditions. Consequently, some seasonal wetland taxa are already very resistant to severe and prolonged drying.

Studies of riparian vegetation along streams have also shown lower in-stream (Stewart et al. 2013) and sediment surface temperatures beneath trees (Stewart et al. 2011) than in streams with no riparian canopy. Thus, riparian vegetation creates refuges from elevated stream temperatures for aquatic invertebrates (Davies 2010). It appears that the tree canopy of fringing vegetation around basin wetlands, where the trees shade the inundated area, may serve the same purpose. The eight wetlands studied here had all retained at least a partial cover of fringing trees, but this is not typical of urban wetlands on the Swan Coastal Plain (Davis and Froend 1999). Indeed, urban wetlands commonly have lost some or all of their native fringing vegetation (e.g. Davis and Froend 1999; Mackintosh et al. 2015), and may thus have lost a temperature refuge for invertebrates that rely on remaining in the sediment when wetlands are dry. These results demonstrate one of the potential mechanisms behind the correlation between fringing vegetation and aquatic macroinvertebrates reported in wetlands surveys (e.g. Mackintosh et al. 2015). Replanting native species of fringing trees is often a part of restoration of freshwater ecosystems because they provide a range of ecosystem services (Bernhardt and Palmer 2007; Boulton et al. 2014); but these trees may serve an additional function by providing a temperature refuge for aquatic invertebrates during dry periods.

Wetland variation and sediment properties

Sediment properties, especially pH, salinity and percent water saturation, were associated with the composition of emerging assemblages. Salinity varies naturally among Swan Coastal Plain

wetlands depending on their underlying groundwater, and it increases when water levels are low (Sim et al. 2013). The salinity measured here arose from salts in the sediment being dissolved during experimental immersion, so salinity levels reflected salt deposition when sediments dried out in the field. In all wetlands (except Joondalup west), salinity was higher in open water because that habitat is the last place to retain surface water, so salts concentrate there.

When saturated, the higher organic matter content in FT sediment releases humic acids, lowering pH. In contrast, sand was the main component of OW sediment, so sediment density was much higher and organic matter content lower than beneath FT. Litter fall from overhanging trees supplies organic matter to FT sediment. *Melaleuca raphiophylla* trees are evergreen and have needle-like leaves and paper-like bark, both of which are shed in large quantities throughout the year. Nevertheless, most tree species growing within and around wetlands are likely to increase sediment organic matter content above that found in open water sediment through the deposition of leaf litter, so these effects are likely to be widespread in vegetated wetlands, providing refuge from dry conditions.

Although the invertebrate assemblages emerging from sediments in this experiment were not particularly diverse (cf Brock et al. 2003) there were still significant differences in composition among wetlands both before and after drying. The drying treatment reduced among-wetland variation in both habitat types, probably because the negative effects on particular taxa (e.g. Collembola) were consistent across all wetlands, making assemblages more similar. Also, although the association between sediment variables and emerging invertebrate assemblages was significant, it was modest ($\approx 25\%$ of the variation), suggesting that other factors were affecting invertebrate assemblage composition. These factors may include past hydroperiod, a range of human impacts and natural spatial and temporal variation. The history of wetland inundation periods varies among these wetlands both spatially and temporally (Sim et al. 2013). For example, Lake Forrestdale, Bibra Lake and North Lake tend to be dry for 5 to 6 months each year, but Lake Booragoon is dry for shorter periods of 1–3 months. These differences in hydroperiod probably had a role in determining which invertebrates emerged from sediments from each wetland during this experiment (Brock et al. 2005). Unfortunately, hydroperiod data is not gathered regularly for most Swan Coastal Plain wetlands, leaving so many gaps in the knowledge of drying patterns that the effects are uninterpretable. All the wetlands retained native fringing trees, but the width and proportion of the edge of each lake covered by these trees, and thus the proportion of the lake covered by this habitat type, varied.

Various human impacts that affect water regime, such as stormwater inputs, land use and clearing of catchment vegetation may affect invertebrate egg banks (Brock et al. 2005) and the effects of these impacts differed among the eight wetlands. For example, North Lake had only a single taxon emerge (Collembola, only from damp FT sediment), something rarely observed in reflooding experiments. However, this wetland has a history of severe eutrophication (Balla and Davis 1995) and its water regime has changed from perennial to seasonal. Recently, its depth has rarely exceeded 0.2 m and the lake bed has become covered with emergent macrophytes. It appears that the invertebrate egg bank in this lake has been damaged by its long history of disturbance. Lake Booragoon, which was also formerly perennial and eutrophic, also had low abundances of invertebrates emerge, although richness was similar to other wetlands. Further research is required into the effects of eutrophication and water regime change on sediment properties and egg banks.

Chelodina Swamp and South Lake were the least disturbed of the eight wetlands. Some taxa that emerged from the open water sediment of Chelodina Swamp were rare in the other wetlands, including aestivating dragonfly and beetle larvae. South Lake has a high level of sediment organic matter, causing cracking of the sediment as the wetland dries and organic matter shrinks. Strachan et al. (2014) showed that many species, especially insects and isopods, took refuge in shallow depressions, cracks and fissures in the sediment of South Lake, rather than relying on dormant stages in surface sediments. This may partially explain the low taxa richness of invertebrates emerging from the surface samples used in the present experiment. It is also possible that methods used in our experiment, such as the potential for predation to have occurred during the 10 days between sampling events, may have led to lower richness or abundance than may occur in the field. If surface sediment does not contain resting stages of a high richness of species, it would still contribute large abundances of cladocerans and ostracods to refilling wetlands. These taxa are both diverse (Horwitz et al. 2009) and abundant in most Swan Coastal Plain wetlands regardless of the level of disturbance (Davis and Christidis 1999). Microcrustaceans such as ostracods, cladocerans and copepods are important in seasonal wetland food webs because their appearance from sediments in large numbers provides food for many predators including invertebrates and waterbirds (Boulton et al. 2014). The drying and storage treatment applied here did not reduce overall abundances of emerging invertebrates compared to damp sediment. However, in the field, effects will be cumulative and the eventual loss of formerly abundant taxa would negatively disrupt food webs.

Not all urban wetlands on the Swan Coastal Plain have fringing trees (due to disturbance or natural variation), although others are completely covered by trees (e.g. *Melaleuca* spp., *Eucalyptus rudis*) or emergent macrophytes. Together with differing hydroregimes, one wetland may stay inundated or damp for longer and be a better refuge from drying in the landscape than another (Chester and Robson 2013). However, many of these urban wetlands appear to contain cool, damp refuges for invertebrates at least one of two spatial scales: beneath bands of FT at the whole wetland (habitat) scale, or at smaller scales in microrefuges such as cracks and deeper fissures that form in some types of wetland sediment (Strachan et al. 2014). The presence of these refuges may at least partially explain the remarkable resistance to drier water regimes reported for this urban wetland fauna (Sim et al. 2013). Although these wetlands are exposed to a range of disturbances, they are natural in origin and appear to have retained some natural ecological processes, especially where native fringing trees have remained. Further research into the ecological function of natural, as opposed to constructed, urban wetlands is needed to inform their management and restoration.

Acknowledgments The authors would like to thank Murdoch University for its support and for providing a PhD scholarship to SRS. Thanks to Peter O’Toole for his help in the field. Sampling was carried out with permits from the Department of Environment and Conservation and the Department of Fisheries, Western Australia.

References

- Balla SA, Davis JA (1995) Seasonal variation in the macroinvertebrate fauna of wetlands of differing water regime and nutrient status on the Swan Coastal Plain, Western Australia. *Hydrobiologia* 299:147–161
- Bayley M, Holmstrup M (1999) Water vapor absorption in arthropods by accumulation of myoinositol and glucose. *Science* 285:1909–1911

- Bernhardt ES, Palmer MA (2007) Restoring streams in an urbanizing world. *Freshw Biol* 52:738–751
- Boulton AJ, Lloyd LN (1992) Flooding frequency and invertebrate emergence from dry floodplain sediments of the river Murray, Australia. *Regul Rivers* 7:137–151
- Boulton AJ, Brock MA, Robson BJ, Ryder DS, Chambers JC, Davis JA (2014) Australian freshwater ecology: processes and management. Wiley-Blackwell, Chichester
- Brendonck L, De Meester L (2003) Egg banks in freshwater zooplankton: evolutionary and ecological archives in the sediment. *Hydrobiologia* 491:63–54
- Brock MA, Nielsen DL, Shiel RJ, Green JD, Langley JD (2003) Drought and aquatic community resilience: the role of eggs and seeds in sediments of temporary wetlands. *Freshw Biol* 48:1207–1218
- Brock MA, Nielsen DL, Crossle K (2005) Changes in biotic communities developing from freshwater wetland sediments under experimental salinity and water regimes. *Freshw Biol* 50:1376–1390
- Chester ET, Robson BJ (2011) Drought refuges, spatial scale and the recolonization of invertebrates in non-perennial streams. *Freshw Biol* 56:2094–2104
- Chester ET, Robson BJ (2013) Anthropogenic refuges for freshwater biodiversity: their ecological characteristics and management. *Biol Conserv* 166:64–75
- Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation. PRIMER-E, Plymouth
- CSIRO (2011) Science and solutions for Australia. In: Cleugh H, Smith MS, Battaglia M, Graham P (eds) Climate change. CSIRO, Collingwood
- Datry T, Corti R, Philippe M (2012) Spatial and temporal aquatic-terrestrial transitions in the temporary Albarine River, France: responses of invertebrates to experimental rewetting. *Freshw Biol* 57:716–727
- Davies PM (2010) Climate change implications for river restoration in global biodiversity hotspots. *Restor Ecol* 18:261–268
- Davis JA, Christidis F (1999) A guide to wetland invertebrates of Southwestern Australia. Western Australian Museum, Perth
- Davis JA, Froend R (1999) Loss and degradation of wetlands in southwestern Australia: underlying causes and consequences and solutions. *Wetl Ecol Manag* 7:13–23
- Gordon ND, McMahon TA, Finlayson BL (1992) Stream hydrology an introduction for ecologists. Wiley, Chichester
- Horwitz P, Rogan R, Halse S, Davis J, Sommer B (2009) Wetland invertebrate richness and endemism on the Swan Coastal Plain, Western Australia. *Mar Freshw Res* 60:1006–1020
- Jenkins KM, Boulton AJ (2007) Detecting impacts and setting restoration targets in arid-zone rivers: aquatic micro-invertebrate responses to reduced floodplain inundation. *J Appl Ecol* 44:823–832
- Lake PS (2000) Disturbance, patchiness, and diversity in streams. *J N Am Benthol Soc* 19:573–592
- Larned ST, Datry T, Robinson CT (2007) Invertebrate and microbial responses to inundation in an ephemeral river reach in New Zealand: effects of preceding dry periods. *Aquat Sci* 69:554–567
- Mackintosh TJ, Davis JA, Thompson RM (2015) The influence of urbanisation on macroinvertebrate biodiversity in constructed stormwater wetlands. *Sci Total Environ* 536:527–537
- Pinder AM, Halse SA, Shiel RJ, McRae JM (2000) Granite outcrop pools in south-western Australia: foci of diversification and refugia for aquatic invertebrates. *J R Soc West Aust* 83:149–161
- Rawls WJ, Pachepsky YA, Ritchie JC, Sobecki TM, Bloodworth H (2003) Effect of soil organic carbon on soil water retention. *Geoderma* 116:61–76
- Ricci C, Pagani M (1997) Desiccation of *Panagrolaimus rigidus* (Nematoda): survival, reproduction and the influence on the internal clock. *Hydrobiologia* 347:1–13
- Schon I, Shearn R, Martens K, Koenders A, Halse S (2015) Age and origin of Australian *Bennelongia* (Crustacea, Ostracoda). *Hydrobiologia* 750:125–146
- Sharitz RR (2003) Carolina Bay wetlands: unique habitats of the southeastern United States. *Wetlands* 23:550–562
- Sim LL, Davis JA, Strehlow K, McGuire M, Trayler KM, Wild S, Papas PJ, O'Connor J (2013) The influence of changing hydroregime on the invertebrate communities of temporary seasonal wetlands. *Freshw Sci* 32: 327–342
- Steward AL, Marshall JC, Sheldon F, Harch B, Choy S, Bunn SE, Tockner K (2011) Terrestrial invertebrates of dry river beds are not simply subsets of riparian assemblages. *Aquat Sci* 73:551–566
- Stewart BA, Close PG, Cook PA, Davies PM (2013) Upper thermal tolerances of key taxonomic groups of stream invertebrates. *Hydrobiologia* 718:131–140
- Strachan SR, Chester ET, Robson BJ (2014) Microrefuges from drying for invertebrates in a seasonal wetland. *Freshw Biol* 59:2528–2538
- Strachan SR, Chester ET, Robson BJ (2015) Freshwater invertebrate life history strategies for surviving desiccation. *Springer Sci Rev* 3:57–75
- Strachan SR, Chester ET, Robson BJ (2016) Habitat alters the effect of false starts on seasonal-wetland invertebrates. *Freshwater Biol*. doi:10.1111/fwb.12738

- Stubbington R, Datry T (2013) The macroinvertebrate seedbank promotes community persistence in temporary rivers across climate zones. *Freshw Biol* 58:1202–1220
- Tronstad LM, Tronstad BP, Benke AC (2005) Invertebrate responses to decreasing water levels in a subtropical river floodplain wetland. *Wetlands* 25:583–593
- Waterkeyn A, Grillas P, Vanschoenwinkel B, Brendonck L (2008) Invertebrate community patterns in Mediterranean temporary wetlands along hydroperiod and salinity gradients. *Freshw Biol* 53:1808–1822
- Wickson SJ, Chester ET, Robson BJ (2012) Aestivation provides flexible mechanisms for survival of stream drying in a larval trichopteran (Leptoceridae). *Mar Freshw Res* 63:821–826
- Zhang Y, Wang X, Pan Y, Hu R (2012) Diurnal relationship between the surface albedo and surface temperature in revegetated desert ecosystems, north-west China. *Arid Land Res Manag* 26:32–43