

Biology and conservation of the unique and diverse halophilic macroinvertebrates of Australian salt lakes

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The authors of the above-mentioned paper regret to inform readers that there were errors published in the systematics of one of the taxa in the manuscript. The list of groups in the *Cladocera* section (on p. F) was published as below:

The bulk of Cladocera that occur in inland waters in Australia are restricted to fresh water, but three groups have representatives in salt lakes. These groups comprise: (1) six species of *Daphniopsis* (or *Daphnia*; see below); (2) two species of *Daphnia* (*Daphnia salinifera* Hebert and *Daphnia neosalinifera* Hebert) from the *Daphnia carinata* (King) subgenus; and (3) three species of chydorid: *Moina baylyi* Forró, *Moina mongolica* Daday and *Extremalona timmsi* Sinev & Shiel.

This text should have been as below (changes underlined):

The bulk of Cladocera that occur in inland waters in Australia are restricted to fresh water, but four groups have representatives in salt lakes. These groups comprise: (1) six species of *Daphniopsis* (or *Daphnia*; see below); (2) two species of *Daphnia* (*Daphnia salinifera* Hebert and *Daphnia neosalinifera* Hebert) from the *Daphnia carinata* (King) subgenus; (3) two *Moina* species (*Moina baylyi* Forró and *Moina mongolica* Daday); and (4) one species of chydorid (*Extremalona timmsi* Sinev & Shiel).

Furthermore, the title of the *Chydorids* section should have been titled *Moinids and chydorids*.

Biology and conservation of the unique and diverse halophilic macroinvertebrates of Australian salt lakes

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Abstract. This study synthesises information on the biology of the unique and diverse halophilic macroinvertebrates of Australian salt lakes, focusing on gastropods and crustaceans. This information is needed to evaluate and manage the threats posed to these invertebrates by increased periods of drought and secondary salinisation. Most of these species are endemic to Australian salt lakes, and some have adapted to extreme conditions (e.g. salinities $>100\text{ g L}^{-1}$ and $\text{pH} < 5$). This study identifies key general findings regarding the taxonomy, ecology and life histories of these invertebrates, such as that many ‘new’ species have been uncovered in the past 20 years, with more likely to come. The study also identifies critical knowledge gaps, such as the need to elucidate the abiotic and biological drivers of the field distributions of species, including why some species are widespread and common whereas other congeneric species are rare or have narrow distributions. Those species that are either restricted to low salinity environments or survive dry periods as aestivating adults (as opposed to desiccation-resistant eggs) are probably the most vulnerable to increasing salinisation and drought. Future work should prioritise the development of a sound taxonomy for all groups, because this is needed to underpin all other biological research.

Keywords: *Coxiella*, crustaceans, halobionts, halophiles.

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Introduction

Salt lakes are defined as enclosed bodies of water with salinity $>3\text{ g L}^{-1}$, although the salinity is usually much greater than this (Williams 1964). Salt lakes are often classed as either athalassic (inland) or coastal (possessing a current or recent connection with the marine environment, including via groundwater; Bayly and Williams 1966).

Australia has a vast number and variety of salt lakes that support unique faunal communities (De Deckker 1983a; Williams 2002). At least in Australia, coastal and athalassic salt lakes are characterised by different faunas. The former mainly contain species that have current or recent marine or estuarine affinities (Timms 2009a, 2010a; Pinder and Quinlan 2015), whereas the latter mainly contain taxa that have evolved in and are restricted to these systems (Bayly 1972). However, some athalassic species occasionally also occur in coastal lakes (Timms 2009a; Pinder and Quinlan 2015). This review focuses on the fauna of Australian athalassic salt lakes but includes data for athalassic species in coastal lakes.

Salt lakes are physically extreme environments, particularly those lakes that are either highly saline or only hold water intermittently (Williams 1985). The physical characteristics of

Australian salt lakes are well established and were reviewed recently by Mernagh *et al.* (2016). Athalassic salt lakes mostly form in locations with semi-arid to arid climates where evaporation exceeds precipitation and drainage is impeded or fully endorheic (Williams 1998a). These lakes vary from expansive playas with long geological records to small, recently formed ponds and wetlands (De Deckker 1983b) that have become saline as a result of the intrusion of saline groundwater. Most Australian salt lakes are alkaline and ionically dominated by NaCl (Bayly and Williams 1966), but some are naturally acidic and can have a pH as low as 3 (Timms 2009b). Some salt lakes hold water permanently but most are either seasonal (usually filling with winter–spring rainfall and drying out over summer–autumn) or episodic (filling only after unseasonal rainfall; Williams 1998a, 1998b).

The terms ‘halotolerant’, ‘halophile’ and ‘halobiont’ are commonly used to classify the aquatic fauna of salt lakes based on their relationship with salinity, although these terms are variously used (Bayly 1972; Williams 1981; Timms 1983; Hammer 1986; Pinder *et al.* 2002). Herein, ‘halotolerant’ describes biota that predominately occur in fresh water (salinity $<3\text{ g L}^{-1}$) but occasionally occur in waters with

salinity up to $\sim 20 \text{ g L}^{-1}$, whereas ‘halophiles’ are biota that occur mostly in athalassic waters (salinity $> 10 \text{ g L}^{-1}$; Williams 1981). We have not attempted to distinguish between ‘high-salinity’ (sometimes called halobiontic) and ‘low-salinity’ (sometimes called halophilic) taxa due to varying definitions (e.g. Timms 1983 v. Williams 1981 v. Bayly 1972) and because many taxa do not neatly fit into one or the other category. It is acknowledged that our definition neglects some species that occur in salt lakes at salinities $> 3 \text{ g L}^{-1}$ but typically less than 10 g L^{-1} that have been described as halophilic elsewhere (e.g. *Eocyzicus* spp. and *Branchinella* spp. in Timms 2007, 2014).

Australian salt lakes support unique communities. Some invertebrate groups, particularly crustaceans, are well represented, with many species, genera and even one family restricted to salt lakes (Halse and McRae 2004; Timms 2014). The gastropod *Coxiella* (which includes the subgenus *Coxielladda*) is unique to these environments and the only gastropod genus anywhere in the world to consist entirely of halophilic species (Williams and Mellor 1991). Insects are commonly encountered, but, with few exceptions, these are halotolerant rather than halophilic (Williams and Kokkinn 1988; Timms 1993; Pinder *et al.* 2005). Fish are rare and are mainly found in low-salinity permanent lakes, but may occur in large episodic lakes during heavy filling events when these lakes become connected to refugia such as mound springs supporting fish (e.g. *Craterocephalus eyresii* (Steindachner) in Lake Eyre and Lake Torrens; Williams and Kokkinn 1988; Williams *et al.* 1998). Numerous waterbirds opportunistically use salt lakes for feeding and even breeding (Weston 2007; Pedler *et al.* 2018) and some, such as banded stilts *Cladorhynchus leucocephalus* (Vieillot), are largely restricted to these lakes (Pedler *et al.* 2014). These birds are probably important vectors of dispersal for salt lake invertebrates (Green *et al.* 2008; Sánchez *et al.* 2012). Australian salt lakes also have distinctive fringing plant communities dominated by genera such as *Tecticornia* (samphires) and *Frankenia* (sea heath; Lyons *et al.* 2004). Salt-tolerant macroalgae such as Characeae and the vascular plants *Ruppia* and *Lepilaena* form thick mats in mildly saline waterbodies (Porter 2007; Casanova 2013), and microalgae such as *Dunaliella* thrive in hypersaline conditions, where they give lakes a characteristic pink hue (Teller 1987).

Salt lakes and their unique biota are threatened globally (Williams 2002). In Australia, reduced rainfall, associated with anthropogenic climate change, is having a widespread and dramatic effect as it causes lakes to fill less often, with shorter hydroperiods (i.e. periods during which water is present) and higher salinities (Hughes 2003; Nielsen and Brock 2009). These changes can have a profound effect on community composition, especially in previously low-salinity or seasonal lakes (Williams 2002; Pinder *et al.* 2005). Secondary salinisation, agricultural and mining activities, groundwater extraction, diversion of surface flows and pollution also present significant threats to Australian salt lakes and have already deleteriously affected these environments in some areas (Williams 1995; Timms 2005). For example, increased salinisation, changes to hydroperiod and, in some cases, acidification associated with secondary salinisation have diminished the faunal communities of some salt lake environments on the Eyre Peninsula, South Australia (Williams 1984; Timms 2009a) and in the Wheatbelt

region of Western Australia (Cale *et al.* 2004). In addition to expirations, there is a risk that these hydrological changes may lead to the extinction of entire species, at least in Western Australia, without intervention (Halse *et al.* 2003). Despite the unique biodiversity and apparent threats, very little has been done to assess the conservation status of salt lake invertebrates (Timms *et al.* 2009).

Conservation planning should be informed by evidence (Sutherland and Wordley 2017). To effectively assess and manage threats to Australian salt lake environments, it is important to synthesise the available information on these environments and use this information to document general trends and highlight critical knowledge gaps. There is, however, no current systematic evaluation of the state of knowledge of the biota of Australian salt lakes. De Deckker (1983b) reviewed the history, chemistry and biota of Australian salt lakes, but our knowledge of these systems has since improved. There have been significant advances in knowledge of the systematics and biology of a range of taxa (Hebert and Wilson 2000; Halse and McRae 2004; Timms 2014) and expanded coverage of some regions (Pinder *et al.* 2002; Timms *et al.* 2006; Timms 2008). The study reviews the current state of knowledge of halophilic macroinvertebrates of Australian salt lakes. It focuses on crustaceans and gastropods because they are an important and conspicuous component of these lakes.

The specific aims of this study were to: (1) synthesise knowledge of halophilic crustaceans and gastropods from Australian salt lakes, focussing on information published since De Deckker (1983b); (2) draw attention to important issues in Australian salt-lake conservation; and (3) identify general trends, gaps in knowledge and directions for future research in this area.

Materials and methods

This study reviews what is known about halophilic macroinvertebrates from Australian salt lakes, focusing on data published since De Deckker’s (1983b) review. For quality control, it mainly relies on peer-reviewed studies, but unpublished theses and reports were used when they contained crucial information that was not otherwise available.

Halophilic macroinvertebrates were identified from published ecological studies of Australian salt lakes (Table 1) and from unpublished data held by the Western Australian Department of Biodiversity, Conservation and Attractions (DBCA). The dataset analysed during this study is available from the corresponding author on reasonable request. In all, 79 described halophilic species in 23 genera were identified. Almost all species were either crustaceans or gastropods. Insects were excluded because most species in Australian salt lakes are halotolerant rather than halophilic (Timms 1993; Pinder *et al.* 2005). Rotifers have also been excluded on the basis that they are microscopic rather than macroscopic (Blinn *et al.* 2004).

Various methods were used to find articles on the biology of the identified halophiles, including searches for keywords ‘salt’, ‘saline’, ‘lake’, ‘wetland’, ‘Australia’, ‘invertebrate’, ‘fauna’, ‘halophile’, ‘halophilic’, ‘halobiont’, ‘crustacean’ and ‘gastropod’ on Scopus and Google Scholar databases. Both databases were last accessed on 1 December 2020.

Table 1. List of field studies used to identify halophilic invertebrate species for each Australian state

Western Australia	South Australia	Victoria	Queensland	New South Wales	Tasmania
Geddes <i>et al.</i> (1981)	Bayly and Williams (1966) ^A	Geddes (1976)	Timms (1987)	Timms (1993)	De Deckker and Williams (1982)
Halse (1981)	Bayly (1970)	Timms (1983)	Timms (1998)	Timms (2018)	
Edward (1983)	Bayly (1976)	Williams <i>et al.</i> (1990)	Timms (2001)		
Doupe and Horwitz (1995)	De Deckker and Geddes (1980)	Williams (1995)	Timms (2008)		
Halse <i>et al.</i> (1998)	Williams (1984)				
Halse <i>et al.</i> (2000a)	Williams and Kokkinn (1988)				
Cale <i>et al.</i> (2004)	Williams <i>et al.</i> (1998)				
Pinder <i>et al.</i> (2005)	Timms (2009a)				
Timms <i>et al.</i> (2006)	Timms <i>et al.</i> (2014)				
Timms (2009b)					
Pinder <i>et al.</i> (2010)					
Pinder <i>et al.</i> (2012)					
Pinder and Quinlan (2015)					
Quinlan <i>et al.</i> (2016)					

^ABayly and Williams (1966) also included some lakes in Victoria

This review includes salinity data from multiple studies. These studies typically estimated salinity (the sum of all ion concentrations per unit solution) from measurements of conductivity (which has particular utility in Australian salt lakes because most have a homogenous ionic composition; Bayly and Williams 1966) or as gravimetric total dissolved solids (TDS; which may include small but variable amounts of organic matter that can result in exaggerated salinity values; Williams and Sherwood 1994). Salinity data reported from gravimetric determination (TDS) in the source article have been converted to grams per litre of dissolved solutes in this review to facilitate comparisons across different studies. This was done using a correction factor of 0.91, which is based on the highly correlated relationship between salinity estimated using conductivity and salinity estimated from gravimetric methods (Bayly and Williams 1966).

Halophilic biota: Crustacea

Anostraca

Three anostracan genera, *Parartemia*, *Branchinella* and *Artemia*, occur in Australian salt lakes (Pinceel *et al.* 2013a; Timms 2014).

Parartemia

The biology of *Parartemia* has been reviewed recently by Timms (2014), so only general points are discussed here.

Taxonomy. *Parartemia*, the only genus in the family Parartemiidae, is unique to Australia and is composed exclusively of halophilic species (Table 2). With 18 described and one undescribed species (Timms 2014), it is one of the most speciose genera in salt lakes.

The taxonomy of *Parartemia* is relatively advanced compared with that of most other Australian salt lake invertebrates, although a substantial number of species (nine) have only been described in the past 10 years (Table 2) and another species is yet to be described (Timms 2014). The most recent taxonomic assessments of *Parartemia* are provided by Timms and Hudson (2009), who described four new species from South Australia, and Timms (2010b), who described six new species from

Western Australia. The taxonomic work is based on morphology, but Remigio *et al.* (2001) used variation in the mitochondrial *16S* gene to confirm that the eight species described at that time were genetically distinct and as evidence of undiscovered species in Lake MacLeod (GenBank Accession number AY014794) and another in 'Scadden East' (GenBank Accession number AY014795) in Western Australia. Whether the undescribed species of Remigio *et al.* (2001) are populations of species subsequently described by Timms (2010b) is not clear.

Ecology. Species diversity in *Parartemia* decreases from western to eastern Australia, with Western Australia having 13 described species (10 endemics) compared with 6 (3 endemics) in South Australia and 2 (no endemics) in the eastern states (Table 2). The ubiquity of species varies, ranging from geographically widespread and known from many sites (e.g. *Parartemia cylindrifera* Linder, *Parartemia longicaudata* Linder and *Parartemia zietziana* Sayce) to only known from one or a few sites in a single region (e.g. *Parartemia triquetra* Timms & Hudson and *Parartemia auriciforma* Timms & Hudson; Timms *et al.* 2009). Knowledge of the distributions of some species is inadequate, especially those like *P. triquetra* and *P. auriciforma*, which occur in remote areas that have been poorly surveyed (Timms and Hudson 2009; Timms 2010b).

Parartemia species occur mainly in ephemeral and seasonal natural salt lakes, surviving dry periods as drought-resistant cysts (Timms 2012a). They are strong hypoosmotic regulators (Geddes 1981) and the most salt-tolerant of the endemic invertebrates in Australian salt lakes (Timms 2014), but little is known about the physiological basis for this. All 15 species for which relevant data are available have been collected from lakes with salinities >90 g L⁻¹, and 8 of these were from lakes with salinities in excess of 200 g L⁻¹ (Table 2). Laboratory experiments by Manwell (1978) suggested that one species, *P. zietziana*, was not able to withstand the highest salinities tolerated by *Artemia*, possibly due to a lesser capacity to produce sufficient haemoglobin to compensate for low oxygen concentrations at very high salinities. Based on field data, the salinity tolerances of *Parartemia* species are very broad and overlap (Table 2). Nevertheless, species rarely co-occur in the same

Table 2. Species of *Parartemia* with their reported salinity range (based on field observations) and geographic distributions

Data from Timms (2014). WA, Western Australia; SA, South Australia; Vic., Victoria; Qld, Queensland; Tas., Tasmania; NSW, New South Wales; NT, Northern Territory; NA, no available data

Species	Description	Salinity range (g L ⁻¹)	Distribution
<i>Parartemia</i>			
<i>acidiphila</i>	Timms and Hudson (2009)	35–210	South-western WA, south-eastern SA
<i>auriciforma</i>	Timms and Hudson (2009)	NA	Central SA
<i>bicornia</i>	Timms (2010b)	22–105	Central WA
<i>boomeranga</i>	Timms (2010b)	50–120	South-western WA
<i>contracta</i>	Linder (1941)	84–240	South-western WA
<i>cylindrifera</i>	Linder (1941)	3–123	South-western WA, south-eastern SA
<i>extracta</i>	Linder (1941)	27–100	South-western WA
<i>informis</i>	Linder (1941)	30–186	South-western WA
<i>laticaudata</i>	Timms (2010b)	8–141	North-west WA, central WA, south-western NT
<i>longicaudata</i>	Linder (1941)	41–240	South-western WA
<i>minuta</i>	Geddes (1973)	2–225	North-western NSW, south-eastern Qld, central SA, Vic.
<i>mouritzi</i>	Timms (2010b)	33–95	South-western WA
<i>purpurea</i>	Timms (2010b)	20–235	South-western WA
<i>serventyi</i>	Linder (1941)	15–262	South-western WA, central WA
<i>triquetra</i>	Timms and Hudson (2009)	NA	Central SA
<i>veronicae</i>	Timms (2010b)	74–225	Central WA
<i>yarleensis</i>	Timms and Hudson (2009)	NA	Central SA
<i>zietziana</i>	Sayce (1903)	27–353	South-eastern SA, Vic., Tas.

waterbody and a combination of physical factors, such as water duration, filling pattern, pH and salinity, are suggested to be important in determining species distributions (Timms 2009c; Timms *et al.* 2009). In addition, *Parartemia* eggs sink and become bound up in sediments, reducing dispersal ability (Timms *et al.* 2009). The majority of species live in alkaline waters, but *Parartemia mouritzi* Timms, *Parartemia contracta* Linder and *Parartemia acidiphila* Timms & Hudson are known to inhabit acidic lakes (Conte and Geddes 1988; Timms 2009b, 2010b; Timms and Hudson 2009).

Life history. Sexes are separate for all *Parartemia* (Timms 2014). Detailed lifecycle and reproductive information is available only for *P. zietziana* (Marchant and Williams 1977a), which reproduces ovoviviparously, producing multiple cohorts so long as conditions are favourable (Timms 2012b) and uses oviparous reproduction to produce highly resistant cysts when conditions become unfavourable (Geddes 1976; Marchant and Williams 1977b). The cysts of *Parartemia laticaudata* and *Parartemia veronicae* have the same stress proteins (p26, artemin and heat shock protein 70) that enable *Artemia* (cysts) to survive severe desiccation (Clegg and Campagna 2006). Cyst hatching appears to follow a ‘bet-hedging’ strategy, whereby some eggs hatch within hours of a filling event but not all eggs hatch at once (in case the water does not persist long enough to allow reproduction; Timms 2012b).

Trophic ecology. Dietary information is available only for *P. zietziana*, which selectively feeds on benthic or suspended particles with a high organic content (Marchant and Williams 1977b). It has been assumed that other species feed similarly (Timms 2014). Timms (2012a) suggested that *Parartemia* mainly feed on organic matter that is resuspended in the water column, which provides limited opportunity for niche diversification based on food resources. Timms (2012a) hypothesised

that this may give a species established in a lake a competitive advantage over a species that recently arrives, and hence explain why lakes typically only contain one *Parartemia* species. Exactly how this may give a resident species a competitive advantage is not clear.

Parartemia are an important food source for waterbirds, such as the banded stilt, that may fly thousands of kilometres to take advantage of booming *Parartemia* populations (Pedler *et al.* 2018).

Conservation status. *Parartemia* is unique among Australian salt lake genera in that its conservation status has been assessed, at least in Western Australia (Timms *et al.* 2009). The dominant threats to *Parartemia* are habitat degradation, including acidification and changes to hydrology (especially prolonged inundation) from secondary salinisation (Timms *et al.* 2009). *Parartemia contracta* is currently the only species listed by the International Union for Conservation of Nature (as vulnerable), although it is one of the more common species and may not be as at risk as previously thought (Timms *et al.* 2009). The species that are regarded as at most risk (*Parartemia extracta* and *Parartemia boomeranga*) are only known from the Wheatbelt region, where altered hydrology and secondary salinisation is widespread (Halse *et al.* 2003). Timms *et al.* (2009) recommended that *P. extracta* be considered as vulnerable because it has disappeared from many sites and is secure only in lakes in the Jurien Bay area (Fig. 1; Timms 2014; Pinder and Quinlan 2015). Another species, namely *P. boomeranga*, may be extinct (Timms 2012b) because it has not been recorded recently and all the lakes this species was known to occur in are affected by secondary salinisation (Fig. 1; Timms *et al.* 2009). Concerns have also been raised for *P. mouritzi* and *Parartemia bicornia*, both of which are only known from a few lakes that are currently being affected by either secondary salinisation or mine dewatering discharge (Timms 2014).

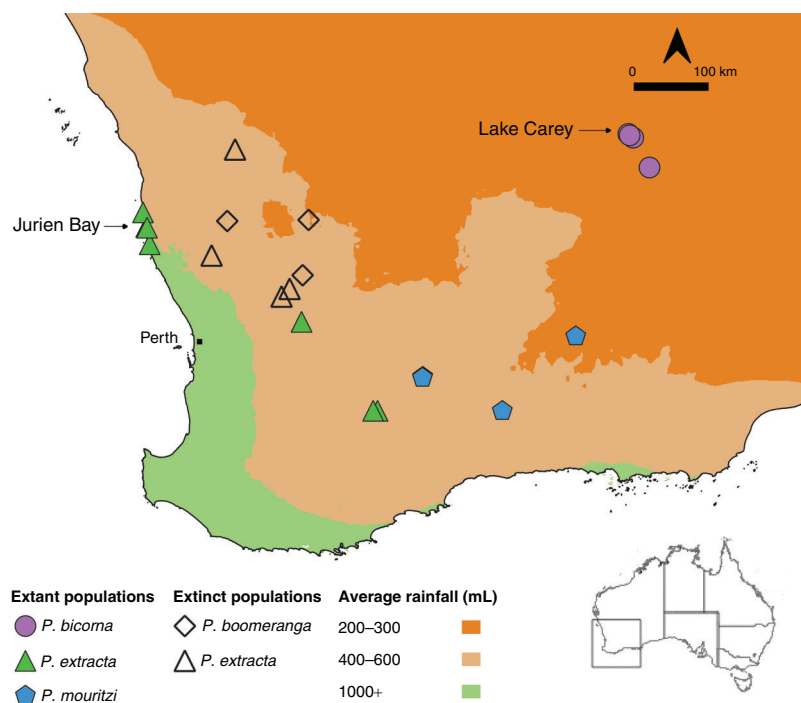


Fig. 1. Reported distributions of four species of *Parartemia* from Western Australia that have been identified as of conservation concern. Likely extinct populations of *P. boomeranga* and *P. extracta* are displayed as open symbols. Data from Timms *et al.* (2009).

Artemia

The genus *Artemia* comprises seven (Rogers 2013) or possibly nine (Naganawa and Mura 2017) species. Although *Artemia* is widespread and common in hypersaline lakes in most continents, only *Artemia franciscana* Kellogg and *Artemia parthenogenetica* Bowen & Sterling are present in Australia (McMaster *et al.* 2007; Asem *et al.* 2018). *A. franciscana* was introduced to Australia by humans to aid in salt production and is overwhelmingly restricted to constructed evaporative ponds (salt works; Timms and Hudson 2009; Asem *et al.* 2018). *A. parthenogenetica* may have also been introduced into salt works by humans (McMaster *et al.* 2007), but its presence in a range of lakes in south-western Australia could be the result of intercontinental bird-mediated dispersal followed by local dispersal (McMaster *et al.* 2007).

All *Artemia* species, including the two species found in Australia, have high dispersal capacity because their cysts float and are effectively transported by animals and wind (Timms and Hudson 2009). Despite this, *A. franciscana* does not seem to be spreading (Timms and Hudson 2009; Asem *et al.* 2018), but the distribution of *A. parthenogenetica* is increasing in south-western Australia, where it is mostly colonising degraded salt lakes (McMaster *et al.* 2007). It is unclear how the further spread of *A. parthenogenetica* may affect *Parartemia* species, but currently *A. parthenogenetica* appears limited to lakes not already occupied by *Parartemia* (McMaster *et al.* 2007).

Branchinella

Branchinella, with 40 described species, is the most speciose of the Australian anostracan genera (Timms 2015a, 2015b). Many species have only recently been described (Timms

2015b), with cryptic lineages identified using genetic data (Pinceel *et al.* 2013b). Only two species, *Branchinella buehnanensis* Geddes and *Branchinella simplex* Linder, are halophiles; the other species are either strictly freshwater or tolerant of only low levels of salinity (Pinceel *et al.* 2013a; Timms 2014). Further work is needed to determine whether *Branchinella halsei* Timms is conspecific with *B. simplex*, because these taxa are morphologically distinct but molecularly congruent (Pinceel *et al.* 2013b).

B. buehnanensis occurs, usually at salinities of $\sim 15 \text{ g L}^{-1}$ (limit 42 g L^{-1} ; Timms 2009c), in Queensland and north-western New South Wales, where it is listed as vulnerable under the *Fisheries Management Act* 1994 (Timms 2014). *B. simplex* is known, usually in salinities of $\sim 30 \text{ g L}^{-1}$ (limit 62 g L^{-1} ; Timms 2015b), from lakes in central Western Australia, northern South Australia and the southern Northern Territory.

The results of a molecular phylogeographic study suggest that the two halophilic species have evolved from different lineages (Pinceel *et al.* 2013b). *B. buehnanensis* and four halotolerant species comprise a clade that is estimated to have evolved from a freshwater ancestor somewhere between c. 62 and 23 million years ago, which coincides with increasing availability of temporary saline aquatic habitats in Australia (van de Graaff 1977; Pinceel *et al.* 2013a).

Notostraca

Triops

Both living notostracan genera, *Triops* and *Lepidurus*, occur in Australia (Pinder *et al.* 2005), although only *Triops* is known from salt lakes (Timms 2009c). Until recently, *Triops* was

thought to be represented in Australia by a single, widespread and morphologically variable species (*Triops australiensis* Spencer & Hall; Timms 2012a). However, a recent molecular appraisal has revealed the presence of a range of putative new species and predicted that further diversity would be found once lakes in central and western Australia are adequately surveyed (Murugan et al. 2009; Meusel and Schwentner 2017). Little ecological information is available for halophilic *Triops* except that undescribed species have been reported from Lake Carey (salinity 11.6–84.3 g L⁻¹, mean 30.3 g L⁻¹ from 10 records; Timms et al. 2006), the Esperance region in Western Australia (salinity 27 and 31 g L⁻¹, 2 records; Timms 2009b), the Paroo wetlands in New South Wales (salinity 0.3–19.3 g L⁻¹; Timms 1993) and Lake Torrens in South Australia (salinity ~16 g L⁻¹; Williams et al. 1998).

Cladocera

The bulk of Cladocera that occur in inland waters in Australia are restricted to fresh water, but three groups have representatives in salt lakes. These groups comprise: (1) six species of *Daphniopsis* (or *Daphnia*; see below); (2) two species of *Daphnia* (*Daphnia salinifera* Hebert and *Daphnia neosalinifera* Hebert) from the *Daphnia carinata* (King) subgenus; and (3) three species of chydorid: *Moina baylyi* Forró, *Moina mongolica* Daday and *Extremalona timmsi* Sinev & Shiel. All species are endemic to Australia except for *M. mongolica*, which is also known from northern Africa, Europe, the middle-east, Russia and China (He et al. 2001), notwithstanding that molecular data suggest that there are many unrecognised species of *Moina* (Bekker et al. 2016).

Colbourne et al. (2006) collected *D. salinifera* from Lake Wyora in Queensland and *D. neosalinifera* from Colac in Victoria and suggested that these species are usually found at lower salinities than the Australian species of *Daphniopsis*. However, apart from this, there are virtually no published data on the former two species, and they are not considered any further herein.

Daphniopsis

Taxonomy. Historically, the daphniids in Australian salt lakes were classified in the genus *Daphniopsis* (Sars) and just one species, *Daphniopsis pusilla* (Serventy), was recognised. Six species, all supported by genetic data (Hebert et al. 2002), have now been described (Sergeev and Williams 1985; Sergeev 1990a, 1990b; Hebert and Wilson 2000). Furthermore, one of six ehippia morphotypes identified by Kokkinn and Williams (1987), namely 'morphotype six' from Lake Eyre South, has not been accounted for by any described species (Hebert and Wilson 2000), and there are reports of undescribed species from salt lakes in the Wheatbelt region in Western Australia (Pinder et al. 2005) and the Eyre Peninsula in South Australia (Timms 2009a). The diversity of *Daphniopsis* in Australia is high, given that *Daphniopsis* is represented by a single species in either fresh or saline water in other regions where it occurs (Bayly 1995; Hebert and Wilson 2000; Gibson and Bayly 2007). Because all the described Australian species form a monophyletic group relative to other daphniids (Colbourne et al. 2006), it appears that this group has undergone a significant radiation in Australia.

The taxonomic status of *Daphniopsis*, specifically its relationship to the genus *Daphnia*, has long been debated (Schwartz and Hebert 1984). Benzie (2005) concluded that *Daphniopsis* as a whole is not morphologically or genetically distinct enough to warrant genus status and suggested that this taxon should be subsumed into the *Daphnia* subgenus *Ctenodaphnia*. Data from three mitochondrial genes support the view that *Daphniopsis* is a component of the genus *Daphnia* (Colbourne et al. 2006). Nevertheless, all the *Daphniopsis* species that were included in the above genetic study formed a monophyletic group, except for *Daphniopsis ephemeralis* (Schwartz & Hebert), which is the only representative of this taxon from the Northern Hemisphere. Most recent studies retain the name *Daphniopsis* (Säwström et al. 2009; Ismail et al. 2010a, 2011a; McCloud et al. 2018; Wang et al. 2019) and this practice has been adopted herein.

Ecology. Given that several species have only been recently described, it is difficult to gauge the reliability of historical accounts of species distributions, although, based on data from recent field records, it appears that south-western Australia has the greatest diversity (Hebert and Wilson 2000). All six described species have been found from at least two sites in this region and two, *Daphniopsis wardi* (Hebert & Wilson) and *Daphniopsis pusilla*, are endemic. Historical reports of the latter species from other parts of southern Australia predate the current taxonomy and are due to misidentification (Hebert and Wilson 2000). Another two species, *Daphniopsis quadrangulus* (Sergeev) and *Daphniopsis australis* (Sergeev & Williams), predominately occur in lakes in south-eastern Australia, but each has been recorded twice in south-western Australia (Fig. 2a). *Daphniopsis truncata* (Hebert & Wilson) and *Daphniopsis queenslandensis* (Sergeev) are common in Western Australia and South Australia, and *D. queenslandensis* also occurs in New South Wales and Queensland (Fig. 2b).

Osmoregulation has been studied in two species of *Daphniopsis* (*D. pusilla* and *D. australis*). Both were determined to be osmoregulators, where the haemolymph is hyperosmotic to the environment at salinities under 8 g L⁻¹, isosmotic in waters with salinity 8–20 g L⁻¹ and hypoosmotic in waters with salinity >20 g L⁻¹ (Aladin and Potts 1995).

All Australian species of *Daphniopsis* are halophilic. Field salinity data suggest that most species are common in 17–30 g L⁻¹, but nevertheless the salinity ranges of most species are very broad (Table 3). The salinity distribution of one species, *D. quadrangulus*, is mostly unknown because there are only two reported occurrences of this species (Table 3). Some reports of species from very high salinities should be viewed with caution because they may relate to preserved dead or dying specimens. For example, experimental data indicate that *D. australis* experiences significant mortality at salinities below 5 and above 33 g L⁻¹ (Ismail et al. 2010a), suggesting that reports of live *D. australis* at a salinity of 154.1 g L⁻¹ by Sergeev and Williams (1985) are unlikely.

Experimental data indicate that growth, reproduction and longevity in *D. australis* are influenced by both temperature and salinity, but the former is especially important between 16 and 25°C and the latter is especially important at salinities of 17–27 g L⁻¹ (Ismail et al. 2011b). *D. australis* experienced significant mortality at temperatures above 28°C (Ismail et al. 2010a), which is consistent with field observations that it occurs

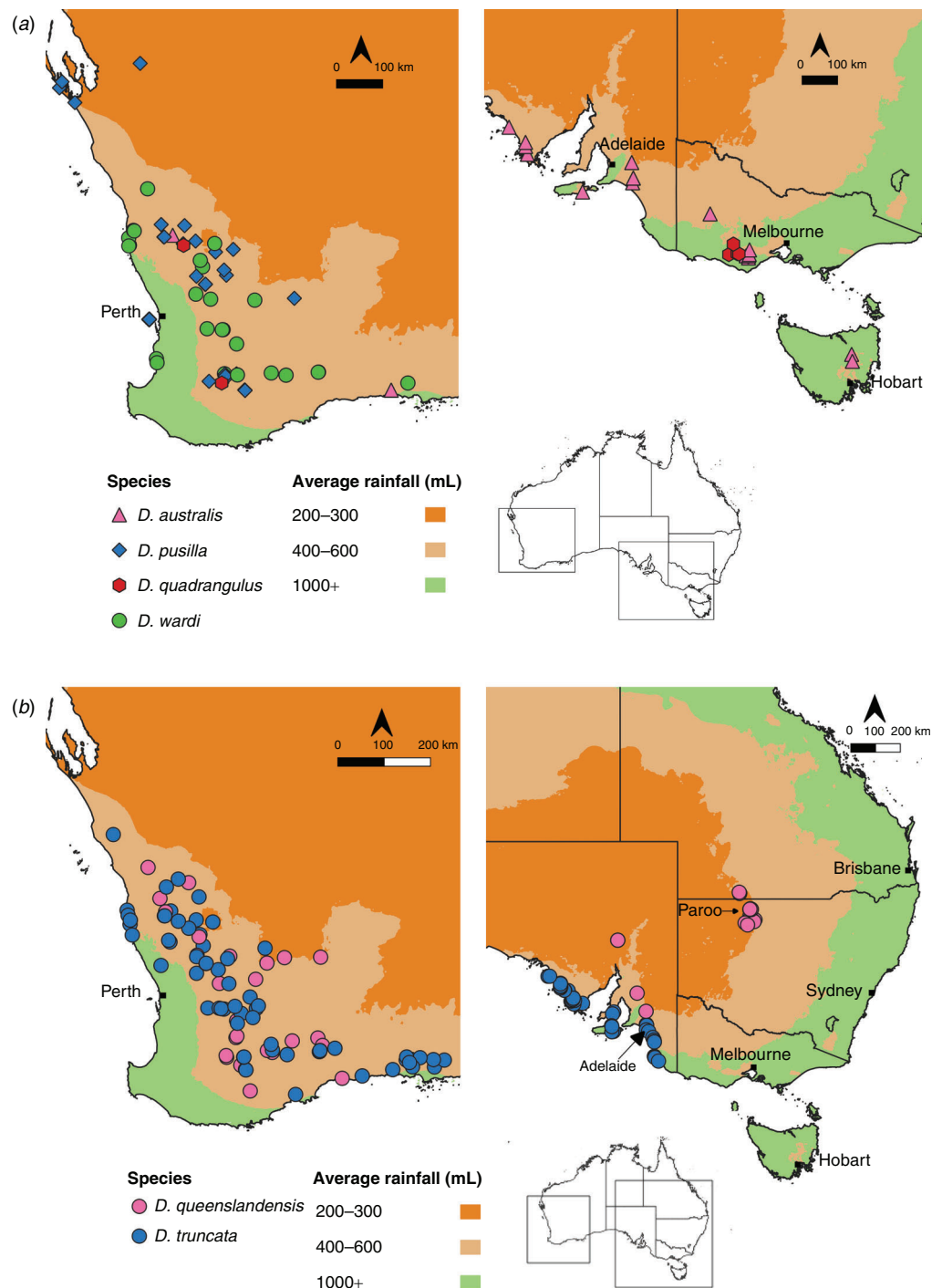


Fig. 2. Recent reported distributions of *Daphniopsis* in Australia. (a) *D. australis*, *D. pusilla*, *D. quadrangulus* and *D. wardi*; (b) *D. queenslandensis* and *D. truncata*. Data are from Edward (1983), Sergeev and Williams (1985), Sergeev (1990a, 1990b), Timms (1993, 1998, 2001, 2009a, 2009b, 2018), Williams *et al.* (1998), Halse *et al.* (2000a, 2000b), Colbourne *et al.* (2006) and unpublished records from the Western Australian Department of Biodiversity Conservation and Attractions.

Table 3. Salinity records for six species of Australian *Daphniopsis* based on field measurements

Sources are as follows: 1, Cale *et al.* (2004); 2, Edward (1983); 3, Halse *et al.* (2000a); 4, Pinder *et al.* (2005); 5, Pinder and Quinlan (2015); 6, Sergeev and Williams (1985); 7, Timms (1993); 8, Timms (1998); 9, Timms (2001); 10, Timms (2009a); 11, Timms (2009b); 12, Western Australian Department of Biodiversity Conservation and Attractions unpublished records; 13, Williams *et al.* (1998)

Species	Salinity (g L ⁻¹)		Sources
	Median (minimum–maximum)	Number of records	
<i>Daphniopsis</i>			
<i>australis</i>	17.2 (4–154.1)	16	4, 6, 10, 12
<i>pusilla</i>	29.7 (0.6–77.3)	42	1–4, 12
<i>quadrangulus</i>	22.7 (7.6–37.8)	2	4, 12
<i>queenslandensis</i>	20 (1–145.6)	45	1, 4, 7–9, 12, 13
<i>truncata</i>	24.1 (0.04–109.2)	60	1, 4, 5, 10–12
<i>wardi</i>	18.9 (5–245.7)	20	1, 4, 5, 12

seasonally in the winter–spring (Campbell 1994). Similarly, *D. queenslandensis* and *D. truncata* have been reported to be more abundant in winter–spring than in summer–autumn (Timms 2008, 2009b, 2018), despite minimal differences in salinity between seasons.

Life history. Like most daphniids, Australian *Daphniopsis* are cyclical parthenogens, although there are interspecific hybrids that reproduce by obligate parthenogenesis (Hebert and Wilson 2000). The switch from parthenogenesis to sexual reproduction and the production of desiccation-resistant ephippial eggs is triggered by unfavourable conditions, possibly one (or a combination) of low food availability, high population density, high salinity and high temperature (Sergeev and Williams 1983; Williams 1986; Ismail *et al.* 2010b). Detailed lifecycle data are available only for *D. australis* under laboratory conditions, as described by Ismail *et al.* (2010b). These data suggest that the parthenogenetic females usually live for 20–30 days, take 6–7 days to reach maturity and produce ~10–12 clutches during their lifetime. The ephippial females have a shorter lifespan and usually produce a maximum of two diapausing eggs. These females are produced under conditions of high population density and can switch from sexual to parthenogenetic reproduction, particularly at low and high food densities in the presence of males whose persistent attempts at mating may stress the females.

Trophic ecology. Little is known about the trophic ecology of *Daphniopsis* in Australian salt lakes. Based on information for other species of *Daphniopsis* (Säwström *et al.* 2009) and *Daphnia* (Taipale *et al.* 2012), these species likely consume microalgae and bacteria and are important herbivores in the lake food webs. Ismail *et al.* (2011a) fed different combinations of three microalgae species commonly used in aquaculture to *D. australis* and found that the composition of algae in the diet influenced the growth and reproductive output of individuals. Based on detailed observations of swimming behaviour under laboratory conditions, McCloud *et al.* (2018) developed the following hypotheses for *D. australis*: (1) males mainly occur in the water column, where they filter feed; (2) parthenogenetic females spend most of their time close to the bottom and mainly rely on benthic resources; and (3) the habits of the ephippial females are intermediate between those of the males and parthenogenetic females. The ostracod *Australocypris insularis* is known to predate on *Daphniopsis* (Campbell 1995).

Chydorids

The endemic halophile *M. baylyi* is widespread in central Australian salt lakes (Timms 2007) and the predominantly Northern Hemisphere *M. mongolica* has been encountered once in a coastal saline lake near Carnarvon in Western Australia (Fig. 3; Halse *et al.* 2000a). Very little information is available for *M. baylyi* other than it is commonly reported at salinities between 2.9 and 60 g L⁻¹ and up to 86.7 g L⁻¹, and is more common during the summer rather than winter filling of lakes (Timms 1987; Williams and Kokkinn 1988; Timms 1993, 2001; Williams *et al.* 1998). The monotypic *E. timmsi* is the most recently described halophilic cladoceran from Australia (Sinev and Shiel 2012) and is known only from two acidic salt lakes near Esperance, Western Australia (as *Alona* spp. in Timms 2009b).

Ostracoda

A diverse and heterogeneous range of halophilic ostracods occurs in Australian salt lakes. These ostracods can be divided into two main groups: (1) giant ostracods from the Australian endemic subfamily Mytilocypridinae (herein called giant ostracods); and (2) non-Mytilocypridinae ostracods (herein called small ostracods).

Giant ostracods

The giant ostracods are >3 mm in length and are a conspicuous component of the biota of Australian salt lakes.

Taxonomy. The morphotaxonomy of giant ostracods is relatively well established from the early work of De Deckker (1978, 1981a) and more recent work by Halse and McRae (2004). Halse and McRae (2004) added 2 new genera and 6 new species, bringing the total to 21 described species in 6 genera, although there are uncertainties regarding the status of a few described species (e.g. whether *Mytilocypris tasmanica* (McKenzie) and *Mytilocypris praenuncia* (Chapman) should be synonymised; Finston 2000). There are also reports of an undescribed species of *Mytilocypris* (Pinder *et al.* 2010; Quinlan *et al.* 2016) and of *Lacrimicypris* (L. Bourke, K. Brown, and G. Paczkowska, unpubl. data, 2018), both from Western Australia. Further species are likely to be found, particularly in remote areas (Halse and McRae 2004). Other than for some allozyme data that have helped resolve species questions in *Mytilocypris*

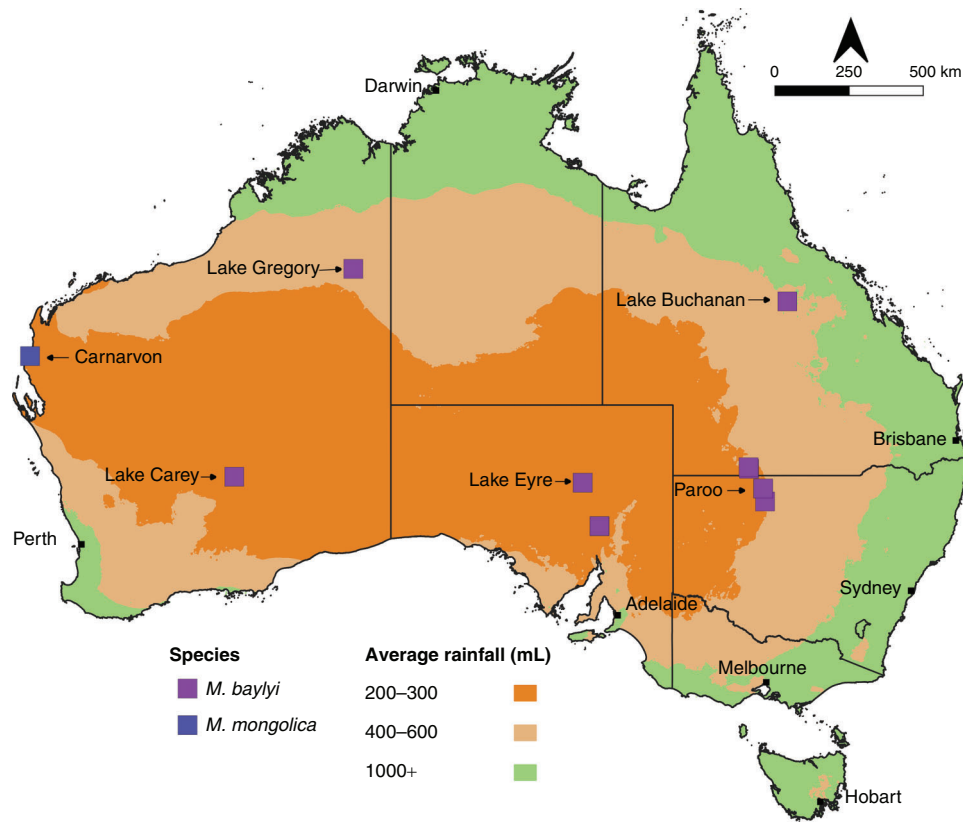


Fig. 3. Reported distributions of halophilic species of *Moina* in Australia. Data are from Timms (1987, 1993, 1998, 2001, 2018), Williams and Kokkinn (1988), Halse *et al.* (1998), Williams *et al.* (1998), Timms *et al.* (2006) and unpublished records from the Western Australian Department of Biodiversity Conservation and Attractions.

(Finston 2000; Halse and McRae 2004), the current taxonomy of giant ostracods is based on morphological characters, mainly the structure of the hemipenis.

Although some giant ostracod species are known only from fresh or low-salinity waterbodies, most are halophiles (Table 4). These halophiles occur in four of six genera: *Australocypris* (all seven species), *Repandocypris* (all two species), *Mytilocypris* (five of seven species, assuming *M. praenuncia* and *M. tasmanica* are distinct) and *Trigonocypris* (one of two species; Table 4). The broad taxonomic distribution of halophilic, low-salinity and freshwater forms suggests that halophily has probably evolved more than once in the Mytilocypridinae.

Ecology. Other than for some taxonomic and distribution information, very little is known about the ecology of giant ostracods, even for *Australocypris*, which is a very diverse, widespread and abundant component of the salt lake ecosystems.

The highest diversity of halophilic giant ostracods is in Western Australia (Table 4), particularly for *Australocypris*, which shows a marked decrease in species richness and endemism from west to east (Table 4). Most halophilic *Mytilocypris* species occur broadly across Australia, although *M. praenuncia-tasmanica* (see above) has only been reported from south-eastern Australia (Table 4). *Repandocypris* has one species only known from Western Australia (*Repandocypris austinensis* Halse & McRae) and another only known from South Australia (*Repandocypris gleneagles* Halse & McRae; Table 4). The

halophilic species of *Trigonocypris* (*Trigonocypris globulosa* (De Deckker)) is found in Western Australia, South Australia, New South Wales and Queensland (Table 4). Most halophilic species of giant ostracod are broadly distributed, although a few seem to have a very narrow range (Halse and McRae 2004). *Australocypris mongerensis* Halse & McRae is only known from a small mildly saline claypan next to Lake Monger in Western Australia (Halse and McRae 2004). However, knowledge of species distributions, particularly for those species first described by Halse and McRae (2004) like *A. mongerensis*, is likely to be incomplete.

With the exception of *A. mongerensis*, the halophilic species of giant ostracod have been collected from a broad and overlapping range of salinities (Table 4). Eight species have been recorded from salinities $>100 \text{ g L}^{-1}$ (Table 4). On average, *Mytilocypris* species tend to occur in a lower and narrower range of salinities than *Australocypris* species (Table 4). However, the salinity distribution of *Mytilocypris mytiloides* (Brady) is very broad and extends into highly saline water (Table 4). Both species of *Repandocypris* have only ever been found at salinities $>40 \text{ g L}^{-1}$ (Table 4), although they are only known from a few sites (Halse and McRae 2004). The salinity range of *T. globulosa* is broad and exceeds 100 g L^{-1} . Based on data for *M. praenuncia*, halophilic giant ostracods are osmoregulators (Aladin and Potts 1996).

All giant ostracods occur in neutral or slightly alkaline waters, but the distributions of *A. insularis* (Chapman),

Table 4. Salinity and distribution data for halophilic Australian giant ostracod species

Source: M. Rahman, Murdoch University, unpublished data. NSW, New South Wales; Qld, Queensland; SA, South Australia; Tas., Tasmania; Vic., Victoria; WA, Western Australia

Species	Salinity (g L ⁻¹)	Distribution
<i>Australocypris</i>		
<i>beaumonti</i>	40.9–73.7	South-western WA
<i>bennetti</i>	25–282.1	South-western WA, central WA
<i>dispar</i>	3.1–128	South-western WA, south-eastern SA
<i>insularis</i>	2–200.2	South-western WA, central WA, south-eastern SA, central SA, Vic.
<i>mongerensis</i>	11	Central-west WA
<i>rectangularis</i>	45.2–198.9	South-western WA ^A , south-eastern SA, Vic.
<i>robusta</i>	4.4–288	South-western WA ^A , central WA ^A , south-eastern SA, central SA, Vic., Tas.
<i>Mytilocypris</i>		
<i>ambigua</i>	1.3–64.6	South-western WA, south-eastern SA, Vic.
<i>henricae</i>	1.5–20	South-western WA ^A , south-eastern SA, Vic., south-eastern NSW
<i>mytiloides</i>	1.3–172.9	South-western WA, central WA, south-eastern SA, Vic., Tas.
<i>splendida</i>	0.3–77.3	South-western WA, south-eastern SA, central SA, Vic., north-western NSW, south-eastern NSW, south-eastern Qld, central Qld
<i>praenuncia</i>	4–51.1	South-eastern SA, Vic., Tas.
<i>tasmanica</i>	4–9	South-eastern SA, Vic., Tas.
<i>Repandocypris</i>		
<i>austiniensis</i>	40–117	Central WA
<i>gleneagles</i>	42–51	Central SA
<i>Trigonocypris</i>		
<i>globulosa</i>	0.7–122	South-western WA, central WA, north-western WA, central SA, north-west NSW, south-eastern Qld, central Qld

^ARecorded once from that area.

Australocypris bennetti Halse & McRae and *M. mytiloides* extend into acidic waters and all have been collected from waters with a pH <4 (Cale *et al.* 2004; Halse and McRae 2004; Timms 2009b). It is not known how these ostracods can survive in such acidic conditions, which are expected to dissolve the calcite carapace (De Deckker 2002).

Life history. All giant ostracods are dioecious and sexually reproducing (De Deckker 1977, 1983a). Giant ostracods produce desiccation-resistant eggs (Halse and McRae 2004), which re-establish populations after unfavourable or dry conditions (De Stasio 1989) and likely facilitate dispersal through attachment to or ingestion by waterbirds (De Deckker 1977; Green *et al.* 2008). Specific information on the life history, reproduction and dispersal of giant ostracods is mainly restricted to species of *Mytilocypris* (De Deckker 1977; Martens 1985; Finston 2000, 2002, 2004, 2007).

Trophic ecology. Giant ostracods tend to actively swim in the water column (De Deckker 1983a). This, and their large size, is likely related to the general absence of fish predators in the salt lakes or temporary freshwater waterbodies they inhabit (De Deckker 1983a). The diet of giant ostracods is poorly understood, although at least *A. insularis* consumes detritus and is also planktivorous and capable of significantly reducing the abundance of *Calamoecia*, *Daphniopsis* and *Diacypis* in microcosm experiments (Campbell 1995).

Small ostracods

Taxonomy. Most of the small ostracods in Australian salt lakes belong to the genera *Diacypis* and *Reticypis*. These genera contain seven and five described species respectively (Table 5), all of which are halophilic (De Deckker 1981b). They comprise the subfamily Diacypridinae, which is endemic to

Australia, and have no known recent freshwater or marine ancestors (De Deckker 1981b). The taxonomy of Diacypridinae has not been addressed since De Deckker (1981a, 1981c), and the extent to which it captures the biodiversity of this group is not clear. There are reports of multiple undescribed species of *Diacypis* and *Reticypis*, predominately from Western Australia (Williams 1984; Williams and Kokkinn 1988; Timms 1993; Pinder *et al.* 2005; Quinlan *et al.* 2016). Species diagnoses are based on the structure of the hemipenis (see fig. 13 in De Deckker 1981c for *Diacypis*). Some characters, such as variation in the carapace shape and size, are ecophenotypic at least in several *Diacypis* and *Reticypis* species (De Deckker 1981c, 1981d).

Other small halophilic ostracods from Australian salt lakes are the endemic *Platycypis baueri* (Herbst), *Patcypris outback* Halse & Martens and *Trilocypis horwitzii* Halse & Martens, which are all in the cosmopolitan subfamily Cyprinoidea (De Deckker and Geddes 1980; De Deckker 1981b; Karanovic 2012; Halse and Martens 2019). In addition, *Billcypris davisae* Halse & Martens has been collected from Lake Lefroy and Lake Cowan in the Goldfields region of Western Australia (Halse and Martens 2019). These are both large hypersaline lakes and this species is likely halophilic, although no information on the salinity at the time of its collection is available (Halse and Martens 2019). The endemic species *Cyprideis australiensis* Hartmann and *Leptocythere lacustris* De Deckker have also been reported from Australian salt lakes but, because these species have marine ancestries, they lack desiccation-resistant eggs and so are restricted to lakes with permanent water (De Deckker 1983a; Pinder *et al.* 2002; Schön *et al.* 2017). A few species of *Cyprinotus*, most notably *Cyprinotus cingalensis* Brady, which is widely distributed in

Table 5. State-based distributions of halophilic small ostracods in Australia

'X' indicates the species has been found in that state. NSW, New South Wales; Qld, Queensland; SA, South Australia; Tas., Tasmania; Vic., Victoria; WA, Western Australia. Sources are as follows: 1, *Cale et al.* (2004); 2, *De Deckker* (1979); 3, *De Deckker and Geddes* (1980); 4, *De Deckker* (1981*d*); 5, *De Deckker* (1981*c*); 6, *De Deckker* (1981*a*); 7, *De Deckker and Williams* (1982); 8, *Doupe and Horwitz* (1995); 9, *Edward* (1983); 10, *Geddes et al.* (1981); 11, *Halse et al.* (2000*a*); 12, *Halse et al.* (2000*b*); 14, *Halse and Martens* (2019); 15, *Pinder et al.* (2005); 16, *Pinder et al.* (2012); 17, *Pinder and Quinlan* (2015); 18, *Timms* (1987); 19, *Timms* (1993); 20, *Timms* (2009*a*); 21, *Timms* (2009*b*); 22, Western Australian Department of Biodiversity Conservation and Attractions; 23, *Williams* (1984); 24, *Williams et al.* (1990); 25, *Williams* (1995); 26, *Williams et al.* (1998); 27, *Williams and Kokkinn* (1988)

Species	WA	SA	Vic.	NSW	Qld	Tas.	Source
<i>Diacypris</i>							
<i>compacta</i>	X	X	X		X		1, 3, 10, 15, 17, 18, 20–26
<i>dictyote</i>	X	X		X			1, 5, 15, 19–23, 26
<i>dietzi</i>	X	X	X	X		X	3, 7, 11, 19, 22, 24, 25
<i>fodiens</i>	X	X					3, 10, 15, 20, 22, 23
<i>phoxe</i>	X	X					5, 15, 22
<i>spinosa</i>	X	X	X			X	1, 5, 7, 8, 9, 12, 15–17, 20–24
<i>whitei</i>	X	X					3, 10, 15, 20–23, 26
<i>Reticypis</i>							
<i>clava</i>	X	X	X				1, 6, 10, 15, 17, 22–24, 26
<i>herbsti</i>		X	X	X			3, 19, 24
<i>kurdimurka</i>	X	X					6, 22, 27
<i>pinguis</i>	X			X			4, 11, 15, 22
<i>walbu</i>	X	X		X	X		1, 2, 6, 15, 18, 19, 26
<i>Platycypis</i>							
<i>baueri</i>	X	X	X				1, 3, 10, 15, 17, 20–24, 26
<i>Patcypis</i>							
<i>outback</i>	X						14
<i>Trilocypis</i>							
<i>horwitzi</i>	X						14

south-east Asia, are found in Australian salt lakes (*Karanovic* 2008), but usually in low-salinity waters, and are more halotolerant than halophilic (*Timms* 1993, 2009*b*; *Pinder et al.* 2002).

Ecology. Knowledge of the biology of the small halophilic ostracods from Australian salt lakes is rudimentary. Two of the Cyprinotinae species (*P. outback* and *T. horwitzi*) have only recently been described (*Halse and Martens* 2019) and thus far reported from only one or a small number of sites in Western Australia. These species are not considered in the following discussion. Understanding the ecology of *Diacypris* and *Reticypis* is complicated by the fact that these taxa are not identified to species level in many studies (*Timms* 1998, 2018; *Timms et al.* 2006).

All described *Diacypris* and *Reticypis* species, as well as *P. baueri*, have broad and overlapping geographic distributions (Table 5). All these species are known from both Western Australia and South Australia, except for *Reticypis herbsti* McKenzie (known from South Australia but not Western Australia) and *Reticypis pinguis* De Deckker (known from Western Australia but not South Australia; Table 5). Some of these species also occur in other states, the exact details of which vary from species to species (Table 5). Many species, such as *Diacypris phoxe* De Deckker, *R. herbsti*, *Reticypis kurdimurka* De Deckker, *R. pinguis* and *Reticypis walbu* De Deckker, are patchily distributed (i.e. reported from a small number of sites that are typically separated by hundreds or even thousands of kilometres; Fig. 4).

Diacypris and *Reticypis* species generally have broad and overlapping salinity tolerances, although some species are more commonly found at higher salinities than others (Fig. 5). For example, *Diacypris spinosa* De Deckker is more common at lower salinities (median 14.7 g L⁻¹) than *Diacypris whitei* (Herbst) (median 69.6 g L⁻¹), *Diacypris fodiens* (Herbst) (median 73.6 g L⁻¹) and *R. herbsti* (median 115.1 g L⁻¹; Fig. 5; De Deckker and Geddes 1980; Pinder et al. 2005). Other species, like *Diacypris compacta* (Herbst) and *P. baueri*, occur across a broad range of salinities, sometimes in excess of 200 g L⁻¹ (Fig. 5; Williams et al. 1990). *D. spinosa* is an osmoregulator (Aladin and Potts 1996), and the other small halophilic ostracods are probably likewise.

It is often said that dispersal of inland ostracods, including halophilic small and giant species, is mediated by birds (De Deckker 1977; Halse 2002). This is supported by the fact that ostracod eggs have been hatched from the faeces of waterbirds that frequent the temporary wetlands in arid Australia, although no information on the species hatched is available (Green et al. 2008).

Copepoda

Copepods are widespread and common in Australian salt lakes, with three orders, namely Calanoida (three species), Cyclopoida (five species) and Harpacticoida (i.e. *Mesochra baylyi* Hamond), represented.

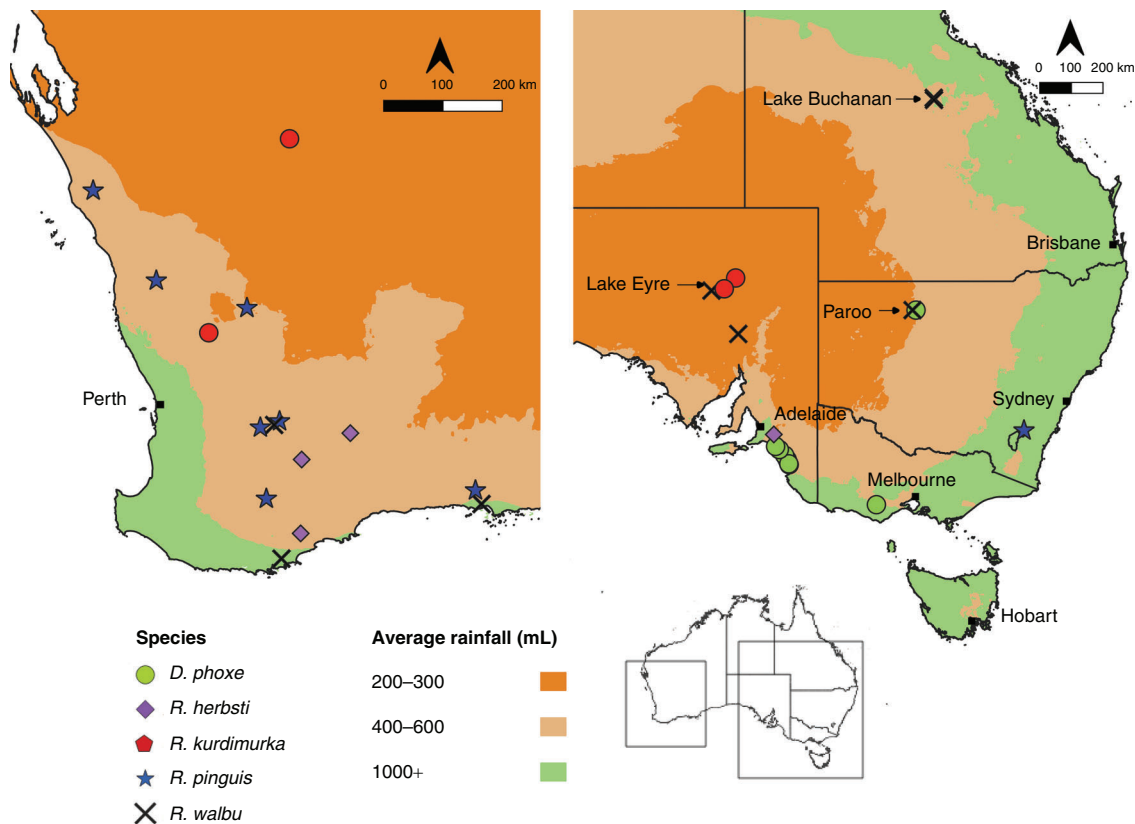


Fig. 4. Reported distributions of four species of *Reticypris* and *Diacypris phoxe* to illustrate the patchy occurrence of small ostracods. Data are from De Deckker (1979, 1981a, 1981c, 1981d), De Deckker and Geddes (1980), Timms (1987, 1993), Williams and Kokkinn (1988), Williams *et al.* (1990, 1998), Halse *et al.* (2000a) and unpublished records from the Western Australian Department of Biodiversity Conservation and Attractions.

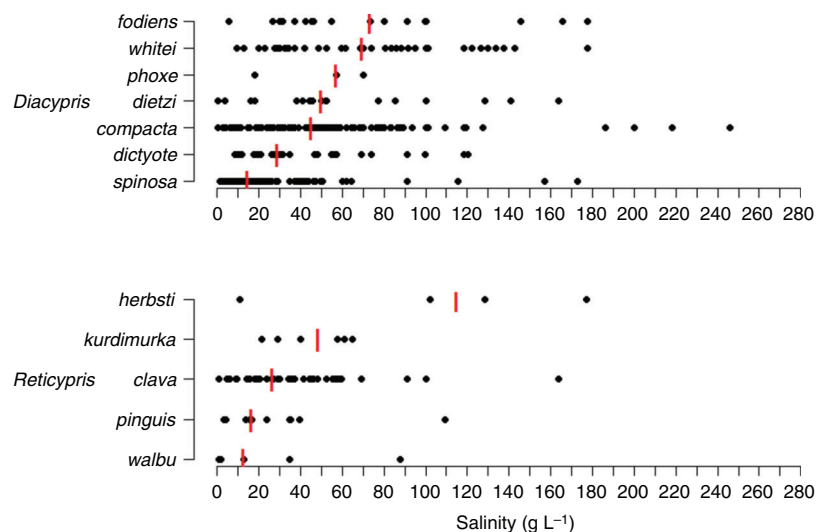


Fig. 5. Salinity distributions of *Diacypris* and *Reticypris* species from field data. The red lines indicate median values. Data are from De Deckker and Geddes (1980), De Deckker (1981a, 1981c, 1981d), Geddes *et al.* (1981), De Deckker and Williams (1982), Edward (1983), Williams (1984, 1995), Williams and Kokkinn (1988), Williams *et al.* (1990, 1998), Doupe and Horwitz (1995), Halse *et al.* (2000a, 2000b), Cale *et al.* (2004), Pinder *et al.* (2005), Timms (2009a, 2009b), Pinder *et al.* (2012), Pinder and Quinlan (2015) and unpublished data from the Western Australian Department of Biodiversity Conservation and Attractions.

Calanoida

Taxonomy. All three halophilic calanoids that occur in Australian salt lakes belong to the genus *Calamoecia*. The taxonomy of these species (*Calamoecia salina* (Nicholls), *Calamoecia clitellata* Bayly and *Calamoecia trilobata* Halse

& McRae) has been unchanged since Bayly (1962), except for the description of *C. trilobata* (Halse and McRae 2001). Other *Calamoecia* occur in Australian freshwater environments (Bayly and Boxshall 2009). Mitochondrial 16S and nuclear 28S gene data do not support suggestions, based on

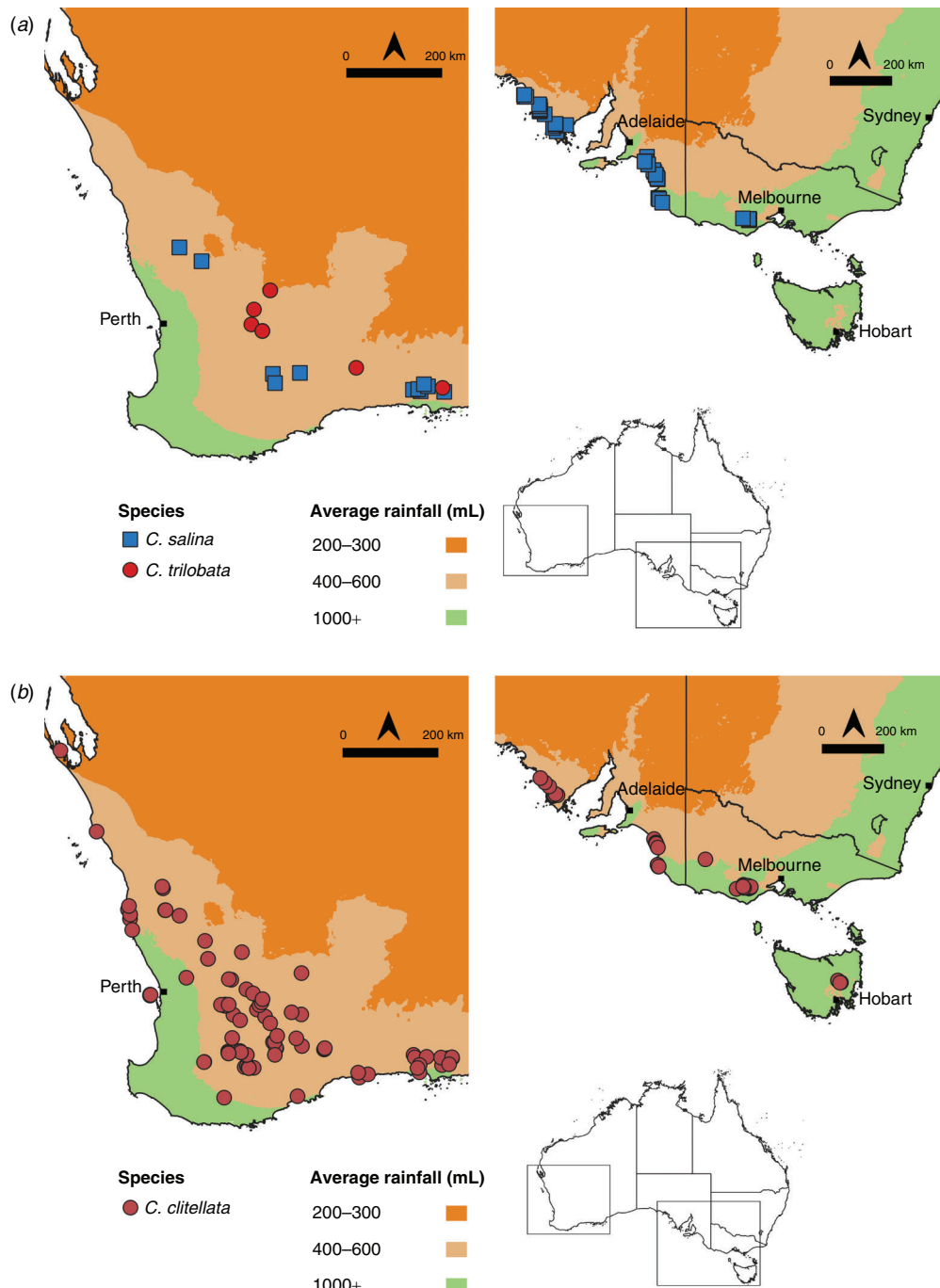


Fig. 6. Reported distribution of *Calamoecia* in Australia: (a) *C. salina* and *C. trilobata* and (b) *C. clitellata*. Data are from Bayly and Williams (1966), Bayly (1970), Geddes (1976), De Deckker and Geddes (1980), Geddes *et al.* (1981), De Deckker and Williams (1982), Edward (1983), Williams (1984, 1995), Williams *et al.* (1990), Timms (2009a, 2009b), Timms *et al.* (2014) and unpublished data from the Western Australian Department of Biodiversity Conservation and Attractions.

morphological data (Bayly 1962), that the salt lake and fresh-water species should be placed in different genera (Adamowicz et al. 2010). In addition, these gene data suggest that *C. clitellata* colonised salt lakes via fresh water (Adamowicz et al. 2010) rather than directly from the marine environment, as has been suggested previously (Maly 1996).

Ecology. Both *C. clitellata* and *C. salina* occur throughout mainland southern Australia; the former is also found in Tasmania (Fig. 6). By contrast, *C. trilobata* is endemic to Western Australia (Fig. 6a).

Despite being osmoconformers (Bayly 1972), these calanoids are often reported from high salinities; for example, *C. clitellata* and *C. salina* have been reported from salinities up to 132 and 195 g L⁻¹ respectively (De Deckker and Geddes 1980; Timms 2009b). Both *C. salina* and *C. clitellata* are often found in the same lake, with *C. salina* succeeding *C. clitellata* at higher salinities, which is attributable to its higher hatching salinity (61.4–82.9 g L⁻¹) than that of *C. clitellata* (20–71 g L⁻¹; Geddes 1976). Less information is available for *C. trilobata*, which has only been reported from acidic salt lakes (pH 2.96–6.3) and primarily occurs at salinities of ~31–63 g L⁻¹ (Pinder et al. 2005; Timms 2009b). Some records of *C. trilobata* at salinities of 160 and 240 g L⁻¹ are probably of dead, brine-preserved individuals (Halse and McRae 2001) and therefore overestimate the upper salinity tolerance of this species (Halse and McRae 2001).

Life history. *Calamoecia*, like most salt lake crustaceans, produces two types of eggs: (1) subitaneous eggs that maintain populations during favourable conditions; and (2) resistant resting eggs that allow populations to persist through unfavourable environmental conditions (Whitehead 2005). These resting eggs are likely important for dispersal. Waterbirds are considered the most likely vector for dispersal (Whitehead 2005), although water or human movement may also be important (Maly et al. 1997). Population genetic data for *C. clitellata* suggest that gene flow is restricted between regions and drainage basins, and sometimes even on fine spatial scales, and therefore populations are typically isolated and self-sustaining (Whitehead 2005). However, occasional dispersal may have significant effects on evolutionary timescales, resulting in secondary contact between highly divergent lineages (Whitehead 2005).

Trophic ecology. Apart from reports that *Calamoecia* feed on microalgae (Whitehead 2005) and are preyed upon by *A. insularis* and potentially other giant ostracods (Campbell 1995), little is known of the trophic ecology of the salt lake calanoids.

Cyclopoidea

In Australian salt lakes, cyclopoids are represented by three endemic species from two genera, as well as the cosmopolitan halophiles *Apocyclops dengizicus* (Lepeshkin) and *Pescecylops arnaudi* (Sars) (Anufrieva 2015). However, the taxonomy of these copepods is confused, due, in part, to a series of name changes (Table 6) and to reports of a significant number of undescribed halophilic species from throughout Australia (De Deckker and Geddes 1980; Brock and Shiel 1983; Williams and Kokkinn 1988; Williams et al. 1990; Timms 1993; Timms and Boulton 2001; Pinder et al. 2005). It is impossible to meaningfully review the biology of these species until the taxonomy is resolved.

Harpacticoida

The harpacticoid genera *Mesochra* and *Schizopera* occur in Australian salt lakes, but only one described species, *M. baylyi*, is known to be halophilic (Hamond 1971; De Deckker and Geddes 1980; Brock and Shiel 1983). Reports of other harpacticoid species from Australian salt lakes are either of undescribed species or of marine and estuarine species that have colonised permanent or semi-permanent coastal salt lakes (Bayly 1970; Hamond 1971; Timms 1993, 2001, 2009b; Pinder et al. 2005). *M. baylyi* is widely distributed in southern Australia (south-western Western Australia, south-eastern South Australia, Victoria and Tasmania) and has been reported in waters with salinities up to 129 g L⁻¹, but is typically reported in waters with salinities below 25 g L⁻¹ (De Deckker and Geddes 1980; De Deckker and Williams 1982; Pinder et al. 2005). It is one of only a few halophilic species suggested to have colonised salt lakes directly from the marine environment (Williams 1981).

Isopoda

The oniscoid *Haloniscus searlei* Chilton is the only described halophilic isopod that occurs in Australia, although recent molecular phylogenetic analyses have suggested that the diversity of this genus is underappreciated (Guzik et al. 2019). The putative new species (revealed by molecular data) are mostly from groundwater, freshwater or semiterrestrial environments, but at least one is from salt lakes (Cooper et al. 2008; Stringer et al. 2019).

Table 6. Names used for *Pescecylops* and *Meridiecylops*
For further details see Fiers (2001), Tang and Knott (2009) and Karanovic et al. (2011).

Current nomenclature	Names used
<i>Pescecylops arnaudi</i> (Sars)	<i>Microcylops arnaudi</i> in Geddes (1976), Morton and Bayly (1977), Geddes et al. (1981) and Williams et al. (1990) <i>Metacylops arnaudi</i> (Sars) in Halse et al. (2000a) and Timms (2009a)
<i>Meridiecylops baylyi</i> Fiers	<i>Microcylops arnaudi</i> in Bayly and Williams (1966) <i>Metacylops arnaudi sensu</i> Kiefer in Halse et al. (2000a) and Pinder et al. (2002). <i>Meridiecylops baylyi</i> in Pinder et al. (2005) and Pinder and Quinlan (2015).
<i>Meridiecylops platypus</i> Fiers	<i>Microcylops platypus</i> in Geddes et al. (1981) and Williams and Kokkinn (1988) <i>Metacylops platypus</i> in Timms (1993) and Timms (2001) <i>Meridiecylops platypus</i> in Timms et al. (2006)

H. searlei sensu lato is geographically widespread, occurring in seasonal and permanent salt lakes in Western Australia, South Australia, Victoria and Tasmania (Williams 1983; Guzik *et al.* 2019). It is a powerful osmoregulator commonly found in salinities from 3.6 to 161 g L⁻¹ (Williams 1983). It primarily grazes on diatoms, but has been noted to occasionally consume chironomid larvae (Blinn *et al.* 1989). This species is unusual among halophilic crustaceans because it has colonised the salt lakes via a terrestrial rather than freshwater ancestor (Ellis and Williams 1970). Related to this is the fact that it survives dry lake periods as an adult rather than with resistant eggs (Williams 1983) and appears unable to colonise lakes that only fill episodically (Williams and Kokkinn 1988; Timms 2008).

Halophilic biota: Gastropoda

Coxiella

All halophilic gastropods in Australian salt lakes belong to the endemic genus *Coxiella*, the only gastropod genus in the world to consist exclusively of halophilic species. *Coxiella* is currently placed within the family Pomatiopsidae, which mainly contains freshwater species (Wilke 2019). However, molecular phylogenetic analysis suggests that *Coxiella* and *Tomichia*, a morphologically similar genus from Africa that includes freshwater, brackish and halophilic species, may merit recognition as a separate family (Tomichiidae; Wilke *et al.* 2013). Despite the ubiquity and abundance of *Coxiella* in Australian salt lakes, the genus is poorly studied (Williams and Mellor 1991; Pinder *et al.* 2002).

Taxonomy

The taxonomy of *Coxiella* has effectively remained unchanged since it was reviewed by Macpherson (1957), who listed 10 species. Kendrick (1978) added one further species (*Coxiella roeae*), known only from fossil material from Western Australia. *Coxiella badgerensis* (Johnston) has since been synonymised with *Coxiella striata* (Reeve) (Smith 1979), and *Coxiella molesta* Iredale and *Coxiella minima* Macpherson have not been collected since they were initially described (for a discussion about *C. molesta*, see Bayly and Williams 1966). Currently, nine extant species in the two subgenera *Coxiella*

(eight species) and *Coxielladda* (one species) are recognised (Davis 1979; Wilke 2019), with seven species having been collected in recent decades. The discussion below focuses on these seven species.

Current species descriptions are based on external shell and operculum characters. Subsequent studies have found single specimens that exhibit the diagnostic morphological characteristics of more than one species (De Deckker and Geddes 1980; Williams and Mellor 1991) or have suggested the existence of undescribed species (Pinder *et al.* 2005; Timms 2009b). In addition, operculum characters have been found to vary with salinity (De Deckker and Geddes 1980) and size (Williams and Mellor 1991). Currently, researchers are unable to confidently identify *Coxiella* material to species level (Williams and Mellor 1991; Pinder *et al.* 2002; Timms 2009b). Owing to this inadequate taxonomy, all species-level information in this group, included that presented herein, must be considered tentative.

Ecology

Coxiella species are mostly found in southern Australia, including Tasmania, but also occur in some parts of central and southern Queensland (Williams and Mellor 1991; Timms 1998). Western Australia is the most diverse area for *Coxiella*, with six described species, including four that are endemic to this region: *Coxiella striatula* (Menke), *Coxiella exposita* (Iredale), *Coxiella glabra* Macpherson and *Coxiella pyrrhostoma* (Cox) (Table 7). *Coxiella glauerti* Macpherson occurs in both Western Australia and South Australia, whereas *C. striata* occurs in South Australia, Victoria and Tasmania, but not Western Australia (Table 7). *Coxielladda gilesi* (Angas) has been reported from remote inland lakes in Western Australia, South Australia and Queensland (Macpherson 1957; Timms 1998).

The geographical ranges of some *Coxiella* species overlap, but different species rarely appear to occur in the same water-body, although there are reports of *C. striata* and *C. glauerti* co-occurring in lakes on the Eyre Peninsula (Timms 2009a). Weston (2007) identified four *Coxiella* species from bird faecal samples collected from a single lake in Western Australia, but the species identifications are questionable.

Table 7. Reported distributions for recently identified *Coxiella* and *Coxielladda* species
Qld, Queensland; SA, South Australia; Tas., Tasmania; WA, Western Australia

Species	Description	Distribution
<i>Coxiella</i>		
<i>exposita</i>	Iredale (1943)	Endemic to south-western WA
<i>glabra</i>	Macpherson (1957)	Endemic to south-western WA
<i>striatula</i>	Menke (1843)	Endemic to south-western WA ^A
<i>pyrrhostoma</i>	Cox (1868)	Endemic to south-western WA
<i>glauerti</i>	Macpherson (1957)	South-western WA and Eyre Peninsula
<i>striata</i>	Reeve (1842)	South-eastern Australia including the Eyre Peninsula and Tas.
<i>Coxielladda</i>		
<i>gilesi</i>	Angas (1877)	Central WA and SA, central and south-eastern Qld ^B

^AReported from fossil deposits in Streaky Bay, South Australia (see Cotton 1942).

^BReported from the Wheatbelt, Western Australia, but the validity of the identification is unclear (see Pinder *et al.* 2002).

Coxiella are osmoconformers (Williams and Mellor 1991). Most field records of active individuals are from a salinity range between 10 and 70 g L⁻¹; the lower and upper recorded ranges are 0.3 and 130 g L⁻¹ (Geddes *et al.* 1981; Timms 1983; Williams *et al.* 1990; Williams and Mellor 1991; Pinder *et al.* 2005). These field data cannot always be accurately ascribed to particular species due to taxonomic uncertainties. Experimental data indicate that the adults of one species (possibly *C. striata*) from Lake Tallinga in South Australia have a broad salinity tolerance, with LD₅₀ limits of 2 and 95.5 g L⁻¹ for gradual acclimation, and 6 and 83 g L⁻¹ for a direct transfer (Williams and Mellor 1991). The extent to which *Coxiella* species vary in salinity tolerance is not clear, but some (e.g. *C. glauerti*) seem to occur at higher salinities than others (e.g. *C. striata*; Timms 2009a; Timms *et al.* 2014).

Life history

The life histories of *Coxiella* species are poorly known. Species are dioecious and reproduction is sexual and probably iteroparous (Williams and Mellor 1991). Individuals are long-lived (compared with most halophilic invertebrates), possibly for as long as 2 years (Williams and Mellor 1991). Related to this, *Coxiella*, like *H. searlei*, aestivate as adults during dry lake periods in areas of high humidity (e.g. under plant or algal mats) or in plates of densely packed individuals to reduce desiccation (Williams 1985; Timms *et al.* 2014). Laboratory experiments suggest that the *Coxiella* from Lake Tallinga can aestivate for at least 2 months with little mortality (Williams and Mellor 1991), whereas aestivating specimens of *C. striata* have been reanimated from lakes known to have been dry for at least 3 months (De Deckker and Geddes 1980). The total length of time that individuals can survive aestivated, and whether this varies among species, is not known. However, it must be limited because *Coxiella* are found in permanent and seasonal lakes, but not in episodic ones (Williams 1998a).

Trophic ecology

The diets of *Coxiella* species have not been investigated directly, but it has been suggested that they feed on benthic algae or detritus (De Deckker 1982; Bayly 1993). *Coxiella* are known to be consumed by native fish (e.g. *Galaxias maculatus* (Jenyns), *Atherinosoma microstoma* (Günther), *Pseudogobius olorum* (Sauvage) and *Philypnodon grandiceps* (Kreffit); Chessman and Williams 1987; Becker and Laurenson 2007) and introduced fish (e.g. *Cyprinus carpio* Linnaeus; Khan 2003) in some waterbodies. They are also an important food source for some waterbirds, such as the hooded plover *Thinornis rubricollis* in south-western Australia, where *Coxiella* has been found to make up to 90% of the diet (Weston 2007).

Discussion

This study synthesises available information on the halophilic macroinvertebrates of Australian salt lakes, focusing on crustaceans and gastropods. The results show that our understanding of the taxonomy and diversity of some groups has improved markedly since the main previous review of these organisms (De Deckker 1983b), as has our knowledge of aspects of the ecology and life histories of a small number of

species, although many knowledge gaps remain. This progress and these gaps, and their conservation implications, are discussed below.

Unique biodiversity

This review highlights the evolutionary distinctiveness of the halophilic macroinvertebrates in Australian salt lakes. The fauna is dominated by crustaceans and molluscs, of which 1 family (Parartemiidae), 2 subfamilies (Diacypriinae and Mytilocypridinae), 11 genera (*Parartemia*, *Extremalona*, *Australocypris*, *Repandocypris*, *Diacypris*, *Reticypis*, *Platycypis*, *Patcypris*, *Trilocypis*, *Meridiacyclops* and *Coxiella*) and 74 of the 79 described species are endemic to these lakes. These high levels of endemism are likely due to a long association between the fauna and Australian salt lake environments or their precursors (De Deckker 1981b; Williams 1981). The number of macroscopic halophilic invertebrate species in Australian salt lakes is also higher than in lakes elsewhere in the world (Alonso 1990; Bayly 1993; Williams *et al.* 1995; De Los Rios-Escalante and Amarouayache 2016). In addition, many components of the Australian fauna are capable of tolerating extreme levels of salinity, and some have other unusual characteristics. For example, although ostracod species are usually absent from environments with pH <5 (because a lower pH inhibits formation of the calcite carapace; Ruiz *et al.* 2013), several species of ostracod occur in highly acidic salt lakes (Timms 2009b). By virtue of its distinctiveness, the invertebrate biodiversity of Australian salt lakes is of high conservation value.

Taxonomy

What we do not know, we cannot protect [Martens and Savatnalinton 2011].

In the past 20 years, considerable progress has been made regarding the discovery and description of species in a few groups of Australian salt lake invertebrates, notably *Parartemia* and giant (Mytilocypridinae) ostracods (Halse and McRae 2004; Timms and Hudson 2009; Timms 2010b). However, the taxonomy of other groups is much less advanced and in some cases (e.g. *Coxiella* gastropods and cyclopoid copepods) the current taxonomy does not allow consistent and accurate species identifications (Williams and Mellor 1991; Pinder *et al.* 2002). Many new species, and sometimes even new genera, have been discovered in those groups that have been subject to recent taxonomic revision, and more biodiversity likely remains to be discovered, especially in poorly studied groups and regions.

Molecular data have substantially changed our understanding of the diversity of many groups, such as *Triops* (Meusel and Schwentner 2017), *Daphniopsis* (Hebert and Wilson 2000), *Parartemia* (Remigio *et al.* 2001), *Mytilocypris* (Finston 2000, 2007), *Branchinella* (Pinceel *et al.* 2013a) and *Haloniscus* (Guzik *et al.* 2019). Nevertheless, the discovery and identification of Australian salt lake invertebrates is still overwhelmingly reliant on morphotaxonomy. Using molecular and morphological data to document the full extent of the diversity of halophilic invertebrates of Australian salt lakes is essential to progress our understanding and conservation of these ecosystems.

Ecology

The species diversity of halophilic invertebrates is highest in Western Australian semi-arid and arid regions. Therefore, this part of Australia is an important region for the conservation of these invertebrates, especially because the salt lakes here are experiencing exceptionally high levels of disturbance due to climate change, secondary salinisation and mining (Halse *et al.* 2003; Timms 2005; Nielsen and Brock 2009).

Conservation planning and assessment requires a sound knowledge of species' distributions and how these are changing through time (Cardoso *et al.* 2011). This point is illustrated by attempts to assess the conservation status of *Parartemia* species, where concerns about *P. contracta* have decreased through time as more intensive sampling has revealed a range of additional populations while concerns about *P. extracta* have increased because temporal sampling suggests that the number of populations and the geographic range of this species are limited and shrinking (Timms *et al.* 2009; Pinder and Quinlan 2015).

Our knowledge of the geographic distribution of most halophilic invertebrates is incomplete. This problem is particularly acute for those species that are difficult to identify because either the existing taxonomy is incomplete or because they cannot be reliably identified using morphological characters (e.g. *Coxiella*). It is also problematic for species that are rare or occur in remote locations. In addition, some older distributional data may be misleading because they are based on outdated taxonomy (e.g. *D. pusilla*). Obtaining a comprehensive inventory of the distribution of halophilic invertebrates in Australian salt lakes is a challenging prospect, partly because there are many lakes that either occur in remote locations or hold water infrequently. Surveying some sites may benefit from a flexible sampling approach, such as raising individuals from egg banks (Timms 2012b). Analysis of environmental DNA in dry sediments could also become an important survey tool but requires a database of reference sequences and a well-developed taxonomy to be effective (Cristescu and Hebert 2018).

The available evidence indicates that most of the halophilic invertebrates in Australia are osmoregulators (e.g. *Parartemia*, giant and small ostracods, *Daphniopsis*), but some are osmoconformers (e.g. calanoid copepods and *Coxiella*). Regardless, most species appear to have broad and overlapping salinity tolerances and many are able to tolerate extremely high salinities, as described above. However, the bulk of information on salinity tolerances in these invertebrates is derived from scattered field data. Such data do not necessarily indicate the optimal conditions for reproduction or completing the lifecycle, which may be much more restrictive than the conditions adults can survive (Hammer 1986). Those species that can only reproduce or complete their lifecycle at low salinity, or within a narrow salinity range, are seemingly more vulnerable to increases or changes in the salinity of the lakes.

Lake Corangamite, a large permanent lake in western Victoria, provides a clear example of how increasing salinity can have a big effect on resident organisms. Due to the diversion of the main inflow creek dating back to the 1960s, water levels in this lake have fallen and salinity has increased, resulting in a change in the biota from one characteristic of moderate salinity (35–50 g L⁻¹) to one of higher salinity (50–100 g L⁻¹;

Williams 1995). Associated with this, populations of halophilic species have been lost from the lake (e.g. *C. striata*). Some salt lakes in central Western Australia and elsewhere are being subjected to the discharge of highly saline waste water from mining activities (Timms 2005; Timms *et al.* 2006). How these lakes are being affected by increased salt loads is unclear (Timms 2005) but, based on the Lake Corangamite example, community changes and local extinctions are possible.

Two interesting features of the distribution of the halophilic invertebrates are that: (1) some species are much more common and broadly distributed than others, even congeners; and (2) congeneric species rarely occur in the same lake, even though many have overlapping geographic and salinity distributions (see above). It is currently unknown whether the common and widespread species have relatively broader ecological tolerances, greater dispersal capacity or both (Williams 1984). The factors controlling the distribution of halophilic invertebrates are likely to be complex. The effects of salinity are correlated with other chemical and physical changes; for example, the availability of dissolved oxygen decreases as salinity (and temperature) increases (Williams 1998a). Thus, although the ecological tolerances of species are usually measured in terms of salinity, this is an oversimplification. Abiotic factors alone are unlikely to explain why congeneric species are rarely found in the same lake, although more intensive sampling and better taxonomy may lead to more examples of co-occurrence. Understanding the relative importance of various abiotic and biotic factors in controlling the distribution of the halophilic invertebrates is critical to predicting how species and communities will respond to perturbations and for developing effective interventions (Nielsen and Brock 2009).

Life history

Detailed life history information is typically available for one species for each of the main types (e.g. ostracod, cladoceran, gastropod) of halophilic macroinvertebrate in Australia. This information indicates that these invertebrates' life histories are fundamentally similar to those of their relatives from other environments (Ellis and Williams 1970; Finston 2002; Ismail *et al.* 2011b). Most species have a rapid life cycle, with short-lived individuals. Multiple generations may be produced while environmental conditions remain favourable and desiccation-resistant eggs are used to survive dry or unfavourable conditions (Timms 2014). By contrast, *H. searlei* and *Coxiella* species survive dry or unfavourable periods as adults (Williams 1983; Williams and Mellor 1991). The total length of time that the aestivating adults can remain viable is not known, but those of *C. striata* can survive for at least 3 months (De Deckker and Geddes 1980) and those of *H. searlei* for at least 1 month depending on humidity (Williams 1983). This time is probably minimal compared with the duration that desiccation-resistant eggs of other taxa may remain viable (Williams and Kokkinn 1988). Consequently, *Coxiella* species and, particularly, *H. searlei* are excluded from waterbodies that dry for extended periods (Williams and Kokkinn 1988), and therefore seem especially vulnerable to a drying climate. Understanding the long-term viability and hatching cues for desiccation-resistant eggs, or the equivalent for the aestivating adults, and how these

vary among species is crucial for assessing the capacity of species to survive as the climate dries.

It is generally believed that halophilic invertebrates in Australia mainly disperse via desiccation-resistant eggs (when present) and that aquatic birds and, to a lesser extent, wind and water flow are important dispersal vectors (Finston 2002; Green *et al.* 2008). Nevertheless, other than for population genetic studies of the copepod *C. clitellata* (Whitehead 2005) and several species of *Mytilocypris* ostracod (Finston 2002), the amount or pattern of dispersal in these invertebrates is unknown. Although it is unlikely that the amount of dispersal is enough to directly affect the population dynamics of a species, if the rate of local extinction is high, a species will need to have a 'reasonable' chance of dispersing into a suitable habitat in order to persist in the landscape.

Biological interactions

Information on biological interactions, such as predation and competition, in Australian salt lake communities is rudimentary (Timms 2021). This makes it difficult to assess the resilience of these systems to the loss of a species. Some waterbirds are known to prey on the invertebrates (Weston 2007; Pedler *et al.* 2018), although comprehensive data on the relationships between these predators and prey are lacking. It is possible that declines in the abundance and availability of the invertebrates (e.g. if salt lakes are dry for longer periods of time and are more saline) will affect the population dynamics of these birds (Senner *et al.* 2018). Fish predation may also be important at certain times in some waterbodies (Chessman and Williams 1987; Becker and Laurenson 2007), although fish are absent from most of the Australian salt lakes, which are typically either ephemeral or highly saline (De Deckker 1983b).

Competitive exclusion (Timms 2012a) may explain why congeneric species in a range of taxa (e.g. *Parartemia*, *Australocypris* and *Coxiella*) rarely co-occur in a single lake, although there is currently no evidence to support that competitive exclusion is more important than niche differentiation or dispersal limitation. The effect of the recent spread of *A. parthenogenetica*, and the potential (although not yet observed) spread of *A. franciscana*, on the native halophilic invertebrates is difficult to predict without detailed information on the ecological requirements of the native species (McMaster *et al.* 2007). However, it is worth noting that *A. franciscana* has out-competed and replaced native *Artemia* species on other continents (Ruebhart *et al.* 2008).

Conclusion

A very diverse and unique range of halophilic invertebrates inhabit Australian salt lakes. These invertebrates are threatened by a range of processes, the most significant of which are increasing periods of extensive drought and secondary salinisation over large parts of the Australian landscape. Populations, and potentially species, have already become extinct (Williams 1995; Timms *et al.* 2009; Timms 2012b) and, without further study, more may be lost without notice (Halse *et al.* 2003). It is currently difficult to properly evaluate the consequences of the threats due to critical gaps in our knowledge of the biology of the

invertebrates. Future studies of Australian halophilic invertebrates should prioritise the following:

- documenting the full extent of biodiversity in these invertebrates; this is the most critical gap to be filled because a sound taxonomy is needed to underpin all other biological research
- developing a better understanding of species' distributions and community composition, particularly in remote regions
- ascertaining species' tolerances to salinity and other physico-chemical parameters across all stages of their lifecycle
- elucidating the long-term viability and hatching cues for desiccation-resistant eggs, and the equivalent for aestivating adults, and how these vary among species
- elucidating the abiotic and biotic factors that control species' distributions, including why congeneric species rarely occur in the same lake despite overlapping geographic and salinity distributions
- determining the patterns and mechanisms of dispersal and how these may influence the capacity of species to persist in the landscape
- elucidating the biological relationships between species, including how the spread of *Artemia* in Australian salt lakes will affect native species
- on a more holistic level, documenting the levels of anthropogenic stressors, including pollution and mining activities, on salt lake environments and identifying and preserving any key habitats that may serve as refugia for Australian halophilic invertebrates, particularly in the face of a drying climate.

Conflicts of interest

The authors declare that they have no conflicts of interest.

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References

- Adamowicz, S. J., Menu-Marque, S., Halse, S. A., Topan, J. C., Zemlak, T. S., Hebert, P. D., and Witt, J. D. (2010). The evolutionary diversification of the Centropagidae (Crustacea, Calanoida): a history of habitat shifts. *Molecular Phylogenetics and Evolution* **55**, 418–430. doi:10.1016/J.YMPEV.2009.12.008
- Aladin, N., and Potts, W. (1995). Osmoregulatory capacity of the Cladocera. *Journal of Comparative Physiology – B. Biochemical, Systemic, and Environmental Physiology* **164**, 671–683. doi:10.1007/BF00389810
- Aladin, N., and Potts, W. (1996). The osmoregulatory capacity of the Ostracoda. *Journal of Comparative Physiology – B. Biochemical, Systemic, and Environmental Physiology* **166**, 215–222. doi:10.1007/BF00263985
- Alonso, M. (1990). Anostraca, Cladocera and Copepoda of Spanish saline lakes. *Hydrobiologia* **197**, 221–231. doi:10.1007/BF00026952

- Angas, G. (1877). Descriptions of a new species of *Bulimus* from Western Australia, and of a *Paludinella* from Lake Eyre, South Australia. *Proceedings of the Zoological Society of London* 170–171.
- Anufrieva, E. V. (2015). Do copepods inhabit hypersaline waters worldwide? A short review and discussion. *Chinese Journal of Oceanology and Limnology* 33, 1354–1361. doi:10.1007/S00343-014-4385-7
- Asem, A., Eimanifar, A., Li, W., Wang, P.-Z., Brooks, S. A., and Wink, M. (2018). Phylogeography and population genetic structure of an exotic invasive brine shrimp, *Artemia* Leach, 1819 (Crustacea: Anostraca), in Australia. *Australian Journal of Zoology* 66, 307–316. doi:10.1071/ZO18077
- Bayly, I. (1962). Additions to the inland water genus *Calamoecia* (Copepoda: Calanoida). *Marine and Freshwater Research* 13, 252–264. doi:10.1071/MF9620252
- Bayly, I. (1970). Further studies on some saline lakes of south-east Australia. *Marine and Freshwater Research* 21, 117–130. doi:10.1071/MF9700117
- Bayly, I. (1972). Salinity tolerance and osmotic behavior of animals in athalassic saline and marine hypersaline waters. *Annual Review of Ecology and Systematics* 3, 233–268. doi:10.1146/ANNUREV.ES.03.110172.001313
- Bayly, I. (1976). The plankton of Lake Eyre. *Marine and Freshwater Research* 27, 661–665. doi:10.1071/MF9760661
- Bayly, I. (1993). The fauna of athalassic saline waters in Australia and the Altiplano of South America: comparisons and historical perspectives. *Hydrobiologia* 267, 225–231. doi:10.1007/BF00018804
- Bayly, I. A. (1995). Distinctive aspects of the zooplankton of large lakes in Australasia, Antarctica and South America. *Marine and Freshwater Research* 46, 1109–1120. doi:10.1071/MF9951109
- Bayly, I. A., and Boxshall, G. A. (2009). An all-conquering ecological journey: from the sea, calanoid copepods mastered brackish, fresh, and athalassic saline waters. *Hydrobiologia* 630, 39–47. doi:10.1007/S10750-009-9797-6
- Bayly, I., and Williams, W. D. (1966). Chemical and biological studies on some saline lakes of south-east Australia. *Marine and Freshwater Research* 17, 177–228. doi:10.1071/MF9660177
- Becker, A., and Laurenson, L. J. (2007). Seasonal and diel comparisons of the diets of four dominant fish species within the main channel and flood-zone of a small intermittently open estuary in south-eastern Australia. *Marine and Freshwater Research* 58, 1086–1095. doi:10.1071/MF06135
- Bekker, E. I., Karabanov, D. P., Galimov, Y. R., and Kotov, A. A. (2016). DNA barcoding reveals high cryptic diversity in the North Eurasian *Moina* species (Crustacea: Cladocera). *PLoS One* 11, e0161737. doi:10.1371/JOURNAL.PONE.0161737
- Benzie, J. (2005). The genus *Daphnia* (including *Daphniopsis*) (Anomopoda: Daphniidae). In 'Guides to the Identification of the Microinvertebrates of the Continental Waters of the World'. (Ed. H. Dumont.) Vol. 21, pp. 32–38 (Backhuys Publishers: Leiden, Netherlands.)
- Blinn, D., Blinn, S., and Bayly, I. (1989). Feeding ecology of *Haloniscus searlei* Chilton, an Oniscoid Isopod living in Athalassic Saline Waters. *Marine and Freshwater Research* 40, 295–301. doi:10.1071/MF9890295
- Blinn, D., Halse, S., Pinder, A., and Shiel, R. (2004). Diatom and micro-invertebrate communities and environmental determinants in the western Australian wheatbelt: a response to salinization. *Hydrobiologia* 528, 229–248. doi:10.1007/S10750-004-2350-8
- Brock, M. A., and Shiel, R. (1983). The composition of aquatic communities in saline wetlands in Western Australia. *Hydrobiologia* 105, 77–84. doi:10.1007/BF00025178
- Cale, D., Halse, S., and Walker, C. (2004). Wetland monitoring in the Wheatbelt of south-west Western Australia: site descriptions, waterbird, aquatic invertebrate and groundwater data. *Conservation Science Western Australia* 5, 20–136.
- Campbell, C. E. (1994). Seasonal zooplankton fauna of salt evaporation basins in South Australia. *Marine and Freshwater Research* 45, 199–208. doi:10.1071/MF9940199
- Campbell, C. E. (1995). The influence of a predatory ostracod, *Australocypris insularis*, on zooplankton abundance and species composition in a saline lake. *Hydrobiologia* 302, 229–239. doi:10.1007/BF00032112
- Cardoso, P., Erwin, T. L., Borges, P. A., and New, T. R. (2011). The seven impediments in invertebrate conservation and how to overcome them. *Biological Conservation* 144, 2647–2655. doi:10.1016/J.BIOCON.2011.07.024
- Casanova, M. T. (2013). *Lamprothamnium* in Australia (Characeae, Charophyceae). *Australian Systematic Botany* 26(4), 268–290. doi:10.1071/SB13026
- Chessman, B., and Williams, W. D. (1987). A note on the diet of *Galaxias maculatus* (Jenyns) (Pisces, Salmoniformes, Galaxiidae) in a closed saline lake in western Victoria. *Bulletin of the Australian Society for Limnology* 11, 43–46.
- Clegg, J. S., and Campagna, V. (2006). Comparisons of stress proteins and soluble carbohydrate in encysted embryos of *Artemia franciscana* and two species of *Parartemia*. *Comparative Biochemistry and Physiology – B. Biochemistry & Molecular Biology* 145, 119–125. doi:10.1016/J.CBMPB.2006.04.014
- Colbourne, J., Wilson, C., and Hebert, P. (2006). The systematics of Australian *Daphnia* and *Daphniopsis* (Crustacea: Cladocera): a shared phylogenetic history transformed by habitat-specific rates of evolution. *Biological Journal of the Linnean Society. Linnean Society of London* 89, 469–488. doi:10.1111/J.1095-8312.2006.00687.X
- Conte, F. P., and Geddes, M. C. (1988). Acid brine shrimp: metabolic strategies in osmotic and ionic adaptation. *Hydrobiologia* 158, 191–200. doi:10.1007/BF00026277
- Cooper, S. J., Saint, K. M., Taiti, S., Austin, A. D., and Humphreys, W. F. (2008). Subterranean archipelago: mitochondrial DNA phylogeography of stygobitic isopods (Oniscidea: *Haloniscus*) from the Yilgarn region of Western Australia. *Invertebrate Systematics* 22, 195–203. doi:10.1071/IS07039
- Cotton, B. C. (1942). Australian Gastropoda of the families Hydrobiidae, Assimineidae and Acmeidae. *Transactions of the Royal Society of South Australia* 66, 124–129.
- Cox, J. C. (1868). 'A Monograph of Australian Land Shells.' (W. Maddock: Sydney, NSW, Australia.)
- Cristescu, M. E., and Hebert, P. D. (2018). Uses and misuses of environmental DNA in biodiversity science and conservation. *Annual Review of Ecology, Evolution, and Systematics* 49, 209–230. doi:10.1146/ANNUREV-ECOLSYS-110617-062306
- Davis, G. (1979). 'Origin and Evolution of the Gastropod Family Pomatiopidae, with Emphasis on the Mekong River Triculinae.' (Allen Press: Lawrence, KS, USA.)
- De Deckker, P. (1977). The distribution of the 'Giant' ostracods Family: Cyprididae (Baird 1845) endemic to Australia. In 'Sixth International Ostracod Symposium'. pp. 285–294. (Junk: The Hague, Netherlands.)
- De Deckker, P. (1978). Comparative morphology and review of mytilocyprinid ostracods (Family Cyprididae). *Australian Journal of Zoology Supplementary Series* 26, 1–62. doi:10.1071/AJZS058
- De Deckker, P. (1979). Ostracods from the mound springs area between Strangways and Curdimurka, South Australia. *Transactions of the Royal Society of South Australia* 103, 155–168.
- De Deckker, P. (1981a). Taxonomy and ecology notes of some ostracods from Australian inland waters. *Transactions of the Royal Society of South Australia* 105, 91–138.
- De Deckker, P. (1981b). Ostracods of athalassic saline lakes. *Hydrobiologia* 81, 131–144. doi:10.1007/BF00048710
- De Deckker, P. (1981c). Taxonomic notes on some Australian ostracods with description of new species. *Zoologica Scripta* 10, 37–55. doi:10.1111/J.1463-6409.1981.TB00483.X

- De Deckker, P. (1981d). On *Reticyprius pinguis* De Decker sp. nov. *Stereo-Atlas of Ostracod Shells* **8**, 93–100.
- De Deckker, P. (1982). Holocene ostracods, other invertebrates and fish remains from cores of four maar lakes in southeastern Australia. *Proceedings of the Royal Society of Victoria* **94**, 183–220.
- De Deckker, P. (1983a). Notes on the ecology and distribution of non-marine ostracods in Australia. *Hydrobiologia* **106**, 223–234. doi:10.1007/BF00008120
- De Deckker, P. (1983b). Australian salt lakes: their history, chemistry, and biota – a review. *Hydrobiologia* **105**, 231–244. doi:10.1007/BF00025191
- De Deckker, P. (2002). Ostracod palaeoecology. In 'The Ostracoda: Applications in Quaternary Research'. (Eds J. Holmes and A. Chivas.) Vol. 131, pp. 121–134. (American Geophysical Union: Washington, DC, USA.) doi:10.1029/131GM06
- De Deckker, P., and Geddes, M. (1980). Seasonal fauna of ephemeral saline lakes near the Coorong Lagoon, South Australia. *Marine and Freshwater Research* **31**, 677–699. doi:10.1071/MF9800677
- De Deckker, P., and Williams, W. D. (1982). Chemical and biological features of Tasmanian salt lakes. *Marine and Freshwater Research* **33**, 1127–1132. doi:10.1071/MF9821127
- De Los Rios-Escalante, P., and Amarouyache, M. (2016). Crustacean zooplankton assemblages in Algerian saline lakes: a comparison with their Chilean Altiplano counterparts. *Crustaceana* **89**, 1485–1500. doi:10.1163/15685403-00003581
- De Stasio, B. T. (1989). The seed bank of a freshwater crustacean: copepodology for the plant ecologist. *Ecology* **70**, 1377–1389. doi:10.2307/1938197
- Doupe, R., and Horwitz, P. (1995). The value of macroinvertebrate assemblages for determining priorities in wetland rehabilitation: a case study from Lake Toolibin, Western Australia. *Journal of the Royal Society of Western Australia* **78**, 33–38.
- Edward, D. (1983). Inland waters of Rottnest Island. *Journal of the Royal Society of Western Australia* **66**, 41–47.
- Ellis, P., and Williams, W. (1970). The biology of *Haloniscus searlei* Chilton, an oniscoid isopod living in Australian salt lakes. *Marine and Freshwater Research* **21**, 51–70. doi:10.1071/MF9700051
- Fiers, F. (2001). *Meridiacyclops*, gen. nov., a new cyclopoid genus (Crustacea: Copepoda: Cyclopidae) from southern Australia. *Invertebrate Systematics* **15**, 893–908. doi:10.1071/IT01003
- Finston, T. (2000). Morphology and molecules conflict to confound species boundaries in salt lake ostracodes of the genus *Mytilocypris* (Crustacea: Ostracoda). *Australian Journal of Zoology* **48**, 393–409. doi:10.1071/ZO00046
- Finston, T. (2002). Geographic patterns of population genetic structure in *Mytilocypris* (Ostracoda: Cyprididae): interpreting breeding systems, gene flow and history in species with differing distributions. *Molecular Ecology* **11**, 1931–1946. doi:10.1046/J.1365-294X.2002.01590.X
- Finston, T. (2004). Effect of a temporally heterogeneous environment on size and shape of the giant ostracods *Mytilocypris* (Ostracoda: Cyprididae) from Australian salt lakes. *Marine and Freshwater Research* **55**, 499–507. doi:10.1071/MF04009
- Finston, T. (2007). Size, shape and development time are plastic traits in salt lake ostracods of the *Mytilocypris mytiloides* (Ostracoda: Cyprididae) species complex. *Marine and Freshwater Research* **58**, 511–518. doi:10.1071/MF06162
- Geddes, M. (1973). A new species of *Parartemia* (Anostraca) from Australia. *Crustaceana* **25**, 5–12. doi:10.1163/156854073X00443
- Geddes, M. (1976). Seasonal fauna of some ephemeral saline waters in western Victoria with particular reference to *Parartemia zietziana* Sayce (Crustacea: Anostraca). *Marine and Freshwater Research* **27**, 1–22. doi:10.1071/MF9760001
- Geddes, M. (1981). The brine shrimps *Artemia* and *Parartemia*: comparative physiology and distribution in Australia. *Hydrobiologia* **81–82**, 169–179. doi:10.1007/BF00048714
- Geddes, M., De Deckker, P., Williams, W. D., Morton, D., and Topping, M. (1981). On the chemistry and biota of some saline lakes in Western Australia. *Hydrobiologia* **81–82**, 201–222. doi:10.1007/BF00048717
- Gibson, J. A., and Bayly, I. A. (2007). New insights into the origins of crustaceans of Antarctic lakes. *Antarctic Science* **19**, 157–164. doi:10.1017/S0954102007000235
- Green, A. J., Jenkins, K., Bell, D., Morris, P., and Kingsford, R. (2008). The potential role of waterbirds in dispersing invertebrates and plants in arid Australia. *Freshwater Biology* **53**, 380–392.
- Guzik, M. T., Stringer, D. N., Murphy, N. P., Cooper, S. J., Taiti, S., King, R. A., Humphreys, W. F., and Austin, A. D. (2019). Molecular phylogenetic analysis of Australian arid-zone oniscidean isopods (Crustacea: *Haloniscus*) reveals strong regional endemism and new putative species. *Invertebrate Systematics* **33**, 556–574.
- Halse, S. (1981). Faunal assemblages of some saline lakes near Marchagee, Western Australia. *Marine and Freshwater Research* **32**, 133–142. doi:10.1071/MF9810133
- Halse, S. (2002). Diversity of Ostracoda (Crustacea) in inland waters of Western Australia. *Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen* **28**, 914–918. doi:10.1080/03680770.2001.11901848
- Halse, S. A., and Martens, K. (2019). Four new genera and five new species of 'Heterocypris' from Western Australia (Crustacea, Ostracoda, Cyprinotinae). *European Journal of Taxonomy* **493**, 1–35. doi:10.5852/EJT.2019.493
- Halse, S., and McRae, J. (2001). *Calamocia trilobata* n sp (Copepoda: Calanoida) from salt lakes in southwestern Australia. *Journal of the Royal Society of Western Australia* **84**, 5–11.
- Halse, S., and McRae, J. (2004). New genera and species of 'giant' ostracods (Crustacea: Cyprididae) from Australia. *Hydrobiologia* **524**, 1–52. doi:10.1023/B:HYDR.0000036197.03776.46
- Halse, S., Shiel, R., and Williams, W. (1998). Aquatic invertebrates of Lake Gregory, northwestern Australia, in relation to salinity and ionic composition. *Hydrobiologia* **381**, 15–29. doi:10.1023/A:1003263105122
- Halse, S., Shiel, R., Storey, A., Edward, D., Lansbury, I., Cale, D., and Harvey, M. (2000a). Aquatic invertebrates and waterbirds of wetlands and rivers of the southern Carnarvon Basin, Western Australia. *Records of the Western Australian Museum* **61**, 217–265. doi:10.18195/ISSN.0313-122X.61.2000.217-265
- Halse, S., Pearson, G., McRae, J., and Shiel, R. (2000b). Monitoring aquatic invertebrates and waterbirds at Toolibin and Walbyring Lakes in the Western Australian wheatbelt. *Journal of the Royal Society of Western Australia* **83**, 17–28.
- Halse, S., Ruprecht, J., and Pinder, A. (2003). Salinisation and prospects for biodiversity in rivers and wetlands of south-west Western Australia. *Australian Journal of Botany* **51**, 673–688. doi:10.1071/BT02113
- Hammer, U. T. (1986). 'Saline Lake Ecosystems of the World.' (W. Junk: Dordrecht, Netherlands.)
- Hamond, R. (1971). The Australian species of *Mesochra* (Crustacea: Harpacticoida), with a comprehensive key to the genus. *Australian Journal of Zoology Supplementary Series* **19**, 1–32. doi:10.1071/AJZS007
- He, Z., Qin, J., Wang, Y., Jiang, H., and Wen, Z. (2001). Biology of *Moina mongolica* (Moinidae, Cladocera) and perspective as live food for marine fish larvae. *Hydrobiologia* **457**, 25–37. doi:10.1023/A:1012277328391
- Hebert, P. D., and Wilson, C. C. (2000). Diversity of the genus *Daphniopsis* in the saline waters of Australia. *Canadian Journal of Zoology* **78**, 794–808. doi:10.1139/Z99-253
- Hebert, P. D., Remigio, E. A., Colbourne, J. K., Taylor, D. J., and Wilson, C. C. (2002). Accelerated molecular evolution in halophilic crustaceans. *Evolution* **56**, 909–926. doi:10.1111/J.0014-3820.2002.TB01404.X
- Hughes, L. (2003). Climate change and Australia: trends, projections and impacts. *Austral Ecology* **28**, 423–443. doi:10.1046/J.1442-9993.2003.01300.X

- Iredale, T. (1943). A basic list of the fresh water Mollusca of Australia. *Australian Zoologist* **10**, 188–230.
- Ismail, H. N., Qin, J. G., and Seuront, L. (Eds) (2010a). Thermal and halo tolerance of a brackish cladoceran *Daphniopsis australis* (Sergeev & Williams). New Oceanography Research Developments: Marine Chemistry, Ocean Floor Analyses and Marine Phytoplankton. (Nova Science Publisher: New York, NY, USA.)
- Ismail, H. N., Qin, J. G., Seuront, L., and Adams, M. (2010b). Impacts of male and food density on female performance in the brackish cladoceran *Daphniopsis australis*. *Hydrobiologia* **652**, 277–288. doi:10.1007/S10750-010-0359-8
- Ismail, H. N., Qin, J. G., and Seuront, L. (2011a). Dietary responses of the brackish cladoceran *Daphniopsis australis* fed on different algal species. *Journal of Experimental Marine Biology and Ecology* **409**, 275–282. doi:10.1016/J.JEMBE.2011.09.008
- Ismail, H. N., Qin, J. G., and Seuront, L. (2011b). Regulation of life history in the brackish cladoceran, *Daphniopsis australis* (Sergeev and Williams, 1985) by temperature and salinity. *Journal of Plankton Research* **33**, 763–777. doi:10.1093/PLANKT/FBQ145
- Karanovic, I. (2008). Three interesting Cyprididae (Ostracoda) from Western Australia. *Records of the Western Australian Museum* **24**, 267–287. doi:10.18195/ISSN.0312-3162.24(3).2008.267-287
- Karanovic, I. (2012). Superfamily Cypridoidea Baird 1845 (Suborder Cypridocopina Jones 1901). In 'Recent Freshwater Ostracods of the World'. pp. 175–564. (Springer: Berlin, Germany.)
- Karanovic, T., Eberhard, S., and Murdoch, A. (2011). A cladistic analysis and taxonomic revision of Australian *Metacyclops* and *Goniocyclops*, with description of four new species and three new genera (Copepoda, Cyclopoida). *Crustaceana* **84**, 1–67. doi:10.1163/001121610X546698
- Kendrick, G. W. (1978). New species of fossil nonmarine molluscs from Western Australia and evidence of late Quaternary climatic change in the Shark Bay district. *Journal of the Royal Society of Western Australia* **60**, 49–60.
- Khan, T. A. (2003). Dietary studies on exotic carp (*Cyprinus carpio*) from two lakes of western Victoria, Australia. *Aquatic Sciences* **65**, 272–286. doi:10.1007/S00027-003-0658-5
- Kokkinn, M. J., and Williams, W. D. (1987). Is ephippial morphology a useful taxonomic descriptor in the Cladocera? An examination based on a study of *Daphniopsis* (Daphniidae) from Australian salt lakes. *Hydrobiologia* **145**, 67–73. doi:10.1007/BF02530266
- Linder, F. (1941). Contributions to the morphology and the taxonomy of the Branchiopoda Anostraca. *Zoologische Beiträge aus Uppsala* **20**, 101–302.
- Lyons, M., Gibson, N., Keighery, G., and Lyons, S. (2004). Wetland flora and vegetation of the Western Australian Wheatbelt. *Records of the Western Australian Museum* **67**, 39–89. doi:10.18195/ISSN.0313-122X.67.2004.039-089
- Macpherson, J. (1957). A review of the genus *Coxiella* Smith, 1894, *sensu lato*. *Western Australian Naturalist* **5**, 191–204.
- Maly, E. J. (1996). A review of relationships among centropagid copepod genera and some species found in Australasia. *Crustaceana* **69**, 727–733. doi:10.1163/156854096X00745
- Maly, E. J., Halse, S. A., and Maly, M. P. (1997). Distribution and incidence patterns of *Boeckella*, *Calamocia*, and *Hemiboeckella* (Copepoda: Calanoida) in Western Australia. *Marine and Freshwater Research* **48**, 615–621. doi:10.1071/MF97015
- Manwell, C. (1978). Haemoglobin in the Australian anostracan *Parartemia zietziana*: evolutionary strategies of conformity vs regulation. *Comparative Biochemistry and Physiology – A. Physiology* **59**, 37–44. doi:10.1016/0300-9629(78)90303-1
- Marchant, R., and Williams, W. D. (1977a). Population dynamics and production of a brine shrimp, *Parartemia zietziana* Sayce (Crustacea: Anostraca), in two salt lakes in western Victoria, Australia. *Marine and Freshwater Research* **28**, 417–438. doi:10.1071/MF9770417
- Marchant, R., and Williams, W. D. (1977b). Field measurements of ingestion and assimilation for the Australian brine shrimp *Parartemia zietziana* Sayce (Crustacea: Anostraca). *Australian Journal of Ecology* **2**, 379–390. doi:10.1111/J.1442-9993.1977.TB01153.X
- Martens, K. (1985). Effects of temperature and salinity on postembryonic growth in *Mytilocypris henricae* (Chapman) (Crustacea, Ostracoda). *Journal of Crustacean Biology* **5**, 258–272. doi:10.2307/1547873
- Martens, K., and Savatnalinton, S. (2011). A subjective checklist of the recent, free-living, non-marine Ostracoda (Crustacea). *Zootaxa* **2855**, 1–79. doi:10.11646/ZOOTAXA.2855.1.1
- McCloud, C. L., Ismail, H. N., and Seuront, L. (2018). Cue hierarchy in the foraging behaviour of the brackish cladoceran *Daphniopsis australis*. *Journal of Oceanology and Limnology* **36**, 2050–2060. doi:10.1007/S00343-018-7335-Y
- McMaster, K., Savage, A., Finston, T., Johnson, M. S., and Knott, B. (2007). The recent spread of *Artemia parthenogenetica* in Western Australia. *Hydrobiologia* **576**, 39–48. doi:10.1007/S10750-006-0291-0
- Menke, K. (1843). 'Molluscorum Novae Hollandiae Specimen.' (Libraria Aulica Hahniana: Hannover, Germany.)
- Mernagh, T., Bastrakov, E., Jaireth, S., de Caritat, P., English, P., and Clarke, J. (2016). A review of Australian salt lakes and associated mineral systems. *Australian Journal of Earth Sciences* **63**, 131–157. doi:10.1080/08120099.2016.1149517
- Meusel, F., and Schwentner, M. (2017). Molecular and morphological delimitation of Australian *Triops* species (Crustacea: Branchiopoda: Notostraca) – large diversity and little morphological differentiation. *Organisms, Diversity & Evolution* **17**, 137–156. doi:10.1007/S13127-016-0306-2
- Morton, D., and Bayly, I. (1977). Studies on the ecology of some temporary freshwater pools in Victoria with special reference to microcrustaceans. *Marine and Freshwater Research* **28**, 439–454. doi:10.1071/MF9770439
- Murugan, G., Obregón-Barboza, H., Maeda-Martínez, A. M., and Timms, B. V. (2009). Co-occurrence of two tadpole shrimp, *Triops* cf. *australiensis* (Branchiopoda: Notostraca), lineages in middle Paroo, north-western New South Wales, with the first record of *Triops* hermaphrodites for the Australian continent. *Australian Journal of Zoology* **57**, 77–84. doi:10.1071/ZO08084
- Naganawa, H., and Mura, G. (2017). Two new cryptic species of *Artemia* (Branchiopoda, Anostraca) from Mongolia and the possibility of invasion and disturbance by the aquaculture industry in East Asia. *Crustaceana* **90**, 1679–1698. doi:10.1163/15685403-00003744
- Nielsen, D. L., and Brock, M. A. (2009). Modified water regime and salinity as a consequence of climate change: prospects for wetlands of Southern Australia. *Climatic Change* **95**, 523–533. doi:10.1007/S10584-009-9564-8
- Pedler, R., Ribot, R., and Bennett, A. (2014). Extreme nomadism in desert waterbirds: flights of the banded stilt. *Biology Letters* **10**, 20140547. doi:10.1098/RSBL.2014.0547
- Pedler, R. D., Ribot, R. F., and Bennett, A. T. (2018). Long-distance flights and high-risk breeding by nomadic waterbirds on desert salt lakes. *Conservation Biology* **32**, 216–228. doi:10.1111/COBI.13007
- Pinceel, T., Brendonck, L., Larmuseau, M. H., Vanhove, M. P., Timms, B. V., and Vanschoenwinkel, B. (2013a). Environmental change as a driver of diversification in temporary aquatic habitats: does the genetic structure of extant fairy shrimp populations reflect historic aridification? *Freshwater Biology* **58**, 1556–1572. doi:10.1111/FWB.12137
- Pinceel, T., Vanschoenwinkel, B., Waterkeyn, A., Vanhove, M. P., Pinder, A., Timms, B. V., and Brendonck, L. (2013b). Fairy shrimps in distress: a molecular taxonomic review of the diverse fairy shrimp genus *Branchinella* (Anostraca: Thamnocephalidae) in Australia in the light of ongoing environmental change. *Hydrobiologia* **700**, 313–327. doi:10.1007/S10750-012-1240-8
- Pinder, A., and Quinlan, K. (2015). Aquatic invertebrate communities of wetlands along the Jurien coast of Western Australia. *Journal of the Royal Society of Western Australia* **98**, 69–88.

- Pinder, A. M., Halse, S. A., Shiel, R. J., Cale, D. J., and McRae, J. M. (2002). Halophile aquatic invertebrates in the wheatbelt region of south-western Australia. *Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen* **28**, 1687–1694. doi:10.1080/03680770.2001.11901909
- Pinder, A. M., Halse, S. A., McRae, J. M., and Shiel, R. J. (2005). Occurrence of aquatic invertebrates of the wheatbelt region of Western Australia in relation to salinity. *Hydrobiologia* **543**, 1–24. doi:10.1007/S10750-004-5712-3
- Pinder, A., Halse, S., Shiel, R., and McRae, J. (2010). An arid zone awash with diversity: patterns in the distribution of aquatic invertebrates in the Pilbara region of Western Australia. *Records of the Western Australian Museum* **78**, 205–246. doi:10.18195/ISSN.0313-122X.78(1).2010.205-246
- Pinder, A., Quinlan, K., Cale, D., and Leung, A. (2012). Aquatic invertebrates of the Hutt River and Hutt Lagoon catchments, Western Australia. *Journal of the Royal Society of Western Australia* **95**, 29–51.
- Porter, J. L. (2007). Contrasting emergence patterns of *Lamprothamnium macropogon* (Characeae, Charophyceae) and *Ruppia tuberosa* (Potamogetonaceae) from arid-zone saline wetlands in Australia. *Charophytes* **1**, 19–27.
- Quinlan, K., Pinder, A., Coppen, R., and Jackson, J. (2016). An opportunistic survey of aquatic invertebrates in the Goldfields region of Western Australia. *Conservation Science Western Australia* **10**, 1–21.
- Reeve, L. (1842) 'Conchologia systematica, or Complete System of Conchology: in which the Lepades and Conchiferous Mollusca are Described and Classified according to their Natural Organization and Habits.' (Wiley and Putnam: New York, NY, USA.)
- Remigio, E., Hebert, P., and Savage, A. (2001). Phylogenetic relationships and remarkable radiation in *Parartemia* (Crustacea: Anostraca), the endemic brine shrimp of Australia: evidence from mitochondrial DNA sequences. *Biological Journal of the Linnean Society. Linnean Society of London* **74**, 59–71. doi:10.1111/J.1095-8312.2001.TB01377.X
- Rogers, D. C. (2013). Anostraca catalogus (Crustacea: Branchiopoda). *The Raffles Bulletin of Zoology* **61**, 525–546.
- Ruebhart, D. R., Cock, I. E., and Shaw, G. R. (2008). Invasive character of the brine shrimp *Artemia franciscana* Kellogg 1906 (Branchiopoda: Anostraca) and its potential impact on Australian inland hypersaline waters. *Marine and Freshwater Research* **59**, 587–595. doi:10.1071/MF07221
- Ruiz, F., Abad, M., Bodergat, A., Carbonel, P., Rodríguez-Lázaro, J., González-Regalado, M., Toscano, A., García, E., and Prenda, J. (2013). Freshwater ostracods as environmental tracers. *International Journal of Environmental Science and Technology* **10**, 1115–1128. doi:10.1007/S13762-013-0249-5
- Sánchez, M. I., Hortas, F., Figuerola, J., and Green, A. J. (2012). Comparing the potential for dispersal via waterbirds of a native and an invasive brine shrimp. *Freshwater Biology* **57**, 1896–1903. doi:10.1111/J.1365-2427.2012.02852.X
- Säwström, C., Karlsson, J., Laybourn-Parry, J., and Granéli, W. (2009). Zooplankton feeding on algae and bacteria under ice in Lake Druzhby, East Antarctica. *Polar Biology* **32**, 1195–1202. doi:10.1007/S00300-009-0619-0
- Sayce, O. (1903). The phyllopods of Australia, including a description of some new genera and species. *Proceedings of the Royal Society of Victoria* **15**, 224–261.
- Schön, I., Halse, S., and Martens, K. (2017). *Cyprideis* (Crustacea, Ostracoda) in Australia. *Journal of Micropalaeontology* **36**, 31–37. doi:10.1144/JMPALEO2016-032
- Schwartz, S. S., and Hebert, P. D. (1984). Subgeneric distinction in the genus *Daphnia*: a new diagnostic trait. *Transactions of the American Microscopical Society* **103**, 341–346. doi:10.2307/3226469
- Senner, N. R., Moore, J. N., Seager, S. T., Dougill, S., Kreuz, K., and Senner, S. E. (2018). A salt lake under stress: relationships among birds, water levels, and invertebrates at a Great Basin saline lake. *Biological Conservation* **220**, 320–329. doi:10.1016/J.BIOCON.2018.02.003
- Sergeev, V. N. (1990a). The ephippial female of a new species of *Daphniopsis* Sars, 1903 (Anomopoda, Daphniidae) from Queensland, Australia. *Crustaceana* **59**, 146–155. doi:10.1163/156854090X00624
- Sergeev, V. N. (1990b). A new species of *Daphniopsis* (Crustacea: Anomopoda: Daphniidae) from Australian salt lakes. *Hydrobiologia* **190**, 1–7. doi:10.1007/BF00020682
- Sergeev, V. N., and Williams, W. D. (1983). *Daphniopsis pusilla* Serventy (Cladocera: Daphniidae), an important element in the fauna of Australian salt lakes. *Hydrobiologia* **100**, 293–300. doi:10.1007/BF00027435
- Sergeev, V. N., and Williams, W. D. (1985). *Daphniopsis australis* nov. sp. (Crustacea: Cladocera), a further daphniid in Australian salt lakes. *Hydrobiologia* **120**, 119–128. doi:10.1007/BF00032132
- Sinev, A. Y., and Shiel, R. J. (2012). *Extremalona timmsi* gen. nov., sp. nov., a new cladoceran (Cladocera: Anomopoda: Chydoridae) from an acid saline lake in southwest Western Australia. *Journal of Natural History* **46**, 2845–2864. doi:10.1080/00222933.2012.727215
- Smith, B. J. (1979). 'Field Guide to the Non-Marine Molluscs of South Eastern Australia.' (Australian National University Press: Canberra, ACT, Australia.)
- Stringer, D. N., King, R. A., Taiti, S., Guzik, M. T., Cooper, S. J., and Austin, A. D. (2019). Systematics of *Haloniscus* Chilton, 1920 (Isopoda: Oniscidea: Philosciidae), with description of four new species from threatened Great Artesian Basin springs in South Australia. *Journal of Crustacean Biology* **39**, 651–668. doi:10.1093/JCBIOL/RUZ044
- Sutherland, W. J., and Wordley, C. F. (2017). Evidence complacency hampers conservation. *Nature Ecology & Evolution* **1**, 1215–1216. doi:10.1038/S41559-017-0244-1
- Taipale, S. J., Brett, M. T., Pulkkinen, K., and Kainz, M. J. (2012). The influence of bacteria-dominated diets on *Daphnia magna* somatic growth, reproduction, and lipid composition. *FEMS Microbiology Ecology* **82**, 50–62. doi:10.1111/J.1574-6941.2012.01406.X
- Tang, D., and Knott, B. (2009). Freshwater cyclopoids and harpacticoids (Crustacea: Copepoda) from the Gngangra Mound region of Western Australia. *Zootaxa* **2029**, 1–70. doi:10.11646/ZOOTAXA.2029.1.1
- Teller, J. T. (1987). The pink colour of lakes, with an example from Australia. *Journal of Arid Environments* **12**, 101–103. doi:10.1016/S0140-1963(18)31179-0
- Timms, B. V. (1983). A study of benthic communities in some shallow saline lakes of western Victoria, Australia. *Hydrobiologia* **105**, 165–177. doi:10.1007/BF00025186
- Timms, B. V. (1987). Limnology of Lake Buchanan, a tropical saline lake, and associated pools, of North Queensland. *Marine and Freshwater Research* **38**, 877–884. doi:10.1071/MF9807877
- Timms, B. V. (1993). Saline lakes of the Paroo, inland New South Wales, Australia. *Hydrobiologia* **267**, 269–289. doi:10.1007/BF00018808
- Timms, B. V. (1998). A study of Lake Wyara, an episodically filled saline lake in southwest Queensland, Australia. *International Journal of Salt Lake Research* **7**, 113–132. doi:10.1007/BF02441882
- Timms, B. V. (2001). A study of the Werewilka Inlet of the saline Lake Wyara, Australia – a harbour of biodiversity for a sea of simplicity. *Hydrobiologia* **466**, 245–254. doi:10.1023/A:1014597131801
- Timms, B. V. (2005). Salt lakes in Australia: present problems and prognosis for the future. *Hydrobiologia* **552**, 1–15. doi:10.1007/S10750-005-1501-X
- Timms, B. V. (2007). The biology of the saline lakes of central and eastern inland of Australia: a review with special reference to their biogeographical affinities. *Hydrobiologia* **576**, 27–37. doi:10.1007/S10750-006-0290-1
- Timms, B. V. (2008). The ecology of episodic saline lakes of inland eastern Australia, as exemplified by a ten year study of the Rockwell-Wombah Lakes of the Paroo. *Proceedings of the Linnean Society of New South Wales* **129**, 1–16.

- Timms, B. V. (2009a). Biodiversity of large branchiopods of Australian saline lakes. *Current Science* **96**, 74–80.
- Timms, B. V. (2009b). Study of the saline lakes of the Esperance Hinterland, Western Australia, with special reference to the roles of acidity and episodicity. *Natural Resources and Environmental Issues* **15**, 215–224.
- Timms, B. V. (2009c). A study of the salt lakes and salt springs of Eyre Peninsula, South Australia. *Hydrobiologia* **626**, 41–51. doi:10.1007/S10750-009-9736-6
- Timms, B. V. (2010a). Blue Lagoon, South Australia: a closed marine lake harbouring potential invaders of continental saline lakes? *Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen* **30**, 1425–1428. doi:10.1080/03680770.2009.11902346
- Timms, B. V. (2010b). Six new species of the brine shrimp *Parartemia* Sayce 1903 (Crustacea: Anostraca: Artemiina) in Western Australia. *Zootaxa* **2715**, 1–35. doi:10.11646/ZOOTAXA.2715.1.1
- Timms, B. V. (2012a). An appraisal of the diversity and distribution of large branchiopods (Branchiopoda: Anostraca, Laevicaudata, Spinicaudata, Cyclestherida, Notostraca) in Australia. *Journal of Crustacean Biology* **32**, 615–623. doi:10.1163/193724012X634198
- Timms, B. V. (2012b). An identification guide to the brine shrimps (Crustacea: Anostraca: Artemiina) of Australia. *Museum Victoria Science Reports* **16**, 1–36. doi:10.24199/J.MVSR.2012.16
- Timms, B. V. (2014). A review of the biology of Australian halophilic anostracans (Branchiopoda: Anostraca). *Journal of Biological Research* **21**, 21. doi:10.1186/2241-5793-21-21
- Timms, B. V. (2015a). A new species of the fairy shrimp *Branchinella* (Crustacea: Anostraca: Thamnocephalidae) from western New South Wales, Australia. *Proceedings of the Linnean Society of New South Wales* **137**, 37–43.
- Timms, B. V. (2015b). A revised identification guide to the fairy shrimps (Crustacea: Anostraca: Anostracina) of Australia. *Museum Victoria Science Reports* **19**, 1–44. doi:10.24199/J.MVSR.2015.19
- Timms, B. V. (2018). On the influence of season and salinity on the phenology of invertebrates in Australian saline lakes, with special reference to those of the Paroo in the semiarid inland. *Journal of Oceanology and Limnology* **36**, 1907–1916. doi:10.1007/S00343-018-7308-1
- Timms, B. V. (2021). Drivers restricting biodiversity in Australian saline lakes: a review. *Marine and Freshwater Research* **72**, 462–468. doi:10.1071/MF20205
- Timms, B. V., and Boulton, A. J. (2001). Typology of arid-zone floodplain wetlands of the Paroo River (inland Australia) and the influence of water regime, turbidity, and salinity on their aquatic invertebrate assemblages. *Archiv für Hydrobiologie* **153**, 1–27. doi:10.1127/ARCHIV-HYDROBIOL/153/2001/1
- Timms, B. V., and Hudson, P. (2009). The brine shrimps (*Artemia* and *Parartemia*) of South Australia, including descriptions of four new species of *Parartemia* (Crustacea: Anostraca: Artemiina). *Zootaxa* **2248**, 47–68. doi:10.11646/ZOOTAXA.2248.1.2
- Timms, B. V., Datson, B., and Coleman, M. (2006). The wetlands of the Lake Carey catchment, northeast Goldfields of Western Australia, with special reference to large branchiopods. *Journal of the Royal Society of Western Australia* **89**, 175–183.
- Timms, B. V., Pinder, A. M., and Campagna, V. S. (2009). The biogeography and conservation status of the Australian endemic brine shrimp *Parartemia* (Crustacea, Anostraca, Parartemiidae). *Conservation Science Western Australia* **7**, 413–427.
- Timms, B. V., Coleman, P., and Cooper, J. (2014). Seagull Lake, Western Eyre Peninsula, South Australia: a saline lake to benefit from climate change? *Transactions of the Royal Society of South Australia* **138**, 161–180. doi:10.1080/03721426.2014.11649007
- van de Graaff, W. E. (1977). Relict early Cainozoic drainages in arid Western Australia. *Zeitschrift für Geomorphologie* **21**, 379–400.
- Wang, M., Zhao, W., Wei, J., Wang, S., and Xie, X. (2019). Acute effects of UVB radiation on the survival, growth, development, and reproduction of *Daphniopsis tibetana* Sars (Crustacea: Cladocera). *Environmental Science and Pollution Research International* **26**, 10916–10925. doi:10.1007/S11356-019-04490-X
- Weston, M. (2007). The foraging and diet of non-breeding hooded plovers *Thinornis rubricollis* in relation to habitat type. *Journal of the Royal Society of Western Australia* **90**, 89–95.
- Whitehead, A. L. (2005). The effects of isolation and environmental heterogeneity on intraspecific variation in *Calamoecia clitellata*, a salt lake-inhabiting copepod. Ph.D. Thesis, University of Western Australia.
- Wilke, T. (2019). Pomatiopsidae Stimpson, 1865. In 'Freshwater Mollusks of the World: a Distribution Atlas'. (Eds C. Lydeard and K. S. Cummings.) pp. 126–130. (John Hopkins University Press: Baltimore, MD, USA.)
- Wilke, T., Haase, M., Hershler, R., Liu, H.-P., Misof, B., and Ponder, W. (2013). Pushing short DNA fragments to the limit: phylogenetic relationships of 'hydrobioid' gastropods (Caenogastropoda: Rissooidea). *Molecular Phylogenetics and Evolution* **66**, 715–736. doi:10.1016/J.YMPEV.2012.10.025
- Williams, W. D. (1964). A contribution to lake typology in Victoria, Australia. *Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen* **15**, 158–168. doi:10.1080/03680770.1962.11895517
- Williams, W. D. (1981). The limnology of saline lakes in Western Victoria. *Hydrobiologia* **81–82**, 233–259. doi:10.1007/BF00048719
- Williams, W. D. (1983). On the ecology of *Haloniscus searlei* (Isopoda, Oniscoidea), an inhabitant of Australian salt lakes. *Hydrobiologia* **105**, 137–142. doi:10.1007/BF00025183
- Williams, W. D. (1984). Chemical and biological features of salt lakes on the Eyre Peninsula, South Australia, and an explanation of regional differences in the fauna of Australian salt lakes. *Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen* **22**, 1208–1215. doi:10.1080/03680770.1983.11897469
- Williams, W. D. (1985). Biotic adaptations in temporary lentic waters, with special reference to those in semi-arid and arid regions. *Hydrobiologia* **125**, 85–110. doi:10.1007/BF00045928
- Williams, W. D. (1986). *Daphniopsis pusilla*, a cladoceran of Australian salt lakes: recognition and ecological data for palaeolimnologists. *Palaeogeography, Palaeoclimatology, Palaeoecology* **54**, 305–316. doi:10.1016/0031-0182(86)90130-6
- Williams, W. D. (1995). Lake Corangamite, Australia, a permanent saline lake: conservation and management issues. *Lakes and Reservoirs: Research and Management* **1**, 55–64. doi:10.1111/J.1440-1770.1995.TB00006.X
- Williams, W. D. (1998a). Salinity as a determinant of the structure of biological communities in salt lakes. *Hydrobiologia* **381**, 191–201. doi:10.1023/A:1003287826503
- Williams, W. D. (Ed.) (1998b). 'Guidelines of Lake Management. Vol. 6. Management of Inland Saline Waters.' (International Lake Environment Committee Foundation: Kusatu, Japan.)
- Williams, W. D. (2002). Environmental threats to salt lakes and the likely status of inland saline ecosystems in 2025. *Environmental Conservation* **29**, 154–167. doi:10.1017/S0376892902000103
- Williams, W. D., and Kokkinn, M. J. (1988). The biogeographical affinities of the fauna in episodically filled salt lakes: a study of Lake Eyre South, Australia. *Hydrobiologia* **158**, 227–236. doi:10.1007/BF00026280
- Williams, W. D., and Mellor, M. W. (1991). Ecology of *Coxiella* (Mollusca, Gastropoda, Prosobranchia), a snail endemic to Australian salt lakes. *Palaeogeography, Palaeoclimatology, Palaeoecology* **84**, 339–355. doi:10.1016/0031-0182(91)90053-T
- Williams, W. D., and Sherwood, J. E. (1994). Definition and measurement of salinity in salt lakes. *International Journal of Salt Lake Research* **3**, 53–63. doi:10.1007/BF01990642

- Williams, W. D., Boulton, A., and Taaffe, R. (1990). Salinity as a determinant of salt lake fauna: a question of scale. *Hydrobiologia* **197**, 257–266. doi:[10.1007/BF00026955](https://doi.org/10.1007/BF00026955)
- Williams, W. D., Carrick, T. R., Bayly, I. A., Green, J., and Herbst, D. B. (1995). Invertebrates in salt lakes of the Bolivian Altiplano. *International Journal of Salt Lake Research* **4**, 65–77. doi:[10.1007/BF01992415](https://doi.org/10.1007/BF01992415)
- Williams, W. D., De Deckker, P., and Shiel, R. J. (1998). The limnology of Lake Torrens, an episodic salt lake of central Australia, with particular reference to unique events in 1989. *Hydrobiologia* **384**, 101–110. doi:[10.1023/A:1003207613473](https://doi.org/10.1023/A:1003207613473)

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