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

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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 d 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.

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 a 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 raphiophylla*, 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 d representing the false start, followed by a dry period of 10, 20 or 30 d representing a range of dry periods at the end of a false start to winter inundation, followed by another inundation period of 5 d representing the start of the ‘true’ winter inundation period (Table 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 1). An additional control of 15 days continuous inundation was added to observe change in assemblage development between 10 and 20 days (Table 1).

Day length increased over the 40 d 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 d inundation: one control (O/FPC5) represented inundation at the start of the experiment and the other (O/FPCE5) represented inundation 40 d later (Table 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 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 d inundation. Treatment jars were placed under lights to dry out by evaporation (surface water disappeared in \approx 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 d. 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 ($t_7 = -4.81$, $P = 0.001$, mean 19.5 °C, Fig. 1a) and mean daily maximum sediment-surface temperature was substantially higher ($t_8 = -3.60$, $P = 0.007$, 25.2 °C, Fig. 1b) in treatments than controls (mean 17.6 °C, mean daily maximum 16.7 °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 1a, b).

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 d 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 (H_1)

Emerging invertebrate assemblages were dominated by crustaceans, but included insects and oligochaete worms (Fig. 2). One cladoceran species, *Ilyocryptus spinifer*, was found and five species of ostracod: *Candonocypris novaezelandiae*, *Bennelongia gwelupensis* (previously *Bennelongia australis*), *Mytilocypris ambigua*, *Diacypris spinosa* and *Cypretta* sp. Insects included two species of Psychodidae larvae (Diptera), adult beetles (identified to Order) and amphibious collembolans. The species present in both habitat types show a range of survival strategies in response to desiccation, including desiccation-resistant eggs and dormancy (Table 2).

Invertebrate assemblages emerging from OW and FT sediment differed markedly (Global $R = 0.595$, $P = 0.001$, Fig. 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. 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. 2). The ostracod *Mytilocypris ambiguosa* and Psychodidae larvae were more abundant in OW.

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. 4a), but in FT, differences were smaller (Global $R = 0.167$, $P = 0.001$) (Fig. 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. 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. 4b). False starts therefore affected the invertebrate assemblages differently in the two habitats.

Pre-planned comparisons – Open water habitat

The composition of emerging invertebrate assemblages differed significantly among OW controls inundated for different periods (Fig. 5a). At 5 d 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 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, $P > 0.127$).

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 2).

Ilyocryptus spinifer and the ostracods *M. ambiguosa*, *B. gwelupensis* and *D. spinosa* emerged in high abundances in controls (Fig. 5a), whereas *C. novaezelandiae* dominated treatment samples, as it did OC5. Also, *I. spinifer* did not emerge from treatments (Table 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 2).

Pre-planned comparisons – Fringing vegetation habitat

Invertebrate composition changed little over time in the controls (Fig. 5b). At 5 days inundation *C. novaezelandiae* and *B. gwelupensis* were the only emerging species, but by 15 days inundation, *I. spinifer* and *Cyprretta* 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. 5b). Most species in this habitat emerged rapidly (in the first 15 days, Fig. 5b) and Collembola did not survive beyond the first 5 days, whereas in OW some species delayed hatching (e.g. *Cyprretta* sp., Table 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 2). *I. spinifer* and *Cyprretta* 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 *Cyprretta* 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 *Cyprretta* 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 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 ($\approx 20\text{ }^{\circ}\text{C}$), so the evaporative drying method effectively dried the sediment but also kept conditions comparable to field conditions. Furthermore, mean maximum temperatures of around $20\text{ }^{\circ}\text{C}$ 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 $35.9\text{ }^{\circ}\text{C}$), and these temperatures were similar to, although slightly cooler than, temperatures measured during wetland drying in South Lake ($37 - 42\text{ }^{\circ}\text{C}$; 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 (H_1) 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. ambigua*, *D. spinosa* and *Cyprretta* sp. survive desiccation through adult dormancy (Strachan *et al.*, 2014). *M. ambigua* and *Cyprretta* sp. showed delayed emergence in OW, and *Cyprretta* sp. also showed delayed emergence from FT sediment. *Diacypriis 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. ambigua*) or the following dry period (e.g. *M. ambigua*, *Cyprretta* 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 zoochorous 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 d 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 raphiophylla*) 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:

- Anderson M.J., Ellingsen A.E. & B.H. McArdle (2006) Multivariate dispersion as a measure of beta diversity. *Ecology Letters*, 9, 683-693.
- Bishop J.A. (1967) Some adaptations of *Limnadia stanleyana* King (Crustacea: Branchiopoda: Conchostraca) to a temporary freshwater environment. *Journal of Animal Ecology*, 36, 599-609.
- Bonada N., Doledec S. & Statzner B. (2007) Taxonomic and biological trait differences of stream macroinvertebrate communities between mediterranean and temperate regions: implications for future climatic scenarios. *Global Change Biology*, 13, 1658-1671.
- Boulton A.J., Brock M., Robson B.J., Ryder D.S., Chambers J.M. & Davis J.A. (2014) *Australian Freshwater Ecology: Processes and Management*. 2nd Edition. Wiley Blackwell, Chichester.

- Brendonck L. (1996) Diapause, quiescence, hatching requirements: what we can learn from large freshwater branchiopods (Crustacea: Branchiopoda: Anostraca, Notostraca, Conchostraca). *Hydrobiologia*, **320**, 85-97.
- Brendonck L. & De Meester L. (2003) Egg banks in freshwater zooplankton: evolutionary and ecological archives in the sediment. *Hydrobiologia*, **491**, 63-54.
- Brock M.A., Nielsen D.L., Shiel R.J., Green J.D. & Langley J.D. (2003) Drought and aquatic community resilience: the role of eggs and seeds in sediments of temporary wetlands. *Freshwater Biology*, **48**, 1207-1218.
- Bunn S.E. (1988) Life histories of some benthic invertebrates from streams of the northern jarrah forest, Western Australia. *Australian Journal of Marine & Freshwater Research*, **39**, 785-804.
- Chaplin J.A. (1991) The effects of reproduction and dispersal on the population structure of a freshwater ostracod. PhD Thesis, University of Wollongong.
- Chessman B.C., Trayler K.M. & Davis J.A. (2002) Family and species-level biotic indices for macroinvertebrates of wetlands on the Swan Coastal Plain, Western Australia. *Marine and Freshwater Research*, **53**, 919-930.
- Chester E.T., Miller A.D., Valenzuela I., S.J. Wickson, & B.J. Robson. (2015) Drought survival strategies, dispersal potential and persistence of invertebrate species in an intermittent stream landscape. *Freshwater Biology*, **60**, 2066-2083.
- Clarke K.R. & Warwick R.M. (2001) *Change in Marine Communities: an Approach to Statistical Analysis and Interpretation*. 2nd editions. PRIMER-E, Plymouth.
- CSIRO (2011) *Climate Change: Science and Solutions for Australia*. CSIRO, Collingwood.
- Davis J. & Christidis F. (1999) *A Guide to Wetland Invertebrates of Southwestern Australia*. Western Australian Museum, Perth.
- De Deckker P. (1983) Notes on the ecology and distribution of non-marine ostracods in Australia. *Hydrobiologia*, **106**, 223-234.
- El Bardicy S., Tadros M., Yousif F. & Hafez S. (2009) Predatory activity of *Psychoda alternata* Say (Diptera: Psychodidae) larvae on *Biomphalaria glabrata* and *Lymnaea*

- natalensis* snails and the free- living larval stages of *Schistosoma mansoni*. *Australian Journal of Basic and Applied Sciences*, **3**, 4503-4509.
- Gooderham J. & Tsyrlin E. (2002) *The Waterbug Book: a Guide to the Freshwater Macroinvertebrates of Temperate Australia*. CSIRO Publishing, Collingwood.
- Hildrew A.G. (1985) A quantitative study of the life history of a fairy shrimp (Branchiopoda: Anostraca) in relation to the temporary nature of its habitat, a Kenyan rainpool. *Journal of Animal Ecology*, **54**, 99-110.
- Hope P.K., Drosowsky W. & Nicholls N. (2006) Shifts in the synoptic systems influencing south-west Western Australia. *Climate Dynamics*, **26**, 751-764.
- Horwitz P., Rogan R., Halse S.A., Davis J.A. & Sommer B. (2009) Wetland invertebrate richness and endemism on the Swan Coastal Plain, Western Australia. *Marine and Freshwater Research*, **60**, 1006-1020.
- Jenkins K.M. & Boulton A.J. (2007) Detecting impacts and setting restoration targets in arid-zone rivers: aquatic micro-invertebrate responses to reduced floodplain inundation. *Journal of Applied Ecology*, **44**, 823-832.
- Johansson F. & Suhling F. (2004) Behaviour and growth of dragonfly larvae along a permanent to temporary water habitat gradient. *Ecological Entomology*, **29**, 196-202.
- Lake P.S. (2011) *Drought and Aquatic Ecosystems: Effects and Responses*. Wiley Blackwell, Chichester.
- Robson B.J., Chester E.T. & Austin C.M. (2011) Why life history information matters: drought refuges and macroinvertebrate persistence in non-perennial streams subject to a drier climate. *Marine and Freshwater Research*, **62**, 801-810.
- Semenuik C.A. & Semenuik V. (2012) The response of basin wetlands to climate changes: a review of case studies from the Swan Coastal Plain, south-western Australia. *Hydrobiologia*, **708**, 47-67
- Sim L.L., Davis J.A. & Chambers J.M. (2009) Development of conceptual models for ecological regime change in temporary Australian wetlands. In: *New Models for Ecosystem Dynamics and Restoration* (eds Hobbs RJ, Suding KN), pp. 259-279, Island Press, Washington DC, USA.

- Sim L.L., Davis J.A., Strehlow K., Mcguire M., Trayler K.M., Wild S., *et al.* (2013) The influence of changing hydroregime on the invertebrate communities of temporary seasonal wetlands. *Freshwater Science*, **32**, 327-342.
- Stanley E.H. & Bushman D.L., Boulton A.J., Grimm N.B. & Fisher S.G. (1994) Invertebrate resistance and resilience to intermittency in a desert stream. *American Midland Naturalist*, **131**, 288-300.
- Strachan S.R. (2016) Invertebrate resistance to wetland drying. PhD Thesis, Murdoch University.
- Strachan S.R., Chester E.T. & Robson B.J. (2014) Microrefuges from drying for invertebrates in a seasonal wetland. *Freshwater Biology*, **59**, 2528-2538.
- Strachan S.R., Chester E.T. & Robson B.J. (2015) Freshwater invertebrate life history strategies for surviving desiccation. *Springer Science Reviews*, **3**, 57-75.
- Stoks R., Geerts A.N. & De Meester L. (2014) Evolutionary and plastic responses of freshwater invertebrates to climate change: realized patterns and future potential. *Evolutionary Applications*, **7**: 42-55.
- Stubbington R. & Datry T. (2013) The macroinvertebrate seedbank promotes community persistence in temporary rivers across climate zones. *Freshwater Biology*, **58**, 1202-1220.
- Tronstad L.M., Tronstad B.P. & Benke A.C. (2005a) Invertebrate seedbanks: rehydration of soil from an unregulated river floodplain in the south-eastern U.S. *Freshwater Biology*, **50**, 646-655.
- Tronstad L.M., Tronstad B.P. & Benke A.C. (2005b) Invertebrate responses to decreasing water levels in a subtropical river floodplain wetland. *Wetlands*, **25**, 583-593.
- Tuytens K., Vanschoenwinkel B., Waterkeyn A. & Brendonck L. (2014) Predictions of climate change infer increased environmental harshness and altered connectivity in a cluster of temporary pools. *Freshwater Biology*, **59**, 995-968.
- Van Leeuwen C.H.A., Huig N., Van der Velde G. *et al.* (2013) How did this snail get here? Several dispersal vectors inferred for an aquatic invasive species. *Freshwater Biology*, **58**, 88-99.

- Vanschoenwinkel B., Gielen S., Seaman M. & Brendonck L. (2008) Any way the wind blows – frequent wind dispersal drives species sorting in ephemeral aquatic communities. *Oikos*, **117**, 125-134.
- Waterkeyn A., Grillas P., Vanschoenwinkel B. & Brendonck L. (2008) Invertebrate community patterns in Mediterranean temporary wetlands along hydroperiod and salinity gradients. *Freshwater Biology*, **53**, 1808-1822.
- Wickson S., Chester E.T. & Robson B.J. (2012) Aestivation provides flexible mechanisms for survival of stream drying in a larval trichopteran (Leptoceridae). *Marine & Freshwater Research*, **63**, 821-826.
- Yousif F., Hafez S., El Bardicy S., Tandros M. & Taleb H.A. (2013) Experimental evaluation of *Candonocypris novaezelandiae* (Crustacea: Ostracoda) in the biocontrol of *Schistosmiasis mansoni* transmission. *Asian Pacific Journal of Tropical Biomedicine*, **3**, 267-272.

Figure Captions:

Figure 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.).

Figure 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).

Figure 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.

Figure 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).

Figure 5. Invertebrate assemblage composition (mean abundance per sample) in controls: (a) open water habitat, (b) fringing vegetation habitat with results from pairwise comparisons. NSD = no significant difference, * $P < 0.05$.

Table 1. Controls and treatments used in the experiment: (O- open water habitat, F- fringing vegetation habitat, C- control, PC – procedural control, T- treatment, PCE – procedural control end of experiment).

Treatment/control name	Initial wet phase	Dry Phase	Second wet phase	Explanation
O/FPC5	5 days	Nil	Nil	Procedural control 5 d inundation
O/FC15	15 days	Nil	Nil	Emergence after 15 d inundation
O/FC20	20 days	Nil	Nil	Emergence after 20 d inundation, control for O/FT20
O/FC30	30 days	Nil	Nil	Emergence after 30 d inundation, control for O/FT30
O/FC40	40 days	Nil	Nil	Emergence after 40 d inundation, control for O/FT40
O/FT20	5 days	10 days	5 days	Effect of a 10 d dry period interrupting inundation. Total duration 20 d
O/FT30	5 days	20 days	5 days	Effect of a 20 d dry period interrupting inundation. Total duration 30 d
O/FT40	5 days	30 days	5 days	Effect of 30 d dry period interrupting inundation. Total duration 40 d
O/FPCE5	Nil	35 days	5 days	Procedural control. 5 d inundation at the end of the 40 d experiment.

Table 2. Desiccation survival strategies used by invertebrate taxa during the experiment and their response to false start treatments in the two habitats.

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

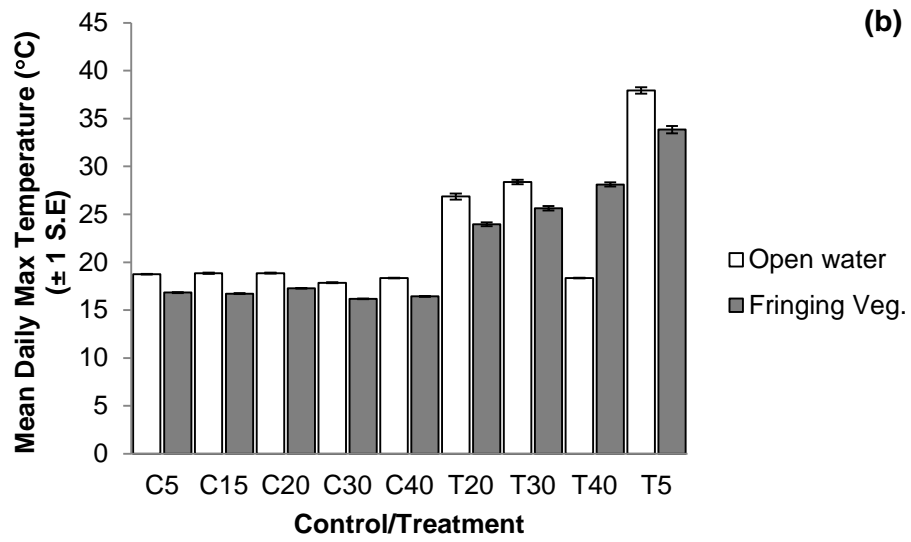
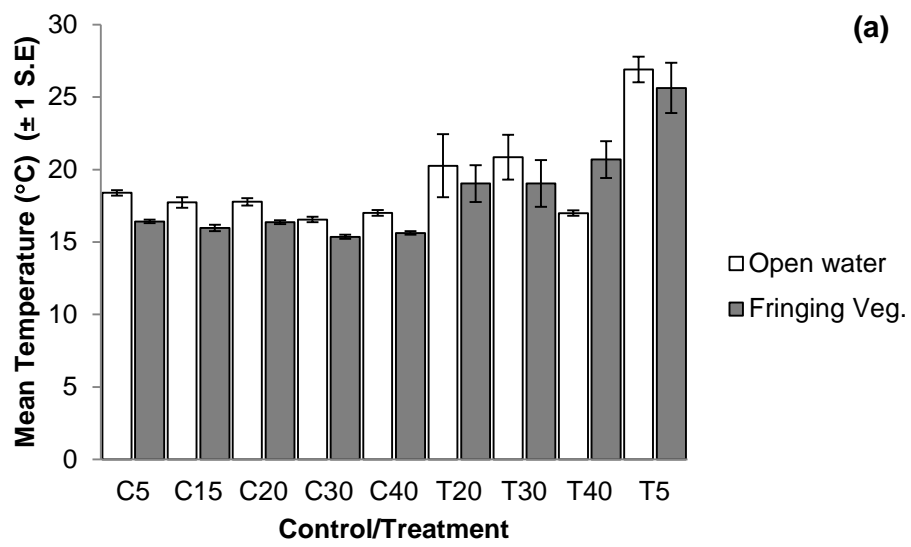


Figure 1

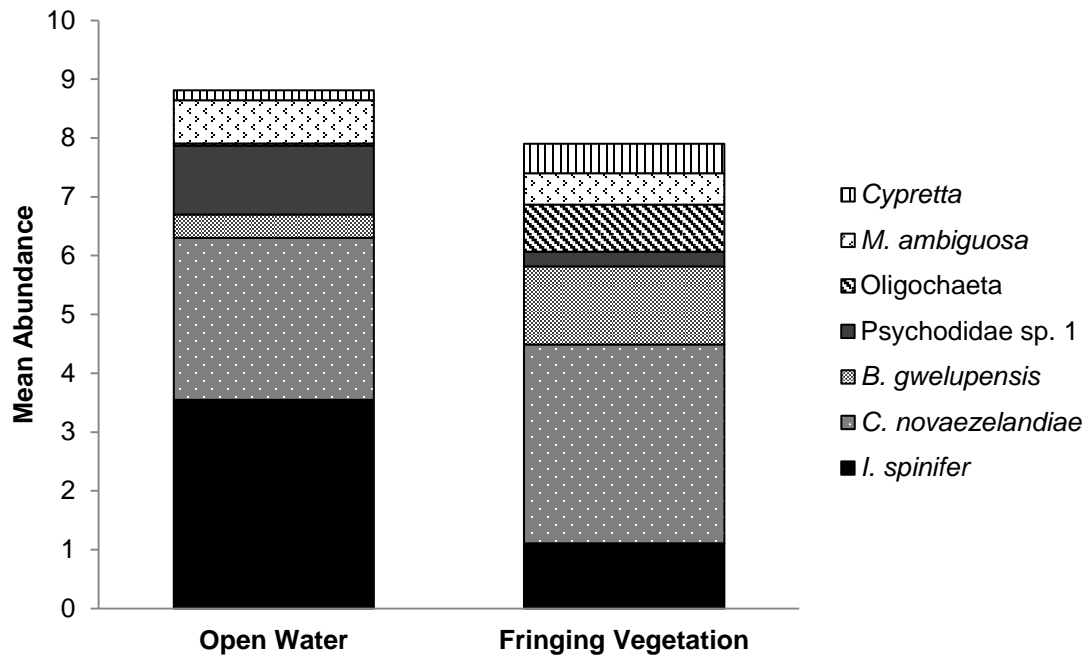


Figure 2

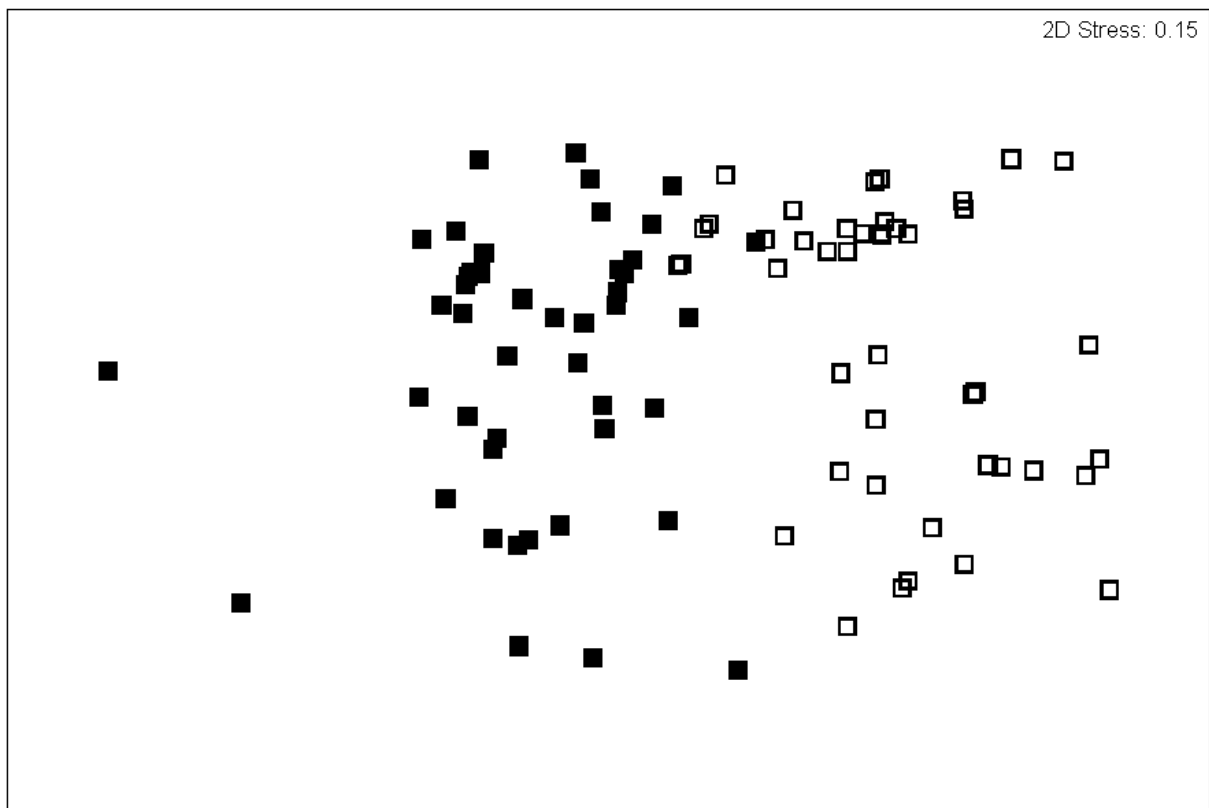


Figure 3

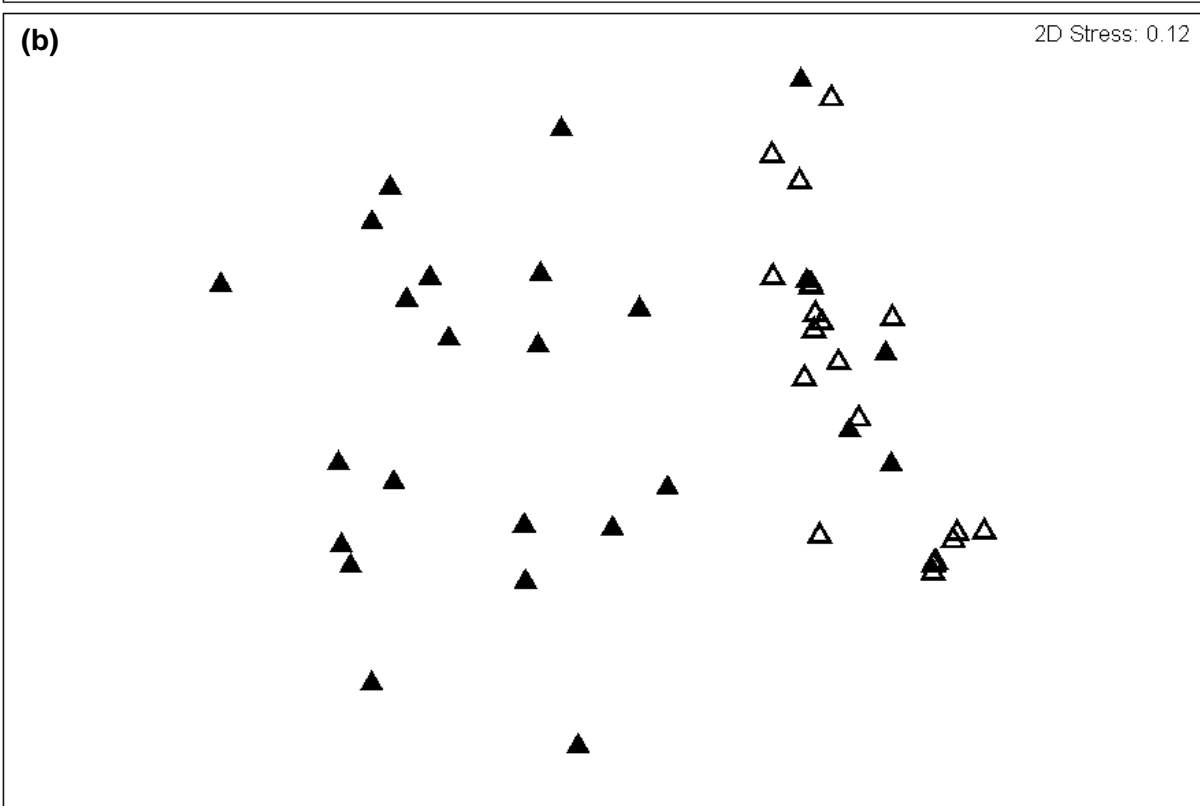
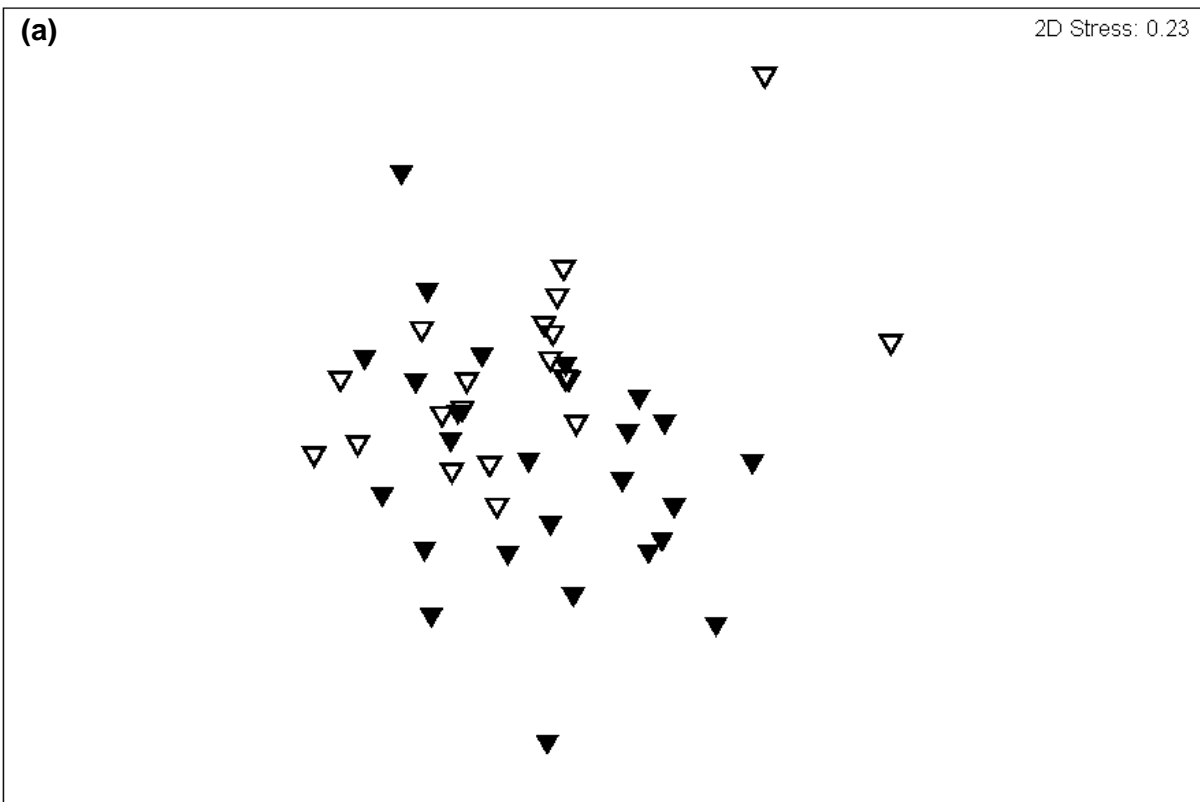


Figure 4

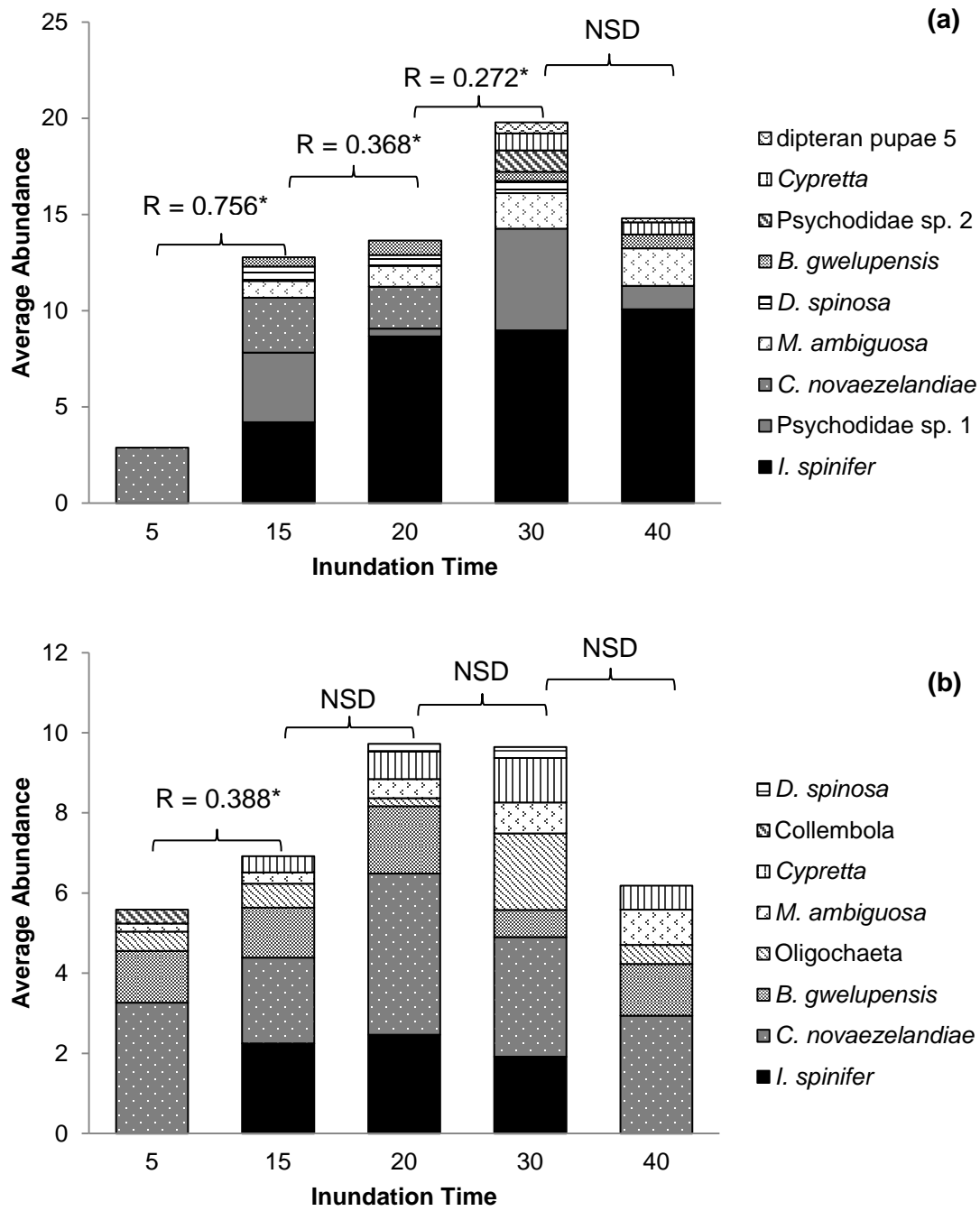


Figure 5