Invertebrate Resistance to Wetland Drying

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Cover photo: three stages of the wetting and drying cycle in South Lake (photos: S. Strachan)
Dedicated to ‘Pa’ Rex Clisty Knight

(1931 - 2014)
Declaration
I declare that this thesis is my own account of my research and contains as its main content work which has not previously been submitted for a degree at any tertiary education institution.

____________________  _____________________
Scott R. Strachan       Date

Statement of Contribution of Others
The contributors to the papers included in this thesis are the supervisors of Scott R. Strachan and have had intellectual input through helping design of experiments, data analysis and writing of papers. But for the most part, this thesis is the work of Scott R. Strachan.

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Permits
 Sampling was carried out with permits from the Department of Environment and Conservation and the Department of Fisheries, Western Australia. Licence to take fauna for scientific purposes, licence number SF008055. Authority to enter CALM land and or waters, licence number CE003225. Fish resources management act 1994 exemption, number 2079.
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Thesis Summary

In regions with a drying climate, as waterbodies dry out more frequently or for longer, species traits interact with aquatic habitat influencing assemblage composition in wetlands. This thesis aimed to identify potential refuges from increased temperatures and altered water regimes for wetland invertebrates that resist drying using resting stages in the sediment. Using the literature on desiccation-responses by freshwater invertebrates, I reviewed relationships between life histories and the degree of desiccation to which individuals are exposed. Sediment microhabitats that retain moisture were sampled, showing that they could provide microrefuges for invertebrates during seasonal drying. Dry sediment was sampled from two habitats (open water (OW) and fringing trees (FT)) in eight wetlands, sediment properties were measured, and invertebrate emergence from inundated damp and artificially dried sediment were observed. FT sediment was cooler, had higher organic matter content, water saturation potential and different invertebrate assemblage composition. For most species the effect of drying depended on habitat; effects included mortality, reduced abundance and increased abundance. False starts occur when dry wetlands receive brief, unseasonable periods of inundation that trigger invertebrate hatching, but then dry out causing abortive hatching. OW and FT sediments were exposed to false starts in the laboratory. In OW, abortive hatching occurred and new assemblages emerged from egg banks during the next inundation. In FT, invertebrates emerged rapidly and survived drying, continuing to develop into assemblages that did not differ from permanently inundated controls. Overall, this research showed that shallow seasonal wetlands contain refuges from higher temperatures and prolonged drying, explaining the resistance of their fauna to drought. To sustain wetland biodiversity, FT vegetation should be protected and replanted (where necessary) and wetland sediment should be protected from degrading processes such as sedimentation and eutrophication, so that it retains microrefuges.
Chapter 1 . General Introduction

Climate change will have serious ramifications for wetlands (Finlayson, 2013). For wetlands in Mediterranean-climate regions where conditions are becoming drier, effects will include prolonged periods of drying, increased air and water temperatures (leading to decreased humidity and increased evaporation rates) and increased frequency and severity of false start events. Some past studies have suggested that these altered environmental conditions will deplete the egg bank (e.g. Jenkins & Boulton, 2007) ultimately resulting in local extinction. Although some aquatic species have resistant behaviour and biological adaptations to survive these conditions, there is not yet enough known about species responses to make sound predictions in the face of climate change (Chessman, 2015). Therefore, the aim of this project was to understand the interaction between species life histories and traits and wetting and drying in wetland environments at three spatial scales: sediment microtopography within habitats, fringing and open water habitats within wetlands and differences among wetlands, to determine some of the ecological mechanisms underlying the responses of invertebrate fauna to climate change.

The three spatial scales addressed were: microhabitat refuge use within a wetland (Chapter 4), habitat-scale differences in emergence between sediment from fringing vegetation and open water habitats (Chapter 5, 6) and differences among wetlands in emergence patterns (Chapter 5). The microrefuge scale is important because this is the scale where individuals encounter and respond to changed environmental conditions. The presence or absence of microrefuges, in conjunction with the survival traits of individual species, is likely to determine population persistence within wetlands. Fringing vegetation with a Melaleuca tree overstorey is common in the study wetlands, providing invertebrate habitat in and around the roots and leaf litter that the trees provide. This habitat is shaded and has sediment that contains more organic matter, so it may also affect population persistence within wetlands by acting as a temperature and moisture refuge. Because many temporary wetland invertebrate species are mobile, and have particular traits and tolerance thresholds (e.g. Calosi et al., 2008), long-term species survival will be determined at the landscape scale (Ruhi et al., 2013). These multiple scales have rarely been covered in a single study, so it has provided a
unique viewpoint of invertebrate habitat and recolonization processes occurring in these wetlands.

The environmental context for this study

Worldwide, the largest climate change impacts on wetlands are expected to occur through changes to hydrology and water regime (Erwin, 2009). Climate change is predicted to increase the frequency and magnitude of extreme events (e.g. droughts, heat waves), to increase both air and water temperature, causing changes in species distributions (pole-wards and to higher altitudes) and fragmenting populations (Davies, 2010). Because south-west Western Australia has no high mountain ranges, and is bordered to the south by the Southern Ocean, it is not possible for species to move pole-wards or to higher altitude (Davies, 2010).

Rainfall in southwest Western Australia decreased by 25% between 1910 and 1995 (Hennessy et al., 1999) and is still declining. Decreasing precipitation can eliminate smaller water bodies, extinguishing the aquatic communities that rely on them (Grimm et al., 1997). The Swan Coastal Plain (SCP) was mostly cleared for agriculture following European settlement and now supports over 60% of Western Australia’s population (2 million) who live in metropolitan Perth (ABS, 2014). In the past, Perth relied on groundwater to supply 60 - 70% of total domestic and industrial water use (Balla & Davis, 1993) because surface run-off has declined so substantially (limiting supply from dams), but now supplements supplies with desalination-plant water. Groundwater extraction together with reduced rainfall has lowered groundwater tables and there is less water available for wetlands, decreasing inundation depth and time.

Climate change-induced increases in air temperature will also increase evaporation rates, which, together with declining rainfall will affect wetland hydrology, stratigraphy, hydrochemistry and biota (Erwin, 2009; Semeniuk & Semeniuk, 2012). Drying and the disappearance of surface water are detrimental to many aquatic organisms, exposing them to high UV light levels and temperature, and to large fluctuations in salinity, pH and oxygen levels (Alekseev et al., 2007). It will also affect behavioural interactions, especially food web structure, arising from changes in either the abundance of producers or top order predators (Wrona et al., 2006). Climate change will reduce the availability of viable aquatic refuges during species’ life cycles, which may lead to local extinction and reductions in geographic range (Robson et al., 2013).
Critical temperatures differ between species and populations depending on their geographical distribution; long term tolerance levels for most animals are thought to be around 45-47°C (Portner & Knust, 2001). Australia has a Gondwanan heritage, so in south-west Western Australia the insect fauna are mainly cool-stenotherms (Davies & Stewart, 2013), with a maximum water-temperature tolerance of about 21 °C (Stewart et al., 2013). However, wetland invertebrates may be more tolerant than stream invertebrates because water temperatures are often higher in open water wetlands than in forested streams and because the fauna is dominated by more tolerant taxa (such as coleopterans and odonates, Stewart et al., 2013). Temperature influences egg incubation period, hatching success, duration of hatching and start and finish of diapause in aquatic insects (Ward & Stanford, 1982). It can also increase invertebrate growth rates which directly affect the duration of life cycles, size at maturity (and thus fecundity) and survival (Anderson & Cummins, 1979).

Recent studies of invertebrates in streams and wetlands have shown the impacts of these effects of climate change. Hogg and Williams (1996) found that with increased thermal regimes (caused by climate change) there will be reductions in total density, increased growth rates, earlier emergence, decreased body size, altered sex ratios and premature breeding of stream invertebrates. The increased rate of early emergence by aquatic insects may cause a mismatch in species’ phenology (e.g. peak abundances of herbivores and their algal prey) that will have ecological and economic consequences (Winder & Schindler, 2004). As a result of these impacts, an increase in mean temperature of 3°C is predicted to result in a loss of 10-25% of the mean species richness in upland streams in the United Kingdom (Durance & Ormerod, 2007). The only published evaluation of climate change impacts on wetland invertebrates in south-western Australia showed that although wetland water regimes had changed substantially, the fauna of the Swan Coastal Plain (SCP) wetlands had not (Sim et al., 2013). The invertebrate fauna was suggested to be both resistant and resilient to warming and drying (Sim et al., 2013), although the mechanisms by which the fauna survives were not investigated. Without an understanding of how the fauna have proved to be both resistant and resilient to climatic drying, it is not possible to predict whether continuing changes in the magnitude and/or duration of drying will enable fauna to persist into the future.
Fringing vegetation is extremely important to ecosystem function in wetlands because, apart from providing shade and habitat, it buffers water temperature, stabilizes and aerates sediments, acts as a wildlife corridor, provides a source of carbon (e.g. woody debris and litter input) and filters material passing into the wetland (e.g. nutrient flux) (Palmer et al., 2000; Zedler & Kercher, 2010; Boulton et al., 2014). The roots of fringing vegetation increase habitat complexity within sediments, increasing their stability and invertebrate diversity, including dormant life-stages (Palmer et al., 2000). Shading is one of the most important impacts of fringing trees because it reduces light availability as well as cooling both water and sediment. These reduced light levels can limit primary productivity in the water column and on the sediment, resulting in the loss of algal-grazing invertebrates (Palmer et al., 2000). In 1996 only 17% of wetlands on the SCP retained a fully vegetated fringing zone, consisting of mainly native species, and 45% of wetlands had lost more than 50% of their fringing vegetation (Hill et al., 1996). It is likely that losses have increased since then although this has not been documented. Loss of fringing vegetation results in elevated water temperature and light levels (promoting algal blooms). Increased UV light, together with loss of vegetation litter input, will also reduce humic inputs and concentrations of tannins and humic acids in the water column resulting in the loss of tannin stained (dystrophic) wetlands and the fauna adapted to them (Davis & Froend, 1999).

SCP wetlands have enormous social importance to the people of Perth (EPA, 1993), a rapidly growing city of over 2 million people. They provide important opportunities for recreation and exercise, have considerable aesthetic value, and provide cooling greenspaces in the urban environment. The latter is especially important in Perth’s mediterranean climate, where summer daytime temperatures frequently exceed 40 °C, and temperatures have been rising steadily over the past 40 years (BOM, 2014). On the SCP, wetlands support more than 80 species of water birds including some globally migratory species (Godfrey, 1989). They also support several species of native frogs and two freshwater turtle species: the long-necked turtle Chelodina colliei and the western swamp tortoise Pseudemydura umbrina, one of the world’s rarest reptiles. The SCP wetlands are thus highly valued and vital for sustaining urban biodiversity in Perth.

Invertebrate dynamics in temporary wetlands in response to drying and inundation

In the past decade, temporary waters have received greater research attention, because their importance and contribution to freshwater biodiversity, globally, has been
recognized (e.g. Nielsen & Brock 2009; Larned et al., 2010). Both physical and biological factors vary during each of the water regime phases seen in temporary waterbodies: rewetting, drying, damp and completely dry (Brock & Jarman, 2000). Temporary waters are typically shallow, heating rapidly through solar radiation, and show fluctuating dissolved oxygen concentrations along with changes in water chemistry related to concentration and dilution effects as water levels change (Williams, 2006). Invertebrates respond directly to these physical and chemical changes, as well as indirectly to changes in biotic interactions. When waterbodies dry out, declining water levels result in a ‘predator-prey soup’ (Lake et al., 1989), where invertebrates become concentrated in the remaining pools of water (e.g. Lind et al., 2007). The subsequent high concentration of prey invertebrates is consumed by both larval invertebrate predators seeking to maximise their growth rate and emerge (Lake et al., 1989); and by mobile adult invertebrate predators (e.g. Dytiscidae) that visit the drying pools to prey on stranded invertebrates (Williams, 2006). When the water level drops completely and the remaining aquatic invertebrates become stranded on the dry bed, a ‘clean-up crew’ of terrestrial invertebrates moves in to scavenge their remains (Steward et al., 2012). On rewetting, there is a rapid shift back to an aquatic invertebrate assemblage because invertebrates with drying-resistant stages emerge from the sediment and large flying invertebrates (e.g. coleopterans and odonates) recolonise (Boulton et al., 2014).

This general pattern of invertebrate dynamics through the wetting and drying cycle appears to be broadly applicable to both streams and wetlands, but much less is known about the specific processes occurring during either drying or re-wetting. For example, although sediment moisture has been identified as a key factor in the ability of invertebrates to take refuge in sediments (Stubbington & Datry, 2013), little is known about how particular moisture levels or other sediment qualities affect invertebrates seeking refuge. Although we now know quite a lot about how invertebrates and algae respond to drought and drying in flowing waters (e.g. Jenkins & Boulton, 2007; Ledger et al., 2008, 2012; Verdonschot et al., 2015) and the refuges that they may use (Tronstad et al., 2005; Robson et al., 2008; Sheldon et al., 2010; Chester & Robson, 2011), much less is known about refuges, habitats or microhabitat types in temporary standing waters. The exception is the egg-bank, which has been the focus of a few studies in temporary wetlands (e.g. Brock et al., 2003, 2005; Angeler & Garcia, 2005;
This thesis has focussed on the processes of drying, and especially re-wetting, of wetland sediments, to contribute to our understanding of different potential refuge and habitat types affecting invertebrate dynamics in temporary wetlands.

Aquatic invertebrates use physiological adaptations and/or behavioural responses to survive adverse conditions. Many invertebrates that inhabit temporary waterbodies have evolved physiological adaptations to survive drying, including desiccation resistant eggs, the capacity to enter a dormant stage, or the use of refuges. Refuges are places, or combinations of time and place, where biota are protected from disturbance and that may act as a source of colonists for the wider landscape once the disturbance ceases (Robson et al., 2013). Some aquatic fauna die within a few hours of loss of surface water if they cannot find a refuge (Datry et al., 2012).

The traits that species possess to cope with disturbances such as drying can be divided into resistance and resilience traits. Resistance traits are those that allow populations to resist the effects of the disturbance and remain within the wetland, such as desiccation resistant eggs in micro-crustaceans (Robson et al., 2011). Resilience traits are those that help populations recover after the disturbance has ceased, usually via dispersal, and include: recolonization through immigration, rapid growth and early reproductive age. Traits are species specific (in some cases even population specific) and therefore each species will react differently to environmental change, including those caused by climate change (Robson et al., 2011). Traits have been grouped into different domains including synchronisation (e.g. diapause and quiescence), dispersal (e.g. active flight and passive transport), reproduction (e.g. egg numbers and per capita investment) and development (e.g. morphology, development time and body size) (Verberk et al., 2008).

Aquatic invertebrates in temporary wetlands use a range of life history strategies to survive, and two strategies in particular are ‘typical’: (1) when wetlands start to dry out most micro-crustaceans form desiccation resistant eggs, from which they hatch when wetlands reflood, (Alekseev et al., 2007); and (2) many insects grow rapidly to reach their final instar and emerge before wetlands dry out, spending the dry phase as aerial adults, and returning to lay their eggs during the following inundation period (Williams, 2006). Although trait-based analyses are popular at present in the northern
hemisphere, relatively little is known of Australian species traits, entailing large assumptions if such analyses are used. In particular, there is a scarcity of information for drought resistance traits even at the family level for Australian freshwater invertebrates (Chessman, 2015), making predictions of the effect of water regime change difficult.

Although climate change may cause an enormous shift in the water regimes of temporary water bodies, little is presently known of the resilience and resistance strategies used by temporary wetland invertebrates in response to drying. Furthermore, the flexibility of these traits and strategies, the role of refuges and the importance of different habitats and microhabitats for invertebrate survival during periods without surface water in wetlands are poorly known. Without this knowledge, it is difficult to make sound predictions about future wetland biodiversity or ecosystem function. The research in this thesis aimed to address these knowledge gaps by developing an understanding of how freshwater wetland invertebrates respond to varying periods of drying and reflooding, and the role of potential microhabitats and habitats in these responses.

*The structure of this thesis*

Prior to carrying out field and laboratory research on invertebrate responses to drying and reflooding, I prepared a literature review that focussed on invertebrate life history strategies for surviving desiccation in wetlands (Chapter 3). This literature review augments and examines the terminology surrounding drying, desiccation and species responses to them, as well as reviewing the range and types of traits and strategies seen in different freshwater invertebrate groups. It also identifies some of the knowledge gaps which I have attempted to address in this thesis. The literature review sought to identify the relevant abiotic factors that are important for invertebrate survival during wetland drying and potential effects of climatic drying on invertebrate survival (Table 1.1). This chapter has been published in the multidisciplinary review journal, Springer Science Reviews (Table 1.1). This review outlined large knowledge gaps including the responses of many aquatic species to drying, responses of survival traits under different environments and conditions, the effects of false start events on aquatic invertebrates. I then sought to understand the interaction between species life histories and traits and the wetland environment (at both the larger habitat and micro-topography scale) under a wetting-drying regime to determine the likely resistance and resilience of
the aquatic invertebrate fauna to climate change (the hypotheses tested in this thesis are listed in Table 1.1).

Following the Introduction, Chapter 2: ‘Study Sites’, describes the SCP wetlands studied in this project in greater detail to provide context and relevant information for the reader. The SCP wetlands are some of the best studied wetlands in Australia, and their invertebrate taxonomy is relatively well known, so they were ideal for this project. Chapter 4: ‘Microrefuges from drying for invertebrates in a seasonal wetland’ used field sampling to investigate the importance of small-scale wetland sediment topography in providing microrefuges for invertebrates and the role they play in invertebrate survival as a wetland dried out and reflooded. Three distinct phases of the water regime were identified: damp, dry and reflooded, and the invertebrates inhabiting each potential microrefuge were sampled at each phase. This Chapter is published in the international journal, Freshwater Biology (Table 1.1). Chapter 5: ‘Fringing trees may provide a refuge from prolonged drying for urban wetland invertebrates’ sampled the egg bank of eight SCP wetlands, quantified a range of sediment variables, rehydrated sediments to examine invertebrate emergence, and manipulated drying to determine the effects of long term drying (12 months) on emergence (Table 1.1). Importantly, Chapter 5 sampled two distinct wetland habitats: sediment from open water areas of wetlands and sediment from beneath the canopy of common wetland trees, *Melaleuca* spp., that grow in the shallows surrounding all eight wetlands. Although hydroperiod duration and salinity have been manipulated in past sediment emergence experiments (e.g. Brock *et al.*, 2005; Jenkins & Boulton, 2007), few rehydration experiments have included a ‘habitat’ factor. That is, few have compared the response to manipulation by invertebrates from different wetland habitats or sediment types within wetlands. As different habitats or sediment types may offer different opportunities to invertebrates seeking refuge from the loss of surface water, this is an important question to address to develop knowledge of invertebrate responses to drying at the wetland-scale. This chapter is in review in the international journal Urban Ecosystems (Table 1.1). Chapter 6: ‘Habitat alters the effect of false starts on seasonal–wetland invertebrates’ used a rehydration experiment to investigate the effects of a false start event comprising varying dry periods, on the emergence of aquatic invertebrates from two wetland habitats, open water and beneath *Melaleuca* trees (Table 1.1). False start events are where a dry wetland receives rainfall which starts to fill the
wetland, but before the emerged invertebrates can reach reproductive age the wetland dries preventing completion of their life cycle. In some mediterranean climate regions, an increased frequency of intense summer or autumn rainfall events with prolonged dry periods between them have been predicted (Evans and Schreider, 2002; CSIRO, 2011; Diodato et al., 2011) which will increase the risk of false start events. These events have not been explored in detail and their effects on aquatic invertebrates are unknown. This chapter is in press in the international journal Freshwater Biology. Chapter 7, the general discussion, provides a synthesis of the results from this thesis with contemporary knowledge of invertebrate responses to wetland drying.

Chapters in this thesis are presented in slightly different styles owing to the different journals for which they are in review or published, and each chapter thus has its own reference list. Although this thesis contains my own work, the text of these thesis chapters uses collective terms (e.g. ‘we’), acknowledging the guidance provided by my supervisors who are also authors on the papers.
### Table 1.1. Research aims, questions or hypotheses for each chapter and publication status.

<table>
<thead>
<tr>
<th>Chapter Title &amp; Research Paper</th>
<th>Research aims</th>
<th>Hypotheses and Research Questions</th>
</tr>
</thead>
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<tr>
<td>Chapter 3. Freshwater invertebrate life history traits for surviving desiccation Strachan S.R., Chester E.T. &amp; Robson B.J. (2015) Freshwater invertebrate life history traits for surviving dry periods: a review. Springer Science Reviews, 3, 57-75.</td>
<td>To review the literature on the physiology and range of species responses to drying. This necessitated clarifying the definitions of the stages of drying and types of resting stages that occur during desiccation, including especially the older ‘pre-electronic’ literature, which often included detailed observations of invertebrate behaviour.</td>
<td>Which abiotic factors are important for macroinvertebrate survival in wetlands that dry out? If wetland water regimes become drier, with shorter periods of inundation and longer dry phases, what effect might this have on macroinvertebrate survival?</td>
</tr>
<tr>
<td>Chapter 4. Microrefuges from drying for invertebrates in a seasonal wetland Strachan S.R., Robson B.J. &amp; Chester E.T. (2014) Microrefuges from drying for invertebrates in a seasonal wetland. Freshwater Biology, 59, 2528-2538.</td>
<td>To investigate potential microhabitat refuges in wetland sediments during dry periods. Three potential microrefuges were studied: surface depressions, shallow cracks and deeper fissures across three stages of the hydroregime (damp, dry and reflooded).</td>
<td>H₁ Because inundation level and temperature in each microrefuge type changed as the wetland dried and reflooded, invertebrate assemblages would also differ among microrefuges. H₂ If deeper fissures in wetland sediments provide a cooler microrefuge for invertebrates in the absence of surface water, then this microrefuge would gain species during the dry phase, as individuals sought out and moved into cooler microhabitats.</td>
</tr>
<tr>
<td>Chapter 5. Fringing trees may provide a refuge from prolonged drying for urban wetland invertebrates Strachan S.R., Chester E.T. &amp; Robson B.J. (2015) Fringing trees may provide a refuge from prolonged drying for urban wetland invertebrates. Urban Ecosystems, In review</td>
<td>To investigate the effects of differences in habitat (open water and fringing vegetation), duration of drying, and sediment properties on emergence and egg bank hatching from sediment from eight SCP wetlands.</td>
<td>H₁ Assemblage composition, diversity and abundance of invertebrates emerging from sediment from open water would differ from that emerging from sediment from beneath fringing trees, because of differences in sediment characteristics. H₂ A higher diversity and abundance of invertebrates, with a different assemblage composition, would emerge from inundated damp sediment taken fresh from the field than from sediment that was dried and stored for a year, because moisture would assist individuals to sustain dormancy.</td>
</tr>
<tr>
<td>Chapter 6. Habitat alters the effect of false starts on seasonal-wetland invertebrates.</td>
<td>To investigate the effects of a false start (where an intense rainfall event occurs, partially filling an intermittent waterbody that then dries out before invertebrates can complete their life cycles) on invertebrate assemblages emerging from the egg bank in two habitats (open water and fringing vegetation) and varying duration of dry periods following the false start.</td>
<td>H₁ the assemblage composition of invertebrates emerging from open water sediment would differ from that emerging from fringing vegetation sediment, because sediment conditions differed between the habitats. H₂ the assemblage composition of invertebrates emerging from sediment exposed to a false start would differ from sediments exposed to continuous inundation, because false starts cause abortive hatching.</td>
</tr>
<tr>
<td>Chapter 7. General Discussion</td>
<td>A synthesis of the results with contemporary knowledge in a global context.</td>
<td></td>
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</tbody>
</table>
References


Balla S.A. & Davis J.A. (1993) Wetlands of the Swan Coastal Plain: Volume 5, managing Perth’s wetlands to conserve the aquatic fauna. Water Authority of Western Australia; Western Australian Environmental Protection Authority, Perth.


Chapter 2. Study Area

Climate, landscape and water regime

Perth has a population of over 2 million (ABS, 2014) and experiences a mediterranean climate where rainfall mostly occurs in the winter (Fig. 2.1). Consequently, most of the wetlands on the Swan Coastal Plain (SCP) are inundated in winter-spring and dry out in summer-autumn. Perth’s annual rainfall has been declining for the last 69 years (Fig. 2.2); winter rainfall has decreased by 25% in south west Western Australia between 1910-1995 (Hennessy et al., 1999) and there have been further declines since (Fig. 2.2). A 15% reduction in rainfall since 1975 has resulted in a 55% decline in runoff due to lowering groundwater tables (CSIRO, 2011). With less rainfall there is less runoff and therefore less surface water in streams, lakes and wetlands, resulting in shorter hydroperiods (CSIRO, 2011).

![Figure 2.1. Perth average monthly rainfall 1945-2013 (BOM, 2014).](image-url)
Figure 2.2. Aggregated annual inflow series for 11 major dams in the Integrated Water Supply Scheme (IWSS). Water year is May to April (Bates et al., 2010).

Altered evaporation rates and rainfall patterns will also change the stratigraphy and hydrochemistry of wetlands (Semeniuk & Semeniuk, 2012). As well as perennial wetlands becoming seasonal, and shallow temporary wetlands being extinguished (Sim et al., 2013), drying increases wetland salinities and reduces sediment moisture levels during dry periods (Semeniuk & Semeniuk, 2012). Prolonged drying may shift wetland sediments from predominantly peat (in natural wetlands in good condition) to more diatomaceous (Semeniuk & Semeniuk, 2012), with flow on effects to the capacity of sediments to form microrefuges such as fissures that connect to groundwater. Plants track these changes in inundation and sediment, and woody plants move towards the centre of basin wetlands: those that require waterlogging move closer to the centre, followed by plants that require drier soils (Semeniuk & Semeniuk, 2012). Furthermore, wetlands respond differently to decadal (or longer) periods of drying because of local differences in age, geographic location, geology and hydrology, that lead to different physical, chemical and ecological processes (Semeniuk & Semeniuk, 2012). These small-scale physical and chemical responses are not well understood, but they are likely
to be important for the survival of invertebrates if they determine sediment properties in wetlands.

The SCP is less than 2.5 million years old and the sediments are the result of marine, aeolian and alluvial deposition (Balla, 1994; Semeniuk & Semeniuk, 2012). Beneath the SCP is a heterogeneous unconfined aquifer, which is recharged by rainfall and forms two mounds, the Gnangara and Jandakot mounds, which sustain natural wetlands on the SCP (Balla & Davis, 1993). The wetlands are mostly surface expressions of the groundwater table (top of the shallow aquifer) therefore surface water levels are influenced by groundwater level as well as rainfall and evaporation rates (Davis & Christidis, 1999). SCP wetlands are typically shallow, interdunal depressions in direct hydraulic connection with the shallow groundwater flow system (Froend et al., 1993). At very small spatial scales (within individual wetlands), depth to the groundwater table determines soil moisture, the duration for which sediments remain damp and whether the zone of capillary-rise of groundwater is subject to evaporation (Semeniuk & Semeniuk, 2012). Recent declines in groundwater tables, due to reduced rainfall and extraction for human use, mean that in some wetlands surface expression of groundwater no longer occurs, even in winter. As a result some wetlands on the SCP are now functionally extinct (Sim et al., 2013). In contrast, urban wetlands that receive stormwater maintain surface water, raising local groundwater levels. In some cases wetlands may now be dependent on stormwater for inundation (Boulton et al., 2014). The loss of groundwater inputs alters the chemistry and light climate of the wetlands, because the groundwater under Bassendean Sands (Fig. 2.3) has high concentrations of humic substances whereas stormwater does not. Urban stormwater may also carry nutrients and other contaminants into wetlands. Changes in wetland inflows may therefore also lead to changes in geomorphological processes, plant and invertebrate species composition, wetland connectivity and ecosystem processes (Semeniuk & Semeniuk, 2012; Boulton et al., 2014). As individual species have specific traits to cope with drying, each species can tolerate a particular inundation period or degree of drying which if changed, may lead to local extinction and changes in assemblage composition.
There are three parallel sand dune systems which make up the SCP: the Bassendean system is the oldest and most easterly, carbonate has leached out of these soils which now consist of siliceous sand; the Spearwood system consists of aeolianite overlain by a hard exterior of yellow and brown sand covered in calcite; the Quindalup system is the youngest and is parallel to the current coastline, consisting of mostly unconsolidated calcareous sand (Fig. 2.3) (McArthur & Bettenay, 1960). The wetlands lie in the depressions between these dune systems and therefore lie in chains running north to south.

**Wetland vegetation**

SCP wetlands are typically shallow and prior to European settlement were extensively vegetated with submerged, emergent and fringing vegetation. Now, few of the remaining wetlands remain fully vegetated with mostly natural vegetation, and only 45% of wetlands retain half of their fringing vegetation (Hill et al., 1996). All the wetlands sampled in this study have some fringing vegetation which varies in both type and extent, from herbland to forest. Lake Booragoon was surrounded by low forest while Lake Joondalup and Lake Forrestdale both had low forest and sedgelands (Semeniuk et al., 1990; Semeniuk & Semeniuk, 2004). Different types of fringing
vegetation may create different habitats for aquatic invertebrates. Vegetation density also has an effect on wetland salinity and water level (Semeniuk & Semeniuk, 2013).

**Invertebrate assemblages**

Wetlands are the most biologically productive area of the Swan Coastal Plain (Balla, 1994), providing habitat for thousands of plant and animal species. Over 280 invertebrate species were identified in a subset of forty SCP wetlands, and of these, more than 25% were aquatic beetles (Davis et al., 1993). Seasonal wetlands have higher invertebrate species richness than perennial wetlands as a result of the greater amount of vegetation present in the water column (Balla, 1994) and the turnover of species through time (Robson & Clay, 2005). Several publications describe the diversity of macroinvertebrates in SCP wetlands (Davis & Christidis, 1999; Horwitz et al., 2009) and relate their distribution to factors related to water regime and water quality (Growns et al., 1992; Davis et al., 1993; Balla & Davis, 1995; Davis et al., 2001; Chessman et al., 2002; Sim et al., 2013), although there are few published studies of the ecology of individual taxa.

Horwitz et al. (2009) analysed previous research on the SCP wetlands and found that the highly diverse invertebrate groups included: 50+ Dytiscidae species (water beetles), 60+ Cladoceran species (water fleas), 30+ copepod species, 40+ ostracod species (seed shrimp), 31 chironomid species (non-biting midges), 10 culicid species (mosquitoes), 9 corixid species (water boatmen), 10 notonectid species (backswimmers), 11 zygopteran species (damselflies), 12 epiproctophoran species (dragonflies), 28 aquatic mite species, 14 aquatic mollusc species and 17 oligochaete (earthworm) species. Compared to the rest of Australia, the SCP wetlands have high overall invertebrate richness and endemicity (15.6% (38 taxa) were found to be endemic to the southwest of Australia, Horwitz et al. 2009). Similarly, Davies and Stewart (2013) found that the lotic waters of south-western Australia have a diverse invertebrate fauna of which 50% of species are endemic to the south-west. This high level of endemicity is not surprising given that south-western Australia is a globally-recognised biodiversity hot spot for a range of other taxa (Davies & Stewart 2013).

It is estimated that 70% of the total wetland land area on the SCP has been lost since European settlement (180 years ago) due to draining and infill (Chessman et al., 2002). Perth’s urban sprawl is partly responsible for the degradation of metropolitan
wetlands and they are increasingly stressed by pollution (especially nutrient enrichment, acidification and stormwater) and hydrological change (Chessman et al., 2002; Sommer & Horwitz, 2009; Horwitz et al., 2009). Development of wetland edges for aesthetic reasons and for recreation has led to the creation of lawns and parklands, which may be fertilized and irrigated. There has also been the introduction of invasive species including mosquito fish (*Gambusia holbrooki*), gold fish (*Carassius auratus*), carp (*Cyprinus carpio*) and the snails *Haita* (formerly *Physa* *acuta*) and *Helisoma* sp. which have contributed to the decline of some native fish and invertebrate species (Davis & Froend, 1999). Exotic plants have also been introduced including submerged weeds such as *Callitriche stagnalis*, *Rorippa nasturtium* (watercress), emergent weeds like *Typha orientalis* and fringing weeds particularly grasses (e.g. *Stenotaphrum secundatum*, *Cynodon dactylon*) and arum lilies (*Zantedeschia aethiopica*), which have changed the native plant composition and increased the fire risk around wetlands (Davis & Froend, 1999).

The study wetlands

The research in this thesis was carried out in eight SCP wetlands: Lake Joondalup West, Lake Joondalup South, Lake Booragoon, North Lake, Bibra Lake, South Lake, Forrestdale Lake and Chelodina Swamp (Fig. 2.4). All the wetlands studied here lie within regional parks and nature reserves and are managed for recreation and conservation. All are seasonally inundated except Lake Joondalup West and Chelodina Swamp, both of which contract to a small central pool in autumn. All eight wetlands also have at least a partial fringe of dense shade provided by a mature canopy of native paperbark trees, *Melaleuca* species (including *Melaleuca rhaphiophylla*, *M. preissiana*, *M. teretifolia*) (Fig. 2.5).
Figure 2.4. Map of Australia, Swan Coastal Plain and Perth showing the eight wetlands studied.
Lake Joondalup West (S31°45.716' E115°47.391') has a total area of 529 ha of which 79 ha is sedgeland (dominant species are: *Baumea articulata*, *Typha orientalis* and *Schoenoplectus validus*) and 64 ha is *Melaleuca/Eucalyptus rudis* woodland (Froend *et al.*, 1993) (Fig. 2.6). The lake is a large, relatively deep linear interdunal depression, with sediments derived from limestone deposits (Arnold, 1990a). Although significant increases in water level have occurred in the past (e.g. Hill *et al.*, 1996), levels dropped in the early 1990’s leading to a seasonal water regime more similar to its original hydrology (Froend *et al.*, 1993). Lake Joondalup South (S31°46.623' E115°47.738'), is part of Lake Joondalup but has been separated from it by the Ocean Reef Road causeway (Fig. 2.6). A series of culverts connect the two basins only in times of high rainfall. Both wetlands are protected within the Yellagonga Regional Park.

**Figure 2.5.** The edge of South Lake when dry, showing the fringing canopy of *Melaleuca* trees.
Figure 2.6. Map of Lake Joondalup West and Lake Joondalup South sites and surrounding remnant vegetation and urban areas (Google Earth, 2015).
Lake Booragoon (S32°02.629' E115°50.602') is 12.3 ha in area and was classed as a permanently inundated basin (Fig. 2.7) (Hill et al., 1996), however, it has returned to a seasonal water regime for the past two decades. It has a dense fringe of *M. rhaphiophylla* trees and its shallow, level basin is almost completely covered with emergent macrophytes. When permanent, the lake water was coloured with tannins that prevented algal blooms despite eutrophication from surrounding land use. Presently, it receives stormwater from the surrounding suburb, so the lake water is more lightly coloured, and incoming nutrient levels are lower due to conversion of the surrounding suburb from septic tanks to sewers in the late 1980s. Lake Booragoon sediment consists largely of organic matter to a depth of 2 m at the centre of the lake, with an increasing proportion of silt and clay to 3m depth (Arnold, 1990b). The fringing trees offer roosting habitat for large numbers of ibis (*Threskiornis molucca, Threskiornis spinicollis*), and several species of egrets (*Ardea alba, Ardea intermedia*) and heron (*Egretta novaehollandiae, Nycticorax caledonicus*).

**Figure 2.7.** Map of Lake Booragoon showing fringing vegetation and surrounding urban area (Google Earth, 2011a).
North Lake (S32°04.652' E115°49.348') is 24.6 ha in area, was classed as a permanently inundated basin (Hill et al., 1996) but like Lake Booragoon, it has returned to a seasonal water regime over the last two decades. It is protected within the Beeliar Regional Park. Formerly up to 4 m deep and receiving high levels of nutrients from inflowing agricultural drainage (Balla & Davis, 1993), it is now seasonal, up to 0.5 m deep and receives only urban stormwater. This change occurred due to cessation of agricultural drainage inputs at the end of the 1990s, combined with a locally declining groundwater table. The perimeter is vegetated by *M. rhaphiophylla*, several species of sedges and *Typha* spp. (Fig. 2.8). A large nature reserve on the eastern side of the lake comprises high quality native bushland and dense wetland vegetation. North Lake in the past has been an excessively eutrophic lake harbouring invertebrate species tolerant of eutrophication and causing nuisance midge problems in the adjacent suburb (Davis *et al.*, 1993). However, in very dry years the lake now does not fill with surface water at all and is highly dependent on stormwater inflow for the presence of surface water. Sediments within the lake bed vary from white sand to highly organic, flocculant sediment (Qiu & McComb, 2000).

*Figure 2.8. Map of North Lake (on the left) and surrounding remnant native vegetation. The adjacent urban area is to the west of this image (Google Earth, 2011b).*
Bibra Lake (S32°05.450' E115°49.278') is 188.7 ha in area and was also a permanently inundated basin in the 1970s – 1990s (Hill et al., 1996). It is protected within the Beeliar Regional Park. Over the past two decades it has become a seasonal wetland, usually retaining a single (hypersaline) pool on the western side of the lake in summer-autumn (Chester, unpublished data). The perimeter is vegetated by *Melaleuca* species, flooded gums (*E. rudis*) and sedges (Fig. 2.9). The western and southern edges comprise lawns and parkland and formerly there was a municipal rubbish dump at the southern end (Davis et al., 1993). Around 50% of the lakebed is vegetated with emergent macrophytes including the exotic *Typha orientalis*. Because of the expansion of *Typha* and the need to protect native vegetation, Bibra Lake is sprayed with herbicide to control *Typha*, annually. In the past, Bibra Lake was an excessively eutrophic lake with tolerant invertebrate species (Davis et al., 1993) and was the source of nuisance midges to surrounding suburbs. Lake sediments now vary from white sand to highly organic flocculant sediment in areas formerly covered by emergent macrophytes.

**Figure 2.9.** Map of Bibra Lake showing remnant fringing vegetation and surrounding urban areas (Google Earth, 2011c).

South Lake (S32°06.227E115°49.125) is a 31.5 ha seasonally inundated basin (Hill et al., 1996) and is protected within the Beeliar Regional Park. It has a dense fringe of native *M. raphiophylla* trees as well as a variety of submerged and emergent
macrophytes (Fig. 2.10). It has extensive beds of emergent macrophytes and does not receive street drainage. It has lightly tannin stained waters and is not eutrophic. South Lake and its sediment are therefore relatively undisturbed by urbanisation and bed modification.

![Figure 2.10. Map of South Lake showing remnant fringing vegetation and surrounding urban and industrial areas (Google Earth, 2011d).](image)

Forrestdale Lake (S32°09.640E115°56.055) is a seasonally inundated, Ramsar-listed lake protected within the Jandakot Regional Park. The total area of a wetland is 247 ha of which is 10.7 ha is sedgeland (predominantly *Typha orientalis*) and 14.8 ha is fringing *Melaleuca* woodland. The lake is a very shallow, flat-bottomed circular basin surrounded by a ring of low dunes (Froend *et al.*, 1993). The perimeter is vegetated by *Melaleuca, Banksia* and *Acacia* woodlands (Fig. 2.11) (Davis *et al.*, 1993). Rural and stormwater drains enter the lake (Froend *et al.*, 1993). The sediment has a (white) clay base which slows water from infiltrating to the ground water (Arnold, 1990c; Qiu & McComb, 2000).
Figure 2.11. Map of Forrestdale Lake showing remnant fringing vegetation, adjacent bushland, agricultural land and the urban area to the north-east (Google Earth, 2008).

Chelodina Swamp (formerly known as Murdoch Swamp) (S32°04.286’ E115°50.096’) is 3.3 ha in area and is a perennially inundated basin connected to the groundwater table. The central area was deepened by 2 m in the late 1930’s to serve as a permanent water source of water for fire control (Hart, 1978). Mature stands of *M. rhaphiophylla* exist in the seasonal wetland area around the deepened pool, which may overflow and flood an area of mature *M. rhaphiophylla*, *Banksia* spp., shrubs and sedges (Fig. 2.12) (Balla & Davis, 1993). No stormwater drains enter Chelodina Swamp however nutrient enriched groundwater enters the wetland from the adjacent farmland. Despite high levels of phosphorus and nitrogen, the high concentrations of humic substances in the water column have prevented algal blooms. Reduced frequency of inundation of fringing vegetation and degradation of humics by UV light in the central pool; have reduced humic concentrations in the last decade (Bryce & Dyer 2009). Chelodina Swamp is one of very few remaining wetlands on the SCP that has both a
perennial section and retains 100% of its native vegetation. Swamp sediments comprise areas of peat and white sand. It is a conservation category wetland protected within the Beeliar Regional Park and lies within the Murdoch University campus where it is managed for conservation and used for teaching and research purposes.

Figure 2.12. Map of Chelodina Swamp showing fringing vegetation and adjacent farmland (to the east) and university car parks (north) (Google Earth, 2011e).

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Chapter 3. Freshwater invertebrate life history traits for surviving desiccation

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Abstract
In many regions, climate change is prolonging dry periods in rivers and wetlands, exposing freshwater invertebrates to increased periods of desiccation. Invertebrates show a range of strategies for surviving desiccation, but the effects of the degree of exposure to desiccation on the expression of particular traits is unknown. This review synthesizes existing information on the desiccation responses of freshwater invertebrates to examine the flexibility of these survival strategies and the relationship between strategies and the degree of desiccation to which individuals are exposed. It focuses on desiccation at the small spatial scales experienced by individuals and clarifies the terminology of resting stages present during desiccation. We provide a key to terminology used for different forms of dormancy, so that appropriate terms may be used. All invertebrate groups showed a range of strategies for surviving desiccation. Sometimes, different traits were expressed among different populations of a species; however, it is unclear how many species show multiple desiccation response strategies. Many crustacean taxa showed physiological dormancy responses to desiccation that enabled survival for long periods (years). Insects often rely on emigration from drying waterbodies as flying adults or on larvae occupying damp refuges on the benthos. Altered water regimes may alter the phenology of desiccation responses, potentially increasing local extinctions, even in species capable of prolonged dormancy because of constraints on life cycles. However, there is limited empirical evidence demonstrating the flexibility of, or limitations to, expression of these survival strategies and their potential fitness costs.

Key words: Climate change, Diapause, Dormancy, Drought, Intermittency, Rivers, Traits, Wetlands
Introduction

It is predicted that, by 2090, the proportion of the global land surface in extreme drought will increase tenfold from current levels [80] leading to decreased hydroperiods in affected wetlands. The areas affected by climatic drying include large areas of southern Australia, north-eastern Brazil, Mexico, the Mediterranean and southern Africa. Many of these areas already contain temporary waterbodies, but climatic drying has the potential to change water regimes from perennial to temporary and for existing temporary waters, hydroperiods are likely to further decrease. Temporary waters are diverse in form and geography; they include small depressions, large lakes, riparian wetlands and ephemeral streams that dry to pools and are found in tropical, arid, semi-arid, temperate and mediterranean climate regions [119, 148]. Many wetland processes are interrelated and will have cumulative or synergistic effects, for example changes in air temperature will affect the biota directly, as well as indirectly via changes in evaporation rates and rainfall patterns, and will influence wetland hydrology, stratigraphy and hydrochemistry [120]. Altered sediment dynamics can have a large effect on the survival of buried eggs (the egg bank, [64]). Furthermore, decreased hydroperiods combined with changes in phenology (arising from increased temperatures) will shift the geographical distribution of many species [62]. For example, an increase in the mean temperature of 3 °C is predicted to result in a loss of 10–25 % of the mean species richness in upland streams in the United Kingdom [52]. In south-western Australia, Sim et al. [122] have documented change in wetland hydroperiods from perennial to seasonal and from seasonal to ephemeral (or terrestrial) arising from the previous 50 years of drying climate in that region. Although many of the plants and animals living in temporary waters possess traits that enable them to survive dry periods, little is known of the flexibility of these traits and whether they will enable populations to withstand prolonged or more frequent dry periods [114]. Conceptually, this scenario is one of the increasingly harsh habitat templets (sensu [126]) interacting with species life histories to determine site occupancy by species [114]. As drying alters the templet, there is an increased risk of species not possessing the traits required for survival in the new water regime. For some taxa, probably those that are good dispersers, existing survival strategies will enable them to withstand prolonged drying (e.g. [122]). For other species, their survival may depend on whether the traits within each population are sufficiently flexible to allow their persistence under
the new water regimes. Existing research shows that many species possess multiple strategies for surviving drying, and these may be used by different life history stages [114]. Thus, the interaction between species survival strategies and aquatic habitat as waterbodies dry out for longer (or fail to fill at all) is likely to be a major driver of reductions in species geographic range. Thus, a review of the existing terminology and knowledge of the strategies available to taxa inhabiting intermittent waterbodies is timely to provide a foundation for hypotheses of change in response to climatic drying.

During summer drying, aquatic animals are exposed to high levels of ultraviolet light, high temperature, large fluctuations in salinity, pH and oxygen and the rapid disappearance of water [2]. The timing and intensity of this combination of conditions determine the species that survive to reproduce or recolonize during the wet phase. The composition of the fauna emerging from dry basins may change dramatically depending on the time of year that inundation occurs [16, 50, 79] and the volume of precipitation that determines habitat area [16, 138]. This dependence on timing is important because changing climates may show increasingly unpredictable timing and frequency of rainfall events and thereby no longer meet the needs of some species. Some changes may benefit species dependent on hatching propagules. For example, species that are able to survive harsh periods in dormancy may profit from habitat instability, as the temporarily unsuitable habitat can exclude all competitors [6]. However, other species will suffer disadvantage due to hatching at inopportune times when they cannot complete their life cycle. With respect to climate change impacts, much emphasis has been placed on species’ changes in phenology driven by changes in temperature, but for aquatic animals, changes in the timing of hydroregime may be of equal significance. Furthermore, in the scenario of warmer, drier conditions, water temperatures will be warmer and waterbodies shallower, so the effects of decreased hydroperiod and increased temperatures are likely to be synergistic [45]. Increased temperatures influence the duration of egg incubation periods, hatching success, duration of hatching and the induction and termination of resting stages [2, 101], minimum size at pupation, sex of insects and increased rate of metabolic function [137]. However, increased temperatures may also exceed physiological tolerances and lead to local extinction [45, 103]. Water quality will also be altered by increased temperatures, influencing oxygen and carbon dioxide levels, salinity and eutrophication in aquatic ecosystems [45, 104]. Although these multiple stressors caused by climate change will all affect aquatic
assemblages, loss of water is among the most deleterious despite many species possessing traits enabling them to survive dry periods [114].

Observations of invertebrates surviving harsh conditions have been made for centuries. Leeuwenhoek (1702 cited in [66]) studied animals that survived loss of all cellular water for prolonged periods. Baker (1764 cited in [65]) revived nematodes after they had been dried for 27 years. Observations of anostracans and notostracans emerging from desiccation-resistant eggs date back to the early 18th century [59]. Straus (1819–1820) recognized that ephippia on Daphnia were used to withstand the northern winter, and this was the first genuine report of diapause [59]. Dormancy in invertebrates is not a single trait but rather a large group of individual strategies and physiological states [30]; and it is only one of the options that species may use to cope with desiccation. The effect of desiccation is different for each life cycle stage of a species, especially under different environmental conditions [41]. This variation may provide opportunities for species to adjust to changed water regimes. For example, copepods that can enter a resting stage as an egg, juvenile or adult, can survive desiccation at any life stage. In contrast, some aquatic taxa sensitive to desiccation die within a few hours of the sediment drying if they cannot find an aquatic refuge [42].

Even though these processes and mechanisms have been studied for a long time, knowledge gaps exist, especially the variation in strategies among related species and the flexibility of these strategies under different environmental conditions. Until relatively recently, dry sediments in temporary aquatic habitats were often considered to be biologically inactive [128, 131].

It is important to correctly identify each desiccation response to make predictions about the effects of increased frequency, duration or intensity of drying upon populations. Similarly, understanding the effects of levels of exposure to desiccation upon the expression of traits increases the ability to predict the consequences of changing climatic regimes for freshwater invertebrates. Therefore, this review aims to synthesize existing information on the desiccation responses of freshwater invertebrates, to examine the flexibility of these strategies and the relationship between survival strategies and the degree of desiccation to which individuals are exposed. That is, responses to desiccation at the small spatial scales experienced by individual invertebrate animals. To do this, we have clarified the definitions of the types of resting stages that occur during desiccation and made an
effort to include the older (pre-electronic) literature which often included detailed observations of invertebrate behaviour.

**What is Desiccation?**

Desiccation from drought is a major factor in mortalities of insects in temporary pools [74, 109], but not all drying leads to complete desiccation. Desiccation arises from different mechanisms leading to the loss of water. In high latitudes, desiccation occurs in systems that freeze in the winter and there is no free water for invertebrates; in lower latitudes, desiccation is associated with long periods of drought. In arid and semi-arid areas where invertebrates are exposed to desiccation for most of the year, they have adapted to cope with a very short period of inundation, and in mediterranean climate ecosystems, drying is usually an annual occurrence [69]. Desiccation tolerance is defined as the ability to dry to equilibrium with air (<0.1 g H2O g-1) that is moderate to extremely dry and then to regain normal function after rehydration [5, 108]. The highest post-desiccation survival rates occur after slow drying that gives individuals sufficient time to adjust their metabolism [111].

While many terms describe individual responses to drying, drying itself is often vaguely defined. A ‘dry’ riverbed or wetland that has no free surface water can have a gradient of sediment moisture levels ranging from totally dry through to saturated, and this gradient will affect the response of individual invertebrates exposed to it. Where groundwater lies below (sometimes metres below) the exposed surface of wetland or riverbeds, but the interstitial spaces are filled with water through wicking, an intermediate degree of drying is created that we term ‘damp’. At the wetter end of the gradient, ‘saturated’ conditions occur when the water table is level with the sediment surface. Neither damp nor saturated sediment conditions are necessarily desiccating for invertebrates (although they may also present other environmental challenges, such as low dissolved oxygen), and they may contain subsurface microhabitats accessible to invertebrates [132].

There is also an important distinction to be made between an organism being desiccated and an environment being desiccated. The absence of surface water does not mean that habitat is desiccated and especially does not mean that the invertebrates in it are also desiccated [132]. A much greater amount of information is necessary about habitat conditions at the scale at which individual animals are exposed to them, to
interpret information on strategies such as dormancy [25]. From afar (as in satellite images), a wetland may appear dry and potentially desiccated, but it may contain damp or inundated microhabitats occupied by invertebrate that do not possess physiological adaptations to desiccation [132]. Microhabitats such as cracks in sediments or crayfish burrows that lead to the groundwater table may allow invertebrates to survive periods without surface water and prevent them from becoming desiccated (e.g. [76]).

**How do Individuals Respond to Desiccation?**

Individual animals survive adverse conditions by using physiological adaptations and/or behavioural responses. Some invertebrate groups have profound physiological adaptations to drying, such as the desiccation-resistant eggs produced by many micro-crustaceans [114]. These physiological responses include strategies that have been defined as resistance traits or strategies because they allow individuals to resist the drying of waterbodies [82, 113] and have been included as forms of refuge from disturbance [32, 115]. Resistance strategies may also include the use of refuge (micro) habitats within the benthos. Other groups, such as adult Coleoptera, have behavioural responses like flying away from drying habitat to more permanent water. Winged stages allow recolonization of habitats that have experienced localized extinction due to drought and serve as an important source of colonizers [28]. These have been termed resilience traits because they permit recovery of populations following loss of individuals during disturbances [32, 82, 113]. These strategies may be stimulated by the degree of desiccation to which individuals are exposed; however, in some cases, behaviour such as flying away from drying habitat may also be triggered by other processes including life history stage or other forms of disturbance. Similarly, some other traits such as a rapid growth rate or early age at reproduction, which may lead to a population being able to respond to the drying of a waterbody through rapid reproduction, are a response that may be triggered by processes other than drying. In the case of rapid reproduction, several traits (and potentially various combinations of traits) from across two trait domains (reproduction and development sensu [139]) are involved in producing the observed response. To describe this complexity clearly, Verberk et al. [139] described suites of co-evolved species traits that combine to make adaptations permitting species to deal with a range of ecological problems as ‘life-history
strategies’. Consequently, because some responses are specific to drying (e.g. aestivation) and others are not (e.g. rapid growth), and some are combinations of traits rather than single traits, we describe them as ‘responses’ to desiccation or as ‘drought survival strategies’.

To maintain life processes, rather than suspending them, many aquatic invertebrates survive dry periods in refuges comprising microhabitats with high humidity; including beneath algal mats [133], in cracks in the sediment [132], damp areas beneath woody debris or stones (e.g. [32, 134]) and inside crayfish burrows (e.g. [76]). Shallow groundwater such as the hyporheic zone present beneath some streams may also provide refuge for species able to access it [134]. The potential for hyporheic refuges from drying is variable and depends on the presence of saturated interstitial spaces, determined by stream gradient and local geology [134]. If the bottom of a waterbody is concave, then resting stages and surviving life stages may move down slope as the water recedes and gather in the deeper zones (‘the coffee ground effect’), which are both the last and first place inundated [135]. Small scale conditions, especially heterogeneity, on the benthos are therefore likely to be important for the survival of invertebrates that seek refuge in the water that remains during the dry period.

The Terminology of Dormancy Responses

Textbook definitions and dictionary meanings of the terminology used to describe resting stages differ markedly (Table 3.1). For example, abiosis and anabiosis are terms used in the literature to describe a state resembling death, but their definitions are broad and imprecise. Similarly, Bishop [20] stated that “students of Crustacea have used the word ‘diapause’ loosely and did not distinguish between diapause and quiescence”. Quiescence is simply the appearance of inactivity, regardless of physical or metabolic state, whereas diapause emphasizes a more profound difference between the active and inactive forms; it might require a physiological change to a specific life stage (Fig. 3.1). A ‘Web of Knowledge’ search showed some broadly defined words being commonly used, while more specific words were used rarely (Table 3.1).
Table 3.1. Terminology and definitions for the ‘dormant stages’ shown by invertebrates in response to habitat drying.

<table>
<thead>
<tr>
<th>Term</th>
<th>Description of meaning</th>
<th>Web of science usage*</th>
<th>Our definition</th>
<th>Taxa shown to use strategy</th>
</tr>
</thead>
<tbody>
<tr>
<td>Resting stages</td>
<td>A broad collective term for the different types of dormancy and diapause; should be used when more specific processes is not understood.</td>
<td>1739</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Resistant stages</td>
<td>A broad collective term for the different types of dormancy and diapause; should be used when more specific processes is not understood.</td>
<td>2394</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Suspension of life</td>
<td>A broad collective term for the different types of dormancy and diapause; should be used when more specific processes is not understood.</td>
<td>536</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dormancy</td>
<td>“Is a suspension of the vital functions in an organism for a certain, sometimes very long, period of time to overcome harsh environmental conditions; with long term cessation of development, growth and breeding. In insects it may occur in embryonic, immature or adult stages” [61]</td>
<td>2956</td>
<td>The slowing of metabolism to overcome a harsh environment</td>
<td></td>
</tr>
<tr>
<td>Hypobiosis</td>
<td>“dormancy” [4]</td>
<td>16</td>
<td>Another term for dormancy</td>
<td></td>
</tr>
<tr>
<td>Term</td>
<td>Definition</td>
<td>Page Numbers</td>
<td>Examples</td>
<td></td>
</tr>
<tr>
<td>----------------------</td>
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<td>--------------</td>
<td>----------------------------------------------------------------------------------------------</td>
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<tr>
<td>Diapause</td>
<td>“Is a type of dormancy; it is determined by a predictive mechanism combining environmental signals and an internal biological clock, driven by hormones and induced by both signal and vital factors (e.g. a larval damselfly or ephippial eggs). Development is not resumed, even if the conditions become favourable, until diapause is broken. It is regarded as adaptive and increases the probability of survival during environmentally unfavourable conditions” [2, 26, 61]</td>
<td>4772</td>
<td>Nematoda, Turbellaria, Oligochaeta, Bivalves, Gastropods, Acarina, Cladocera, Copepoda, Conchostracha, Ostracoda, Anostraca, Notostraca, Chironomidae, Diptera, Culicidae, Ephemeroptera, Odonata, Plecoptera, Trichoptera Rotifers</td>
<td></td>
</tr>
<tr>
<td>Quiescence</td>
<td>“Quiescence is an immediate response to a limiting factor, and metabolism and development is resumed as soon as conditions permit” [2, 26, 61]</td>
<td>1389</td>
<td>Bivalves, Gastropods, Acarina, Cladocera, Copepoda, Conchostracha, Ostracoda, Plecoptera, Trichoptera</td>
<td></td>
</tr>
<tr>
<td>Aestivation</td>
<td>“Is a physical state in which an organism is metabolically inactive or physically dormant during summer or during periods of continued high temperatures in temperate areas or during a dry season in tropical areas” [61]</td>
<td>543</td>
<td>Nematodes, Hirudinea, Amphipoda/Isopoda, Decapoda, Odonata, Trichoptera</td>
<td></td>
</tr>
<tr>
<td>Hibernation</td>
<td>“winter dormancy, a period of suspended development in organisms that occurs during seasonally low temperatures” [61]</td>
<td>2515</td>
<td>Acarina, Cladocera, Ostracoda, Trichoptera</td>
<td></td>
</tr>
<tr>
<td>Athermopause</td>
<td>“Is a physiological condition or expression of dormancy that is influenced by one or more non-thermal factors” [61]</td>
<td>0</td>
<td>Diapause that occurs in the summer months triggered by cues such as day length and temperature</td>
<td></td>
</tr>
<tr>
<td>Summer diapause</td>
<td>May be induced obligatorily or facultatively by such seasonal cues as day length and temperature, different from winter diapause as the two types involve different physiological processes [110]</td>
<td>591</td>
<td>Diapause that occurs in the summer months triggered by cues such as day length and temperature</td>
<td></td>
</tr>
<tr>
<td>Term</td>
<td>Definition</td>
<td>Articles</td>
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<tr>
<td>Abiosis</td>
<td>“Is suspension of life, a mode of living, vitality” [61]</td>
<td>1</td>
<td></td>
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<tr>
<td>Anabiosis</td>
<td>“A condition of apparent death or suspended animation where productive metabolic process in which biochemical reactions within the animal body produces proteins, fats and carbohydrates from food material” [61, 85]</td>
<td>66</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Superpause</td>
<td>“Is diapause for more than 1 year” [61]</td>
<td>0</td>
<td></td>
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<tr>
<td>Mesopause</td>
<td>“Is diapause for between 3-12 months” [61]</td>
<td>12</td>
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<tr>
<td>Oligopause</td>
<td>“Is diapause for less than 3 months” [61]</td>
<td>13</td>
<td></td>
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<tr>
<td>Cryptobiosis</td>
<td>“Is a hidden life, continuing at a low metabolic level, without obvious signs of activity” [9] (e.g. Collembola).</td>
<td>118</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anhydrobiosis</td>
<td>“Is the maintenance of life in the absence of water induced by low humidity or by desiccation” [9, 61]</td>
<td>305</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cyclomorphosis</td>
<td>“Seasonal changes in body shape found in rotifers and in cladocerans. In cladocerans the changes in shape involve the head, which is rounded from midsummer to spring and then progressively becomes helmet shaped from spring to summer reverting to the rounded shape by midsummer. The process is poorly understood and may be a result of genetic factors interacting with external conditions (e.g. temperature)” [3, 149]</td>
<td>143</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Web of science search conducted on 6/11/12; related search included web of science categories: anatomy morphology, biodiversity conservation, biology, cell biology, developmental biology, ecology, entomology, environmental sciences, environmental science ecology, evolution biology, fisheries, limnology, marine freshwater biology, microbiology, physiology, reproductive biology and zoology. Usage: numbers are numbers of articles identified in the search as using a particular term.
Figure 3.1. Key to terminology of the types of dormancy shown by freshwater invertebrates. Using literature listed in the Table 3.1, this key was constructed to assist researchers to identify the correct terminology for dormant states. Begin on the left hand side and proceed according to the level of knowledge about the physiology and traits of a particular species.
It is important that researchers use the correct terminology to describe species responses to drying, because these terms may describe physiological mechanisms and thereby indicate how much is known about the particular physiological process used (Fig. 3.1). We have constructed a key to assist researchers to identify the correct term for a species under study, reflecting what is known of its response to drying (Fig. 3.1). Use of precise terminology also enables more accurate prediction of the outcome of environmental change for species. Usually, the appropriate term can be determined by the degree of knowledge of the physiological processes involved in producing the observed state, such as by following the key to terms shown in Fig. 3.1. Often, authors do not know which process or mechanism is occurring and wrongly use a precise term such as ‘diapause’ where they should be using the term ‘dormancy’ instead.

**Desiccation Resistance Among Freshwater Invertebrates**

Most taxonomic groups have several strategies for surviving drought (Table 3.2), so although individual species might only use one method, ancestral genotypes contained the potential for multiple survival strategies. Some taxa have extraordinary abilities to resist desiccation *in situ.*
Table 3.2. Drought survival strategies across life stages in freshwater invertebrate taxa and their known duration of dormancy (where applicable). Strategies and life stages in bold are specific responses to desiccation, others are used for other types of disturbance.

<table>
<thead>
<tr>
<th>Group</th>
<th>Survival strategy</th>
<th>Aestivation</th>
<th>Anhydrobiosis</th>
<th>Cryptobiosis</th>
<th>Diapause</th>
<th>Hibernation</th>
<th>Quiescence</th>
<th>Cohort splitting</th>
<th>Commensalism</th>
<th>Rapid growth</th>
<th>Sealing Shell/carapace</th>
<th>Burrows</th>
<th>Arial adults</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nematoda</td>
<td></td>
<td>X</td>
<td>X</td>
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<tr>
<td>Turbellaria</td>
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<td>X</td>
<td>X</td>
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<td>Hirudinea</td>
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<td>Oligochaeta</td>
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<tr>
<td>Bivalves</td>
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<td>X</td>
<td>X</td>
<td>X</td>
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<td>Gastropoda</td>
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<td>X</td>
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<td>X</td>
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<tr>
<td>Acarina</td>
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<td>X</td>
<td>X</td>
<td>X</td>
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<td>X</td>
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<td>Rotifers</td>
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<td>X</td>
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<td>Cladocera</td>
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<td>X</td>
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<td>Copepoda</td>
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<tr>
<td>Conchostrachae</td>
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<td>X</td>
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Anhydrobiosis

Although many taxa have desiccation-resistant eggs, some also have desiccation-resistant larvae and adults capable of entering anhydrobiosis (dehydrated state). Nematodes, for example, may produce a resistant third-stage juvenile known as ‘‘daver larvae’’ which have a modified cuticle to withstand drying (Wharfton 1986 cited in [30]) and may survive extended dry periods (longer than 200 days) in a state of anhydrobiosis [63, 84]. Rotifers also use anhydrobiosis, and some (Musibila sp.) can survive nine years in a desiccated state [63]. Some leeches are also capable of anhydrobiosis ([78], Table 3.2); for example, a leech survived drying at 13 °C for 17 days [65]. However, the physiological mechanism and fitness cost of anhydrobiosis in most species is unknown. For example, it is not known whether animals can enter and emerge from anhydrobiosis repeatedly. Consequently, while anhydrobiosis is a strategy specific to surviving desiccation and appears to be suitable for long periods without surface water, it is not clear whether it is a flexible or costly strategy for individuals.

Diapause

Diapause is present in life cycles of the majority of crustaceans (Table 3.2), and usually only one form of diapause is specific to order (but exceptions are not rare; [2]). Diapause may be used to survive drying, but also freezing, or may occur as part of the life cycle in the absence of disturbance. Copepods have diapausing eggs, juveniles [37] and adults [99], late copepodites [118] and adults may encyst [155], and the eggs of some species are very resistant to desiccation [151]. It has even been reported that some copepods were ‘‘desiccation’’ resistant for 200 years or more (Hairston et al. 1995 cited in [19]). Although copepods are probably very desiccation resistant, the mechanisms that allow prolonged diapause are unknown and therefore the likely effects of drier water regimes on populations cannot be predicted. This is true for other taxa that use diapause to resist drying, such as some stonefly species that have early instars capable of diapause.

Alternative Life Cycle

For some taxa, the life cycle changes profoundly at the onset of a disturbance such as drying. This type of response to declining water levels comprises reproductive flexibility and the capacity to alter development; it thus combines traits from two
Male Cladocera (water fleas, Crustacea) occur in populations only at the onset of unfavourable conditions; usually, populations are entirely made up of females reproducing parthenogenetically. Following fertilization, females produce a resting egg (ephippium) by thickening a section of the carapace which forms the ephippium (after her death, [151]). Ephippia have been successfully hatched from dry pond sediments after 200 years [60], and they can withstand both freezing and desiccation [96], suggesting that they would be a robust response to prolonged drying. However, in floodplain sediments, Jenkins and Boulton [75] found that “cladoceran production fell by more than an order of magnitude as the duration of drying increased from 6 to 20 years”, showing that the effects of prolonged drying can be detected in wild populations, and indicating that climate change may affect the viability of ephippia.

**Resistant Eggs and Cysts**

There are a wide range of other taxa that produce forms of resistant eggs or cysts, some of which must experience a period of dormancy (either quiescence or diapause) prior to hatching. The physiological processes leading to the formation of eggs and cysts differ markedly, and eggs may be formed parthenogenetically or through meiosis and sexual reproduction. Even the details of the parthenogenetic process differ among species. In most cases, little is known of the processes by which eggs or cysts develop in response to drying or the triggers that commence these processes. Many Crustacea, such as anostracans (brine shrimp) and copepods, produce desiccation-resistant eggs. Anostracan eggs can survive 15–20 years of desiccation ([33]; Steiert 1995 cited in [17]) and may persist in the sediment over many hydrological cycles. Hildrew [70] used an experiment where 28-day wet/dry periods were oscillated nine times over a 504-day period and observed anostracans hatching during every wet phase. This shows that egg banks can supply hatchlings over repeated cycles of wetting and drying without new egg production contributing to the egg bank. Some genera (e.g. *Branchinella*) require the desiccation of eggs as part of their life history [151]. Notostraca (tadpole shrimp) are one of the few invertebrate groups found only in temporary waters, and their desiccation-resistant eggs last for long periods; in at least one species, eggs require desiccation for further development [58, 151]. Conchostracan
(clam shrimp) eggs are also desiccation resistant although the free swimming stages are killed by drying [21]. Anostracans and notostracans are likely to be taxa that adapt well to prolonged dry periods.

Other taxa have resting stages that may last for shorter periods, but still up to around 2 years, representing a form of quiescence. Turbellarians (flatworms, Platyhelminthes) have dormant eggs lasting up to 2 years [156] and may also form resistant cysts enclosing young, adults or fragments of animals; they also may survive in permanent pools ([31], Table 3.2). Oligochaetes (Annelida) also have resistant cysts enclosing young and can also survive as adults or fragments of adults or dormant eggs [78]. The rotifer *Bdelloidea* sp. secretes a cyst with a layer of protective gel [2, 149], which is thick shelled and only hatches after a dormant period [151].

Insects, including many dipterans and some coleopterans, may produce desiccation-resistant eggs. For example, the chironomid midge *Polypedilum vanderplanki* produces desiccation-resistant eggs capable of surviving drying for 17 years (Adams 1985 cited in [108]). Simulidae (black flies) and Culicidae (mosquitoes) have drought-resistant eggs which hatch once the water returns (Hawley 1988 cited in [7; 114]). *Aedes aegypti* and *A. albopictus* eggs become resistant to desiccation approximately 24–48 h after deposition (Christophers 1960 cited in [125]). *Eurosta solidaginis* (Diptera: Tephritida) found in North America withstand exceptionally dry conditions for 6–8 months, among the driest reported for any insect [106]. Some species of Plecoptera (stoneflies) have eggs that pass through dormancy periods (Table 3.2), while other species show delayed hatching (e.g. members of the Perlidae, Perlodidae and Pteronarcyidae) [94]. These are forms of quiescence and diapause, respectively.

**Aestivation**

Some taxa rely on shorter term resistance to drying by constructing special resistant structures in which to aestivate or hibernate (Fig. 3.1). Some species of Hirudinea are able to survive the summer and autumn period buried in the ground, and some surround themselves in a secreted layer of slime in small cavities in the dry mud, forming an aestivation chamber (Herter 1937 cited in [78; 44, 65]). Enchytraeids (oligochaetes) use two survival strategies to survive drying: migration to deeper and moister microhabitats (only for periods of days) or a desiccation-tolerant cocoon stage [91]. Burial in deeper, moister sediment is also a strategy used by some bivalve
molluscs (Table 3.2). Hyriidae (freshwater mussels) are able to tolerate prolonged dry spells by burying themselves in the mud and sealing their shell (quiescence). Sphaeriidae may survive drying for short periods [46], by closing their shells. Many sphaerids are endemic to ephemeral waters where they survive drying for many months [95].

Aestivation has not been recorded for amphipods and has only been observed in isopods in two studies: Chester and Robson [32] observed adult Synamphisopus doegi (erroneously named Paraphreatoicus relictus) aestivating in damp sediment beneath stones in dry stream beds; Mackie et al. [89] found two species of isopod (Heterias sp. and S. doegi) aestivating under boulders in damp places in intermittent streams; both studies were in the Victoria Range, western Victoria, Australia. Aquatic amphipods and isopods therefore probably have a reliance on permanent water sources (e.g. [98]). Under climate change, these refuges may be more difficult to access. If the ability to aestivate is rare among amphipods and isopods, this could place them at significant risk of local extinction during climatic drying.

Similarly, freshwater crayfish may construct aestivation chambers [32], burrow down to the water table [151]; Fig. 3.2), or enter the burrows of other crayfish species [76]. Some are able to survive several years of drought in burrows connected to the water table, and some species seal the burrow entrance with a mound of excavated earth to further reduce drying [112], another form of aestivation. Responses to prolonged drying and water regime change arising from climatic drying will probably vary widely among freshwater crayfish species. Aestivation is rarer among insects than crustaceans but has been recorded for some caddisfly (Leptoceridae, [145]) and dragonfly larvae (Telephlebiidae, [32]). The caddisflies seal their cases up with silk, and the dragonfly larvae burrow beneath stones on the streambed. For all the taxa that aestivate, the construction of aestivation chambers probably entails fitness costs.
Figure 3.2. Refuges that aquatic animals use to survive dry periods in wetlands. Image: South Lake, Perth.
False start events may occur where an intense rainfall event causes the partial filling of a dry waterbody, which then dries out again before aquatic invertebrates can complete their life cycles. Mortality will occur in some species, and other species may encounter a fitness cost such as having to repeatedly construct (and emerge from) aestivation chambers. An experiment with caddisfly larvae showed that drier sediment conditions reduced the success of aestivation [145], so aestivation will have limits to its viability that may be exceeded for some species and some locations as a result of climatic drying.

**Resistance by Use of Moist Microhabitat Refuges Within a Waterbody**

Where invertebrates survive drying within moist sites within a waterbody, they are resisting desiccation in that waterbody. However, there are other survival strategies that involve invertebrates leaving the waterbody to seek out moist or wet habitats elsewhere and these are resilience strategies (discussed below).

Some species exploit damp microrefuges on the benthos (Fig. 3.2). For example, the adults of some cladoceran and gastropod species can survive and remain active in damp sediment. Other freshwater gastropods, both adults and young, survive drying in patches of moist air and sediment beneath dried algal mats [56, 133]. The production of an epiphragm or operculum to seal the shell aperture and retain moisture prolongs the time that they can remain in these microrefuges. However, juvenile gastropods are more susceptible to drying than adults [56], so if a false start occurs and they hatch out, the whole cohort may be killed. These types of microrefuge are likely to become smaller and occur less frequently under drier climates.

Amphipods and isopods have been commonly found in temporary ponds where they take advantage of the pholeteros (burrow water; [81]); but they are also found in waterbodies without crayfish burrows [68], so they exploit refuges such as the groundwater table, which they access by burrowing (Fig. 3.2; [150]), or perennial springs associated with temporary waters [98]. Shallow groundwater can be a refuge and corridor for dispersal for these crustaceans [68], and cracks in the substrate may give access to ground water, as observed for *Paramphisopus palustris* [132]. If groundwater tables decline with climatic drying, these refuges are likely to become
unavailable in some places, leading to local extinction of species like these that have few alternatives (Table 3.2).

**Desiccation Resilience Among Freshwater Invertebrates**

**Cohort Splitting**

Cohort splitting occurs when a single generation divides because of differing duration of a dormant stage [27, 114]. This mechanism occurs together with diapause, where individuals remain viable for longer than their usual life cycle, and may occur in the absence of disturbances as well as in response to disturbances, including drying [27]. Unlike the strategies listed above, it occurs at the population level. For example, Hildrew [70] found that during inundation in a Kenyan rain pool, only about 3% of the fairy shrimp population hatched and this reproductive population produced offspring equalling 7 times the population, showing the productive potential of egg banks. Female conchostracans also use cohort splitting where they deposit very large numbers of eggs at times of favourable conditions, so that they can persist for the next few years even if the conditions become unfavourable [51]. Cohort splitting probably occurs in many groups of invertebrates as a means of resisting desiccation but goes unnoticed, being difficult to detect unless studied directly. It may become more important as climate change progresses and warrants further research to determine the limits to its flexibility. A few studies of the egg bank and aestivation are beginning to address these questions (e.g. [75, 135, 145]).

**Dependence on Perennial Waters**

Lastly, some species rely on perennial waters, such as permanent pools that exist amongst temporary wetlands or streams (e.g. Figure 7.19 in [24; 32, 98, 107]). Those insect larvae unable to accelerate their growth or enter a dormant state to avoid desiccation may rely entirely on perennial waters. They include some species of mayfly (Ephemeroptera), water pennies (Psephenidae: Coleoptera), as well as some Crustacea such as decapod shrimps, some isopod and amphipod species and some freshwater crayfish [24].
Rapid Growth

Rapid growth during periods of inundation in temporary waters is a strategy used to complete the aquatic stage of a life cycle seen in several invertebrate groups, particularly insects (Table 3.2). This strategy is not confined to drought but is potentially beneficial for a range of circumstances. Furthermore, under warmer conditions, many invertebrates are likely to increase their growth rate. For example, mosquitoes take advantage of small temporary waters to reproduce and rapidly complete their life cycle as an aerial adult. Odonates may respond to drying by developing faster, reducing their size at metamorphosis [97]. However, final instar size may be directly related to fecundity in females [48, 116], so this may entail a fitness cost.

Ostracods that live in temporary waters may grow rapidly and are short lived, potentially having multiple generations in one season, permitting cohort splitting [92] and showing how resistance and resilience traits can combine to create highly effective strategies for surviving desiccation. Hatching has been observed in sediment during damp periods, but most hatching occurs after refilling [1, 132] suggesting quiescence. With immature stages already in the dry soil, ostracods may have a developmental head start when the water returns and an advantage over other species of invertebrates, given that they are already well developed [71]. It also appears likely that the amount of time juvenile ostracods take to become active once reimmersed is proportional to the duration of desiccation [1, 71]. Strachan et al. [132] observed two strategies for surviving drying among six species of ostracods (Cyprididae) in one intermittent wetland: one group (4 species) closed their carapace and aestivated and the other group (2 species) relied on the hatching of desiccation-resistant eggs.

Emigration by Flying Adults

Emigration is a drought-avoidance strategy seen in many insects but also in most species of Acarina (water mites). They have larvae that attach to migrating insect hosts and leave the water (phoresis), remaining attached to their host throughout its stay in permanent water and returning to temporary waterbodies with the host when water returns [147]. Insects generally have a separate aquatic larval stage and an aerial adult stage with varying degrees of dependence on water, so this form of resilience strategy is
common (Table 3.2). Therefore, once hatched, insects may have to complete their aquatic life stage before surface water disappears, although the ability of most species to accelerate their growth, and any associated fitness costs, is unknown (except for some odonates e.g. [48]).

Aquatic coleopterans (beetles) show a range of traits to resist drying including recolonizing adults (Table 3.2, Jackson 1956 cited in [149]). Aquatic Hemiptera (true bugs) do not appear to have life stages tolerant to drying, instead relying on recolonizing adults (Macan 1939 cited in [149]), but like beetles they are able to efficiently exploit temporary water bodies. Adult beetles are usually capable of flying away and effectively avoid drought through rapid colonization of more permanent waters via flight (Wissinger 1995 cited in [123]). Many predatory adult water beetles and bugs are able to survive in harsh aquatic environments such as drying pools where levels of dissolved oxygen are low [10], because they are air-breatheers, in order to prey or scavenge upon trapped animals.

Although short lived, Ephemeroptera (mayflies) have mobile adult stages that may fly to permanent water [86, 151] as do the Plecoptera (stoneflies). Wing length is important in flight dispersers; rare species frequently have relatively shorter wings, while common species have long wings and are therefore better dispersers [90]. Ephemeroptera are susceptible to drying and while a few species have desiccation-resistant eggs [114, 151], most species survive in permanent water and repopulate temporary waters via oviposition. Most Plecoptera have a mobile adult stage that migrates by flight to survive the summer around permanent water [24, 67]. Some species are very selective in their choice of oviposition sites, for example, ovipositing almost exclusively on substrata that protrude above the water surface [83], which may provide a humid environment that keeps eggs moist.

**Life History Strategies That Combine Desiccation Resistance and Resilience Traits may Show the Greatest Flexibility Despite Their Complexity**

Odonata (dragonflies and damselflies) and Trichoptera (caddisflies) have some of the most complex combinations of drought survival strategies, including diapausuing eggs within desiccation-resistant gelatinous egg masses and terrestrial pupae (Trichoptera); desiccation-resistant nymphs (odonates) and recolonizing adults. Most species that inhabit temporary waterbodies show rapid growth [47, 142, 146], and some
species of caddisfly have larvae that can burrow and survive deep in substrata [146]; and probably undergo quiescence. Larvae of the dragonflies *Telephlebia* and *Antipodophlebia* can be found quiescent in damp leaf litter; *Petaluridae* larvae are semi-aquatic burrowers, while *Archipetaliidae* and *Austropetaliidae* larvae are semi-terrestrial and can be found under damp logs [39, 60]. Some damselfly species in wetlands deposit eggs endophytically (within the stems of vegetation) [121] where they undergo quiescence until the habitat refloods. When nymphs of the dragonfly *Anax* sp. reach their last instar, they either metamorphose or enter mesopause (Fig. 3.1) depending on the photoperiod; in long photoperiods, the dragonfly will metamorphose within a couple of days, but if the photoperiod is shorter, it will enter mesopause where it will stay for at least 105 days [38].

Those trichopterans having cases built from silk, twigs, leaves or stones probably experience some protection from drying. Some species deposit their eggs in a terrestrial location which is thought to reduce the risk of autumn rain providing a ‘false start’ [154]. *Leptoceridae* and *Limnephilidae* may enter dormancy as eggs [146], a form of hibernation; the eggs are also capable of diapause and the aquatic larvae of aestivation [35, 145]. Diapause [35] has also been shown in larvae of the *Glossosomatidae* [11], *Sericostomatidae* [55] and *Calamoceratidae* [12]. Life histories for Trichoptera can differ considerably from one location to another within the same species [54] suggesting that the use of these survival traits might vary among populations. For example, the suspension-feeding caddisfly *Smicrophylax australis* (Hydropsychidae) showed autumn–winter hatching, followed by rapid growth in spring and adult emergence in late summer in a warm shallow perennial stream. In contrast, in a nearby cooler and deeper stream, larval growth rates of *S. australis* were slower: larvae hatched in autumn–winter failed to emerge the following summer and instead emerged the following year over a shorter period during spring and early summer [27]. Both populations showed cohort splitting [27], but the pattern differed between streams, presumably because the warmer stream facilitated faster growth but perhaps also provided a cue (warm shallow conditions) to larvae to accelerate growth to avoid potential stream drying, because these larvae lack a desiccation resistance mechanism. Other caddisfly strategies can include migration from intermittent habitats shortly before drying [e.g. some species of the genus *Ironquia* sp. (Limnephiloidea)]; *I. plattenis* migrate as a fifth instar and aestivate for 4 months before pupating [57, 144].
Although some caddis larvae aestivate by sealing their cases with silk (e.g. [145]), it is unclear whether they can repeatedly emerge from and re-enter this state, as would be required with increased occurrence of false start events during dry periods. However, even if they can repeatedly aestivate, emerge and aestivate again, there is likely to be an eventual fitness cost for adults.

The capacity for survival strategies to differ between populations in some species permits adaptation to local conditions, a form of flexibility that will assist species to adapt to climatic drying. For example, the bivalve *Pisidium moitessieranum* in southern Finland produces only one cohort per year, eggs are laid in the summer and shelled larvae emerge the following spring. But in the Upper Rhone (France), the same species produces two cohorts per year and the first cohort is incubated in the mother’s shell for three months and then released [92]. Similar examples have been reported for other invertebrate species, but more research is required into the flexibility of life history traits related to surviving desiccation and whether there is a possibility of species being able to switch from one strategy (combination of traits) to another and maybe ‘hedging their bets’ with multiple strategies among populations.

**Invertebrate Life Cycles and Their Interaction with Drying Climates**

There are many advantages for species that can persist *in situ* despite desiccation. Aestivation allows species to exploit habitats not available to other taxa and potentially to dominate temporary waterbodies through early emergence [132], as does the ability to hatch and develop in damp sediment [71, 114, 145]. However, life cycle lengths for aquatic invertebrates differ under different temperatures and among species (e.g. [100]). This is important because where hydroperiods decrease, species with shorter life cycles may be more likely to survive than species with longer life spans, depending on which life stage is affected. However, if species able to survive desiccation as an egg experience hydroperiods too short for hatchlings to reach either emergence or reproductive age, the population risks localized extinction unless cohort splitting prevents all the eggs from hatching. So far, studies suggest that delayed hatching occurs in many, perhaps most, species that rely on desiccation-resistant eggs, but further research is needed to determine how hatching cues will respond to drier water regimes.
The biggest difference in traits related to desiccation is between crustaceans and insects. Many crustacean taxa have physiological adaptations to survive desiccation, although most amphipods, isopods and decapod shrimp are exceptions. Crustaceans can also survive for longer periods of time in resting states compared to insects. Insects mainly rely on either emigration as adults to permanent waterbodies or as larvae dwelling in either damp microrefuges or inundated refuge habitat to survive. However, we do not know whether survival in microrefuges occurs because individuals are simply in the right spot at the right time when drying occurs or whether individuals are capable of seeking out and moving into suitable microrefuges [115], although there is increasing evidence of deliberate movement into refuges by some species (e.g. [76, 88, 132]).

Overall, crustaceans are more likely to emerge in large numbers from refuges on the bed when surface water becomes available, provided that fine sediments are present to harbour them [135]. Thus, it appears likely that crustaceans will be more resistant to climatic drying than insects, although, because of other climatic changes that accompany drying, species with resilience traits may ultimately adapt more successfully [32].

The altered timing of seasonal floods that may accompany climatic drying could limit distributions of more desiccation-resistant species by disrupting matches between life stages and resource availability [127]. For example, emergence following dormancy may coincide with an abundance of food, but with altered flood timing there may be more missed opportunities where emergence and the abundant food source no longer coincide. These effects may be transmitted to all trophic levels, with ecological and environmental consequences [153]. Although this review demonstrates knowledge of a range of desiccation resistance and resilience traits, less is known about the phenology of these traits, their flexibility or the potential fitness costs entailed by climate change. This comprises a large knowledge gap in our ability to predict the consequences of climate change on ecosystems.

Some desiccation survival traits are better developed to survive higher temperatures and longer dry periods than others, but all traits have limits. Aerial adults may be the most successful way for insects to survive drying as they are able to disperse to find permanent water; however, drier landscapes with little vegetation may also limit adult movement [36]. However, we know from genetic studies that many aquatic insects are surprisingly poor dispersers [72]. Insect larvae need to have a hydroperiod duration
sufficient to reach their final larval instar, and then, depending upon their dispersal ability, (or the availability of ‘stepping stones’), the length of the adult life stage will determine whether they reach suitable habitat. A few longterm studies of the impact of drought and increasingly intermittent flow regimes now show that some taxa will be ‘filtered out’ by prolonged drying, reducing biodiversity and leading to lasting change in community composition [23, 127]. The most successful strategies for surviving prolonged drying and higher temperatures are shown by crustaceans with eggs that are viable for long periods and capable of cohort splitting and by insects with strongly dispersing flying adults and rapidly growing larval stages. More research is required into invertebrate physiology, so we can predict the mechanisms involved in survival of desiccation and the environmental limits of these mechanisms. Furthermore, studies are now showing that even congeneric species can show remarkably different trait functions (e.g. [100]), meaning that more species-level investigations are needed to understand the diversity of responses to environmental change.

This review has highlighted the need for further research into life history traits and strategies, their flexibility and the physiological processes used in resisting desiccation. One difficulty for research is that traits for surviving dry periods are species or life stage specific, even different populations of the same species may display different survival strategies. However, initial responses to climate change in ecological communities will be by individuals and thus will be reflected in the population dynamics of individual species. Groups of species, whether functional or taxonomic, will not respond as a single unit [130], so species responses must be investigated to predict the outcomes of climate change.

One of the questions we posed at the beginning of this article was: does the degree of exposure to desiccation affect the expression of life history strategies for surviving desiccation? Unfortunately, the knowledge we have about species responses to desiccation does not yet enable us to answer this question. More field and laboratory studies are needed to investigate the tolerances of species, the flexibility of their life history traits and the effects of water regime change on individual and population fitness. Specifically, how much moisture is retained in different habitats as they dry and the effect of this on species responses is a key knowledge gap that limits our ability to predict the consequences of changes in water regime in both running and standing waters. Those few studies that have examined different degrees of drying [132, 135]
suggest that moisture content will be a key variable in invertebrate persistence in freshwater ecosystems.

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Chapter 4. Microrefuges from drying for invertebrates in a seasonal wetland

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**Summary**

1. Seasonally intermittent freshwater environments show large temporal changes in area and environmental conditions (which may be harsh). We investigated whether microhabitats that retain moisture could provide a refuge during drying in a seasonal wetland.

2. We investigated occupancy by invertebrates of three potential microrefuge types: surface depressions, shallow cracks and deeper fissures in the sediment of a wetland in Western Australia. Our aims were to determine whether the assemblages occupying these microrefuges differed and whether they changed as the wetland dried and reflooded.

3. Ten microrefuges of each type were sampled for invertebrates, sediment and temperature during each of three hydrological phases: the damp phase (surface water absent but sediment moist), the dry phase (groundwater at its lowest level) and the reflooded phase (surface water present). Sediment samples taken from each microrefuge in the damp and dry phases were reflooded in the laboratory to reveal species aestivating or present as eggs, and sediment organic matter content was measured.

4. Sediment organic matter content did not change between wetland phases. The invertebrate assemblage in the microrefuges showed almost complete species turnover between phases. Invertebrate composition differed between microrefuges, and temperature in the deeper fissures was on average >10 °C lower than in surface depressions and shallow cracks.

5. Microcrustaceans and gastropods survived the drier months as resting stages in the microrefuges and either emerged or hatched from eggs upon reflooding. Several species, including isopods and caddisflies, were collected only from cracks and fissures as the wetland dried. During drying, a high diversity of carnivorous species was observed in the microrefuges.

6. Sediment microrefuges apparently underpin resistance to drought by invertebrates in South Lake. Those species that depend on sediment fissures to survive may be threatened by the declining groundwater table in the region. Changes to wetland hydrology and other human activities that affect wetland sediment or vegetation will affect the range of microrefuges available to invertebrates to survive drying and may thus alter wetland biodiversity.

*Keywords*: drought, egg bank, mediterranean climate, refuges, temperature, temporary wetlands.
Introduction

Loss of water is the most deleterious factor influencing aquatic animals and although it occurs annually in seasonal wetlands, its effect on individual species and their survival is poorly understood (Sim et al., 2013). Seasonally intermittent wetlands in regions with a Mediterranean climate show large temporal changes in habitat area and conditions, ranging from extensive surface water in the winter, to a dry landscape and harsh conditions in summer. During summer drying, freshwater animals are increasingly exposed to ultraviolet light, high temperature, large fluctuations in salinity, pH and oxygen and the rapid disappearance of surface water (Alekseev, De Stasio & Gilbert, 2007). Increased temperature may exceed physiological tolerances and lead to high mortality or local extinction (Maxted, McCready & Scarsbrook, 2005). Temperature influences the duration of egg incubation, hatching success, duration of hatching and the induction and termination of resting stages (Oliver, 1971; Alekseev et al., 2007), as well as minimum size at pupation, sex ratios in insects, increased metabolic rate (Terblanche et al., 2005), changes in food availability and food-web structure (Rosenzweig et al., 2008). Given the range of physical changes that occur during drying, invertebrates that live in intermittent aquatic environments often show adaptive traits.

Species may show several types of response to adverse conditions: life-history adjustments (altered phenology), morphological, behavioural and physiological responses (Lytle & Poff, 2004; Robson, Chester & Austin, 2011). Some crustaceans produce drought resistant eggs or cysts (Datry, Corti & Philippe, 2012; Stubbington & Datry, 2013). Other groups, such as many large predators (e.g. Dytiscidae), show behavioural responses including dispersal by flight to wetter areas (Boulton & Lake, 2008), while other species may move into refuges when drying occurs (Robson et al., 2011). Refuges support populations of species not able to live in the surrounding environment due to the effects of disturbance; a refuge is also a source of colonists for the surrounding environment once the disturbance has passed (Robson et al., 2013). Many types of refuge have been identified in flowing waters (e.g. Lancaster, 2000; Chester & Robson, 2011; Robson et al., 2013; Stubbington & Datry, 2013), but relatively few in standing waters, aside from studies of wetland seed and egg banks (e.g. Brock et al., 2003; Jenkins & Boulton, 2007; Tuckett et al., 2010).

Refuges may be large, such as perennial waterbodies, or they may be smaller habitats and occur within waterbodies (Stubbington & Datry, 2013). These smaller
refuges were described as microhabitat sources of colonists by Stubbington & Datry (2013) and are termed microrefuges here. Microrefuges include cracks in sediments, damp areas beneath algal mats (Strandine, 1941), stones (Chester & Robson, 2011) or leaf litter and areas with high humidity such as crayfish burrows (Stubbington & Datry, 2013 and references therein), all of which may occur in wetlands.

Sediment characteristics will partially determine the types and frequency of microrefuges in wetlands. For example, the organic matter content of the sediment can affect drying rates, because organic matter can hold up to 20 times its mass in water and improves water retention (Reddy & DeLaune, 2008). Sediment moisture content has been shown to be a major determinant of seedbank viability (Stubbington & Datry, 2013). Therefore, patches of wetland sediment with higher organic matter content may hold moisture for longer periods, increasing the capacity for aquatic organisms to survive dry summer conditions. Small differences in organic matter content between microrefuges could mean that certain areas within a wetland are more likely than others to provide refuges during summer.

We chose three potential microrefuge types: surface depressions, shallow cracks and deeper fissures in wetland sediment, to investigate invertebrate occupancy, including resting stages. These potential microrefuges were the main water-retaining physical features found on the wetland bed in open water areas; no other refuge types were apparent. The hypotheses were that invertebrate assemblages occupying these microrefuge types would differ because of differences in temperature and level of inundation and that assemblages would change over time as the wetland dried and reflooded. We expected that assemblages in the deep fissures would gain species during the dry phase because the deeper fissures would provide a cooler microenvironment for invertebrates.

**Methods**

**Study site**

South Lake (32°06.2270S, 115°49.1250E), in suburban Perth, Western Australia (with a Mediterranean climate) has a maximum area of 31.5 ha and is a seasonally inundated groundwater-dependent basin, protected within the Beeliar Regional Park (Hill et al., 1996). It is surrounded by native vegetation, has extensive beds of emergent macrophytes and does not receive street drainage. South Lake and its sediment are therefore relatively undisturbed by urbanisation and bed modification. The lake has a
faunal assemblage similar to other natural wetlands on the Swan Coastal Plain. The invertebrate fauna of these wetlands is well known and further descriptions may be found in Davis & Christidis (1999), Horwitz et al. (2009) and Sim et al. (2013).

**Water regime**

Maximum wetland depth usually occurs in spring (September–October) and the dry phase in autumn (March–April) (Davis & Froend, 1999). After the surface water disappears from South Lake (during summer and autumn), the water table drops between 0.1 and 1 m below the sediment surface. As the water level drops, the sediment cracks and tessellates, creating shallow cracks and deeper fissures that may connect to the groundwater table (Fig. 4.1). During the damp phase (March 2012), the water in a drying pool had a temperature of 27.1 °C, conductivity of 5.49 mS cm\(^{-1}\) and pH of 8.21. In the reflooded phase (May 2012), when the wetland had started to refill, water temperature was 19.2 °C, conductivity was 1.90 mS cm\(^{-1}\) and pH was 8.43, these recordings were from a single point.

**Sampling and laboratory procedure**

The three microrefuge types were surface depressions (on the surface of the sediment where water may pool during drying), shallow cracks (in soft sediment and of restricted depth, c. <8 cm and with a firm bottom) and deep fissures (in the substratum, c. >15 cm deep, which had very loose sediment at the bottom sometimes mixed with filaments of iron bacteria, suggesting possible connection to the deeper groundwater). During the damp phase (March 2012), 90 microrefuges (30 of each type) were marked on the bed of South Lake (Fig. 4.1). Ten microrefuges of each type were randomly sampled at each of the three sampling times, chosen to represent particular stages in the wetting and drying cycle: the damp phase (early autumn, late March), the dry phase (midautumn, April) and the reflooded phase (late autumn, May) 2012. Different microrefuges were sampled on each occasion, so that no microrefuge was sampled twice.
Figure 4.1. Microrefuges and the inundation level at the three sampling times. In the damp phase, South Lake is drying out and water levels have dropped: (a) only the cracks and fissures are inundated; (b) a dry surface microrefuge. During the dry phase, the water table has dropped below the surface: (c) crack microrefuges and (d) a fissure still containing water. In the reflooded phase: (e) South Lake starting to reflood and (f) a submerged fissure.
In the damp phase, daytime air temperatures were high (31.3 °C, mean daily maximum, Jandakot Airport, BOM, 2013) and the wetland sediment remained damp. The water table had dropped just below the sediment surface and water filled the cracks and fissures (Fig. 4.1). In the dry phase, air temperatures and day length had declined (26.0 °C, mean daily maximum, Jandakot Airport, BOM, 2013) and the water table had dropped so that only the fissures still contained standing water (Fig. 4.1). The day following the dry phase sampling, rainfall was recorded nearby (28 mm Jandakot Airport; BOM, 2013) and the wetland began to refill. By the sampling date during the reflooded phase a further 97 mm of rain had fallen (BOM, 2013), and air temperatures and day length were at their lowest (22.7 °C mean daily maximum, Jandakot Airport, BOM, 2013). Fissures, cracks and surface depressions were all underwater (Fig. 4.1).

Data loggers (HOBO pendant temp/light, 64k UA- 002-064; Onset Computer Corporation, Bourne, MA, U.S.A.) were used to record temperature in the different microrefuge types. Loggers were randomly placed in three of each of the refuge types: in depressions, cracks and fissures. Loggers in fissures were suspended 10 cm below the surface on monofilament line, while others were pegged directly to the substratum at the deepest point for that microhabitat. Temperature was logged every half an hour from the 23 March 2012 to the 8 May 2012 during the period when the wetland dried out and then refilled.

Different refuge types and inundation phases necessitated somewhat different collection methods, but each sample comprised an equivalent sampled area (0.2 m length of crack, fissure, depression), amount of sediment (c. 500 g) and volume of water (c. 2 L, damp and reflooded phases). Invertebrates were collected from the free water in cracks and fissures (Fig. 4.1) during the damp phase using a net (250 µm mesh, c. 30 s sweep). In the dry phase, sediment was collected using a trowel. In the reflooded phase when the microrefuges were submerged (Fig. 4.1), a hand pump and hose was used to collect water from within microrefuges and passed through a 125 µm sieve; sediment was collected using a trowel. Sediment was placed in thick plastic bags and transported back to the laboratory for preservation in 70% ethanol. Invertebrates were removed from all samples, counted and identified to the lowest possible taxonomic level.

The organic content of the sediment was determined by loss on ignition, for damp and dry phase samples only. Samples could not be collected effectively in the reflooded phase when the lake was inundated. Subsamples of sediment (10 g) from each
invertebrate sample were heated at 500 °C for 6 h to burn off the organic matter and then reweighed (nearest mg) to determine the loss.

**Invertebrate resting stages**

To separate the invertebrates that were active in the wetland from those which hatched out from the egg bank or emerged after aestivation, a 200 g subsample was taken from each of the dry sediment samples prior to preservation of the remaining sample. The subsample was placed in 1-L jars and inundated with 400 mL of distilled water to permit hatching of eggs/cysts in the sediment or emergence of aestivating individuals. On day three, the water was decanted from the jars and passed through a 125 µm sieve and the captured material preserved. The jars were refilled with distilled water and allowed to sit in the laboratory until day 20, whereupon the water was again decanted, sieved and preserved, and the sediment also preserved. Invertebrates were counted and identified to the lowest possible taxonomic level.

**Data analysis**

Sampling was randomised, with different, interspersed microrefuges sampled independently at each time. The design was therefore fully factorial. The organic content of sediment in each microrefuge for damp and dry phases was analysed using a two-factor analysis of variance (ANOVA) (time, two levels, fixed; microrefuge type, three levels, fixed) in SPSS (version 21), normality and homogeneity of variance assumptions were met without transformation. Using logger data, mean maximum daily temperatures were calculated for each phase (damp: 27 March–4 April; dry: 13 April–27 April; reflooded: 28 April–5 May). As a measure of daily variation in temperature in each microrefuge type, squared differences were calculated for 12 h lags (i.e. intervals with the highest negative correlation) for each logger, within each phase; square roots of the averages of these were then analysed in three single-factor ANOVAs (microrefuge type, three levels).

Patterns in invertebrate assemblage composition were similar for both abundance and presence/absence data so only the latter are presented here. Multivariate analyses were conducted using the PRIMER package (Clarke & Warwick, 2001). Ordination plots (non-metric Multidimensional Scaling, nMDS) based on a Bray–Curtis similarity matrix were used to display differences between inundation phase and microrefuges (default settings were used). A two-factor analysis of similarity (ANOSIM) (inundation phase, three levels; microrefuge type, three levels) was used to
determine whether assemblage composition differed between inundation phases and microrefuges (Clarke, 1993). However, the effect of inundation phase was so large that differences between microrefuge types were then analysed separately in three, single-factor (microrefuge type, three levels) ANOSIMs, one for each phase. SIMPER analyses were used to identify the taxa associated with differences between sampling times, and associated with each microrefuge type (Clarke & Warwick, 2001). For the invertebrate resting stages samples, a two-factor (sampling time, two levels, day 3 and 20; microrefuge type, three levels) ANOSIM was used to determine whether the composition of taxa present as resting stages differed among microrefuge types.

Results

Sediment composition and temperature in microrefuges

There was no difference in the organic content of the sediment between times (range of means: 37.4–38.2%; $F_{1,54} = 3.24$, $P = 0.08$), or microrefuges (range of means: 38.4–40.9%; $F_{2,54} = 1.57$, $P = 0.22$). Generally, loggers in surface depressions and shallow cracks recorded lower temperature maxima after inundation (average 27.6 °C), than before (Fig. 4.2a). In all phases of inundation, fissures had significantly lower daily temperature maxima ($F_{2,4} = 18.8–20.1$, $P < 0.005$), ranging from 19.7 to 20.8 °C, than the other microrefuges, which did not differ. Light intensity (lux) records (not presented) confirmed that there was complete darkness inside fissures. Surface depressions and cracks were similarly exposed to solar radiation, with maxima at 37.3–42.1 °C during drying (Fig. 4.2a). However, one logger in a crack recorded lower daily maxima at all times (26.5–28.4 °C).
Figure 4.2. Temperature logger data within each microhabitat, n = 3, for each inundation phase: (a) mean maximum daily temperature (+1 SE); (b) mean 12-h fluctuation (+1 SE). Temperatures within microrefuges differed at each phase: damp (F\(_{2,8} = 18.77, P = 0.002\)), dry (F\(_{2,8} = 24.43, P = 0.001\)) and reflooded (F\(_{2,8} = 20.15, P = 0.002\)).

Daily variation in temperature (12-h temperature differences) followed the same pattern, but variation in fissures was very low compared with the other refuge types, with average fluctuations of <2 °C over 12 h during the dry season, compared with 13–16 °C at the surface or in shallow cracks (Fig. 4.2b). When the wetland surface was dry, temperature in shallow cracks and surface depressions varied from 6.5 to 16.6 °C, but after inundation temperature was less variable, being 6.2–10.3 °C. Moisture content in the sediment beneath surface depressions and cracks exceeded 50% at all times because interstitial water was present, although the sediment surface was dry.

Invertebrate dynamics through the inundation cycle

Sixty-four taxa were recorded in samples from the three microrefuges during this study from a total of 97 129 individuals collected (Chapter 8, Appendix, Table 8.1). The fauna comprised cnidarians (Hydra), annelids, arthropods and a mollusc (Physa acuta). All were found in the refuges during the study (Table 4.1), but crustaceans dominated the sediment reflooded in the laboratory (Table 4.2).
Table 4.1. Dominant invertebrate taxa collected for each time and microrefuge, identified through SIMPER analysis.

<table>
<thead>
<tr>
<th>Water regime phase</th>
<th>Microrefuge</th>
<th>Dominant invertebrate taxa</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Damp phase</strong></td>
<td>Surface</td>
<td>Oligochaeta, <em>Physa acuta</em>, Dolichopodidae (L), <em>Mytilocypris ambiguosa</em>, Stratiomyidae (L), <em>Cypretta</em> sp., <em>Dicypris spinosa</em>.</td>
</tr>
<tr>
<td></td>
<td>Cracks</td>
<td><em>P. acuta</em>, Dolichopodidae (L), Stratiomyidae (L), <em>M. ambiguosa</em>, <em>Cypretta</em> sp., Oligochaeta, <em>D. spinosa</em>.</td>
</tr>
<tr>
<td></td>
<td>Fissures</td>
<td><em>P. acuta</em>, <em>Cypretta</em> sp., <em>Triplectides australis</em>, <em>D. spinosa</em>, Oligochaeta, <em>M. ambiguosa</em>, <em>Paramphisopus palustris</em>, <em>Paranisops</em> sp. (A), small damselfly (L), small dragonfly (L), Dytiscidae sp. (A) Orthocladiinae (L).</td>
</tr>
<tr>
<td><strong>Dry phase</strong></td>
<td>Surface</td>
<td>Ceratopogonidae (L), Noteridae (A), <em>P. acuta</em>, dipteran (P), Hydrophilidae (L), <em>D. spinosa</em>, Dolichopodidae (L), Orthocladiinae (L), <em>Cypretta</em> sp.</td>
</tr>
<tr>
<td></td>
<td>Cracks</td>
<td><em>P. acuta</em>, Dolichopodidae (L), Ceratopogonidae (L), Orthocladiinae (L), Noteridae (A), <em>Cypretta</em> sp., <em>D. spinosa</em>, <em>M. ambiguosa</em>, dipteran (P), Forcipomyiinae.</td>
</tr>
<tr>
<td></td>
<td>Fissures</td>
<td><em>Cypretta</em> sp., Noteridae (A), <em>D. spinosa</em>, Ceratopogonidae (L), <em>M. ambiguosa</em>, Dolichopodidae (L), <em>P. acuta</em>, Forcipomyiinae, Orthocladiinae (L).</td>
</tr>
<tr>
<td></td>
<td>Fissures</td>
<td>Oligochaeta, Ilyocryptidae sp., <em>P. acuta</em>, <em>Cypretta</em> sp., <em>C. novaezelandiae</em>.</td>
</tr>
</tbody>
</table>

Taxa listed comprised approximately 90% of the differences between the microrefuges and times. Taxa are listed in descending order of dominance. Life history phase: larvae (L), adult (A) and pupae (P).
Table 4.2. Dominant taxa in the invertebrate resting stages samples (hatching experiment) for each time and microrefuge identified through SIMPER analysis.

<table>
<thead>
<tr>
<th>Time period</th>
<th>Microhabitat</th>
<th>Dominant invertebrate taxa</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Three days</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Surface</td>
<td></td>
<td>Collembola, <em>Cypridopsis funebris</em>, <em>Diacypris spinosa</em></td>
</tr>
<tr>
<td>Cracks</td>
<td></td>
<td>Collembola, <em>D. spinosa</em>, <em>C. funebris</em>, Oligochaeta</td>
</tr>
<tr>
<td>Fissures</td>
<td></td>
<td>Collembola, <em>Candonocypris novaezelandiae</em>, <em>D. spinosa</em>, <em>C. funebris</em>, Oligochaeta</td>
</tr>
<tr>
<td><strong>Twenty days</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Surface</td>
<td></td>
<td>Collembola, Ilyocryptidae sp., <em>C. funebris</em></td>
</tr>
<tr>
<td>Cracks</td>
<td></td>
<td>Collembola, Calanoida, <em>Physa acuta</em>, Ilyocryptidae sp., Oligochaeta</td>
</tr>
<tr>
<td>Fissures</td>
<td></td>
<td>Ilyocryptidae sp., Collembola, <em>C. funebris</em>, Calanoida, Oligochaeta</td>
</tr>
</tbody>
</table>

Taxa listed comprised approximately 90% of the differences between the microrefuges and times. Taxa are listed in descending order of dominance.

The almost complete turnover of the invertebrate assemblage between sampling times was the largest source of variation in species composition at South Lake (Global $R = 0.918$, $P < 0.001$, Fig. 4.3a). Sediment organic matter did not differ between inundation phases or microrefuges, so it probably had little effect on species turnover. Instead, the rapid species turnover, which occurred over an 8-week period, coincided with marked changes in water level and temperature. Similarly, pairwise tests showed that the largest differences in composition were between the reflooded phase and the other phases (dry cf. reflooded: $R = 0.981$, $P < 0.001$; damp cf. reflooded samples: $R = 0.981$, $P < 0.001$). The difference in assemblage composition between damp and dry samples was not as large ($R = 0.782$, $P < 0.001$). This is because some invertebrates present in the reflooded phase were absent at the two earlier phases (Table 4.1), or were present only as dormant stages in the sediment, as shown by the composition of the resting stage samples (see below).

Species composition during the reflooded phase was dominated by invertebrates that emerged from the dry sediment, mostly microcrustaceans such as ostracods, cladocerans and copepods as well as gastropods (*P. acuta*) that were aestivating during
the previous phase. The dominant insect taxa present in the microrefuges in the damp, and dry phases were carnivores preying and scavenging upon stranded and dying invertebrates (Table 4.1). Mostly, the predators were rapidly completing their aquatic life stage to emerge as terrestrial adults before the wetland refilled. For example, we observed stratiomyid larvae foraging in surface depressions, preying on stranded and dying invertebrates. These insects, along with hydrophilid beetle larvae, were completing their larval stage. Some of these carnivores, such as the noterid and dytiscid beetles, were already adults, able to fly from place to place to feed.

**Microrefuges for invertebrates**

Assemblage composition also differed between microrefuges (Global $R = 0.217$, $P < 0.001$, Fig. 4.3b), but the microrefuges were more similar to each other at the same time than they were to the same microrefuge type at different times. Consequently, assemblages among microrefuges were analysed for each phase separately. In the damp phase when the wetland had just dried at the surface, assemblage composition differed between microrefuges (Global $R = 0.373$, $P < 0.001$), because the assemblage in the deeper fissures differed from that in the cracks ($R = 0.549$, $P = 0.002$) and the surface depressions ($R = 0.637$, $P = 0.001$). Shallow crack and surface assemblages did not differ ($R = -0.011$, $P = 0.51$, Fig. 4.3b). Surface depressions and cracks were characterised by the presence of the gastropod *P. acuta*, ostracod species and a variety of dipteran larvae including scavenging *Stratiomyidae*. The deeper fissures differed owing to the presence of isopods (*Paramphisopus palustris*), early instar odonates and backswimmers (*Paranisops* sp.) (Table 4.1).
In the dry phase when only the deeper fissures contained free water, there was no difference between assemblages in the microrefuges (Global $R = 0.08$, $P = 0.4$). There were fewer species of ostracod present, and several types of dipteran larvae were common, along with adult Noteridae beetles (Table 4.1).

Oligochaetes, *P. acuta* and ilyocryptids (cladocerans) were abundant in all three microrefuges during the reflooded phase (Table 4.1) but assemblage composition differed among the microrefuges (Global $R = 0.198$, $P < 0.001$) due to the different distribution patterns of three ostracod species. *Cypretta* sp. was only found in the fissures, whereas *Diacypris spinosa* and *Bennelongia australis* were found in the depressions ($R = 0.438$, $P < 0.001$). All three species were found in the crack microrefuge, so it did not differ from either the surface or fissures (Table 4.1).

Some species, although not found in large numbers, showed interesting distribution patterns (Table 4.1). The shredding caddisfly *Triplectides australis* was recorded in the fissures during the damp phase, but were less frequent in the dry phase when they were present in the shallow cracks as well as the fissures. By the reflooded phase, they were largely absent. Similarly, carnivorous Ceratopogonidae larvae were found occasionally in the damp phase in the surface depressions and shallow cracks and in the dry phase were found frequently in all microrefuges. Adult noterid beetles were found in some samples from all microrefuges in the damp phase. In the dry phase, they were often found in samples from the fissures, but were absent by the reflooded phase.
The isopod *P. palustris* was prevalent in the fissures and also occurred in low numbers in the surface and cracks in the damp phase, but in the dry phase were found only in the fissures.

There were changes in the dominant taxa that emerged from resting stages in the sediment between days 3 and 20 (Global $R = 0.162$, $P = 0.001$, Table 4.2). Collembola was the most abundant taxon at all times and microrefuges except for the deeper fissures on day 20. At day three, ostracods emerged from aestivation, dominating the samples. After 20 days, cladocerans and copepods had hatched from the egg bank and the gastropod *P. acuta* and the ostracod *Cypridopsis finebris* had emerged from aestivation (Table 4.2). Microrefuge types also differed (Global $R = 0.458$, $P = 0.001$): composition differed between surface depressions and crack samples ($R = 0.184$, $P = 0.001$), surface and fissure samples ($R = 0.171$, $P = 0.002$) and crack and fissure samples ($R = 0.135$, $P = 0.009$). Fewer species emerged from surface depressions than from cracks or fissures and *Candonocypris novaezelandiae* only emerged from fissure samples.

**Discussion**

*Microrefuge characteristics*

There was a large difference between both the mean temperature and range of temperatures in the microrefuges. Fissures provided a thermal refuge for invertebrates during the hottest and driest periods and more generally, a refuge for invertebrates intolerant of emersion. The cooler and very consistent temperatures in the deeper fissures arose because they are in darkness, but also due to upwelling groundwater, indicated by the presence of iron bacteria in the bottom of the fissures where deeper hypoxic water was upwelling (Emerson, Fleming & McBeth, 2010). Importantly, the fissures in the lake bed persist through the year and do not completely close-up, potentially creating a continuous link to the groundwater. Access to groundwater appears to be important for invertebrates without a terrestrial or desiccation-resistant life stage, such as isopods (e.g. *P. palustris*) or amphipods, to take refuge from drying (Gouws & Stewart, 2007). Also, the temperature differences between the microrefuges persisted even when the whole lake bed was inundated, suggesting that animals may have access to lower temperature microhabitats during hot weather even in inundated wetlands. There may also be places outside fissures with more moderate temperature fluctuations, perhaps with significant shading provided by small-scale topography (Sim *et al.*, 2013).
Patterns of microrefuge use

Although we did not directly measure invertebrate movement, some of the patterns observed here are consistent with movement between microrefuges. For example, the ostracod *Mytilocypris ambiguosa* was found in all microrefuges in the damp phase but in the dry phase was present only in cracks and fissures, suggesting that individuals were moving into the cooler refuges, avoiding the surface depressions. Some larger crustaceans, such as isopods, burrow down towards the groundwater table when surface waters disappear (Williams & Hynes, 1976). The isopod *P. palustris* was prevalent in the surface depressions and shallow cracks in the damp phase, but in the dry phase they were only found in the deeper fissures, which are both the last and first place inundated. It appears probable that these isopods were actively using deeper fissures as a microrefuge during wetland drying.

Some microcrustaceans such as ostracods can withstand drying by entering a state of quiescence, where they close their carapace and metabolic activity is lowered (Delorme, 1991). Emergence has been observed in sediment during damp periods but mostly occurs after refilling (Aguilar-Alberola & Mesquita-Jones, 2011) as observed here. With immature stages already in the dry sediment, these ostracods may have a developmental head start when the water returns (Horne, 1993).

Several insect taxa showed a distribution pattern consistent with a larval stage present during the drying phase, but absent by the time reflooding occurred, because they had emerged as flying adults. For example, predatory dolichopodid larvae were present at the surface and in shallow cracks in the damp and dry phases, but were not found in any of the microrefuges in the reflooded phase. Similarly, ceratopogonid larvae were found in all three microrefuge types in the dry phase only, preying upon the other macroinvertebrates. Orthocladiinae were present in the fissures in the damp phase, while in the dry phase they were found in all of the microrefuges and in the reflooded phase were rare. The availability of stranded invertebrates as prey for predatory coleopteran and dipteran larvae makes the drying phase particularly suitable for these taxa by assisting them to complete their larval life stage (Boulton & Lake, 1992).

Some of the insects with carnivorous larvae that consume stranded and dying invertebrates on the sediment surface were uncommon. Predatory noterid beetle adults were present in all microrefuges in the damp phase, but were more common during the dry phase. As these beetles were absent when the wetland refilled, they were probably preying upon invertebrates trapped in the microrefuges. The predatory larvae of the
Forcipomyiinae occurred only in the cracks and fissures in the dry phase. This dipteran sub-family is semi-terrestrial (Gooderham & Tsyrlin, 2002) and when water is scarce they complete their life cycle rapidly.

Predators such as odonates that inhabit temporary waterbodies may grow rapidly (Watson, Theischinger & Abbey, 1991; De Block, McPeek & Stoks, 2008) although deteriorating conditions in drying waterbodies may limit the growth rate of some species (De Block & Stoks, 2005). In the present study, small newly hatched damselflies and dragonflies were found frequently only in cool, wet fissures during the damp phase; no odonates were found after this time. This suggests either that larvae of these species grew quickly and emerged in the 4 weeks before the next samples were taken, or that they were consumed by predators (Morin, 1984). Some potential predators of juvenile odonates such as adult Paranisosps and diving beetles (Dytiscidae) were also only found in the fissures during the damp phase and may have consumed the odonate larvae.

Some non-predatory insects also apparently moved into the fissure microrefuges in the dry phase. For example, larvae of the caddisfly T. australis were present in the surface depressions and shallow cracks in the damp phase but in the dry phase were mostly found in deeper fissures and were absent from surface depressions. Larvae probably pupated in the fissures and emerged prior to reflooding (e.g. Jannot, 2009), explaining their absence from reflooding samples. Oviposition may be triggered by rain (St Clair, 1993) and may occur during reflooding.

The role of resting stages in the sediment

Resting stages in wetland sediments have previously been identified as a major source of recolonists when inundation occurs (Brock et al., 2003; Jenkins & Boulton, 2007; Tuckett et al., 2010), especially the microcrustacea. Ephippia (a thickened section of the carapace that protects the eggs of Cladocera; Williams, 1988) were present in every microrefuge during the damp and dry phases but were less common in samples taken in the reflooded phase. This correlated with the appearance of cladocerans in both the 20 day resting stage samples and the reflooded microrefuges. Although these cladocerans (Ilyocryptidae) were found in the field only in the reflooded phase, they were present in all microrefuges, indicating that they had survived the dry period as desiccation-resistant eggs. Some ephippia were still present in the reflooded samples and had not hatched. This may have been because they were buried and did not receive
their hatch cue (Alekseev et al., 2007), or because of a form of cohort splitting that relies on prolonged diapause (Robson et al., 2011). Similarly, invertebrate assemblages emerging from dry phase sediment inundated in the laboratory differed between 3 and 20 day periods of inundation, because of different hatching times among taxa (Paltridge et al., 1997; Brock et al., 2003).

Two ostracod species, *C. novaezelandiae* and *B. australis* (both from the family Cyprididae) were also found commonly only during the reflooded phase. Some ostracods in temporary waters use a form of diapause, where development of the young does not follow immediately after deposition of the eggs and may be delayed for up to several years if conditions are unfavourable (Williams, 1988). We observed hatching of *C. novaezelandiae* eggs in the resting stage samples although, oddly, *B. australis* was not also found. Possibly, *B. australis* eggs were not laid in the microrefuges we sampled or we did not replicate the necessary hatching cue. Four other ostracod species [*Cypretta* sp., *M. ambiguosa*, *D. spinosa*, *C. funebris* (all Cyprididae)] closed their carapace and aestivated in response to drying and then emerged from dormancy when reflooded. Thus, ostracod species from the family Cyprididae present in South Lake showed two alternative strategies for surviving drying.

*The role of wetland microrefuges in a drying climate*

Most taxa present during the drying phase were more common in shallow cracks and/or deeper fissures than in surface depressions. Recent studies of other seasonal wetlands on the Swan Coastal Plain show that the climatic drying is causing shorter hydropériods in seasonal wetlands and that some are no longer inundated by groundwater (Sim et al., 2013). Although Sim et al. (2013) did not observe significant aridification of this fauna, some taxa are at risk from declining groundwater tables. Gouws & Stewart (2007) identified the endemic isopod *P. palustris* as at risk from groundwater decline, given its poor dispersal capacity, dependence on aestivation and high genetic diversity within the region. Our results support the proposition that *P. palustris* depends on connections to the groundwater, because we observed it only within deep fissures when surface water was absent from South Lake. This species and others with similar traits are likely to be negatively affected by further regional drying.

A few studies have now described the mechanisms by which stream and river fauna survive drying, focussing on the interaction between species traits and potential refuge habitat (e.g. Sheldon et al., 2010; Chester & Robson, 2011; Stubbington &
Datry, 2013). It is well known that some wetland invertebrates aestivate or produce eggs resistant to desiccation in response to the loss of surface water (Brock et al., 2003; Jenkins & Boulton, 2007). However, other responses to drying by wetland invertebrates are less well known, as are the interactions between species responses and environmental conditions in wetlands (Sim et al., 2013). This study shows that small-scale dynamics occur between microhabitats and invertebrates in wetlands, just as they do in streams. Furthermore, these dynamics occur over a relatively short time period (8 weeks). Further studies of wetland microhabitats are needed to understand the role of different types of sediment and vegetation on the ability of species to resist desiccation, and to identify microrefuges in wetlands. Knowledge of the types and distribution of microrefuges used by wetland species is necessary to manage wetland biodiversity across mosaics of intermittent and perennial wetlands (Sim et al., 2013). Changes to water regimes along with human activities that affect the structure of sediment or vegetation in wetlands will affect the range of microrefuges available to invertebrates during annual drying, and may thereby alter wetland biodiversity.

Acknowledgments
The authors would like to thank Murdoch University for its support and for providing a PhD scholarship to SRS. Sampling was carried out with permits from the Department of Environment and Conservation and the Department of Fisheries, Western Australia.

References


**Supporting Information**

Additional Supporting Information may be found in the online version of this article:

**Appendix Table 8.1.** Species list of invertebrates found in this study [adult (A), juvenile (J), larvae (L)].
Chapter 5. Fringing trees may provide a refuge from prolonged drying for urban wetland invertebrates

Submitted to Urban Ecosystems

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Abstract

Climate change is causing prolonged drying in many temporary 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
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, temporary 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. in press). Although sediment from open water at the centre of a wetland is expected to have a longer hydperiod, 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 (Stubbington 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 5.1). All are temporary wetlands 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 rhaphiophylla*, Table 5.1) 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 six or seven months in winter–spring and dry out for five to six months in summer–autumn (Table 5.1), 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).
Table 5.1. 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). * Joondalup West and Joondalup South are part of the same system but separated by Ocean Reef Road causeway.

<table>
<thead>
<tr>
<th>Wetland name and area</th>
<th>Location</th>
<th>2009 dry period and duration</th>
<th>2010 dry period and duration</th>
<th>2011 dry period and duration</th>
<th>Fringing tree cover (percent of wetland perimeter)</th>
<th>Average width of tree fringe (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Joondalup West, 529 ha*</td>
<td>S31°45.716’ E115°47.391’</td>
<td>No record</td>
<td>No record</td>
<td>No record</td>
<td>70</td>
<td>260</td>
</tr>
<tr>
<td>Joondalup South, 529 ha*</td>
<td>S31°46.623’ E115°47.738’</td>
<td>No record</td>
<td>No record</td>
<td>No record</td>
<td>80</td>
<td>80</td>
</tr>
<tr>
<td>Booragoon Lake, 12.3 ha</td>
<td>S32°02.629’ E115°50.602’</td>
<td>May, &gt;4 weeks</td>
<td>January–April, 3 months</td>
<td>May, &gt;4 weeks</td>
<td>100</td>
<td>95</td>
</tr>
<tr>
<td>North Lake, 24.6 ha</td>
<td>S32°04.652’ E115°49.348’</td>
<td>February–June, 5 months</td>
<td>January–June, 5 months</td>
<td>November 2010–June, 7 months</td>
<td>70</td>
<td>80</td>
</tr>
<tr>
<td>Bibra Lake, 188.7 ha</td>
<td>S32°05.450’ E115°49.278’</td>
<td>March–July, 5 month</td>
<td>February–July, 5 months</td>
<td>December 2010–July, 6 months</td>
<td>80</td>
<td>200</td>
</tr>
<tr>
<td>South Lake, 31.5 ha</td>
<td>S32°06.227’ E115°49.125’</td>
<td>February–July, 6 months</td>
<td>January 2010–July 2011, 17 months</td>
<td>Dry all year</td>
<td>100</td>
<td>245</td>
</tr>
<tr>
<td>Forrestdale Lake, 247 ha</td>
<td>S32°09.640’ E115°56.055’</td>
<td>January–June, 6 months</td>
<td>December 2009–July, 6 months</td>
<td>December 2010–June, 6 months</td>
<td>100</td>
<td>140</td>
</tr>
<tr>
<td>Chelodina Swamp, 3.3 ha</td>
<td>S32°04.286’ E115°50.096’</td>
<td>No record</td>
<td>No record</td>
<td>No record</td>
<td>100</td>
<td>130</td>
</tr>
</tbody>
</table>
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 10cm of sediment using a trowel (newly deposited organic matter lying on the sediment surface was not collected). 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, 64k 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 12h 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 hours for 180 hours. The organic content of the sediment was determined by loss on ignition (ten grams of sediment heated for 500°C for 6 hours). 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 900mL 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 (125µm 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 (125µm 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 hours 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 twelve 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 hour 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 5.2). A PCA ordination was carried out on the Euclidean distance matrix to identify the variables separating the habitats and wetlands.

**Table 5.2.** 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.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Wetland</th>
<th>pH</th>
<th>Conductivity (mS cm(^{-1}) at 25 °C)</th>
<th>Water retention potential (g/h @ 40 °C)</th>
<th>Density (g/cm(^{2}))</th>
<th>Organic content (%)</th>
<th>Water saturation (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Open water</td>
<td>Joondalup West</td>
<td>6.76 - 7.11</td>
<td>0.68</td>
<td>-0.011</td>
<td>3.65</td>
<td>3.6</td>
<td>40.74</td>
</tr>
<tr>
<td></td>
<td>Joondalup South</td>
<td>5.50 - 6.98</td>
<td>3.35</td>
<td>-0.008</td>
<td>1.20</td>
<td>34.2</td>
<td>181.35</td>
</tr>
<tr>
<td></td>
<td>Booragoon Lake</td>
<td>4.87 - 5.96</td>
<td>18.51</td>
<td>-0.007</td>
<td>1.25</td>
<td>58.0</td>
<td>153.33</td>
</tr>
<tr>
<td></td>
<td>North Lake</td>
<td>4.18 - 4.66</td>
<td>12.94</td>
<td>-0.008</td>
<td>1.63</td>
<td>48.5</td>
<td>107.08</td>
</tr>
<tr>
<td></td>
<td>Bibra Lake</td>
<td>6.46 - 8.00</td>
<td>16.25</td>
<td>-0.008</td>
<td>2.19</td>
<td>23.1</td>
<td>102.09</td>
</tr>
<tr>
<td></td>
<td>South Lake</td>
<td>6.63 - 7.89</td>
<td>5.66</td>
<td>-0.006</td>
<td>1.16</td>
<td>62.9</td>
<td>216.64</td>
</tr>
<tr>
<td></td>
<td>Forrestdale Lake</td>
<td>7.94 - 8.21</td>
<td>5.60</td>
<td>-0.008</td>
<td>1.80</td>
<td>29.5</td>
<td>135.77</td>
</tr>
<tr>
<td></td>
<td>Chelodina Swamp</td>
<td>4.29 - 5.34</td>
<td>2.16</td>
<td>-0.009</td>
<td>1.88</td>
<td>25.8</td>
<td>111.13</td>
</tr>
<tr>
<td>Fringing vegetation</td>
<td>Joondalup West</td>
<td>6.89 - 7.62</td>
<td>1.10</td>
<td>-0.008</td>
<td>1.18</td>
<td>46.0</td>
<td>192.30</td>
</tr>
<tr>
<td></td>
<td>Joondalup South</td>
<td>6.43 - 7.03</td>
<td>1.36</td>
<td>-0.022</td>
<td>1.02</td>
<td>54.9</td>
<td>193.88</td>
</tr>
<tr>
<td></td>
<td>Booragoon Lake</td>
<td>4.43 - 6.00</td>
<td>2.79</td>
<td>-0.008</td>
<td>0.75</td>
<td>68.8</td>
<td>307.17</td>
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<tr>
<td></td>
<td>North Lake</td>
<td>5.07 - 6.18</td>
<td>0.44</td>
<td>-0.007</td>
<td>1.52</td>
<td>24.4</td>
<td>167.64</td>
</tr>
<tr>
<td></td>
<td>Bibra Lake</td>
<td>6.50 - 7.23</td>
<td>0.91</td>
<td>-0.006</td>
<td>1.66</td>
<td>29.3</td>
<td>144.52</td>
</tr>
<tr>
<td></td>
<td>South Lake</td>
<td>5.67 - 6.58</td>
<td>2.73</td>
<td>-0.009</td>
<td>0.82</td>
<td>66.9</td>
<td>260.27</td>
</tr>
<tr>
<td></td>
<td>Forrestdale Lake</td>
<td>6.71 - 7.78</td>
<td>0.62</td>
<td>-0.007</td>
<td>1.76</td>
<td>27.8</td>
<td>185.90</td>
</tr>
<tr>
<td></td>
<td>Chelodina Swamp</td>
<td>4.14 - 5.77</td>
<td>0.91</td>
<td>-0.006</td>
<td>1.30</td>
<td>47.6</td>
<td>150.81</td>
</tr>
</tbody>
</table>

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 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 log$_{10}$ 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. 5.1) (Global \( R = 0.437, P = 0.001 \)) and between wetlands (Global \( R = 0.344, P = 0.001 \), Table 5.2). Moisture content and organic matter content were higher in FT sediment than in OW sediment, which had higher EC and density (Table 5.2). 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 5.2). Electrical conductivity was higher in OW sediment (8.14 ± 2.40 mS/cm) compared to FT sediment (1.36 ± 0.32 mS/cm). 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/cm²) had much higher density than FT sediment (1.27 ± 0.13 g/cm²) because of its lower organic content. The two habitats were distinguished by percent water saturation and EC (Fig. 5.1, Table 5.2). 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.
Figure 5.1. 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, Ms = conductivity (milliSiemens), Sat % = water saturation percentage, WRetention = water retention potential. 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.

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 Chyadoridae, copepods (Harpactacoida, Cyclopoida) and three commonly occurring species of Cyprididae ostracod: *Bennelongia gwelupensis* (previously *Bennelongia australis*), *Cypretta* sp. and *Diacypris spinosa* (Tables 5.3, 5.4). 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 5.3, 5.4).
Table 5.3. 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).

<table>
<thead>
<tr>
<th>Species</th>
<th>Open water damp treatment</th>
<th>Open water dried treatment</th>
<th>Fringing Vegetation damp treatment</th>
<th>Fringing vegetation dried treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ilyocryptus spinifer</em></td>
<td>1.51</td>
<td>2.30</td>
<td>1.20</td>
<td>0.54</td>
</tr>
<tr>
<td><em>Bennelongia gnelupensis</em></td>
<td>0.84</td>
<td>0.97</td>
<td>0.83</td>
<td>0.00</td>
</tr>
<tr>
<td>Chydoridae sp.</td>
<td>0.67</td>
<td>0.87</td>
<td>1.18</td>
<td>0.75</td>
</tr>
<tr>
<td><em>Diacypris spinose</em></td>
<td>0.39</td>
<td>0.32</td>
<td>1.24</td>
<td>0.30</td>
</tr>
<tr>
<td>Cypretta. sp.</td>
<td>0.37</td>
<td>0.14</td>
<td>0.56</td>
<td>0.04</td>
</tr>
<tr>
<td>Cyclopoida sp.</td>
<td>0.18</td>
<td>0.08</td>
<td>0.57</td>
<td>0.00</td>
</tr>
<tr>
<td>Orabatidae sp. 1 (A)</td>
<td>0.04</td>
<td>0.16</td>
<td>Absent</td>
<td>Absent</td>
</tr>
<tr>
<td>Collembola</td>
<td>0.04</td>
<td>0.00</td>
<td>1.47</td>
<td>0.04</td>
</tr>
<tr>
<td><em>Berosus sp. 1 (A)</em></td>
<td>0.11</td>
<td>0.00</td>
<td>Absent</td>
<td>Absent</td>
</tr>
</tbody>
</table>
Table 5.4. SIMPER analysis of invertebrate data (total number of individuals in n = 6 replicates pooled), comparing habitat within each wetland (damp treatment only).

<table>
<thead>
<tr>
<th>Site</th>
<th>Species</th>
<th>Open average abundance</th>
<th>Fringing Veg average abundance</th>
<th>Contribution %</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Joondalup West</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>average dissimilarity</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>56%</td>
<td>Cyclopoida sp.</td>
<td>0.19</td>
<td>23.82</td>
<td>37.53</td>
</tr>
<tr>
<td></td>
<td><em>Ilyocryptus spinifer</em></td>
<td></td>
<td>38.06</td>
<td>34.13</td>
</tr>
<tr>
<td></td>
<td>Harpacticoida sp.</td>
<td>0.00</td>
<td>4.17</td>
<td>6.90</td>
</tr>
<tr>
<td></td>
<td><em>Diacypris spinosa</em></td>
<td>0.38</td>
<td>3.69</td>
<td>6.78</td>
</tr>
<tr>
<td></td>
<td><em>Bennelongia gwelupensis</em></td>
<td>5.12</td>
<td>3.45</td>
<td>6.65</td>
</tr>
<tr>
<td><strong>Joondalup South</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>average dissimilarity</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>82.5%</td>
<td>Chydoridae sp.</td>
<td>11.73</td>
<td>27.19</td>
<td>40.10</td>
</tr>
<tr>
<td></td>
<td><em>Ilyocryptus spinifer</em></td>
<td></td>
<td>27.19</td>
<td>40.10</td>
</tr>
<tr>
<td></td>
<td><em>D. spinosa</em></td>
<td>0.77</td>
<td>17.02</td>
<td>21.29</td>
</tr>
<tr>
<td></td>
<td><em>B. gwelupensis</em></td>
<td>6.24</td>
<td>0.00</td>
<td>13.01</td>
</tr>
<tr>
<td><strong>Booragoon Lake</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>average dissimilarity</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>91.4%</td>
<td><em>Ilyocryptus spinifer</em></td>
<td>7.69</td>
<td>22.51</td>
<td>35.62</td>
</tr>
<tr>
<td></td>
<td><em>B. gwelupensis</em></td>
<td>0.00</td>
<td>17.58</td>
<td>30.18</td>
</tr>
<tr>
<td></td>
<td>Collembola</td>
<td>0.16</td>
<td>4.75</td>
<td>12.75</td>
</tr>
<tr>
<td></td>
<td><em>Cypretta sp.</em></td>
<td>0.00</td>
<td>7.11</td>
<td>9.79</td>
</tr>
<tr>
<td></td>
<td>Chydoridae sp.</td>
<td>0.00</td>
<td>2.26</td>
<td>5.33</td>
</tr>
<tr>
<td><strong>North Lake</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>average dissimilarity</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>100%</td>
<td>Collembola</td>
<td>0.00</td>
<td>63.49</td>
<td>90.21</td>
</tr>
<tr>
<td><strong>Bibra Lake</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>average dissimilarity</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>95.4%</td>
<td><em>Ilyocryptus spinifer</em></td>
<td>12.94</td>
<td>7.81</td>
<td>52.85</td>
</tr>
<tr>
<td></td>
<td>Chydoridae sp.</td>
<td>0.04</td>
<td>9.36</td>
<td>17.95</td>
</tr>
<tr>
<td></td>
<td>Collembola</td>
<td>0.00</td>
<td>4.66</td>
<td>14.64</td>
</tr>
<tr>
<td></td>
<td><em>D. spinosa</em></td>
<td>0.23</td>
<td>3.67</td>
<td>8.06</td>
</tr>
<tr>
<td><strong>South Lake</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>average dissimilarity</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>65.5%</td>
<td><em>D. spinosa</em></td>
<td>3.43</td>
<td>27.29</td>
<td>32.06</td>
</tr>
<tr>
<td></td>
<td>Chydoridae sp.</td>
<td>10.58</td>
<td>24.41</td>
<td>21.66</td>
</tr>
<tr>
<td></td>
<td><em>B. gwelupensis</em></td>
<td>18.33</td>
<td>7.97</td>
<td>19.75</td>
</tr>
<tr>
<td></td>
<td>Collembola</td>
<td>0.00</td>
<td>5.52</td>
<td>8.85</td>
</tr>
<tr>
<td></td>
<td><em>Ilyocryptus spinifer</em></td>
<td>3.02</td>
<td>3.35</td>
<td>5.78</td>
</tr>
<tr>
<td></td>
<td><em>Orithabida sp.</em></td>
<td>0.95</td>
<td>4.09</td>
<td>5.43</td>
</tr>
<tr>
<td><strong>Forrestdale Lake</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>average dissimilarity</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>100%</td>
<td>Collembola</td>
<td>0.00</td>
<td>95.32</td>
<td>88.57</td>
</tr>
<tr>
<td></td>
<td><em>Cypretta sp.</em></td>
<td>3.72</td>
<td>0.00</td>
<td>3.06</td>
</tr>
<tr>
<td><strong>Chelodina Swamp</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>average dissimilarity</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>99.7%</td>
<td>Collembola</td>
<td>0.00</td>
<td>68.39</td>
<td>63.98</td>
</tr>
<tr>
<td></td>
<td>Chydoridae sp.</td>
<td>0.60</td>
<td>17.72</td>
<td>15.71</td>
</tr>
<tr>
<td></td>
<td><em>Orthocladiinae sp.</em></td>
<td>8.45</td>
<td>0.00</td>
<td>7.69</td>
</tr>
<tr>
<td></td>
<td><em>Berosus sp.</em></td>
<td>2.40</td>
<td>0.00</td>
<td>2.44</td>
</tr>
<tr>
<td></td>
<td><em>Hemicordulia tau larvae</em></td>
<td>1.67</td>
<td>0.00</td>
<td>1.92</td>
</tr>
</tbody>
</table>
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 5.3, 5.4). Some taxa occurred in both habitat types, such as \textit{I. spinifer}, \textit{B. gwelupensis}, Chydroridae sp., \textit{D. spinosa}, while others predominated in one habitat or the other (e.g. Collembola in FT; Orabatidae and \textit{Berosus} sp. 1 in OW, Table 5.3). Within damp sediment samples, Collembola, Chydroridae and \textit{D. spinosa} always emerged more commonly from FT than from OW samples (Table 5.4), presumably because they are detritivores. Two common taxa, \textit{Ilyocryptus spinifer} and the ostracod \textit{B. gwelupensis}, varied in their emergence pattern between habitat types and wetlands. \textit{B. gwelupensis} emerged in higher abundances from OW samples from Joondalup West and South Lake, but only emerged from sediment beneath FT in Lake Booragoon samples. \textit{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 5.4). 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 5.3, 5.4). Collembola and \textit{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 5.3). The drying treatment also had positive effects, or no effect, on some species (Table 5.3). More \textit{Ilyocryptus spinifer} (Cladocera) emerged from dried OW samples than from damp OW samples, although the effect was reversed in FT samples (Table 5.3). The drying treatment did not affect emergence by the ostracod \textit{Bennelongia gwelupensis} in OW samples (Table 5.3), but prolonged drying led either to mortality or exceptionally delayed emergence (beyond the 30 d duration of this experiment) (Table 5.3). 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 \((\rho = 0.476, P = 0.001)\).
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. 5.2). 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 5.3), 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 *Diacypris spinosa* and a species of Chydoridae cladoceran than did open water or dried FT sediment (Table 5.3). Another ostracod, *Cypretta* sp., was rare in the dried samples but of moderate abundance in the damp sediment samples (Table 5.3). 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.

**Figure 5.2.** 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.
Taxa richness of assemblages emerging from damp sediment differed between the two habitats, but this pattern differed among wetlands (habitat x wetland interaction: $F_{5,51} = 3.34$, $P = 0.011$ (Appendix, Table 8.2-8.5)). In Lake Joondalup South, Lake Forrestdale and Chelodina Swamp, more taxa 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 x wetland interaction: $F_{5,32} = 4.78$, $P = 0.002$ (Appendix, Table 8.2-8.5)). 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 $F_{5,32} = 4.42$, $P < 0.01$ (Appendix, Table 8.2-8.5)). 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 $F_{5,28} = 1.7$, $P > 0.05$ (Appendix, Table 8.2-8.5)). 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 5.2). 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 (≈ 35 °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. in press).

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. Cypretta 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 Cypretta sp., were inhibited by experimental drying. Diacypris was most affected in FT sediment, but Cypretta 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 (Chydroridae 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 temporary 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 (Steward 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 rhaphiophylla* 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 (≈ 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 five to six 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 ten 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 temporary 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.

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Chapter 6. Habitat alters the effect of false starts on seasonal-wetland invertebrates

Freshwater Biology, in press

Scott R. Strachan, Edwin T. Chester & Belinda J. Robson
Summary:

1. Climate change is modifying the timing of the onset of winter rainfall in southern Australia, at times creating brief inundation events in seasonal wetlands, termed ‘false starts’. False starts may cause abortive hatchings of fauna emerging from sediment egg banks because wetlands dry out before invertebrates can complete their life cycle or reach a drying-resistant life stage.

2. A laboratory emergence experiment was used to determine whether the abortive hatching caused by false starts alters assemblage composition in the subsequent hydroperiod; and whether the length of the dry period following a false start alters subsequent assemblage composition. Sediment for the experiment was collected from Lake Joondalup South, Swan Coastal Plain (SCP), Western Australia, because it has a relatively diverse assemblage of desiccation-resistant invertebrate propagules. Most wetlands on the SCP are seasonal and groundwater-fed and the region has a mediterranean-type climate.

3. Two different habitat types (open water (OW) and fringing trees (FT)) with distinct freshwater invertebrate assemblages are commonly found in SCP wetlands. We repeated the experiment in sediment from both habitats to determine whether false starts had the same effect on the two assemblages. Replicate sediment samples from both habitats were placed in microcosms randomly allocated to treatments or controls. To simulate false starts of differing dry-period duration, treatments were inundated for five days, then allowed to dry out for different time periods (10, 20, 30 days) then inundated for five days. Controls were inundated for time periods equivalent to the total duration of each false start treatment (20, 30, 40 days).

4. FT sediment had higher organic matter and moisture content than OW sediment. The composition of the emerging assemblage differed between habitats, and emergence was slower from OW than FT sediment. Abortive hatching followed the false start in OW sediment, but subsequently the same assemblage emerged, showing reliance on the egg bank to re-supply lost populations. Abortive hatching was not observed in FT sediment, where invertebrates survived drying during the false start, continuing to develop for up to 30 days without surface water, because those sediments retained moisture.

5. Provided that winter-spring hydroperiods continue to inundate OW for several months, these results indicate that invertebrates will be able to complete their
life cycles and replenish egg banks following abortive hatching, demonstrating resilience to false starts. False starts to winter inundation rarely occur more than a month prior to the start of ‘true’ winter rains, so FT assemblages are resistant to false starts, showing the ability to survive dry periods of up to 30 days. Furthermore, survival in damp FT sediment also gave these populations a ‘head start’, because the surviving assemblage was identical to the continuously inundated control.

6. Assemblages emerging from beneath FT may potentially recolonise inundated OW habitat. So far, changes to SCP seasonal-wetland hydroperiods will be within the coping range of their invertebrate assemblages. As FT assemblages were more resistant to false starts, restoration schemes that increase shading by fringing vegetation should be encouraged.

**Keywords:** aestivation, desiccation tolerance, egg bank, species traits, temporary ponds, temporary wetlands
Introduction:

Despite the challenge of regular drying, temporary wetlands provide important habitat for many freshwater organisms (Tuytens et al., 2014). However, in regions where rainfall is declining, shortened hydroperiods present a serious threat to freshwater animals that complete their entire life cycle in freshwater (molluscs, crustaceans, fish) and to those that must complete an freshwater life stage prior to reproduction (amphibians, insects) (Waterkeyn et al., 2008; Sim et al., 2013; Stoks et al., 2014; Tuytens et al., 2014). In mediterranean climates, rainfall is strongly seasonal with at least 80% of annual rainfall occurring in the winter-spring period; many streams and wetlands are intermittent, and animal life histories are adapted to these conditions (Bunn, 1988; Bonada et al., 2007). However, as autumn and early-winter rainfall has declined in mediterranean-climate regions of southern Australia, winter rains may commence briefly but then cease for several weeks (Hope et al., 2006), creating brief periods (days to 1-2 weeks) of inundation in intermittent wetlands, followed by loss of surface water (3-6 weeks) until winter rainfall commences and uninterrupted inundation occurs. These brief inundation events have been termed ‘false starts’, that is, they are false starts to the inundation period in intermittent waterbodies (Sim et al., 2009; Lake, 2011). However, the effect of false starts on freshwater invertebrate assemblages remains largely unknown (Lake, 2011).

False starts have the potential to disrupt the life cycles of wetland animals, especially those that rely on dormant life stages resting in the surface sediments of dry wetlands that hatch upon inundation. During a false start, invertebrates may emerge from the sediment in response to inundation, but then cannot complete their life cycle because the wetland dries out again too quickly, causing mass mortality events termed ‘abortive hatchings’ (e.g. conchostracans, Bishop, 1967; anostracans, Hildrew, 1985; Tuytens et al., 2014). Abortive hatchings caused by false-start events may deplete egg or seed banks and, if repeated, even lead to extinction of populations (Brendonck, 1996; Sim et al., 2009; Tuytens et al., 2014). Evidence from abortive hatchings suggests that invertebrates do not survive the dry period following a false start. Indeed, temporary wetlands are often viewed as being ‘reset’ by dry periods, such that differently structured ecosystems may emerge following dry periods in the same wetland (Sim et al., 2009). However, few studies (e.g. Tronstad et al., 2005b) have followed
invertebrate survival through the dry period in wetlands to determine whether this is true.

Studies of alternating longer wetting and drying events found seed banks (*sensu* Stubbington & Datry, 2013) to be resilient to drying because propagules were abundant, not all propagules hatched in each inundation period and most taxa had been able to complete their life history (Brock *et al.*, 2003; Stubbington and Datry, 2013). These findings have led to the assumption that seed banks will be resilient to false starts, because even with abortive hatchings, other eggs will be present in sediments to supply future hydroperiods. False starts could have negative effects on subsequent assemblages if abortive hatchings occurred among a wide range of species, or repeatedly through time, depleting the store of eggs, but this is not the only potential mechanism for negative effects. Studies based on sediment rehydration (e.g. Brock *et al.*, 2003; Jenkins & Boulton, 2007) often focus on hatching of desiccation-resistant eggs, overlooking species that rely on aestivation (a time of slowed metabolism usually during summer (Strachan *et al.*, 2015)) to survive dry periods (e.g. some species of: larval caddisflies, Wickson *et al.*, 2012; crayfish, Stubbington and Datry, 2013; isopods, ostracods Strachan *et al.*, 2014; 2015). False starts may force aestivating species to emerge from and then re-enter dormancy repeatedly, with probable fitness costs, and recent studies show that a considerable proportion of invertebrate propagules in wetland sediments may be aestivators (Strachan *et al.*, 2014). To detect any negative effects of false starts that last beyond abortive hatchings, it is necessary to examine the invertebrate assemblages that develop in the ‘true’ inundation period following a false start in a range of habitat and sediment types.

Different habitats (and corresponding sediment types) vary in moisture content, affecting the composition of dormant assemblages (Strachan, 2016). Temporary wetlands are often fringed by trees that become inundated during the wet season, although they are inundated for shorter periods than open water (OW) in the centre of a wetland (Strachan *et al.*, 2015). Invertebrate taxa with propagules resting in dry sediments beneath wetland trees may therefore have been exposed to shorter prior hydroperiods than propagules in dry OW sediment. Also, sediment beneath fringing trees differs from OW sediment, having a higher organic matter and moisture content, resulting in a slower drying process. It is also shaded and thus cooler than sediment in OW habitat (Strachan, 2016), leading to different conditions for the survival of eggs or
aestivating invertebrates. As far as we are aware, no prior studies of invertebrate emergence from wetland sediments have compared different habitat types or the effects of altered water regimes on emergence from different sediment habitat types.

We used a laboratory experiment to determine whether a hydrological false start will disrupt invertebrate life cycles and thereby alter the species composition of the invertebrate assemblage emerging from wetland sediment in the subsequent inundation period. Sediment samples were taken from both OW and FT to compare invertebrate responses to a false start in these two different habitats. Multiple treatments and matching controls were chosen to test the capacity of egg banks and dormant invertebrates to survive a short period (5 days) of inundation followed by varying durations of drying. The hypotheses tested were: (H₁) the assemblage composition of invertebrates emerging from OW sediment would differ from that emerging from fringing tree (FT) sediment; (H₂) the assemblage composition of invertebrates emerging from sediment exposed to hydrological false start of different duration would differ from each other, and from sediments exposed to continuous inundation.

Methods:

Study site

The Swan Coastal Plain (SCP) wetlands in south-west Western Australia are shallow, groundwater fed wetlands underlain by sandplain, in a region with a highly seasonal mediterranean climate (Sim et al., 2013). Most are inundated in winter–spring and dry out in summer–autumn, but groundwater extraction together with climatic drying is prolonging dry periods (CSIRO, 2011; Sim et al., 2013). The invertebrate assemblage of these wetlands is well known (Davis & Christidis, 1999; Chessman et al., 2002; Horwitz et al., 2009; Sim et al., 2013). A study of invertebrate emergence from sediment from eight SCP wetlands (Strachan, 2016) showed that the seasonally inundated (and fishless) Lake Joondalup South (S31°46.623′ E115°47.738′) had the highest diversity and abundance of freshwater invertebrates emerging from dry sediment, so was chosen for this experiment. Lake Joondalup South has an intact band of the native fringing tree Melaleuca rhaphiophylla, and is managed for recreation and conservation. Sediment from beneath FT in Lake Joondalup South had a higher organic matter content (55%) than did sediment from OW (34%), a narrower pH range (FT: 6.4
– 7.0, OW: 5.5 – 7.0) and slightly higher water saturation potential (FT: 194%, OW: 181%) (Strachan, 2016).

Field Sampling

The top 10 cm of lake-bed sediments are the source of most emerging invertebrates in wetlands (Brendonck and De Meester 2003). Therefore, 90 replicate random samples were taken from the top 10 cm of lakebed sediment in Lake Joondalup South during the summer-autumn dry period (May 2011) using a trowel. Surface water was absent from the lake at that time. Forty-five sediment samples were taken from beneath fringing trees and 45 were taken from the area of dry lake bed where open water had stood during winter-spring. An equivalent volume (∼ 250 mL) of this sediment was placed into 90, 900ml wide-mouthed jars for use in the experiment. Each sample jar thus represented an independently collected sample of dry surface sediment from Lake Joondalup South.

Experimental design and procedure

Controls and treatments were kept indoors under identical conditions, to represent effects of a false start unconfounded by other wetland recolonization processes such as aerial or wind dispersal. An identical experimental design was used for sediment samples from the two habitats, although this meant that FT sediment was not shaded, as it would be in the field for at least part of the day. Air temperatures and light conditions (natural light through large laboratory windows supplemented with halogen lights on an 8h on 16 h off regime) similar to those that would occur during false start events on the SCP, occurring in late autumn or early winter, were used. The experiment was run in September 2011, when mean daily maximum air temperature was 20 °C and mean daily minimum was 8.1 °C. These temperatures were very similar to those in late autumn (May) and early winter (June), that we were trying to mimic, both in 2011 (mean daily maximum air temperatures: May 23.5 °C, June 19.6 °C; mean daily minimum: May 9.7 °C, June 9.3 °C) and to the long-term averages (mean daily maximum: May 22 °C, June 19 °C; mean daily minimum: May 9.4 °C, June 7.4 °C). To quantify temperatures at the sediment surface, temperature loggers were placed in one randomly chosen replicate for each habitat, control and treatment. These temperatures were measured hourly throughout the experiment. Halogen lights were used to mimic the solar-evaporative drying that occurs in SCP wetlands during late autumn and early winter. Dry periods of between 10 and 30 d were used, following the false start, based
on observations of the timing of autumn rain events prior to the commencement of winter rains on the SCP (authors’ unpublished observations).

Experimental treatments comprised an initial inundation period of 5 days representing the false start, followed by a dry period of 10, 20 or 30 days representing a range of dry periods at the end of a false start to winter inundation, followed by another inundation period of 5 days representing the start of the ‘true’ winter inundation period (Table 6.1). Three controls (20, 30, 40 d of continuous inundation) were needed in each habitat type, paired with treatments of equal total duration (e.g. FT20 equalled FC20, Table 6.1). An additional control of 15 days continuous inundation was added to observe change in assemblage development between 10 and 20 days (Table 6.1).

**Table 6.1.** Controls and treatments used in the experiment: (O- open water habitat, F- fringing vegetation habitat, C- Control, T- treatment).

<table>
<thead>
<tr>
<th>Treatment name</th>
<th>Initial wet phase</th>
<th>Dry Phase</th>
<th>Second wet phase</th>
<th>Explanation</th>
</tr>
</thead>
<tbody>
<tr>
<td>O/FC5</td>
<td>5 days</td>
<td>Nil</td>
<td>Nil</td>
<td>Procedural control 5 d inundation</td>
</tr>
<tr>
<td>O/FC15</td>
<td>15 days</td>
<td>Nil</td>
<td>Nil</td>
<td>Emergence after 15 d inundation</td>
</tr>
<tr>
<td>O/FC20</td>
<td>20 days</td>
<td>Nil</td>
<td>Nil</td>
<td>Emergence after 20 d inundation, control for O/FT20</td>
</tr>
<tr>
<td>O/FC30</td>
<td>30 days</td>
<td>Nil</td>
<td>Nil</td>
<td>Emergence after 30 d inundation, control for O/FT30</td>
</tr>
<tr>
<td>O/FC40</td>
<td>40 days</td>
<td>Nil</td>
<td>Nil</td>
<td>Emergence after 40 d inundation, control for O/FT40</td>
</tr>
<tr>
<td>O/FT20</td>
<td>5 days</td>
<td>10 days</td>
<td>5 days</td>
<td>Effect of a 10 d dry period interrupting inundation. Total duration 20 d</td>
</tr>
<tr>
<td>O/FT30</td>
<td>5 days</td>
<td>20 days</td>
<td>5 days</td>
<td>Effect of a 20 d dry period interrupting inundation. Total duration 30 d</td>
</tr>
<tr>
<td>O/FT40</td>
<td>5 days</td>
<td>30 days</td>
<td>5 days</td>
<td>Effect of 30 d dry period interrupting inundation. Total duration 40 d</td>
</tr>
<tr>
<td>O/FT5</td>
<td>Nil</td>
<td>35 days</td>
<td>5 days</td>
<td>Procedural control. 5 d inundation at the end of the 40 d experiment.</td>
</tr>
</tbody>
</table>

Day length increased over the 40 days experiment, which received natural light through the laboratory windows. Procedural controls were used to determine whether day length affected assemblages because freshwater invertebrates may respond rapidly to changes in photoperiod (Stoks et al., 2014). Two procedural controls were used and both were sampled following 5 days inundation: one control (O/FPC5) represented
inundation at the start of the experiment and the other (O/FPCE5) represented inundation 40 days later (Table 6.1).

Experimental treatments were allocated randomly to the 45 jars within each habitat type, with five replicate jars for each treatment and control from each habitat (Table 6.1). At the start of the experiment, each jar was inundated with distilled water for 5 days. Control jars were sampled after 15, 20, 30 and 40 days inundation. Treatment jars were placed under lights to dry out by evaporation (surface water disappeared in ≈ 5 days and samples were completely dry by day 11, drying rates comparable to field conditions [e.g. Strachan et al., 2014]) for their specified period, after which they were again inundated for 5 days. At the end of the experiment, samples (sediment and water) were preserved in ethanol for counting and identification. Each jar was therefore sampled only once, at the end of the experiment for each treatment. Invertebrates were identified to lowest possible taxonomic level.

Data analysis

Assemblage composition (species x abundance matrix) was the dependent variable used to test the hypotheses. Species composition in controls was compared between the two habitat types to test hypothesis 1. To test hypothesis 2, assemblage composition was compared among all treatments and controls within each habitat type separately, to generate pre-planned comparisons of each false start treatment to its corresponding control (of equal total duration), and to the 5 day inundation control. These pre-planned comparisons showed how false starts of different duration affected invertebrate emergence and the development of assemblages. This enabled the effects of false starts to be separated from the effect of total time available for invertebrate emergence, and comparison with the 5 day control showed whether the assemblage was simply the product of recent emergence following an abortive hatching. Pairwise comparisons were also used to compare pairs of controls of increasing duration, within each habitat type, to describe species emergence patterns during the first 40 days of inundation.

Although experimental conditions were kept as similar as possible, the treatments and habitats were expected to result in different sediment-surface temperatures, due to differing moisture content. Mean temperature and mean daily maximum temperature for each habitat, treatment and control were calculated. T-tests
were used to compare mean temperature and mean daily maximum temperature in samples from the two habitats (OW and FT) and between treatment and controls.

Using Primer version 6 (Clarke & Warwick, 2001), invertebrate species by abundance data were square-root transformed to reduce the influence of highly abundant taxa, then a Bray-Curtis resemblance matrix was calculated. Assemblage composition in the two procedural controls for each habitat was compared as a preliminary analysis (using analysis of similarity, ANOSIM (Clarke & Warwick, 2001)) to determine whether invertebrate emergence differed in response to inundation at the start or the end of the experiment. ANOSIM was used to test whether invertebrate assemblage composition differed between habitats (habitat, 2 levels: OW, FT, controls only), and relationships among samples were displayed using an ordination plot (non-metric multidimensional scaling (nMDS)). Invertebrate assemblage composition was found to differ markedly between habitats, so hypothesis two was analysed separately within each habitat using a single factor (treatment, 9 levels: 5 controls and 4 treatments) ANOSIM. Pre-planned pairwise comparisons were used to compare matched pairs of treatments and controls of equal duration, to compare false start treatments to 5 day controls to identify abortive hatching, and to compare pairs of controls of increasing duration. Ordination plots (nMDS) were used to display differences in assemblage composition among treatments. The index of multivariate dispersion (IMD) was calculated to describe the variance among samples within factor levels (Anderson et al., 2006). PERMDISP, a permutation test, was used to determine whether among-sample variance differed among the factor levels (Anderson et al., 2006). Similarity percentages (SIMPER) analysis was used to identify the species associated with each habitat and the species characterising each treatment and control.

**Results:**

**Temperature**

Mean \((t_{16} = 0.60, \ P = 0.55)\) and mean daily maximum \((t_{16} = 0.32, \ P = 0.75)\) sediment-surface temperatures during the experiment did not differ between sediments from the two habitats. In contrast, mean sediment-surface temperature was higher \((t_{7} = -4.81, \ P = 0.001, \ \text{mean} \ 19.5\ ^\circ\text{C}, \ \text{Fig. 6.1a})\) and mean daily maximum sediment-surface temperature was substantially higher \((t_{8} = -3.60, \ P = 0.007, \ 25.2\ ^\circ\text{C}, \ \text{Fig. 6.1b})\) in treatments than controls \(\text{mean} \ 17.6\ ^\circ\text{C}, \ \text{mean daily maximum} \ 16.7\ ^\circ\text{C}\). This difference
was due to the controls being inundated for the whole experiment, while the treatments dried out. The procedural control (O/FT5) had the highest mean temperatures because it was dry until the final 5 days (mean 26.3 °C, mean daily maximum 35.9 °C, Fig 6.1a, b).

Figure 6.1. Mean temperature for each control or treatment in the two habitat types during the laboratory experiment: (a) temperature across experiment (± 1 S.E.), (b) daily maximum (± 1 S.E.).

Procedural controls

In both habitats, there was no difference between the invertebrate assemblage emerging from 5 d inundation at the start of the experiment compared to 5 days.
inundation at the end of the experiment (OW $R = -0.2$, $P = 0.905$; FT $R = -0.056$, $P = 0.635$). There was thus no effect of seasonal change in day length on emergence, so the remaining hypothesis tests could be interpreted as planned.

**Invertebrate emergence from open water and fringing vegetation sediment (H₁)**

Emerging invertebrate assemblages were dominated by crustaceans, but included insects and oligochaete worms (Fig. 6.2). One cladoceran species, *Ilyocryptus spinifer*, was found and five species of ostracod: *Candonocypris novaezelandiae*, *Bennelongia gwelupensis* (previously *Bennelongia australis*), *Mytilocypris ambiguosa*, *Diacypris spinosa* and *Cypretta* sp. Insects included two species of Psychodidae larvae (Diptera), adult beetles (identified to Order) and amphibious collemboles. The species present in both habitat types show a range of survival strategies in response to desiccation, including desiccation-resistant eggs and dormancy (Table 6.2).

![Figure 6.2](image)

**Figure 6.2.** Mean abundances per sample of the top 90% of invertebrate taxa in the two habitats from the SIMPER analysis (key and stacks are in the same order).
Table 6.2. Desiccation survival strategies used by invertebrate taxa during the experiment and their response to false start treatments in the two habitats.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Desiccation survival strategy</th>
<th>Response to false start treatment in OW</th>
<th>Response to false start treatments in FT</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oligochaeta</td>
<td>Absent</td>
<td>Absent</td>
<td>Remained active</td>
</tr>
<tr>
<td><em>Ilyocryptus spinifer</em></td>
<td>Ephippia</td>
<td>Delayed hatching</td>
<td>Hatched and remained active</td>
</tr>
<tr>
<td><em>Candonocypris novaezelandiae</em></td>
<td>Desiccation-resistant eggs</td>
<td>Abortive hatching</td>
<td>Hatched and remained active</td>
</tr>
<tr>
<td><em>Bennelongia gwelupensis</em></td>
<td>Desiccation-resistant eggs</td>
<td>Abortive hatching</td>
<td>Hatched and remained active</td>
</tr>
<tr>
<td><em>Mytilocypris ambiguosa</em></td>
<td>Adult dormancy</td>
<td>Did not emerge from dormancy</td>
<td>Emerged from dormancy and remained active</td>
</tr>
<tr>
<td><em>Diacypris spinosa</em></td>
<td>Adult dormancy</td>
<td>Did not emerge from dormancy</td>
<td>Emerged from dormancy and remained active</td>
</tr>
<tr>
<td><em>Cypretta</em> sp.</td>
<td>Adult dormancy</td>
<td>Did not emerge from dormancy</td>
<td>Emerged from dormancy and remained active</td>
</tr>
<tr>
<td><em>Collembola</em></td>
<td>Absent</td>
<td>Absent</td>
<td>Amphibious (remained active)</td>
</tr>
<tr>
<td><em>Psychodidae</em> spp.</td>
<td>Desiccation-resistant eggs</td>
<td>Delayed hatching</td>
<td>Delayed hatching</td>
</tr>
<tr>
<td><em>Dipteran pupae</em></td>
<td>Dormant pupae</td>
<td>Remained dormant</td>
<td>Absent</td>
</tr>
</tbody>
</table>

Invertebrate assemblages emerging from OW and FT sediment differed markedly (Global $R = 0.595$, $P = 0.001$, Fig. 6.3), so Hypothesis 1 was supported. This difference comprised both species composition and relative abundance; that is, the two habitats shared some species in common, but their relative abundances differed (Fig. 6.2). SIMPER showed fewer Cladocera (*I. spinifer*) emerged from the sediment in FT samples than OW samples, but FT had more Oligochaeta and Ostracoda: *Candonocypris novaezelandiae*, *Bennelongia gwelupensis* and *Cypretta* sp (Fig. 6.2). The ostracod *Mytilocypris ambiguosa* and Psychodidae larvae were more abundant in OW.
**Figure 6.3.** Non-metric multidimensional scaling ordination plot of all invertebrates that emerged from the two habitats in the laboratory: open water – white squares; fringing vegetation – black squares.

*Effects of the false start on emerging invertebrate assemblages (H2)*

In OW, invertebrate assemblages in treatments and controls differed strongly (Global $R = 0.474$, $P = 0.001$) (Fig. 6.4a), but in FT, differences were smaller (Global $R = 0.167$, $P = 0.001$) (Fig. 6.4b), so Hypothesis 2 was supported in both habitat types. Furthermore, in OW habitat, dispersion was much higher amongst control samples (IMD = 1.23) than among treatments (IMD = 0.635; Fig. 6.4a), indicating that false start treatments made assemblages more uniform among samples ($F_{1,43} = 20.6$, $P = 0.002$). This occurred because only two species, the ostracods *C. novaezelandiae* and *B. gwelupensis*, hatched in OW sediment during the periods of inundation in the false start treatments, regardless of the length of the intervening dry period. This pattern was not evident in FT sediment (control IMD = 1.09; treatment IMD = 0.85; $F_{1,43} = 1.36$, $P = 0.27$; Fig. 6.4b). False starts therefore affected the invertebrate assemblages differently in the two habitats.
Figure 6.4. Non-metric multidimensional scaling ordination plot of invertebrate assemblages emerging from controls and treatments. Controls – black triangles, treatments – white triangles: (a) open water habitat, (b) fringing vegetation habitat (note the high stress value).

Pre-planned comparisons – Open water habitat

The composition of emerging invertebrate assemblages differed significantly among OW controls inundated for different periods (Fig. 6.5a). At 5 days inundation, only *C. novaezelandiae* had emerged, but over longer inundation periods, Ilyocryptidae cladocerans (*I. spinifer*) and Psychodidae sp. 1 larvae appeared in the controls. *Cypretta* sp. emerged by 30 days, and assemblages did not differ between 30 and 40 days in the controls (Fig 6.5a). In contrast, invertebrate assemblages emerging from the 20, 30, and 40 day treatments did not differ (*R* values ranged from 0.06 – 0.25, *P >* 0.127).
Figure 6.5. Invertebrate assemblage composition (average abundance per sample) in controls: (a) open water habitat, (b) fringing vegetation habitat with results from pairwise comparisons. NSD = no significant difference. * P < 0.05.

The composition of invertebrate assemblages that emerged following either 10 or 20 days of drying was identical to the assemblage that emerged after only 5 days of inundation (OPC5 vs either OT20 (R = -0.144, P = 0.944) or OT30 day (R = -0.004, P = 0.421)). The negative R values show that variation was greater among samples within
each treatment than between the treatments and the 5 day control. Also, OT20 and OC20 differed significantly \((R = 0.792, P = 0.008)\), showing that while the control assemblage had continued to develop for twenty days, the treatment assemblage had not. Thus, the false start treatment caused abortive hatching: mortality occurred during drying, and then upon re-wetting a new cohort of propagules emerged from the egg bank (Table 6.2).

*Ilyocryptus spinifer* and the ostracods *M. ambiguosa*, *B. gwelupensis* and *D. spinosa* emerged in high abundances in controls (Fig. 6.5a), whereas *C. novaezelandiae* dominated treatment samples, as it did OC5. Also, *I. spinifer* did not emerge from treatments (Table 6.2) despite the presence of large numbers of ephippia in the samples (unpublished data). OT30 and OC30 also differed significantly \((R = 0.856, P = 0.008)\), because *I. spinifer*, Psychodidae sp. 1, *M. ambiguosa*, dipteran pupae sp. 5 and Psychodidae sp. 2 were found only in controls, whereas *C. novaezelandiae* again dominated treatments. The same response patterns were observed when OT40 was compared to OPC5 \((R = -0.1, P = 0.73)\) and OC40 \((R = 0.948, P = 0.008)\), showing that the false start treatment had the same effects on the assemblage, regardless of duration (Table 6.2).

*Pre-planned comparisons – Fringing Melaleuca rhaphiophylla habitat*

Invertebrate composition changed little over time in the controls (Fig. 6.5b). At 5 days inundation *C. novaezelandiae* and *B. gwelupensis* were the only emerging species, but by 15 days inundation, *I. spinifer* and *Cypretta* sp. began to emerge. Assemblage composition then changed little over time among the 20, 30 and 40 day treatments \((R\) values ranged from -0.07 - 0.184, \(P > 0.071)\), although a few *D. spinosa* emerged by 20 days (Fig. 6.5b). Most species in this habitat emerged rapidly (in the first 15 days, Fig. 6.5b) and Collembola did not survive beyond the first 5 days, whereas in OW some species delayed hatching (e.g. *Cypretta* sp., Table 6.2).

In contrast to OW sediment, the difference between assemblages emerging from FC5 and FT20 was large \((R = 0.428, P = 0.008)\), showing that abortive hatching did not occur (Table 6.2). *I. spinifer* and *Cypretta* sp. were found only in FT20, and *B. gwelupensis*, *C. novaezelandiae* and *M. ambiguosa* were present in higher mean abundances in FT20 than in FC5. In contrast, Oligochaeta, Collembola and an adult beetle species were all found in higher abundances in FC5. However, FT20 and FC20 also differed significantly \((R = 0.368, P = 0.024)\), showing that the false start treatment
had delayed the development of the assemblage. *I. spinifer* were present and *C. novaezelandiae* and *Cypretta* sp. occurred in higher mean abundances in FC20. In contrast, *B. gwelupensis*, Oligochaeta and *M. ambiguosa* were present in higher abundances in FT20.

The assemblage that emerged from FC5 also differed significantly from both FT30 ($R = 0.56, P = 0.008$) and FT40 ($R = 0.228, P = 0.048$). *C. novaezelandiae* was present in higher abundances and Collembola were found only in FC5, whereas *Cypretta* sp. only occurred in FT30, 40. However, there was no significant difference in assemblage composition between FC30 and FT30 ($R = 0.092, P = 0.25$) or between FT40 and FC40 ($R = 0.12, P = 0.87$). That is, the assemblage that had developed in the false start treatments with a 20 or 30 day dry period was the same as the assemblage that developed in the equal duration control, so the assemblage in dry FT sediment had continued to develop and was the same as the continuously inundated control. Overall, whether they hatched from eggs or emerged from dormancy, invertebrates in FT sediment continued to emerge and remained active in the sediment throughout the experiment (Table 6.2) regardless of the false start treatment.

**Discussion:**

**Experimental conditions**

Mean sediment-surface temperatures during the experiment were similar to mean maximum air temperatures in autumn–early winter ($\approx 20 ^\circ C$), so the evaporative drying method effectively dried the sediment but also kept conditions comparable to field conditions. Furthermore, mean maximum temperatures of around $20 ^\circ C$ were recorded in fissure microrefuges in another SCP wetland, South Lake, where a wide range of invertebrates survived the dry period (Strachan et al., 2014). Mean maximum sediment-surface temperatures were highest in the 5 day controls (OT5 and FT5 $35.9 ^\circ C$), and these temperatures were similar to, although slightly cooler than, temperatures measured during wetland drying in South Lake ($37 – 42 ^\circ C$; Strachan et al., 2014). Similarly, no seasonal effects were evident on faunal emergence because the assemblages that emerged from the procedural controls did not differ from the five day controls. Experimental conditions, although controlled, were thus a reasonable representation of field conditions.
Invertebrate emergence from open water and fringing vegetation sediment

The hypothesis (H₁) that the assemblage composition of invertebrates emerging from OW sediments would differ from the assemblage emerging from FT sediment was supported. Although most species were present in both habitats, we observed higher abundances of taxa that included amphibious species (e.g. oligochaetes and collembolans) in FT sediment than in OW sediment. The temporal pattern of emergence also differed between the habitats because species emerged more rapidly from FT sediment (regardless of whether species were found in both habitats or only in FT), a response that may enable them to make use of shorter inundation periods. In contrast, after 5 days of inundation in OW, only *C. novaezelandiae* emerged; other species showed delayed responses suggesting that they may already show resistance to short false-start events.

Fringing trees may create conditions in sediments that slow the rate of drying (shading, high organic matter content and water retention), partially compensating for shorter hydroperiods. Furthermore, amphibious taxa have been shown not to follow retreating water levels as wetlands dry out (Tronstad *et al.*, 2005b), allowing them to remain in the moist environment beneath fringing trees. Although sediment beneath FT has somewhat higher water saturation potential, it is inundated for shorter periods than is OW, because it is at higher elevation than the centre of the wetland basin (which fills first and dries last). This may mean that species or populations present beneath FT may have to be more capable of surviving brief inundation periods than those in OW. However, freshwater crustaceans have been shown to follow retreating water levels as they decline (Tronstad *et al.*, 2005b), so the presence of desiccation-resistant eggs and dormant adults beneath fringing trees may seem surprising. Another study of a different SCP wetland has shown that wetland crustaceans may take refuge in depressions and cracks in wetland sediments as they dry (Strachan *et al.*, 2014), suggesting that not all individuals migrate to the centre of drying wetlands.

The impact of false starts on invertebrate emergence

The hypothesis (H₂) that the assemblage composition of invertebrates emerging from sediment exposed to false starts of different duration would differ from sediments exposed to continuous inundation was supported in both habitats, although abortive hatching was only observed in OW sediment. In FT, the assemblages exposed to the false start treatments continued to develop during the dry periods following the first
inundation period. Treatments that applied false starts with different dry-period duration caused different patterns of invertebrate emergence from FT sediment. Unexpectedly, an identical assemblage emerged in OW regardless of the duration of the false start dry-period. So, the response to the false start treatments differed markedly between the habitats.

Overall, three types of response to false starts were observed in this experiment. Firstly, species that hatched from desiccation-resistant eggs immediately upon immersion but showed abortive hatching in response to false starts. Secondly, species with delayed emergence (> 5 days) which responded differently in the two habitats: in OW sediment they did not emerge in response to false starts; in FT sediment they emerged rapidly and survived in the damp sediment without surface water in response to the false start. Thirdly, amphibious species in FT sediment that readily survived the false start. It is likely that other types of response to false starts may be observed in other types of wetland sediment or regions with different faunal composition of temporary wetland assemblages.

Invertebrate assemblages in OW became uniform in response to false starts because two ostracod species hatched rapidly from desiccation-resistant eggs and the dry periods following the false starts caused their mortality (i.e. abortive hatching). C. novaezelandiae and B. gwelupensis may produce desiccation-resistant eggs either parthenogenetically (De Deckker, 1983; Chaplin, 1991) or through meiosis, and the minimum time from maturity to sexual production of eggs in C. novaezelandiae is > 40 days (Chaplin, 1991). It seems unlikely that either species produced new eggs during the first inundation period, so the egg supply for the second hatching came from the egg bank. Adult C. novaezelandiae lay desiccation-resistant eggs that hatch rapidly in both field and laboratory, and most eggs may hatch in response to inundation (Strachan et al., 2014), showing little resistance to false starts. However, C. novaezelandiae prey on the desiccation-resistant eggs of other invertebrate species (Yousif et al., 2013) so a food source is immediately available to them upon hatching. Although parthenogenetic life histories permit rapid egg-laying, assisting survival in unpredictable environments, they may be inflexible and have few other options to respond to drying. They may also be heavily reliant on dispersal to provide genetic diversity to populations (Chaplin, 1991). Species with both resistance (desiccation-resistant eggs) and resilience traits (abundant supply of eggs in egg-bank, cohort-splitting) have been thought better equipped to
survive the impacts of climate change (e.g. Chester et al., 2015), but repeated false-start events without a long intervening hydroperiod may comprise a limit to their effectiveness.

In contrast, in FT, all invertebrate assemblages from the false start treatments differed from the assemblage in the 5 d control, showing that these assemblages did not experience abortive hatching. Invertebrates emerged more rapidly in FT than OW and were a mixture of species hatching from desiccation-resistant eggs and those emerging from dormancy. When exposed to the false start, these assemblages continued to develop in the absence of surface water (the sediment remained damp). Although emergence in the treatments was initially slower than in controls, the developing assemblage caught up to controls by 30 days. Few studies have observed freshwater invertebrates remaining active in damp sediment. Tronstad et al. (2005a) showed that some freshwater dipteran larvae (Chironomidae, Ceratopogonidae) remained active in river floodplain sediment during periods without surface water, and as a result, were able to complete larval growth, pupate and emerge within as little of 10 days of inundation. However, we do not know of any other study documenting the continued emergence, activity and growth of freshwater invertebrates in the absence of inundation. This response was probably possible because FT sediment retains moisture more effectively than OW sediment, creating a humid environment. Sediment moisture has been identified in several studies as a crucial factor for invertebrate survival in dry streambeds (Stubbington & Datry, 2013), but usually in relation to the survival of dormant, not active, invertebrates.

Although drying following the false start in OW sediment caused abortive hatching by B. gwelupensis, in FT sediment hatchlings survived the false start. Other ostracods, such as M. ambiguosa, D. spinosa and Cypretta sp. survive desiccation through adult dormancy (Strachan et al., 2014). M. ambiguosa and Cypretta sp. showed delayed emergence in OW, and Cypretta sp. also showed delayed emergence from FT sediment. Diacypris spinosa adults and I. spinifer ephippia showed delayed emergence in controls in both habitats, suggesting the potential for resistance to false starts in some widespread species. Therefore, species that emerged very rarely (or not at all) from OW sediment following the false start, emerged or hatched from FT sediment during either the inundation period (e.g. M. ambiguosa) or the following dry period (e.g. M.
ambiguosa, Cypretta sp.). These responses indicate that (damp) sediment beneath FT may provide a refuge from false starts for a range of wetland invertebrates.

The results from Lake Joondalup South show that habitat type alters individual species responses (and therefore invertebrate assemblage response) to false-start events. The differences between habitats are likely to be associated with differences in sediment conditions, as well as the past hydroperiod to which the sediments were exposed (but not shading because FT sediment was not shaded during the experiment as it would be in the field). This experiment used sediment from only one wetland, but the wetlands on the SCP have a wide range of sediment properties, hydroperiod duration and assemblage composition (Sim et al., 2013) which may affect invertebrate responses to false-start events. So, while this study shows some of the invertebrate responses to false starts that may occur, other response patterns may exist. Also, laboratory experiments do have some limitations for understanding ecological processes. For example, the deaths of Collembola after 5 days of inundation in FT samples were almost certainly an artefact of the microcosms, because they prevented Collembola from migrating away from the flooding; in the field they would have migrated up-slope to remain in damp sediment as the wetland refilled (Tronstad et al., 2005a). Also, larger animals (such as birds) are present in drying wetlands and may feed on invertebrates active in FT sediments (Boulton et al., 2014), and wind-borne (Vanschoenwinkel et al., 2008) or zochorous dispersal may also occur (Van Leeuwen et al., 2013); such processes are not easily represented in laboratory experiments. False-start events will have species-specific effects that need to be investigated more widely (Robson et al., 2011; Strachan et al., 2015), and more field-based observations and experiments are needed to examine small-scale processes in wetlands because invertebrate responses to drying operate at these small scales (e.g. Tronstad et al., 2005b, Strachan et al., 2014) but have wider-scale influences on food web development during the hydroperiod.

Species responses and trait flexibility

None of the species observed here are rare or threatened however, cladocerans and ostracods have important roles in wetland ecology. Both taxa reach high abundances in temporary wetlands during the hydroperiod and are consumed by a wide variety of invertebrate and vertebrate predators (Boulton et al., 2014). Herbivorous nektonic cladocerans like I. spinifer are important phytoplankton grazers in wetlands (Davis & Christidis, 1999) and ostracods are benthic detritivores, consuming fine-
particulate organic matter and providing a detrital basis for wetland food webs (Gooderham & Tsyrlin, 2002). Thus, the dynamics of these taxa and their responses to changes in temperature and water regime are important for sustaining ecosystem function in temporary wetlands.

Species respond individually to climatic events such as false starts according to the plasticity of their survival traits. But there are trade-offs associated with life cycles lived in different types of habitat (Johansson & Suhling, 2004): for example, accelerated development may increase predation risk arising from more time spent feeding. Rate of drying may also affect invertebrate survival: slow drying (3-4 days, as applied here) has been found to retain higher invertebrate abundance and diversity than fast drying (2 hours) (Stanley et al., 1994). Habitat structure (e.g. presence of fringing trees) and quality (e.g. sediment properties) will determine whether microrefuges (e.g. sediment cracks) or refuges (e.g. FT) from drying are present in wetlands. However, wetland invertebrates must still possess the traits required to use these refuges to survive drying, although comparatively little is known of how altered water regimes may alter the phenology of desiccation responses (Strachan et al., 2015).

One of the most urgent questions in conservation ecology is the degree to which species survival traits are flexible, that might enable autonomous adaptation to climate change. Species able to adjust the timing or use of particular traits should survive better than less flexible species (Wickson et al., 2012). Some species in the present study showed different responses to the false start treatment in different habitats, suggesting that habitat conditions do permit flexibility in hatching/emergence times in response to inundation and drying. For example, the cypridid ostracod *M. ambiguosa* emerged from aestivation immediately in FT samples, regardless of the false start, whereas they failed to emerge from false start treatment samples in OW. Another aestivating cypridid, *Cypretta* sp., also failed to emerge from false start treatments in OW, but in FT they showed delayed emergence. Both of these species are known to respond to wetland drying by retreating into damp cracks and crevices (microrefuges) in the sediment where they become dormant (Strachan et al., 2014), suggesting that sediment moisture facilitates both their survival and activity. These species have at least two options for refuge from desiccation in wetlands: microrefuges in open-water sediment and sediment beneath fringing trees. Species possessing more than one refuge option may be more resilient to hydrological change driven by climate change (Robson et al., 2011). The
complexity of species responses to the pattern of wetting and drying suggests that some will be difficult to predict, despite being partially habitat-dependent.

*Ilyocryptus spinifer* ephippia did not hatch in OW and rarely hatched in FT sediment following the false start, despite hatching in all controls inundated for > 5 days and the presence of large numbers of ephippia in all samples. Cladocerans are among the most abundant animals in wetlands, having an important role in food webs and ephippia are known to withstand drying for very long periods (up to 200 years (Gooderham & Tsyrlin, 2002)), although their viability declines over time (Jenkins & Boulton, 2007). This species appeared to delay hatching beyond the duration of the false starts applied in this experiment. However, their presence in controls inundated for ≥ 15 days suggests that a false start inundation that lasted for longer than 15 days might have caused abortive hatching.

Abortive hatching may benefit predatory or scavenging invertebrates such as some Stratiomyidae and Psychodidae dipteran larvae, which are known to feed on stranded invertebrates in drying wetlands (El Bardicy *et al*., 2009; Strachan *et al*., 2014). These insect larvae may benefit from abortive hatchings by feeding rapidly, pupating and emerging as flying adults during the dry period. Large numbers of dipterans have been observed pupating and emerging from recently exposed sediments in a drying floodplain wetland (Tronstad *et al*., 2005b). However the species of Psychodidae in this experiment were present mostly in OW sediment and hatched from eggs only from controls, indicating that they may have been unable to respond to brief periods (5 days) of inundation.

As climate change progresses and water regimes in SCP wetlands become drier (Sim *et al*., 2013), refuges from drying will become increasingly important for species both capable and incapable of desiccation resistance (Strachan *et al*., 2015). However, lower volumes of wetland inundation may cause FT to be left ‘high and dry’ in some wetlands. Although the fringing vegetation around wetlands responds to lower water levels, it can take decades for fringing trees (such as *Melaleuca rhaphiophylla*) to establish a shady canopy further into a wetland basin (Semenuik & Semenuik, 2012). If sediment under FT is a refuge from the drying and warming effects of climate change then planting locally-native wetland tree species deeper into wetland basins could be a useful action to assist wetland biodiversity to adapt to climate change, especially where
other factors (e.g. groundwater extraction, clearing of fringing vegetation) are placing stress on wetland ecosystems.

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**References:**


Chapter 7. General Discussion

Climate change will have serious ramifications for Swan Coastal Plain wetlands, including prolonged periods of drying, increased air and water temperatures (leading to decreased humidity and increased evaporation rates) and increased frequency and severity of false start events. Some past studies have suggested that these altered environmental conditions will deplete the egg bank (e.g. Jenkins & Boulton, 2007) ultimately resulting in local extinction. Although some aquatic species have resistant behaviour and biological adaptations to survive these conditions, there is not yet enough known about species responses to make sound predictions in the face of climate change (Chessman, 2015). Therefore, the aim of this project was to understand the interaction between species life histories and traits, and wetting and drying in wetland environments at three scales: sediment microtopography within habitats, fringing and open water habitats within a wetland and different wetlands. Addressing the different scales enabled the project to encompass the whole life cycle of different species to better holistically determine the ecological mechanisms underlying the responses of invertebrate fauna to the effects of climate change.

The three spatial scales addressed incorporated microhabitat refuge use within a wetland (Chapter 4), habitat-scale differences in emergence from sediment between fringing vegetation and open water habitats (Chapter 5, 6) and differences among wetlands in emergence patterns (Chapter 5). The microrefuge scale is where individuals encounter and respond to changed environmental conditions. The presence or absence of microrefuges, in conjunction with the survival strategies of individual species, is likely to determine the persistence of populations of many invertebrate species within temporary wetlands. The Melaleuca species-dominated fringing vegetation common to many SCP wetlands provides invertebrate habitat in and around the roots and leaf litter that the trees provide. This habitat is associated with sediment that is less dense, has more organic matter, is cooler and retains more moisture than open-water sediment, so it may also affect population persistence within wetlands by acting as a temperature refuge. It certainly contains a different composition of invertebrate propagules than found in open water sediment. Because many temporary wetland invertebrate species are mobile, and have particular traits and tolerance thresholds (e.g. Calosi et al., 2008), long-term species survival will be determined at the landscape scale (Ruhi et al., 2013). The multiple scales covered in this study show that temporary wetlands provide a
mosaic of habitat and micro-habitat as well as a variety of water regimes, that facilitate invertebrate resistance to drying, but may also sustain resilience (recolonization processes) occurring after drying in wetlands.

*The physiology and variety of species responses to drying*

Most groups of aquatic macroinvertebrates contain some species that possess physiological or behavioural traits to survive dry periods (Robson *et al*., 2011). These traits are species specific and sometimes have even been shown to be population specific (Chapter 3), so under different conditions, different species may be better able to survive dry periods. There has been confusion in the literature about the terminology surrounding drying and associated traits (Chapter 3), leading to a misuse of terms and therefore misunderstanding of the processes and states that actually occur. I believe this has hindered progress, or even caused a regression in scientific understanding of desiccation responses, because many of the pre-electronic era papers correctly identified the degree of drying and the survival mechanisms used by species. For this reason, the review provided a table listing freshwater invertebrate families and summarising the survival strategies they use, the life stage that can survive drying, the length of dry period they can survive and the best references for these survival strategies. Future publications need to be as specific as possible about the type of desiccation response being examined and how it may relate to conditions in the environment. There is also a role for more studies of invertebrate physiology and biochemistry as it relates to desiccation resistance.

*Microhabitat refuges in wetland sediments during dry periods*

I observed a significant and rapid change in the assemblage composition of invertebrates while South Lake dried and reflooded (Table 7.1) (Chapter 4). During these rapid changes, different invertebrate species responded differently: some retreated into cooler microrefuges, while others produced desiccation resistant stages or emigrated from the wetland. As has been shown for dry riverbeds (Steward *et al*., 2012), when wetlands have no surface water they are not biologically inactive, because there are many aquatic species present in microrefuges and as resistant life stages. The observations from South Lake (Chapter 4) demonstrated that small scale microhabitats and processes can be important for individual survival and species persistence. Fissure microhabitats in particular were significantly cooler and had more stable temperatures than the lakebed surface. As climate change progresses on the SCP, air temperatures
and evaporation rates will increase, changing physical conditions in the sediment (Fig. 7.1). The effects of these changes will vary depending on the type of sediment present in a wetland. Three main types of surface sediment are found in SCP wetlands: peat-like sediment with high organic matter content; sandy sediment with low organic matter content; and an organic floc found in eutrophic wetlands (Fig. 7.1). The latter occurs in perennial wetlands experiencing anthropogenic eutrophication and repeated algal blooms, however, as many SCP wetlands have become intermittent in recent decades (Sim et al., 2013), some wetlands with this floc now dry out, appearing to retain few invertebrate propagules (e.g. North Lake, Lake Booragoon, Chapter 5). Wetlands with sandy sediments, low in organic matter show surface depressions when the lake beds are dry, but do not form cracks or fissures. Wetlands with sediments with a higher organic matter content, like South Lake, show all three of these microrefuges, because the sediment shrinks markedly during drying (Fig. 7.2). Sediments with high organic matter content also retain moisture for longer during drying (Chapters 5, 6) creating temperature and moisture-retaining microrefuges for invertebrates (Fig. 7.1). The results from South Lake showed that different invertebrate species were found in different microrefuges, but also that a variety of life history strategies were used to survive drying in conjunction with these microrefuges. Of the invertebrates that aestivated, some were found only in fissures (e.g. caddisfly larvae *Triplectides australis*), but others were found in surface depressions and in sediment more generally (e.g. some ostracods, Fig. 7.1). The outcome of aestivation also differed between these taxa: *T. australis* pupated and flew away from drying wetlands, but the ostracods emerged from aestivation once the wetlands reflooded, giving them a developmental head start on taxa emerging from eggs (e.g. cladocerans, ostracods: *C. novaezelandiae*). Species such as the isopod *Paramphisopus palustris* did not appear to enter any form of dormancy but relied on the cool, damp and dark fissures to survive drying. The adult beetles found in all microrefuges preyed on trapped invertebrates and flew away before the wetland dried completely (Fig. 7.1). So, although a variety of microrefuges may be available within a wetland, the species using those microrefuges may also vary in their life-history responses to drying.
### Table 7.1. Research aims, hypotheses and outcomes.

<table>
<thead>
<tr>
<th>Chapter Title &amp; Research Paper</th>
<th>Research aims</th>
<th>Hypotheses and Research Questions</th>
<th>Outcome</th>
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<tbody>
<tr>
<td><strong>Chapter 3. Freshwater invertebrate life history traits for surviving desiccation</strong>&lt;br&gt;Strachan S.R., Chester E.T. &amp; Robson B.J. (2015) Freshwater invertebrate life history traits for surviving dry periods: a review. <em>Springer Science Reviews, 3</em>, 57-75.</td>
<td>To review the literature on the physiology and range of species responses to drying. This necessitated clarifying the definitions of the stages of drying and types of resting stages that occur during desiccation, including especially the older ‘pre-electronic’ literature, which often included detailed observations of invertebrate behaviour.</td>
<td>Which abiotic factors are important for macroinvertebrate survival in wetlands that dry out? If wetland water regimes become drier, with shorter periods of inundation and longer dry phases, what effect might this have on macroinvertebrate survival?</td>
<td>Insufficient data</td>
</tr>
<tr>
<td><strong>Chapter 4. Microrefuges from drying for invertebrates in a seasonal wetland</strong>&lt;br&gt;Strachan S.R., Chester E.T. &amp; Robson B.J. (2014) Microrefuges from drying for invertebrates in a seasonal wetland. <em>Freshwater Biology, 59</em>, 2528-2538.</td>
<td>To investigate potential microhabitat refuges in wetland sediments during dry periods. Three potential microrefuges were studied: surface depressions, shallow cracks and deeper fissures across three stages of the hydroregime (damp, dry and reflooded).</td>
<td>H$_1$ Because inundation level and temperature in each microrefuge type changed as the wetland dried and reflooded, invertebrate assemblages would also differ among microrefuges. H$_2$ If deeper fissures in wetland sediments provide a cooler microrefuge for invertebrates in the absence of surface water, then this microrefuge would gain species during the dry phase, as individuals sought out and moved into cooler microhabitats.</td>
<td>H$_1$ Accepted  H$_2$ Accepted</td>
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<td>Chapter 5</td>
<td>Fringing trees may provide a refuge from prolonged drying for urban wetland invertebrates.</td>
<td>To investigate emergence and egg bank hatching from sediment from eight SCP wetlands and the effects of differences in habitat (open water and fringing vegetation), duration of drying, and sediment properties.</td>
<td>$H_1$ Assemblage composition, diversity and abundance of invertebrates emerging from sediment from open water would differ from that emerging from sediment from beneath fringing trees, because of differences in sediment characteristics. $H_2$ A higher diversity and abundance of invertebrates, with a different assemblage composition, would emerge from inundated damp sediment taken fresh from the field than from sediment that was dried and stored for a year, because moisture would assist individuals to sustain dormancy.</td>
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<td>Chapter 6</td>
<td>Habitat alters the effect of false starts on seasonal-wetland invertebrates.</td>
<td>To investigate the effects of a false start (where an intense rainfall event occurs, partially filling an intermittent waterbody that then dries out before invertebrates can complete their life cycles) on invertebrate assemblages emerging from the egg bank in two habitats (open water and fringing vegetation) and varying duration of dry periods following the false start.</td>
<td>$H_1$ the assemblage composition of invertebrates emerging from open water sediment would differ from that emerging from fringing vegetation sediment, because sediment conditions differed between the habitats. $H_2$ the assemblage composition of invertebrates emerging from sediment exposed to a false start would differ from sediments exposed to continuous inundation, because false starts cause abortive hatching.</td>
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Figure 7.1. Relationship between climate and sediment type in temporary wetlands and effects on benthic invertebrates (Solid triangles indicate increasing levels of variable).
Increasingly, the temperature tolerances of freshwater invertebrates are being measured, often as upper thermal limits/tolerances (e.g. Calosi et al., 2008, 2010; Stewart et al., 2013). Studies of some species of wetland-dwelling diving beetles showed that their upper thermal limits were generally above 40 °C (Calosi et al., 2010) because Dytiscidae are among the most tolerant insect taxa (Stewart et al., 2013). Surface lake-bed temperatures in South Lake also reached 40 °C and showed diurnal fluctuations averaging 15 °C (Chapter 4), but temperatures measured simultaneously inside fissures averaged only 20 °C with daily fluctuations of less than 2 °C. This means that those species with lower tolerances or poorer acclimation abilities (such as some
long-lived adult beetles, (e.g. Calosi et al., 2008) could seek refuge in fissures during hot periods, thereby remaining in those wetlands despite the warmer conditions.

Therefore, observations from South Lake show how very small scale differences in (micro)habitat may result in large scale effects (population persistence within wetlands), which will become increasingly important under climate change. Although these observations were only made in one wetland, they show how invertebrates that lack desiccation resistant stages (e.g. P. palustris) can survive in wetland sediments. It is likely that these processes also occur in other wetlands with similar sediment properties, because crevices and fissures are commonly observed in the dry beds of wetlands in good ecological condition (Fig. 7.2). Further research needs to be carried out in other wetlands with similar sediment structure to that observed in South Lake, as well as lakes with other types of sediment (e.g. clay, cobbles). Given that negative impacts on wetlands such as eutrophication (with repeated algal blooms) or invasion by exotic emergent macrophytes (e.g. Typha orientalis) can profoundly alter sediment properties, they appear likely to reduce or entirely eliminate crack and fissure-type microhabitat refuges in wetland sediments. So, wetlands retaining these microrefuges should be protected as drought refuges for aquatic invertebrates. Other microrefuges such as woody debris, emergent vegetation and leaf litter may exist in other wetlands (Chapter 3) and should be investigated for their capacity to provide drought refuges for invertebrates as more wetlands become intermittent.

*Emergence and egg bank hatching from two different sediment habitats*

Invertebrate assemblages emerging from open water sediment differed from those emerging from fringing vegetation sediment in eight SCP wetlands (Table 7.1) (Chapter 5). These two habitats also differed in sediment composition (density, organic matter content, moisture content) and sediment temperature. Some species that were present in both habitat types showed different responses to inundation in each habitat, while others did not (Fig. 7.3). Despite the eight wetlands differing in a range of variables (Fig. 7.3), differences in invertebrate emergence from the two habitat types were consistent among wetlands (except North Lake, from which nothing emerged), showing the importance of local habitat conditions. Furthermore, the application of the prolonged drying treatment showed that sediment properties altered invertebrate responses to prolonged drying, for example the ostracod *D. spinosa* delayed emergence following prolonged drying only in fringing vegetation sediment (Fig. 7.3). The
ostracod *B. gwelupensis* showed delayed emergence in both damp and dried treatments in open water and in the damp fringing vegetation treatment, but failed to emerge at all from the dried fringing vegetation sediment, showing either mortality or prolonged delay in emergence in response to drying (Fig. 7.3). In contrast, some species responses remained unaltered (e.g. *I. spinifer*, Fig. 7.3).

**Figure 7.3.** Summary of results for fringing trees may provide a refuge from prolonged drying for urban wetland invertebrates. Solid triangles indicate peak species emergence, coloured dots represent wetlands.

North Lake differed from the other wetlands because no invertebrates emerged from sediments collected there, and emergence was also limited from Lake Booragoon. Both wetlands were formerly perennial and experienced decades of eutrophication and algal blooms (Balla & Davis, 1995, Robson pers comm, 2013). Now that both dry out,
very few invertebrate taxa that can emerge from resting stages in the sediment are present in either wetland, probably because sediment microrefuges were destroyed by the deposition of thick layers of organic floc for many years. This appears likely to have damaged the invertebrate faunal assemblage, which is now mainly comprised of mobile insects, such as Corixidae and Notonectidae, and chironomid larvae (Robson pers comm, 2013).

As climate change increases ambient temperatures, the cooler refuge under fringing vegetation may become increasingly important for invertebrate survival. Stewart *et al.*, (2013) identified 21 °C as the threshold for temperature-sensitive stream invertebrates in south-western Australia and noted that this temperature is frequently exceeded in streams lacking riparian vegetation. Fringing vegetation alongside streams has been shown to create temperature refuges for freshwater invertebrates (Davies, 2010) and my results indicate that a similar process may occur in wetlands because sediment surface temperatures were on average five degrees cooler beneath fringing vegetation at South Lake (Chapter 4). However, my results also showed that the sediment from beneath fringing trees, even when unshaded (in the laboratory), remained around six degrees cooler when drying than did open water sediment. Temperature differences of the magnitude of five to six degrees Celsius will be sufficient to improve survival rates for some freshwater invertebrate species, especially differences between temperatures above or below 30 °C, which is the region in which many species upper thermal limits lies (Stewart *et al.*, 2013). Drying rates will also be slower beneath fringing trees, allowing invertebrates more time to prepare for desiccation, which is important for their survival (Stanley *et al.*, 1994). Thus it appears that fringing vegetation may provide a temperature refuge in wetlands and that there is another temperature-moderating mechanism driven by fringing vegetation (cooler sediment during drying) that operates in wetlands but has not been described in streams. There are many other possibilities for refuge habitats in wetlands, such as amongst emergent vegetation, beneath different types of fringing vegetation (e.g. heath vegetation, nitrogen fixing trees or understorey plants), upon or beneath woody debris, and beneath mats of dried submerged vegetation. Further research is needed to determine what other habitat types provide drought refuges and how often these habitat types occur in intermittent wetlands.
This emergence experiment was carried out in the laboratory and even though conditions were similar to average wetland conditions, experimental conditions cannot be the same as those occurring in situ in wetlands. For example, distilled water was used in the experiments but in the field, groundwater (mostly) refloods these wetlands, and it contains elements such as iron. These differences may have altered emergence patterns of some taxa. Similarly, taxa such as the collembolans that might retreat upslope from encroaching surface waters were unable to escape within the microcosms and mortality ensued. These limitations are common to all similar laboratory experiments and are widely recognised (e.g. Stubbington & Datry, 2013), but they do facilitate controlled comparisons of emergence under different conditions (Chapters 4, 5).

Invertebrate dynamics within different habitats in wetlands have been studied much less than habitat types in rivers and streams. How different habitat types affect invertebrate responses to disturbances, such as drying, has been studied even less often. This study shows the role of both shading and (several) sediment properties and the effect they can have on strategies for surviving drying used by aquatic invertebrates. More studies of different habitat types in different kinds of intermittent wetlands are urgently needed to expand our understanding of species responses to drying, the role of habitat in sustaining biodiversity and to identify refuges which will assist species and ecosystems to cope with climate change.

The effects of a false start on invertebrate emergence

The open water and fringing vegetation habitats differed in invertebrate assemblage composition, and emergence was slower in open water than from fringing vegetation sediment (Fig. 7.4). In open water sediment, total mortality occurred during the dry period following the false start and so subsequent assemblage composition reflected only the following 5 d of immersion (Fig. 7.4). Remarkably, in fringing vegetation sediment, the emerged fauna was able to persist and continued to develop without surface water for at least a 30 d dry period. The false start experiment also showed that some species delayed emergence in both continuously inundated and false start treatments (Fig. 7.4). So, in false start treatments in open water samples were not inundated for long enough to trigger emergence in species with delayed emergence, but in fringing vegetation, sufficient moisture was present to enable emergence and continued development. Species that hatch from eggs immediately upon inundation did so, but then died in open water samples (Fig. 7.4). The continuous development of
invertebrates in fringing vegetation sediments was somewhat slower following false starts than in controls but caught up to controls by 30 days. This showed that had the second period of inundation been the true start of the wet season, the assemblage beneath fringing vegetation would have been very well developed compared to that in open water areas of a wetland.

![Diagram](image)

**Figure 7.4.** Effect of false start events on seasonal-wetland invertebrates (d-number of days that the control or treatment lasted, solid triangle shows high or low levels of variables).

It is important to note that the sediment for this experiment was collected from one wetland only (Lake Joondalup South). Although previous experiments (Chapter 5) showed that this wetland had the highest diversity of emerging invertebrates, it would have been interesting to see whether invertebrates in fringing vegetation showed the same abilities in other wetlands. The presence of many of the same species in sediment from beneath the fringing trees of the other seven wetlands, and similarities in sediment...
qualities from this habitat (Chapter 5) suggests that they are likely to show a similar capacity to continue development without surface water. I am aware of no other studies showing that wetland invertebrates can survive and grow in damp sediment, in the absence of inundation, so this experiment discovered new survival abilities by freshwater invertebrates that are facilitated by particular habitat conditions. Such discoveries are vital because they show that wetland invertebrates may be more resistant to some climate change impacts, such as false start events, than previously thought, provided that suitable habitats are available and have remained in good condition. Unfortunately, fringing trees have been cleared from many SCP wetlands (Chester et al., 2013) and wetlands elsewhere in the world. If false start events increase in frequency and severity some invertebrates will be unaffected, some may benefit while many will be negatively impacted. Research exploring more severe false starts is also required to identify any negative impacts on invertebrates and whether repeated false starts will lead to local extinction (e.g. Jenkins & Boulton, 2007).

This study needs to be repeated in other wetland clusters to determine how widespread these abilities and associated habitat conditions are. A recent study of the freshwater snail Havia (Physa) acuta in SCP wetlands showed that it uses anhydrobiosis to survive drying (Chester, unpublished data), but populations of this species in Europe do not, showing relatively quick mortality in response to desiccation (Costil et al., 2001; Collas et al., 2014). This suggests that populations of some taxa on the SCP have adapted to intermittency, which occurs often in these wetlands. Furthermore, showed that H. acuta collected from perennial wetlands were as able to use anhydrobiosis as individuals collected from intermittent wetlands, showing that the regional population pool for this species all retained this survival trait, regardless of the water regime to which they were exposed at the time of collection. Consequently, invertebrates in SCP wetlands may be more resistant to the effects of wetland drying than invertebrates from regions where most wetlands are perennial.

Invertebrate responses across spatial scales

Some of the invertebrate species studied here showed flexible traits depending on the microhabitat, habitat or wetland that they emerged from, while others did not. A variety of life history strategies were compiled from responses observed in Chapters 4 – 6, and are described here to illustrate how invertebrates respond to desiccation and habitat across spatial scales.
Cypretta sp. is a commonly occurring ostracod species in SCP wetlands (Davis & Christidis, 1999) and was found in all microrefuges except surface depressions (during reflooding), and mostly in open water. In response to desiccation, Cypretta sp. closed their bivalve carapace and entered a dormant state. They emerged rapidly following reimmersion, but in response to the false start they delayed their emergence in both habitats. Aestivation, by definition, ends when reimmersion occurs. To delay emergence for more than five days following immersion, Cypretta sp. may be using a form of diapause with no environmental cue for emergence, or there may be another dormancy process occurring. Further research is needed to determine the physiology of these response patterns, however, this was the only species studied here that appeared to show two different types of dormancy.

Bennelongia gwelupensis is another commonly occurring ostracod that uses desiccation-resistant eggs to survive drying. It was found mostly in the surface depression microrefuge but it did not hatch from dry sediment collected from these microrefuges. Eggs that may have been in this sediment either did not receive the correct hatching cue or delayed hatching for longer than the duration of the experiment. B. gwelupensis did show delayed hatching (> 30 d) from open water sediment (Chapter 5), but in that experiment it did not hatch from dried fringing vegetation samples (Fig. 7.3). The difference in habitat and the manipulated drying regime changed the hatching pattern of this species. In contrast, B. gwelupensis from fringing vegetation in Lake Joondalup South were observed hatching rapidly from eggs in both 5 day controls and false-start treatment samples with various lengths of dry period (Chapter 6). They also hatched in open water controls, but took longer to appear. Although sediment beneath fringing trees may be exposed to longer dry periods than open water sediment, effects of past hydroperiods on dormant eggs are only possible if individuals beneath fringing vegetation and open water are from separate populations that do not mix when wetlands are inundated. This seems unlikely, so B. gwelupensis eggs probably show flexible hatching responses to patterns of wetting and drying. Alternatively, given the high, but cryptic, species diversity of Bennelongia in Western Australia (Schon et al., 2015), we may have inadvertently collected different species of this genus in different wetlands, where different species show different responses to habitat and drying.

Collembolans are amphibious invertebrates and were abundant beneath fringing trees during dry periods. As collembolans are semi-aquatic detritivores, this is ideal
habitat, being high in organic matter, relatively humid and sporadically inundated (Gooderham & Tsyrlin, 2002). Collembola died during prolonged (> 5 d) inundation in the laboratory experiments probably because they could not escape from the microcosms. In wetlands, they probably advance across lake beds as water levels decline to feed on newly exposed detritus and then retreat upslope as wetlands refill. In some wetlands, Collembola were found only in the fringing vegetation samples and almost complete mortality was observed in response to drying treatments. Adult collembolans may be intolerant of desiccation, relying on their desiccation resistant eggs in dry open water areas (which I observed hatching from open water sediment in Chapter 5), but surviving dry periods in damp fringing tree sediment. Therefore, if adults are able to produce eggs before they are killed by desiccation, they may survive further climatic drying.

The cladoceran *Ilyocryptus spinifer* was only found in microrefuges in the reflooded phase because they emerged from ephippia following inundation (Kotov & Dumont, 2000). As the wetland dried, they formed ephippia, thereby avoiding the drying phase and the intense predation that can occur then (Boulton et al., 2014). Across all wetlands, *I. spinifer* showed delayed emergence of between ten and twenty days after immersion, but varied in habitat occupancy. They occurred in high abundance in fringing vegetation at Lake Joondalup west, in open water in Lake Joondalup south and in both habitats in Lake Booragoon and South Lake. After a false start event, *I. spinifer* showed delayed hatching of more than 15 days. Cladocerans emerge from ephippia in response to environmental cues (Gooderham & Tsyrlin, 2002), although the cue for this species is not known (Kotov & Dumont, 2000). Clearly, *I. spinifer* in SCP wetlands shows a delayed response to inundation (although it may actually be responding to another cue entirely) that avoids hatching in response to short false starts. This may be because females have to have reached at least their fourth instar to be able to form an ephippium, and formation requires a further two moults (Kotov & Dumont, 2000), meaning that false starts could cause widespread mortality of hatchlings. A delay of more than ten days following inundation also permits the microalgal food of this large (relative to other Cladocera) herbivore to grow in abundance so that when it emerges, food is readily available. However, I also observed ephippia present in sediments that did not emerge, that is, not all of the ephippia present in the sediment hatched in response to one inundation event. Ephippia are known to be long-lived and resistant to
poor environmental conditions (Mellors, 1975), and bet-hedging in the form of cohort-splitting is likely to be a common occurrence, making this species quite resistant to climate change and local extinction.

*C. novaezelandiae* is another commonly occurring ostracod with desiccation resistant eggs that always hatched immediately after inundation. Even when exposed to a false start treatment (Chapter 6) there was no delay in the hatching of *C. novaezelandiae* and individuals were killed by subsequent drying. *C. novaezelandiae* may rely on sheer numbers (of eggs stored in the sediment) to persist in temporary environments.

Life history flexibility is extremely important for surviving climate change. Species with narrow or no flexibility will be pushed beyond their tolerances leading to local extinction (Steffen *et al.*, 2009). Species with greater flexibility will be able to adapt to the new environmental conditions caused by climate change. Species that are able to cope with temporarily unsuitable conditions will be favoured, although in each habitat this may be a different species (Verberk *et al.*, 2008). Species with few life history options for desiccation resistance (e.g. isopods) or little flexibility may use refuges either microhabitat (e.g. fissures) or habitat to survive (Steffen *et al.*, 2009). But these refuges must be present in the wetland for them to be accessed by poorly-dispersing sensitive species. Loss of these refuges may thus result in the loss of the sensitive species from the ecosystem.

*Spatial scale, emergence after wetland drying and the effects of drying climate*

Invertebrate dynamics across the three spatial scales in response to wetland drying can affect each other and therefore it is important that we understand these dynamics for management of biodiversity at the landscape scale. At a landscape scale, climate change is increasing temperatures, reducing rainfall and changing rainfall patterns on the SCP (CSIRO, 2011). This changes factors such as the timing of first inundation and drying, length of hydroperiod, depth and extent of inundation (determining whether the fringing vegetation becomes inundated), rate of drying (determining whether invertebrates complete their life cycles) and the frequency and duration of false start events and subsequent drying. Stubbington and Datry (2013) found that moisture was the most important variable for aquatic invertebrate survival in sediments, and my results also show its importance, but very little is known about the
interaction of sediment moisture at very small scales with individual invertebrates. Further research at this fine scale is required to understand the total effects of moisture loss. In a drier climate, some wetlands will no longer be perennial, may dry more rapidly or fail to fill at all (e.g. Sim et al., 2013, Fig. 7.5 vi). Such changes to water regime may affect the microrefuge scale: if fissures do not stay inundated or moist, part of their value as refuges from drying will be lost (they may still be cooler through shading) and the invertebrates relying on them may become locally extinct (Fig. 7.5 i - iii). Importantly, these fissures remain during inundation (Fig. 7.6) (Chapter 4) and may last for many years through cycles of wetting and drying.
Figure 7.5. The effects of climate change on the aquatic environment, using the SCP as an example. In microhabitats, inundation levels may be much lower (i-iii): and wetlands may dry out quicker (i) resulting in just the fissures being inundated; in the dry period (ii) the water table drops below the fissures so that there are no damp sediment refuges in the wetland, and in the reflooded stage (iii) the wetland may not become as deep as it once did. At the wetland level (iv,v) (South Lake), in winter (iv) the wetland may fail to fill or water may not reach fringing trees, and in summer (v) changes in sediment properties may cause the loss of sediment microrefuges. In the landscape (vi) some wetlands may be no longer perennial (orange cross), dry very rapidly or fail to fill at all (red cross), or contain no sediment refuges (red circle).
All the wetlands studied here have some fringing vegetation that provided an alternative habitat for invertebrates. In winter, when wetland water levels are at their highest, the area beneath fringing trees becomes flooded, but it is the last area to become inundated and the first from which water recedes, so this area has a much shorter hydroperiod than does the open water (Fig. 7.5 iv-v, 7.7). Because fringing vegetation sediment has a much higher organic matter content and shading, temperatures are cooler there and drying occurs much more slowly, giving invertebrates time to prepare for desiccation. In contrast, the open water habitat is inundated for longer, but drying occurs rapidly and invertebrates are exposed to UV light and higher temperatures than invertebrates beneath the shady trees.

**Figure 7.6.** Underwater photo of a sediment fissure surrounded by Charophyte growth, after the wetland had refilled.
Figure 7.7. Changing inundation patterns in groundwater-fed temporary basin wetlands will change the duration of inundation in different habitat types and moisture levels in the sediment. (a) past inundation patterns: both habitats inundated in winter-spring and dry in summer-autumn, with some variation in extent among years. Sediment retains some moisture content; (b) present and future inundation patterns: both habitats have drier sediment in summer-autumn and in winter-spring, the variation in inundation extent among years means that fringing vegetation is partially inundated in some years and other years it is not inundated. Size of arrows indicates volume of groundwater and rainfall inputs.
At the wetland scale, fringing vegetation may act as a refuge for wetland invertebrates during dry periods that will become increasingly important with changed climate conditions. However, not all SCP wetlands have fringing *Melaleuca* trees, either because of vegetation clearing or because other tree species (e.g. *Eucalyptus rudis*, *Casuarina* spp.) are present instead. Further research on the effects of other tree species in Australia and elsewhere is needed to see whether they also create a drought refuge, although river research suggests that they will (e.g. Davies, 2010). Replanting fringing trees around wetlands, or facilitating their establishment downslope in basin wetlands experiencing lower water levels, could re-establish this refuge from drying and increasing temperatures.

The spread of some invasive plant species will be facilitated by the effects of climatic drying on wetland water regimes. Spread of *Typha* spp. in particular, is facilitated by periods of unusually low water levels in SCP wetlands (pers. obs.). It has to be sprayed with herbicide to prevent it forming a monoculture in Bibra Lake and by 2013 it had completely covered the bed of South Lake. The spread of exotic trees and invasive emergent macrophytes will alter sediment properties by out-competing native species, altering the cycling of carbon and nitrogen and increasing the amounts of organic material (in response to eutrophication) deposited onto wetland sediments to such high levels that sediment anoxia may occur (Anderson & Mitsch, 2006; Tuchman *et al.*, 2009; Angeloni *et al.*, 2013). This process may also remove microrefuges, leaving some invertebrate taxa (e.g. amphipods, isopods) with nowhere to shelter from drying and high temperatures. Introduced trees and macrophytes may create new refuges for aquatic invertebrates, and further research is required to investigate their effects on refuge availability and occupancy.

Changes at smaller scales that alter microrefuge availability or fringing vegetation, may result in losses at the landscape scale (Fig. 7.5 vi). Losses of natural refuges will increase the importance of perennial anthropogenic waterbodies (e.g. water retention sumps, farm dams) which may buffer the effects of climate change (Chester & Robson, 2013). Shorter hydroperiods and lower inundation levels will cause fringing vegetation to be inundated for shorter periods of time or potentially not at all in drier years (Fig. 7.7). This may affect the role of the fringing vegetation as a refuge, and the seed/egg bank may become less viable (Jenkins & Boulton, 2007). Fringing trees will slowly move inward towards the centre of the wetland via seedlings but this is a slow
process compared to the rate of declining water levels (Semenuik & Semenuik, 2012). This may be mitigated by tree planting between the natural fringing vegetation and the new maximum inundation level, which may eventually provide similar ecosystem benefits as the current fringing vegetation. It may be more difficult to restore sediment microrefuges once they are lost, increasing the importance of protecting those wetlands that still retain them, from threatening processes such as formation of a monoculture of invasive emergent macrophytes.

My research shows some of the mechanisms by which SCP wetland invertebrates are able to persist despite prolonged drying, explaining the widespread tolerance of drier water regimes that was observed by Sim et al., (2013) in their long-term SCP wetland dataset. For example, even where wetland water regimes are drier, if fringing vegetation sediment retains moisture, some invertebrate species can survive in the absence of surface water. These survival strategies may exist among SCP wetland invertebrates because the pre-existing mediterranean climate shows high inter-annual variability in many of these factors (Bonada et al., 2008). However, much remains to be discovered about long-term population persistence in these wetlands. Since they were first surveyed for macroinvertebrates in the 1980s, many wetlands have changed from perennial to seasonally-inundated (Fig. 7.7, Sim et al., 2013) and consequently, the frequency of occurrence of amphipods, isopods and decapod shrimp has declined (Chester et al., 2013). They are now absent from many formerly perennial wetlands (e.g. North Lake, Lake Booragoon) where previously they were abundant (Davis & Christidis, 1999) and this may be due to the loss of perennial water in wetlands where no cracks or fissures exist in dry sediment.

Changes in water regime as the climate dries mean that some wetlands in the landscape act as refuges because they are perennial (Fig. 7.5; 7.8, Chester et al., 2013; Choney et al., 2014). Good dispersers (e.g. adult Odonata, Diptera and Coleoptera) survive the harsh dry summer by emigrating to perennial waterbodies and moving back to temporary wetlands when the water returns (Boulton et al., 2014). Other temporary wetlands do not have the correct sediment properties (i.e. sediment with high coarse organic matter content which shrinks and cracks during drying, Fig. 7.5), so invertebrates which require high humidity (e.g. collembolans) may die quickly. However, these wetlands may dry out slowly enough for invertebrates with desiccation-resistant resting stages (eggs, ephippia, pupae) to reach their resting stages and survive.
Those wetlands with sediment properties that allow crack and fissure microhabitats to form during the drying process will sustain many different species through the dry period.

Figure 7.8. Example landscape dynamics of the study wetlands on the SCP. In winter all the wetlands are inundated (blue). In summer, they either dry out, some very rapidly (red cross), and may contain microrefuges (blue circle), or may not contain microrefuges (red circle), some of the perennial wetlands provide refuges (blue cross).

Stream research has repeatedly concluded that perennial streams amongst a network of intermittent streams form important refuges against drying (Chester & Robson, 2011, Sheldon et al., 2010, Robson et al., 2013). It seems likely that perennial wetlands within a mosaic of temporary wetlands will perform a similar function. As in streams, it appears that the presence of particular habitats or microhabitats within wetlands will play an important role in the quality of individual wetlands as refuges. Studies such as these have concluded that resilience traits are more important for the survival of stream invertebrates than resistance traits. The opposite may be true in wetlands and my research shows that even invertebrates with no desiccation-resistant life stage may be able to resist drying by surviving within sediment microrefuges. The
presence of these types of refuges may potentially be more common than in streams, although debate remains about the relative importance of sediments and the eggbank compared to perennial pools/reaches in rivers and streams (see Stubbington, 2012; Stubbington & Datry, 2013).

**Management implications**

Unlike stream reaches connected by flowing water, wetlands are commonly viewed as individual units. Individual basin wetlands can be very different to others nearby, differing in hydroperiod, water regime, submerged, emergent and fringing vegetation types and in substratum type. However, wetlands may be connected though groundwater and by the immigration/emigration of aquatic fauna. It is becoming increasingly clear that wetland invertebrates can and do disperse within wetland mosaics and sometimes over surprisingly long distances (Green & Figuerola, 2005; Van Leeuwin et al., 2013; Schon et al., 2015). This means that wetlands need to be managed across multiple scales. At the landscape scale, a mosaic of wetlands with different hydroperiod and sediment types will support a wider diversity of invertebrates than single wetlands, or groups of similar wetlands. Mosaics also provide refuges and recolonization sources for areas where disturbance causes local extinction (at the wetland scale). Other studies have suggested that perennial wetlands act as an important refuge in mosaics of mainly temporary wetlands (Chester & Robson, 2013). The present study shows that temporary wetlands with sediment microrefuges and bands of native fringing trees may also act as important refuges at the wetland and landscape scales.

My thesis shows that we cannot assume that egg banks will survive the wide range of environmental changes that are occurring through climate change, because species survival will also be determined by differences in habitat and microhabitat (within and between wetlands), sediment type and biotic processes as well as water regime. The survival and persistence of aquatic invertebrate species may be enhanced by protecting and/or restoring fringing trees around wetlands, as well as assisting vegetation patches to grow downslope, following retreating waterlines as the area covered by surface water shrinks. Identifying and protecting temporary wetlands that contain sediment microrefuges such as crevices and fissures could be a means of allowing species with no desiccation tolerant life stage to survive wetland drying. As with streams, perennial wetlands in good condition could be particularly valuable refuges during supraseasonal droughts. Protecting those wetlands from degradation and
restoring them may have value wider than simply sustaining biodiversity within that single wetland. Future studies of a wider variety of habitats and microhabitats in various wetland types should provide much valuable information on any potential role that they might play during disturbances, including dry periods. Importantly, understanding the function of these habitats for invertebrate survival should provide insights into how to manage temporary wetlands and their fauna to sustain biodiversity. In the southwest Western Australian biodiversity hotpot, flora and fauna are trapped by climate change because they are surrounded by ocean and desert, and there are no mountains to provide cooler refuges (Davies, 2010; Stewart et al., 2013). The inability of species to move their geographic range polewards or to higher altitude forces them to rely on refuges within the landscape to survive drying and higher temperatures (Steffen et al., 2009). Therefore, it is important to discover new refuges within wetlands, such as habitats and microhabitats that may provide hitherto unknown options for species survival.

References


Chapter 8. Appendices

Chapter 5. Microrefuges from drying for invertebrates in a seasonal wetland.

Table 8.1. Species list of invertebrates found in this study (adult (A), juvenile (J), larvae (L)).

<table>
<thead>
<tr>
<th>Cnidaria</th>
<th>Berosus sp. (A), Berosus sp. (L), Noteridae sp. (A)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hydra</td>
<td>Hydrophilidae sp. (L)</td>
</tr>
<tr>
<td>Oligochaeta</td>
<td>Limnichidae (A)</td>
</tr>
<tr>
<td>Mollusca, Haïta acuta</td>
<td>Haliplidae sp. (L)</td>
</tr>
<tr>
<td>Ferrissia sp.</td>
<td>Unknown Beetle (A)</td>
</tr>
<tr>
<td>Arthropoda, Arachnida</td>
<td>Arthropoda, Insecta, Diptera</td>
</tr>
<tr>
<td>Pionidae sp., Piona cumberlandensis</td>
<td>Chironomidae</td>
</tr>
<tr>
<td>Oribatida sp. 1 (A, J), Unknown mite, Arthropoda, Crustacea, Copepoda</td>
<td>Orthocladiinae (L)</td>
</tr>
<tr>
<td>Calanoida</td>
<td>Chironominae (L)</td>
</tr>
<tr>
<td>Cyclopoida</td>
<td>Culicidae</td>
</tr>
<tr>
<td>Harpacticoida</td>
<td>Culex (L)</td>
</tr>
<tr>
<td>Arthropoda, Crustacea, Cladocera</td>
<td>Ceratopogonidae sp. 1 (L)</td>
</tr>
<tr>
<td>Chydoridae, Ilyocryptus spinifer</td>
<td>Ceratopogonidae sp. 2 (L)</td>
</tr>
<tr>
<td>Arthropoda, Crustacea, Ostracoda</td>
<td>Forcipomyiinae sp. (L)</td>
</tr>
<tr>
<td>Bennelongia gwelupensis (formerly australis)</td>
<td>Dolichopodidae sp. (L)</td>
</tr>
<tr>
<td>Candonocypris novaezelandiae</td>
<td>Stratimyidae sp. (L)</td>
</tr>
<tr>
<td>Cypridopsis funebris, Cypretta sp.</td>
<td>Syrphidae sp. (L)</td>
</tr>
<tr>
<td>Diacypris spinosa</td>
<td>Unidentified Dipteran (L)</td>
</tr>
<tr>
<td>Mytilocypris ambigua</td>
<td>Arthropoda, Insecta, Hemiptera</td>
</tr>
<tr>
<td>Ilyodromus sp.</td>
<td>Candonocypris novaezelandiae</td>
</tr>
<tr>
<td>Arthropoda, Crustacea, Amphipoda</td>
<td>Corixidae sp. 1 (J)</td>
</tr>
<tr>
<td>Austrochiltonia subtenuis</td>
<td>Micronecta robusta (A, J)</td>
</tr>
<tr>
<td>Arthropoda, Crustacea, Isopoda</td>
<td>Sigara sp. (A)</td>
</tr>
<tr>
<td>Paramphipus palustris</td>
<td>Notonectidae sp. 1 (J)</td>
</tr>
<tr>
<td>Arthropoda, Collembola</td>
<td>Paronisops sp. (A)</td>
</tr>
<tr>
<td>Arthropoda, Insecta, Coleoptera</td>
<td>Gerridae sp. (A)</td>
</tr>
<tr>
<td>Dytiscidae sp. (A)</td>
<td>Nepidae sp. (A)</td>
</tr>
<tr>
<td>Dytiscidae sp. (L),</td>
<td>Arthropoda, Insecta, Odonata</td>
</tr>
<tr>
<td></td>
<td>Anisoptera (L)</td>
</tr>
<tr>
<td></td>
<td>Zygoptera (L)</td>
</tr>
<tr>
<td></td>
<td>Arthropoda, Insecta, Trichoptera</td>
</tr>
<tr>
<td></td>
<td>Leptoceridae</td>
</tr>
<tr>
<td></td>
<td>Notalina sp. (L)</td>
</tr>
<tr>
<td></td>
<td>Triplectides australis (L)</td>
</tr>
</tbody>
</table>
Chapter 5. Fringing trees may provide a refuge from prolonged drying for urban wetland invertebrates

Table 8.2. SPSS ANOVA table restricted version, damp species richness

<table>
<thead>
<tr>
<th>Source</th>
<th>Sum of Squares</th>
<th>df</th>
<th>Mean Square</th>
<th>F</th>
<th>Sig.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat</td>
<td>0.171</td>
<td>1</td>
<td>0.171</td>
<td>0.032</td>
<td>0.865</td>
</tr>
<tr>
<td>Error</td>
<td>26.794</td>
<td>5.021</td>
<td>5.325</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wetland</td>
<td>39.440</td>
<td>1</td>
<td>7.888</td>
<td>1.470</td>
<td>0.341</td>
</tr>
<tr>
<td>Error</td>
<td>26.822</td>
<td>5.021</td>
<td>5.364</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Habitat * Wetland</td>
<td>39.440</td>
<td>5</td>
<td>7.888</td>
<td>4.9</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Error</td>
<td>81.833</td>
<td>51</td>
<td>1.605</td>
<td></td>
<td></td>
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</tbody>
</table>

Table 8.3. SPSS ANOVA table restricted version, damp species abundance

<table>
<thead>
<tr>
<th>Source</th>
<th>Sum of Squares</th>
<th>df</th>
<th>Mean Square</th>
<th>F</th>
<th>Sig.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat</td>
<td>0.411</td>
<td>1</td>
<td>0.411</td>
<td>1.188</td>
<td>0.325</td>
</tr>
<tr>
<td>Error</td>
<td>1.751</td>
<td>5.064</td>
<td>0.346</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wetland</td>
<td>3.844</td>
<td>5</td>
<td>0.769</td>
<td>2.215</td>
<td>0.202</td>
</tr>
<tr>
<td>Error</td>
<td>1.736</td>
<td>5</td>
<td>0.347</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Habitat * Wetland</td>
<td>3.844</td>
<td>5</td>
<td>0.769</td>
<td>3.63</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Error</td>
<td>10.803</td>
<td>51</td>
<td>0.212</td>
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<td></td>
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</tbody>
</table>

Table 8.4. SPSS ANOVA table restricted version, dry species richness

<table>
<thead>
<tr>
<th>Source</th>
<th>Sum of Squares</th>
<th>df</th>
<th>Mean Square</th>
<th>F</th>
<th>Sig.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat</td>
<td>1.658</td>
<td>1</td>
<td>1.658</td>
<td>1.003</td>
<td>0.359</td>
</tr>
<tr>
<td>Error</td>
<td>9.066</td>
<td>5.480</td>
<td>1.654</td>
<td></td>
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</tr>
<tr>
<td>Wetland</td>
<td>6.312</td>
<td>5</td>
<td>1.262</td>
<td>0.652</td>
<td>0.675</td>
</tr>
<tr>
<td>Error</td>
<td>9.680</td>
<td>5</td>
<td>1.936</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Habitat * Wetland</td>
<td>6.312</td>
<td>5</td>
<td>1.262</td>
<td>3.12</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>Error</td>
<td>12.950</td>
<td>32</td>
<td>0.405</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 8.5. SPSS ANOVA table restricted version, dry species abundance

<table>
<thead>
<tr>
<th>Source</th>
<th>Sum of Squares</th>
<th>df</th>
<th>Mean Square</th>
<th>F</th>
<th>Sig.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat</td>
<td>0.425</td>
<td>1</td>
<td>0.425</td>
<td>3.530</td>
<td>0.099</td>
</tr>
<tr>
<td>Error</td>
<td>0.922</td>
<td>7.661</td>
<td>0.120</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wetland</td>
<td>2.831</td>
<td>5</td>
<td>0.566</td>
<td>4.777</td>
<td>0.056</td>
</tr>
<tr>
<td>Error</td>
<td>0.593</td>
<td>5</td>
<td>0.119</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Habitat * Wetland</td>
<td>2.831</td>
<td>5</td>
<td>0.566</td>
<td>4.42</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Error</td>
<td>4.099</td>
<td>32</td>
<td>0.128</td>
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</tr>
</tbody>
</table>