The impacts of an invasive herbivore (*Camelus dromedaries*) on arid zone freshwater pools: An experimental investigation of the effects of dung on macroinvertebrate colonisation

Glenis McBurnie [a, b, *], Jenny Davis [c], Ross M. Thompson [c], Catherine Nano [a], Jayne Brim-Box [a]

[a] Northern Territory Department of Land Resource Management, P.O. Box 1120, Alice Springs NT 0870, Australia
[b] School of Biological Sciences, Monash University, Clayton, VIC, Australia
[c] Institute for Applied Ecology, University of Canberra, Bruce, ACT, Australia

ARTICLE INFO

ABSTRACT

Aquatic ecosystems in arid environments provide important refugia and 'stepping-stones' of connectivity for aquatic fauna. Aquatic ecosystems in central Australia are vulnerable to degradation due to the impacts of invasive herbivores such as camels, which degrade small desert waterbodies through drinking, trampling, and fouling with dung. In this study we assessed the impacts of camel dung on the water quality and macroinvertebrate colonization and community composition of small arid zone freshwater pools using experimental mesocosms.

Camel dung (2 kg) was added to half the mesocosms (the treatment), the remaining mesocosms (without camel dung) acted as the controls. All mesocosms were sampled weekly for water quality, nutrients, chlorophyll *a* and macroinvertebrate richness and abundance, over an eight week period during summer.

Macroinvertebrate abundance was higher in the control mesocosms in comparison to the treatment mesocosms. Pollution tolerant taxa such as mosquito larvae were common in treatment mesocosms, while sensitive fauna, such as larval mayflies and dragonflies were more common in the controls. The latter are predators and appeared to have a major influence on community composition.

Our results reinforce the need for active management of invasive herbivores to protect aquatic biodiversity and to manage potential disease-vector species in central Australia waterbodies.

© 2014 Published by Elsevier Ltd.

1. Introduction

Arid environments cover 47% of the earth (Kingsford and Thompson, 2006) and include a number of threatened ecosystems and associated flora and fauna (Byrne et al., 2008; Murphy et al., 2009; Anthelme et al., 2011). Arid waterbodies are considered "islands of water in a sea of dry land" (Faulks et al., 2010) but have been the focus of relatively few ecological studies (Sada et al., 2005; De Los Rios et al., 2010; Kirkman et al., 2012). Given their isolation within an inhospitable arid landscape, waterbodies are analogous to islands (Ward and Blaustein, 1994; March and Bass, 1995; Angeler and Alverez-Cobales, 2005; Murphy et al., 2009) and in this sense are instructive for studying fundamental ecological processes such as assembly dynamics and the role of refugia (Davis et al., 2013). Waterbodies are particularly useful in assessing the interplay between local conditions, dispersal and colonisation (Jenkins and Buikema, 1998; Thompson and Townsend, 2006; Zickovich and Bohonak, 2007; Jeffries, 2011) and various aspects of Island Biogeography Theory (Ward and Blaustein, 1994; Bohonak and Jenkins, 2003). Invertebrate colonisation of waterbodies has been the focus of many studies because the site scale is relatively discrete, small and easy to comprehend, and the turnover rate of colonists is rapid enough to provide a feasible timeframe for research (Layton and Voshell, 1991; Clifford et al., 1992; Bohonak and Jenkins, 2003; Williams et al., 2008).

Degradation of aquatic ecosystems in arid regions is a major issue because of their biological, social and economic importance (Williams, 2000; Box et al., 2008; Kirkman et al., 2012). For example, springs in arid areas may provide the only reliable source of water (Sada et al., 2005), are geographically isolated (Box et al., 2008) and in

---

many cases support an endemic aquatic fauna (Wilmer and Wilcox, 2007; Murphy et al., 2009). Many aquatic ecosystems in arid Australia are culturally significant to Aboriginal people, who have relied on permanent and temporary water to survive for thousands of years (Bayly, 1999). In central Australia, aquatic habitats provide a scarce and critical resource for flora and fauna (Davis et al., 1993; Box et al., 2008) and like other areas of the world are regarded as "precious jewels of the desert", a status that reflects their importance to both aquatic and terrestrial biodiversity (Box et al., 2008). It is evident that the conservation of arid zone aquatic ecosystems is critical, particularly in the face of globally developing threats to water resources in arid regions (Vorosmarty et al., 2010).

Water resources in arid regions are under pressure from increasing human populations and the associated requirements of major industries such as mining and agriculture (Murphy et al., 2009). These factors in turn influence multiple and interacting stressors that include salinisation, weed invasion, pollution, aquifer drawdown and unmanaged feral herbivores (Sada et al., 2005; Box et al., 2008; Lindenmayer et al., 2010).

Australia has the largest feral population of dromedary camels (Camelus dromidarius) in the world. Their numbers increased since first being imported from their regions of origin (Afghanistan, Pakistan and northern India) between 1840 and 1907, with numbers reaching an estimated peak population of 1 million in 2008 (Dorges and Heucke, 1996; Edwards et al., 2010; Saalfeld and Edwards, 2010). Invasive herbivores such as the camel are a major problem in central Australia (Edwards et al., 2010). At high densities they have a large negative impact on environmental, cultural and economic resources by damaging infrastructure, vegetation and aquatic habitats (Edwards et al., 2010; Saalfeld and Edwards, 2010). While it is well established that various invasive herbivores pose a threat to aquatic ecosystems, there is a need to focus specifically on the impacts of camels due to their wide distribution and commonly unrestricted access to waterbodies throughout arid Australia. Camels can cause significant damage to waterbodies by trampling vegetation and eroding banks, by depletion of permanent springs, and by fouling through defecation (Brim-Box et al., 2010; Edwards et al., 2010), which can lead to eutrophication, and serious consequences for aquatic fauna (Smith et al., 1999).

Eutrophication, the excessive input of nitrogen and phosphorus into aquatic ecosystems, is one of the major threats to freshwater ecosystems globally (Smith and Schindler, 2009; Kneitel and Lessin, 2010; Teissier et al., 2012). The negative effects of eutrophication include major compositional and functional shifts in ecosystem components, changes in trophic levels, increases in invasive species, and an increased risk of emerging diseases (Smith and Schindler, 2009; Kneitel and Lessin, 2010). Consideration of eutrophication is important because it provides a basis to better understand ecological processes and interactions in seasonal ecosystems, information which is fundamental for effective management (Kneitel and Lessin, 2010).

The objective of this study was to investigate the impacts of camels on the water quality and invertebrate ecology of simulated arid zone waterbodies. We assessed the effects of camel dung on aquatic habitats by measuring changes in: i) physico-chemical variables and phytoplankton; ii) macroinvertebrate richness and abundance; and iii) macroinvertebrate community composition, over time in experimental mesocosms located in the central Australian arid zone.

2. Methods

2.1. Experimental mesocosms

Eighteen mesocosms (artificial pools), arranged in three groups of six, approximately 80 m apart, were placed in the Arid Zone Research Institute compound (133° 52′E, 23° 46′S) in Alice Springs, in the Northern Territory, Australia. The plastic 100 L, 1 m × 0.5 m pools were typical (in dimensions and volume) of small arid zone waterbodies. Within each group, three treatment mesocosms (with camel dung added) and three control mesocosms (without dung) were located 5 m apart in an alternating pattern. The closest known source of dispersing macroinvertebrate communities was the wastewater treatment ponds situated approximately 3 km north of the site.

Each mesocosm contained an identical substrate of clean sand sourced from a terrestrial site isolated from potential sources of aquatic fauna. Locally sourced native leaf litter (60 gms), a commercial de-chlorinator (5 ml), a commercial bacterial treatment (10 ml) and 90 L of tap water were added to each mesocosm. An imitation 'log' constructed from 25 mm PVC pipe with sealed ends was also added, with one end emerging from the water, to provide an oviposition site and an artificial substrate for invertebrate colonisation and emergence.

Two 200 L water drums were placed near each of the groups and were filled with tap water one week prior to mesocosm assembly and treated with a de-chlorinator. The water drums were used as reservoirs throughout the experiment to maintain constant water levels within the mesocosms. The drums had a small 10 cm aperture at the top, which may have permitted colonisation of the water source. However the same water was used to fill both the treatment and control pools to ensure minimal effects.

A 2 kg bag of camel dung was added to each treatment mesocosm at the beginning of the experiment. Field observations indicated that some small pools and springs can be almost completely filled with camel dung. We estimated that 2 kg of dung was the equivalent of a moderate quantity of dung in a similar-sized pool. Fresh camel dung was rinsed, crushed and mixed before being packed into calico bags. These bags were removed after 6 weeks, and replaced with 2 kg bags of fresh dung, to imitate camels re-visiting pool sites. Identical calico bags, without dung, were added to each control mesocosm. These bags were also replaced after 6 weeks to control for any effect of increased habitat (created by the bag) or disturbance due to bag removal and replacement.

2.2. Water quality and macroinvertebrate sampling

The mesocosms were sampled weekly over an eight week period during summer (October–December), 2012. Physico-chemical parameters (i.e. temperature, pH, conductivity, dissolved oxygen and turbidity) were measured at midday using a Horiba U-10 multi-parameter water quality meter (Kyoto, Kansai, Japan). Total nitrogen (TN) and total phosphorus (TP) concentrations were measured at weeks one, four and eight, on bulked water samples which were prepared by combining equal volumes (150 ml) of water from each set of control mesocosms and each set of treatment mesocosms within each cluster. Bulked samples were frozen and subsequently analysed using standard methods (APHA, 2005) at the Water Studies Centre (National Association of Testing Authorities accredited) at Monash University.

The concentration of chlorophyll a (a measure of algal biomass) in the water column was measured in each mesocosm, every second week, by filtering 100 ml of water through a Whatman 4.7 cm glass microfibre filter. The pigment was extracted in acetone and then measured spectrophotometrically according to standard methods (APHA, 2005).

Macroinvertebrates were sampled once a week for eight weeks by sweeping a long handled net (250 micron mesh) in a zig-zag motion across each mesocosm. A fixed volume of water (approximately 94 L) was filtered through the net in each mesocosm on each sampling occasion. The artificial 'log' was removed and shaken

over a tray of water, on each sampling occasion, to capture associated invertebrates.

Invertebrates captured were sorted, identified to the highest possible taxonomic resolution, counted, recorded, and released alive back into the same mesocosm directly after sampling. At the end of the experimental period (8 weeks) the same methods were used to exhaustively sample all macroinvertebrates present in the mesocosms. All specimens were stored in 95% ethanol for later identification using a stereomicroscope and online keys (e.g. www.mdfrc.org.au/bugguide/.

2.3. Data analysis

We used a repeated measures ANOVA to determine differences over time in physico-chemical parameters, chlorophyll *a*, taxa richness and taxa abundance, between treatment and control mesocosms, using the GLM RM procedure in R Project software (R Development Core Team, 2008). We plotted the abundance of selected taxa present over time, and the concentration of dissolved oxygen, in treatment and control mesocosms.

We used multivariate techniques available in the PRIMER 6 software package with PERMANOVA + add-on (Plymouth Marine Laboratory; Clarke and Gorley, 2006; Anderson et al., 2008) to determine changes in invertebrate assemblage changes over time and in response to the presence of dung. A species by pool cluster matrix was constructed using summed abundances across three replicates (i.e. three mesocosms per site per treatment) and adjusted Bray−Curtis similarity on transformed (log X + 1) abundance data was carried out.

Non-metric multidimensional scaling (MDS) was used to visually examine patterns within the data cloud in relation to dung and time effects. The main and interactive effects of dung pollution and time on assemblage composition were then directly tested using the PERMANOVA routine. The design included three factors: dung (fixed, 2 levels dung added & no dung added), time (random, eight levels) and pool cluster (random, three levels). The inclusion of pool cluster as a factor in the model incorporated the clustering structure inherent through time, thus creating a 'repeated measures' design (after Sim et al., 2013).

Similarity percentage analysis (SIMPER) was used to determine discriminating species for within and between-group comparisons according to dung treatment.

3. Results

3.1. Physico−chemical parameters

The average air temperature varied greatly over the eight-week experimental period, reaching a maximum of 38.7 °C and average water temperatures (recorded at the time of sampling each week) were high (~32 °C) (Table 1). Little precipitation (7 mm) was recorded during the same period. Significant differences in conductivity and pH were recorded over time and between the treatment and control mesocosms (Table 2), however, the differences were not large (Table 1). The presence of dung resulted in significantly different TN and TP concentrations (Table 2) which were higher in the treatment mesocosms than controls (Table 1). The initially high concentrations of both TN and TP in the treatment mesocosms declined over time, but increased again following the addition of fresh dung in week 6. In contrast, TN and TP concentrations were lower in the control mesocosms and changed little over the duration of the experiment.

Chlorophyll *a* concentrations were higher in treatment mesocosms (Table 1) and changed significantly over time in both control and treatment groups, however these changes were not

Table 1
Summary (means ± standard errors) of the effects of camel dung on the physico-chemistry and phytoplankton (chlorophyll *a*) of experimental arid zone mesocosms.

Parameter	Control	Treatment
PH	9.16 (SE ± 0.04)	9.51 (SE ± 0.05)
Conductivity (mS/cm)	2.07 (SE ± 0.07)	2.56 (SE ± 0.08)
Dissolved Oxygen (%)	88.47 (SE ± 2.64)	121.04 (SE ± 6.20)
Temperature (°C)	31.9 (SE ± 0.43)	32.8 (SE ± 0.45)
Total Phosphorus (mg/L)	0.15 (SE ± 0.02)	3.96 (SE ± 0.35)
Total Nitrogen (mg/L)	2.38 (SE ± 0.16)	23.56 (SE ± 1.66)
Chlorophyll *a* (mg/L)	3.25 (SE ± 0.58)	8.41 (SE ± 2.92)

significantly different between the groups. Measurement of chlorophyll *a* was made only on samples taken from the water column. Visual assessment revealed the development of high densities of benthic (i.e. attached) algae on the walls of the mesocosms over time. As a consequence our measurement of water column chlorophyll *a* provided only a partial assessment of total algal biomass and eutrophication.

Dissolved Oxygen (DO) levels in the mesocosms differed significantly between treatment groups (Table 1). Repeated measures ANOVA revealed significant effects of dung, time and dung over time on DO (Table 2). Initial concentrations of DO fluctuated greatly in the treatment mesocosms in comparison to the controls (Fig. 1).

3.2. Effects of dung on macroinvertebrate colonisation

Macroinvertebrate richness varied significantly between the treatment and control mesocosms and over time (Table 2). The sequence of macroinvertebrate colonisation varied between treatments and controls, and by taxa (Table 3). Invertebrate colonists included a range of functional feeding groups (shredders, collectors and predators) (Table 3) and the majority of taxa that colonised both the control and treatment mesocosms are considered to be pollution tolerant (www.mdfrc.org.au/bugguide; Hawking et al., 2009, Table 3). The exceptions were mayflies, and water mites which are considered to be sensitive to pollution and were only recorded in the control mesocosms. Two species of Hydrophilidae (adults) were also only recorded from the control mesocosms but their pollution tolerance is not known.

Water mites appeared in the controls in week 5 and mayfly larvae from week 6, (Table 3). The subsequent disappearance of water mites (from week 6) from the control mesocosms corresponded with the presence of high numbers of predatory dragonfly larvae and the arrival of other predators such as adult hemipterans (*Anisops* and *Agraptocorixa*) (Table 3).

3.3. Effects of dung on macroinvertebrate community composition

Significant changes occurred in macroinvertebrate community composition over time as revealed by PERMANOVA ($F_{7,14}$ 8.5, $P < 0.001$). The assemblages that were present in weeks 1 and 2 differed markedly from those present later in the experimental period (Fig. 2). There was a strong effect of dung on community composition ($F_{1,14} = 3.6, P < 0.01$) which was significant over time ($F_{7,14} = 3.4, P < 0.001$) (Fig. 2).

Dissimilarity in invertebrate composition between the control and treatment mesocosms was largely due to differing numbers of larval dragonflies, larval chironomids, larval mosquitoes, *Allodessus* beetle larvae and mosquito pupae (Table 4). These five taxa accounted for up to 70% of the dissimilarity between controls and treatments. The striking difference in composition between the control and treatment mesocosms was the high abundance of larval

Table 2
Repeated Measures ANOVA summary for the effects of camel dung on the physico-chemistry, phytoplankton and macroinvertebrates of experimental arid zone mesocosms.

Parameter	Dung	Time	Dung*Time
pH	$F_{1,16} = 27.4, p < 0.001$[a]	$F_{7,112} = 38.5, p < 0.001$[a]	$F_{7,112} = 3.2, p < 0.001$[a]
Conductivity (mS/cm)	$F_{1,16} = 137, p < 0.001$[a]	$F_{7,112} = 1133.7, p < 0.001$[a]	$F_{7,112} = 13.3, p < 0.001$[a]
Dissolved Oxygen (%)	$F_{1,16} = 59.5, p < 0.001$[a]	$F_{7,112} = 17.5, p < 0.001$[a]	$F_{7,112} = 8.3, p < 0.001$[a]
Temperature (°C)	$F_{1,16} = 5, p < 0.05$[a]	$F_{7,112} = 433.2, p < 0.001$[a]	$F_{7,112} = 1.3, p = 0.238$
Total Phosphorus (mg/L)	$F_{1,4} = 141.1, p < 0.001$[a]	$F_{2,8} = 1.4, p = 0.3$	$F_{2,8} = 1.3, p = 0.3$
Total Nitrogen (mg/L)	$F_{1,4} = 283.1, p < 0.001$[a]	$F_{2,8} = 2.8, p = 0.122$	$F_{2,8} = 2.6, p = 0.134$
Chlorophyll a (mg/L)	$F_{1,15} = 4.2, p = 0.06$	$F_{3,47} = 4.3, p < 0.001$[a]	$F_{3,47} = 2, p = 0.13$
Abundance	$F_{1,16} = 6.6, p < 0.05$[a]	$F_{7,112} = 17.6, p < 0.001$[a]	$F_{7,112} = 2.3, p < 0.05$[a]
Richness	$F_{1,16} = 1.9, p = 0.19$	$F_{7,112} = 36, p < 0.001$[a]	$F_{7,112} = 7.3, p < 0.001$[a]

[a] Indicates significant result.

dragonflies in the controls in contrast to the high abundance of mosquito larva and pupa in the treatments (Table 4).

3.4. Interactions between water quality, treatments and macroinvertebrates

There was a strong interaction between the effects of camel dung on water quality, algae, sequence of colonization and community composition. The arrival of dragonfly larvae in treatment mesocosms coincided with the three week period when DO was stable and similar to DO in the control mesocosms (Figs. 1 and 3). Larval dragonfly abundance declined from week 6 in treatment mesocosms, corresponding with the spike in DO saturation following the second dung treatment.

Dragonfly larvae colonised the controls earlier (week 2) than treatment mesocosms (week 4) and were much more abundant in the controls (Fig. 3). The peak abundance in the control mesocosms occurred between weeks four and six, corresponding with a decline and re-colonisation of mosquito larvae and a complete absence of mosquito pupae in week four (Fig. 3). Mosquito larvae and pupae were present in treatment (dung) mesocosms for the entire eight week experimental period, declining slightly in week 5 when larval dragonfly numbers were highest, but otherwise remaining relatively consistent and almost double the abundance of mosquito larvae and pupae recorded in the controls.

4. Discussion

Aquatic ecosystems are biologically important yet often overlooked features of arid landscapes that are useful for assessing anthropogenic disturbances (Williams, 2000; Box et al., 2008; Patten et al., 2008; Becerra Jurado et al., 2009; Davis et al., 2013). We sought to investigate how the impacts of camel dung affected the invertebrate colonisation of arid zone freshwater pools using experimental mesocosms. We assessed the effect of the addition of camel dung by measuring water quality, macroinvertebrate richness and abundance, and macroinvertebrate community composition over time.

4.1. Interactions and effects of camel dung on water quality

Nutrients are considered the main determinant of phytoplankton biomass in aquatic ecosystems (Teissier et al., 2012) and in this study were assessed by measuring total nitrogen and phosphorus, and phytoplankton biomass as chlorophyll a. Excessive nutrient input from animal waste is a major concern for surface waters globally, impacting on water quality, human health and ecosystem function (Burkholder et al., 2007; Smith and Schindler, 2009). Dung can enter water directly when herbivores stand in waterbodies to drink, or indirectly via runoff from adjacent land (Croel and Kneitel, 2011). Similar to cattle waste, camel dung can pose a threat to shallow lentic systems by fostering eutrophic conditions and stimulating algal blooms (Croel and Kneitel, 2011). The addition of camel dung to the treatment mesocosms significantly increased TN and TP concentrations in comparison with the control mesocosms. Although we cannot directly associate an increase in algal biomass with the presence of dung because of the limitations of our measurements, it is highly likely that the high algal biomass covering the walls of the treatment mesocosms was a direct consequence of the nutrient loading associated with the presence of dung.

Changes in water quality parameters such as pH, conductivity and DO provided indirect evidence of eutrophication caused by
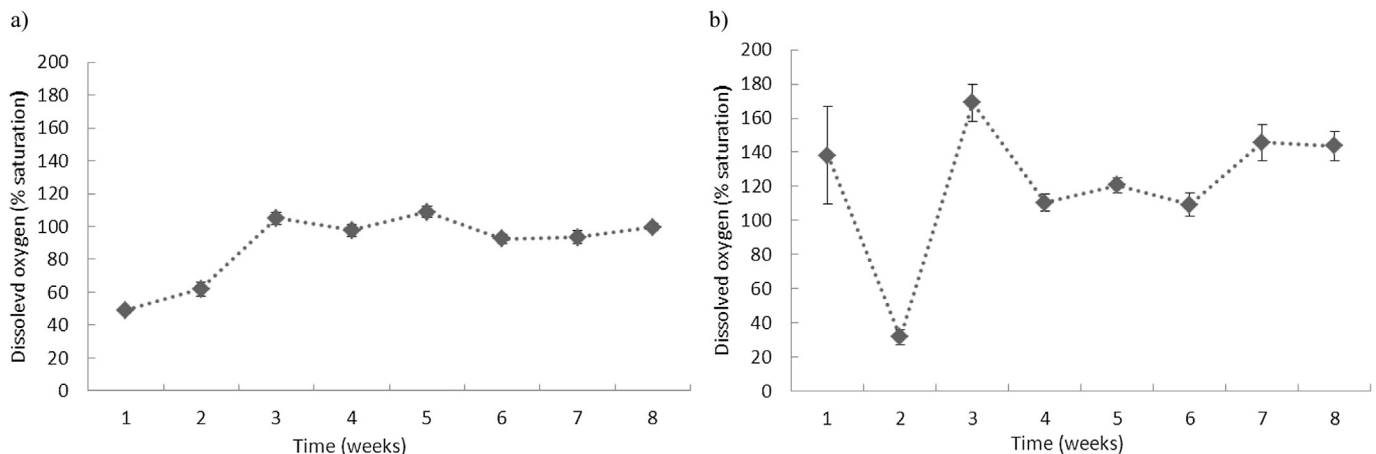

Fig. 1. Changes over time in dissolved oxygen saturation (mean% ± SE) in a) control and b) treatment mesocosms. 100% saturation indicates that DO is diffusing back into the atmosphere and can be indicative of eutrophication.

Table 3
List of macroinvertebrate taxa, and the week of arrival, recorded in the experimental mesocosms. Sensitivity to organic pollution is shown based on www.mdfrc.org.au/bugguide; Hawking et al. (2009). Dispersal type is based on Bilton et al. (2001).

Taxa	Life stage	Functional feeding group	Sensitivity to pollution	Mode of dispersal[a]	Week of arrival Control	Week of arrival Treatment
Chironomidae (bloodworm)	Larva	Gathering collector	Tolerant	WTA/WF	2	2
Chironomidae	Pupa	NA	NA	WTA/WF	2	3
Culicidae (mosquito)	Larva	Filtering –Collector	Very tolerant	WTA/WF	1	1
Culicidae	Pupa	NA	NA	WTA/WF	2	2
Allodessus sp. (beetle)	Adult	Unknown	Unknown	WTA/SF	1	1
Allodessus sp.	Larva	Predator	Unknown	WTA/SF	2	2
Tabanidae (horsefly)	Larva	Unknown	Unknown	WTA/WF	2	1
Anisoptera spp (dragonfly)	Larva	Predator	Mixed	WTA/SF	2	4
Elmidae (riffle beetle)	Adult	Shredder	Very tolerant	WTA/WF	2	–
Hydrophilidae 1 (beetle)	Adult	Unknown	Unknown	WTA/WF	1	–
Hydrophilidae 2	Larva	Unknown	Unknown	WTA/SF	5	5
Micronecta (water boatman)	Larva	Predator	Very tolerant	WTA/SF	3	3
Micronecta	Adult	Predator	Very tolerant	WTA/SF	1	1
Psychodidae (moth fly)	Larva	Unknown	Unknown	WTA/WF	–	3
Hydrophilidae 3 (beetle)	Adult	Unknown	Unknown	WTA/SF	5	–
Hydracarina (water mite)	Adult	Predator	Sensitive	Phoresy	5	–
Anisops (backswimmer)	Adult	Predator	Very tolerant	WTA/SF	6	6
Agraptocorixia (boatman)	Adult	Predator	Very tolerant	WTA/SF	8	6
Ephemeroptera sp (mayfly)	Larva	Scraper	Sensitive	WTA/SF	6	–
Total number of taxa recorded					18	14

[a] WTA = Winged Terrestrial Adult, W = Weak Flyer, SF = Strong Flyer.

the addition of camel dung. The slightly higher values of pH recorded in the treatment mesocosms were likely due to higher rates of primary productivity driven by the nutrients provided by dung, while the slightly higher conductivities could be attributed to higher ionic concentrations associated with decomposing dung. The high dissolved oxygen (DO) saturations in the treatment mesocosms were indicative of changes in algal growth. The treatment mesocosms were supersaturated (DO > 100%) in week 1 when phytoplankton were visually abundant, DO declined rapidly in week 2 when the initial bloom collapsed (and microbial uptake would have been high), DO increased in week 3 as benthic algae established on the mesocosm walls, and supersaturation persisted for the remainder of the experimental period. These results demonstrate how vulnerable small eutrophic waterbodies are to large changes in DO as a result of the interplay between algal growth, when photosynthetic activity elevates DO concentrations, and the rapid uptake of DO by microbial communities responding to dying algal blooms.

The occurrence of supersaturation (DO > 100%) indicated the likelihood of large diurnal fluctuations in DO. Although we only recorded spot measurements (once a week at midday) it is known that maximum DO concentrations usually occur mid-afternoon when photosynthesis greatly exceeds respiration. At night the reverse situation occurs: the lack of light restricts photosynthetic activity and the uptake of oxygen by respiration greatly exceeds that produced by photosynthesis (Williams, 2006; Reddy and DeLaune, 2008). This can have a direct impact on aquatic organisms that are sensitive to low or fluctuating DO concentrations. Certain aquatic invertebrates including larval dragonflies, larval beetles and larval mayflies are particularly susceptible to low DO (Gullan and Cranston, 1994).

4.2. Effects of camel dung on macroinvertebrates

Colonisation, leading to the establishment of new populations, is essential for the persistence of species inhabiting aquatic ecosystems and is important in a wider landscape context (Williams, 2006; Jeffries, 2011; Bogan and Boersma, 2012). The pools in this experiment were readily colonised by a suite of taxa representative of temporary or ephemeral freshwater pools, (i.e. Coleoptera,
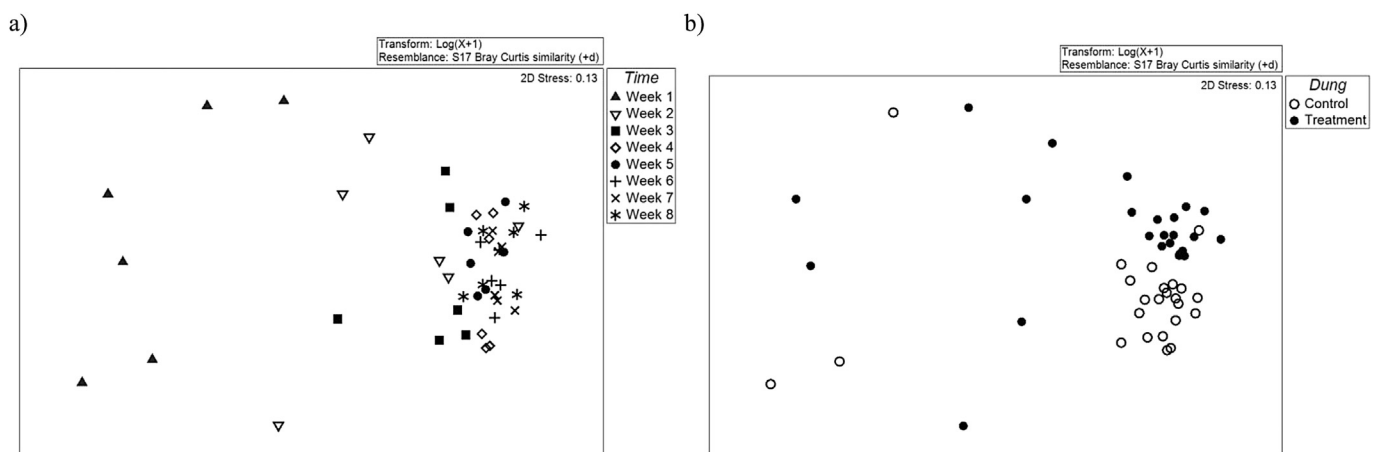
a)

b)

Fig. 2. NMDS ordination showing the changes in macroinvertebrate invertebrate community composition in arid zone mesocosms: a) over time and b) between treatment (camel dung) and control (no dung) mesocosms.

Table 4
Taxa contributing up to 90% of the average Bray–Curtis between-group dissimilarity (using SIMPER analysis) averaged over the 8 sample times on transformed (log X + 1) data. Average abundances indicate relative differences in abundance between treatment and control mesocosms. Column 4 shows the ratio of the average dissimilarity (column 3) divided by the standard deviation (SD). Number of samples = 48. The first five taxa make up to 70% of the between group dissimilarity.

Taxa	Average similarity		Average dissimilarity	Diss/SD	% contribution	Cumulative %
	Control (no dung)	Treatment (dung)				
Anisoptera (larva)	4.33	1.7	9.61	1.33	17.71	17.71
Chironomidae (larva)	4.06	4.4	8.29	0.99	15.27	32.98
Culicidae (larva)	2.23	3.37	6.73	1.1	12.4	45.38
Allodessus (larva)	2.05	1.96	5.16	1.11	9.51	54.89
Culicidae (pupa)	0.8	1.97	4.77	1.23	8.79	63.67
Tabanidae (larva)	0.45	1.15	4.37	0.58	8.06	71.73
Allodessus (adult)	1.35	1.11	3.05	1.03	5.63	77.36
Chironomidae (pupa)	0.07	1.12	2.77	0.97	5.11	82.47
Micronecta (nymph)	0.41	0.8	2.25	1	4.14	86.61
Micronecta (adult)	0.37	0.58	1.95	0.83	3.6	90.2

Diptera, Ephemeroptera and Hemiptera) (Williams, 2006). However, microcrustaceans such as Copepoda and Cladocera that have been recorded in similar studies (Barnes, 1983; Jeffries, 2011) were not present. Microcrustaceans establish in temporary pools either by emerging from sediment egg banks or by passive, wind-borne dispersal of resistant eggs (Caceres and Soluk, 2002). All taxa recorded in the treatment and control mesocosms were insects with a flying adult stage, except water mites, which are passively dispersed by phoresy (Bilton et al., 2001; Williams, 2006). Pioneer taxa such as chironomids, mosquitoes and adult beetles were first to colonise regardless of treatment, which is consistent with other studies (Barnes, 1983; Becerra Jurado, 2009; Jeffries, 2011; Bogan and Boersma, 2012).

Temporary waters are typically inhabited by highly resistant and dispersive taxa that either have high mobility, can transport via hosts or have life stages that are resistant to desiccation (Williams, 2006; Green et al., 2008). The mesocosm in this experiment were constructed with new materials, clean sand and treated water (suitable for domestic consumption), so that only highly mobile fauna could colonise. This excluded desiccation-resistant zooplankton such as copepods and cladocerans, and larger crustaceans such as the clam shrimps (Laevicaudata/Spinicaudata), fairy shrimps (Anostraca) and shield shrimps (Notostraca) that commonly hatch from the egg banks of temporary pool sediments (Barnes, 1983; Jeffries, 2011). Future experiments could use sediment inoculations from nearby natural pools to determine the responses of other aquatic fauna to eutrophication.

There was a difference in colonisation rates and composition between the treatment (dung) and control mesocosms. Most taxa that colonised the mesocosms were classed as tolerant to organic pollution by Australian rating systems (www.mdfrc.org.au/bugguide; Hawking et al., 2009). Some taxa, such as adult Allodessus beetles and adult hemipterans, Agraptocorixa, Anisops and Micronecta, are capable of relocating when conditions deteriorate and likely moved frequently between pools to feed and escape poor water quality (Barnes, 1983; Bogan and Boersma, 2012). Larval dragonflies, however, were unable to move between pools until after emergence as adults. Their greater abundance in the control mesocosms in comparison to the treatments suggests that the species present were sensitive to eutrophication and associated poor water quality. This is somewhat surprising in that most families were ranked as only mildly sensitive or pollution tolerant. The sensitivity of individual species could not be fully determined because it was not possible to undertake species determinations on live specimens.

Larval dragonflies colonised the control mesocosms rapidly, appearing from week 2, whereas they did not colonise the treatment mesocosms until week 4. This coincided with the stabilisation of DO levels in the treatment mesocosms, which suggested that the dragonfly larvae present were sensitive to DO fluctuations. Accordingly, the treatment mesocosms did not support the large numbers observed in control mesocosms. Larval mayflies were not recorded in any treatment mesocosms, indicating that they were very sensitive to the negative effects of camel dung on water
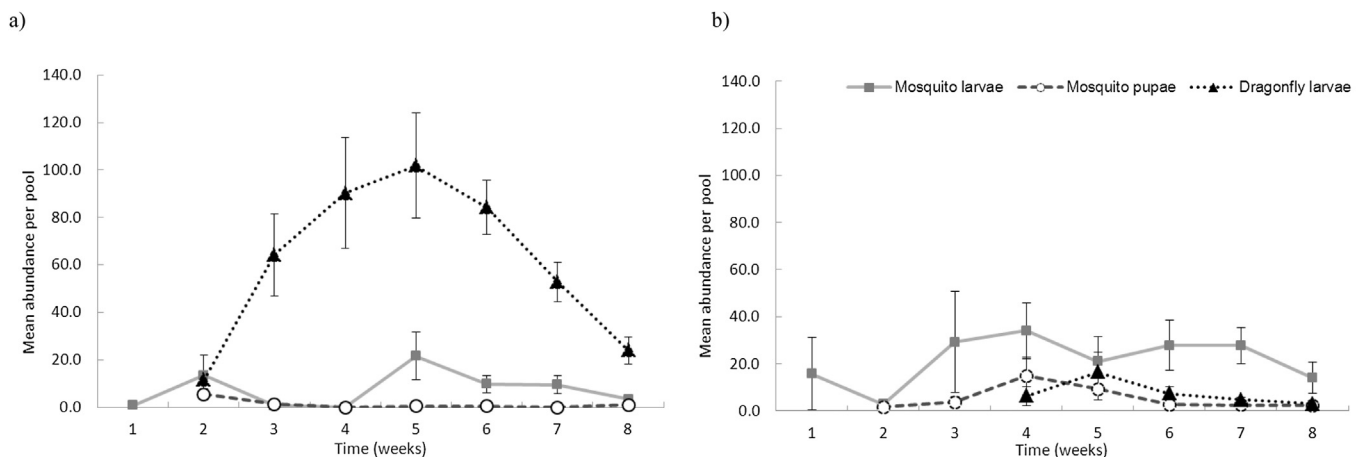

Fig. 3. Changes in the abundance of dragonfly larvae and mosquito larvae and pupae (means ± SE) over time in control (a) and treatment (camel dung) (b) mesocosms. The colonisation of dragonfly larvae coincided with a reduction in mosquito larvae and pupae in control mesocosms.

quality. This result corresponded with the high sensitivity rating assigned to mayflies (www.mdfrc.org.au/bugguide; Hawking et al., 2009).

In addition to the interacting effects of hydrological regime and water quality, strong biological interactions can also have a major influence on the composition of macroinvertebrate communities in temporary pools (Jeffries, 2011). The presence of predatory species is particularly important in driving assemblage composition (Stav et al., 2000; Bogan and Boersma, 2012), as was observed in this study. For example, as dragonfly abundance rose in the control mesocosms, the abundance of mosquito larvae and pupae declined considerably. This supports other studies that found fewer adult mosquitoes were recorded in pools containing dragonfly larvae (Stav et al., 2000). In contrast larval dragonfly abundance was much lower in the treatment mesocosms, and larval and pupal mosquito abundances remained relatively high and stable throughout the experiment. The treatment mesocosms were therefore potentially producing more adult mosquitoes than the controls. The presence of large numbers of mosquitos in arid waterbodies is a potential human health concern, as some mosquitos are known vectors of major diseases, including dengue and viral encephalitis (Chase and Knight, 2003; Williams, 2006).

Larval mosquitoes have respiratory syphons that enable them use atmospheric oxygen, and thereby survive in even the most polluted waters (Williams, 2006). However, to use atmospheric oxygen they must frequently rise to the surface, which exposes them to predators (De Szalay and Resh, 2000; Stav et al., 2000). Larval mosquitoes are heavily preyed upon by various taxa (Blaustein et al., 2005), including larval dragonflies, which are often the top aquatic predator in waterbodies that lack vertebrate predators such as fish (Stav et al., 2000). Larval dragonflies have been found to significantly reduce the abundance of larval mosquitoes by direct consumption, and because the presence of dragonfly nymphs repels oviposition by female mosquitoes (Stav et al., 2000). Our study confirmed that invertebrate predators are important determinants of aquatic community structure in temporary pools lacking vertebrate predators and have an important role in reducing mosquito populations in unpolluted systems.

5. Implications for natural waterbodies

This study provides experimental evidence of the negative impacts of camel dung on arid zone waterbodies. The effects, and interactions, of dung and water quality are likely to be exacerbated in natural pools, particularly in dry summers. As the landscape dries, aquatic sites evaporate and shrink in volume, which reduces habitat and concentrates solutes, especially nutrients (Williams, 2006). The deposition of dung is non-random at the landscape scale as feral camels move in from dry areas and concentrate in high numbers around aquatic sites to drink (Edwards et al., 2001; Brim-Box et al., 2010; Croel and Kneitel, 2011). Not only do the large numbers of camels utilising a water source have a direct physical impact (Brim-Box et al., 2010), the large biomass of dung, coupled with evaporation, reduces the amount of free water available and creates a thick dung 'soup'. These impacts, combined with negative chemical and biological impacts create conditions that are intolerable for most aquatic species. While this study focussed on the impacts of camel dung on aquatic species, it is likely that the poor water quality created by camels also affects the terrestrial species (birds, wallabies, kangaroos and dingoes) that drink from these pools.

Various native vertebrates, including wallabies and kangaroos, have been observed drinking at pools and springs, however they are unlikely to have the same impact on water quality as camels. Red kangaroos (the largest native herbivores in arid Australia) can weigh up to 90 kg, approximately one quarter of the weight of an adult camel, and in hot conditions only need to drink approximately 100 ml/day of water compared to 200 L/day for a camel. In addition, kangaroos have efficient urine concentrating abilities (Dawson et al., 1975). The largest native herbivores in central Australia are therefore much smaller, don't drink as much water nor deposit as much waste as camels.

Permanent waterbodies such as springs and rockholes provide important evolutionary refugia in arid landscapes and are often hotspots of biodiversity (Davis et al., 1993; Keleher and Rader, 2008). Temporary or ephemeral waterbodies are also critical to biodiversity as they provide ecological 'stepping-stones' in an otherwise unhospitable landscape by facilitating the dispersal and colonisation of aquatic fauna (Williams, 2000; De Meester et al., 2005; Williams, 2006; Bogan and Boersma, 2012; Sim et al., 2013). Introduced herbivores such as camels may therefore be contributing to fragmentation of aquatic ecosystems in the arid zone by disturbing the connectivity of these stepping stones.

Aquatic ecosystems in arid regions are particularly vulnerable to degradation because of their isolation coupled with the negative impacts of introduced herbivores (Sada et al., 2005; Box et al., 2008; Murphy et al., 2009; Brim-Box et al., 2010; Woodward et al., 2010; Sim et al., 2013). This study highlights the need for active management of invasive herbivores, such as camels, around arid zone waterbodies to reduce the amount of dung entering surface waters. This would lower the likelihood of eutrophication and associated loss of aquatic biodiversity, particularly the invertebrate predators which are important for mosquito control. It is essential that populations of feral camels and other invasive herbivores continue to be reduced, actively managed and monitored to ensure that the integrity of arid zone aquatic ecosystems is maintained and their persistence is supported over the long term.

Acknowledgements

References

Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER. PRIMER-E Ltd, Plymouth UK.

Angeler, D.G., Alverez-Cobelas, M., 2005. Island biogeography and landscape structure: integrating ecological concepts in a landscape perspective of anthropogenic impacts in temporary wetlands. Environ. Pollut. 138, 420—424.

Anthelme, F., Abdoulkader, A., Viane, R., 2011. Are ferns in arid environments underestimated? contribution from the Saharan mountains. J. Arid Environ. 75, 516—523.

APHA, 2005. Standard Methods for the Examination of Water and Wastewater, twenty-first ed. American Public Health Association, Wasington DC.

Barnes, L.E., 1983. The colonisation of ball-clay ponds by macroinvertebrates and macrophytes. Freshw. Biol. 13, 561—578.

Bayly, I.A.E., 1999. Review of how indigenous people managed for water in desert regions of Australia. J. R. Soc. West. Aust. 82, 17—25.

Becerra Jurado, G., Callanan, M., Gioria, M., Baars, J.R., Harrington, R., Kelly-Quinn, M., 2009. Comparison of macroinvertebrate community structure and driving environmental factors in natural and wastewater treatment ponds. Hydrobiologica 634, 153—165.

Bilton, D.T., Freeland, J.R., Okamura, B., 2001. Disperal in freshwater invertebrates. Annu. Rev. Ecol. Syst. 32, 159—181.

Blaustein, L., Blaustein, J., Chase, J., 2005. Chemical detection of the predator Notonecta irrorata by ovipositing Culex mosquitoes. J. Vector Ecol. 30, 299—301.

Bohonak, A.J., Jenkins, G., 2003. Ecological and evolutionary significance of dispersal by freshwater invertebrates. Ecol. Lett. 6, 783—796.

Bogan, M.T., Boersma, K.S., 2012. Aerial dispersal of aquatic invertebrates along and away from arid-land streams. Freshw. Sci. 31 (4), 1131—1144.

Box, J.B., Duguid, A., Read, R.E., Kimber, R.G., Knapton, A., Davis, J., Bowland, A.E., 2008. Central Australian waterbodies: the importance of permanence in a desert landscape. J. Arid Environ. 72, 1395—1413.

Brim-Box, J., Guest, T., Barker, P., Jambrecina, M., Moran, S., Kulitja, R., 2010. Camel usage and impacts at a permanent spring in central Australia: a case study. Rangel. J. 32, 55–62.

Burkholder, J., Libra, B., Weyer, P., Heathcote, S., Koplin, D., Thorne, P.S., Wichman, M., 2007. Impacts of waste from concentrated animal feeding operations on water quality. Environ. Health Perspect. 115 (2), 308–312.

Byrne, M., Yeates, D.K., Joseph, L., Kearney, M., Bowler, J., Williams, A.J., Cooper, S., Donnellan, S.C., Keogh, J.S., Leys, R., Melville, J., Murphy, D.J., Porch, N., Wyrwoll, K.-H., 2008. Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota. Mol. Ecol. 17, 4398–4417.

Caceres, C.E., Soluk, D.A., 2002. Blowing in the wind: a field test of overland dispersal and colonization by aquatic invertebrates. Oecologia 131, 402–408.

Chase, J.M., Knight, T.M., 2003. Drought-induced mosquito outbreaks in wetlands. Ecol. Lett. 6, 1017–1024.

Clarke, K.R., Gorley, R.N., 2006. PRIMER V6: User Manual/Tutorial. PRIMER-E Ltd, Plymouth Marine Laboratories PL, United Kingdom.

Clifford, H.F., Casey, R.J., Saffran, K.A., 1992. Short-term colonisation of rough and smooth tiles by benthic macroinvertebrates and algae. North Am. Benthol. Soc. 11, 304–315.

Croel, R.C., Kneitel, J.M., 2011. Cattle waste reduces plant diversity in vernal pool mesocosms. Aquat. Bot. 95, 140–145.

Dawson, T.J., Denny, M.J.S., Russel, E.M., Ellis, B., 1975. Water usage and diet preferences of free ranging kangaroos, sheep and feral goats in the Australian arid zone during summer. J. Zool. 177 (1), 1–23.

Davis, J.A., Pavlova, A., Thompson, R., Sunnucks, P., 2013. Evolutionary refugia and ecological refuges: key concepts for conserving Australian arid zone freshwater biodiversity under climate change. Glob. Change Biol. 19, 1970–1984.

Davis, J.A., Harrington, S.A., Friend, J.A., 1993. Invertebrate communities of relict streams in the arid zone- the Gorge Gill Range, Central Australia. Aust. J. Mar. Freshwater Res. 44, 483–505.

De Los Rios, P., Adamowicz, S.J., Witt, J.D.S., 2010. Aquatic fauna in the driest desert on earth: first report on the crustacean fauna of the Loa River (Atacama Desert, Antofagasta region, Chile). Crustaceana 83, 257–266.

De Meester, L., Declerck, S., Stokes, B., Louette, G., Van De Muetter, F., De Bie, T., Michels, E., Brendonck, L., 2005. Ponds and pools as model systems in conservation biology, ecology and evolution biology. Aquat. Conser. Mar. Freshwater Ecosyst. 15, 715–725.

De Szalay, F.A., Resh, V.H., 2000. Factors influencing macroinvertebrate colonisation of seasonal wetlands: responses to emergent plant cover. Freshw. Biol. 45, 295–308.

Dorges, B., Heucke, J., 1996. Ecology, Social Organization & Behavior of the Feral Dromedary Camelus Dromedarius (L. 1758) in Central Australia. B. Dorges & J. Heucke.

Edwards, G.P., Eldridge, S.R., Wurst, D., Berman, D.M., Garbin, V., 2001. Movement patterns of female feral camels in central and northern Australia. Wildl. Res. 28, 283–289.

Edwards, G.P., Zeng, B., Saalfeld, W.K., Vaarzon-Morel, P., 2010. Evaluation of the impacts of feral camels. Rangel. J. 32, 43–54.

Faulks, L.K., Gilligan, D.M., Beheregaray, L.B., 2010. Islands of water in a sea of dry land: hydrological regime predicts genetic diversity and dispersal in a widespread fish from Australia's arid zone, the golden perch (*Macquaria ambigua*). Mol. Ecol. 19, 4723–4737.

Green, A.J., Jenkins, K.M., Bell, D., Morris, P.J., Kingsford, R.T., 2008. The potential role of waterbirds in dispersing invertebrates and plants in arid Australia. Freshw. Biol. 53, 380–392.

Gullan, P.J., Cranston, P.S., 1994. Aquatic insects. In: The Insects: an Outline of Entomology. Chapman & Hall, London, UK, pp. 224–246.

Hawking, J.H., Smith, L.M., Le Busque, K., 2009. Identification and Ecology of Australian Freshwater Invertebrates. Murray-Darling Freshwater Research Centre (Accessed October–November 2012). http://www.mdfrc.org.au/bugguide.

Jeffries, M.J., 2011. The temporal dynamics of temporary pond macroinvertebrate communities over a 10-year period. Hydrobiologica 661, 391–405.

Jenkins, D.G., Buikema, A.L., 1998. Do similar communities develop in similar sites? A test with zooplankton structure and function. Ecol. Monogr. 68, 421–443.

Keleher, M.J., Rader, R.B., 2008. Dispersal limitations and history explain community composition of metaphyton in desert springs of the Bonneville Basin, Utah: a multiscale analysis. Am. Soc. Limnol. Oceanogr. 53, 1604–1613.

Kingsford, R.T., Thompson, J.R., 2006. Desert or dryland rivers of the world: an introduction. In: Kingsford, R.T. (Ed.), Ecology of Desert Rivers. Cambridge University Press, UK, pp. 3–10.

Kirkman, L.K., Smith, L.L., Quintana-Ascencio, P.F., Kaeser, M.J., Golladay, S.W., Farmer, A.L., 2012. Is species richness congruent among taxa? surrogacy, complementarity and environmental correlates among three disparate taxa in geographically isolated wetlands. Ecol. Indic. 18, 131–139.

Kneitel, J.M., Lessin, C.L., 2010. Ecosystem-phase interactions: aquatic eutrophication decreases terrestrial plant diversity in California vernal pools. Oecologia 163, 461–469.

Layton, R.J., Voshell, J.R.J., 1991. Colonisation of new experimental ponds by benthic macroinvertebrates. Environ. Entomol. 20, 110–117.

Lindenmayer, D.B., Burbidge, A.A., Hughs, L., Kitching, R.L., Musgrave, W., Stafford Smith, M., Werner, P.A., 2010. Conservation strategies in response to rapid climate change: Australia as a case study. Biol. Conserv. 143, 1587–1593.

March, F., Bass, D., 1995. Application of island biogeography theory to temporary pools. J. Freshw. Ecol. 10, 83–85.

Murphy, N.P., Adams, M., Austin, A.D., 2009. Independent colonization and extensive cryptic speciation of freshwater amphipods in the isolated groundwater springs of Australia's Great Artesian Basin. Mol. Ecol. 18, 109–122.

Patten, D.T., Rouse, L., Stromberg, J.C., 2008. Isolated spring wetlands in the Great Basin and Mojave deserts, USA: potential response of vegetation to groundwater withdrawal. Environ. Manag. 41, 398–413.

R Development Core Team, 2008. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Reddy, K.R., DeLaune, R.D., 2008. Biochemistry of Wetlands: Science and Applications. Taylor & Francis Group, CRC Press, United States of America.

Saalfeld, W.K., Edwards, G.P., 2010. Distribution and abundance of the feral camel (*Camelus dromedarius*) in Australia. Rangel. J. 32, 1–9.

Sada, D.W., Fleishman, E., Murphy, D., 2005. Associations among spring-dependent aquatic assemblages and environmental and land use gradients in a Mojave Desert mountain range. Divers. Distrib. 11, 91–99.

Sim, L.L., Davis, J.A., Strehlow, K., McGuire, M., Trayler, K.M., Wild, S., Papas, P.J., O'Connor, J., 2013. The influence of changing hydroregime on the invertebrate communities of temporary seasonal wetlands. Freshw. Sci. 32, 327–342.

Smith, V.H., Tilman, G.D., Nekola, J.C., 1999. Eutrophication: impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. Environ. Pollut. 100, 179–196.

Smith, V.H., Schindler, D.W., 2009. Eutrophication science: where do we go from here? Trends Ecol. Evol. 24 (4), 201–207.

Stav, G., Blaustein, L., Margalit, Y., 2000. Influence of nymphal *Anax imperator* (odonata: aeshnidae) on oviposition by the mosquito *Culiseta longiareolata* (diptera: culicidae) and community structure in temporary pools. J. Vector Ecol. 25, 190–202.

Teissier, S., Peretyatko, A., De Backer, S., Triest, L., 2012. Strength of phytoplankton-nutrient relationship: evidence from 13 biomanipulated ponds. Hydrobiologica 689, 147–159.

Thompson, R., Townsend, C., 2006. A truce with neutral theory: local deterministic factors, species traits and dispersal limitation together determine patterns of diversity in stream invertebrates. J. Anim. Ecol. 75, 476–484.

Vorosmarty, C.J., McIntyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P.A., Glidden, S., Bunn, S.E., Sullivan, C.A., Reidy, C.A., Davies, P.M., 2010. Global threats to human water security and river biodiversity. Nature 467, 555–561.

Ward, D., Blaustein, L., 1994. The overriding influence of flash floods on species-area curves in ephemeral Negiv Desert pools- a consideration of the value of island biogeography theory. J. Biogeogr. 21, 595–603.

Williams, D.D., 2006. The Biology of Temporary Waters. Oxford University Press, New York.

Williams, P., Whitfield, M., Biggs, J., 2008. How can we make new ponds biodiverse? A case study monitored over 7 years. Hydrobiologica 597, 137–148.

Williams, W.D., 2000. Biodiversity in temporary wetlands of dryland regions. Int. Assoc. Theor. Appl. Limnol. Proc. 27, 141–144.

Wilmer, J.W., Wilcox, C., 2007. Fine scale patterns of migration and gene flow in the endangered mound spring snail, *Fonscochlea accepta* (mollusca : hydrobiidae) in arid Australia. Conserv. Genet. 8, 617–628.

Woodward, G., Perkins, D.M., Brown, L.E., 2010. Climate change and freshwater ecosystems: impacts across multiple levels of organisation. Phil. Trans. R. Soc. B 35, 2093–2106.

Zickovich, J.M., Bohonak, A.J., 2007. Dispersal ability and genetic structure in aquatic invertebrates: a comparative study in southern California streams and reservoirs. Freshw. Biol. 52, 1982–1996.