Corrigendum

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

Angus D'Arcy Lawrie, Jennifer Chaplin and Adrian Pinder

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 <u>four</u> 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; <u>(3) two *Moina* species (*Moina baylyi* Forró and *Moina mongolica* Daday); and (4) one species of chydorid (*Extremalona timmsi* Sinev & Shiel).</u>

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 g L^{-1} and 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.

Introduction

Salt lakes are defined as enclosed bodies of water with salinity >3 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 1983*a*; 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 2009*a*, 2010*a*; 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 2009*a*; 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 1998*a*). These lakes vary from expansive playas with long geological records to small, recently formed ponds and wetlands (De Deckker 1983*b*) 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 2009*b*). 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 1998*a*, 1998*b*).

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 predominantly occur in fresh water (salinity <3 g L^{-1}) but occasionally occur in waters with

salinity up to ∼20 g L^{-1}, whereas 'halophiles' are biota that occur mostly in athalassic waters (salinity >10 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 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 2009*a*) 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 (1983*b*) 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 (1983*b*); (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 (1983*b*) 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 *et al.* (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 *et al.* (1990)	Timms (2001)		
Doupe and Horwitz (1995)	De Deckker and Geddes (1980)	Williams (1995)	Timms (2008)		
Halse *et al.* (1998)	Williams (1984)				
Halse *et al.* (2000*a*)	Williams and Kokkinn (1988)				
Cale *et al.* (2004)	Williams *et al.* (1998)				
Pinder *et al.* (2005)	Timms (2009*a*)				
Timms *et al.* (2006)	Timms *et al.* (2014)				
Timms (2009*b*)					
Pinder *et al.* (2010)					
Pinder *et al.* (2012)					
Pinder and Quinlan (2015)					
Quinlan *et al.* (2016)					

[A]Bayly 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.* 2013*a*; 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 (2010*b*), 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 (2010*b*) 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 2010*b*).

Parartemia species occur mainly in ephemeral and seasonal natural salt lakes, surviving dry periods as drought-resistant cysts (Timms 2012*a*). 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
Parartemia			
acidiphila	Timms and Hudson (2009)	35–210	South-western WA, south-eastern SA
auriciforma	Timms and Hudson (2009)	NA	Central SA
bicorna	Timms (2010*b*)	22–105	Central WA
boomeranga	Timms (2010*b*)	50–120	South-western WA
contracta	Linder (1941)	84–240	South-western WA
cylindrifera	Linder (1941)	3–123	South-western WA, south-eastern SA
extracta	Linder (1941)	27–100	South-western WA
informis	Linder (1941)	30–186	South-western WA
laticaudata	Timms (2010*b*)	8–141	North-west WA, central WA, south-western NT
longicaudata	Linder (1941)	41–240	South-western WA
minuta	Geddes (1973)	2–225	North-western NSW, south-eastern Qld, central SA, Vic.
mouritzi	Timms (2010*b*)	33–95	South-western WA
purpurea	Timms (2010*b*)	20–235	South-western WA
serventyi	Linder (1941)	15–262	South-western WA, central WA
triquetra	Timms and Hudson (2009)	NA	Central SA
veronicae	Timms (2010*b*)	74–225	Central WA
yarleensis	Timms and Hudson (2009)	NA	Central SA
zietziana	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 2009*c*; 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 2009*b*, 2010*b*; 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 1977*a*), which reproduces ovoviviparously, producing multiple cohorts so long as conditions are favourable (Timms 2012*b*) and uses oviparous reproduction to produce highly resistant cysts when conditions become unfavourable (Geddes 1976; Marchant and Williams 1977*b*). 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 2012*b*).

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 1977*b*). It has been assumed that other species feed similarly (Timms 2014). Timms (2012*a*) 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 (2012*a*) 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 2012*b*) 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 bicorna,* 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).
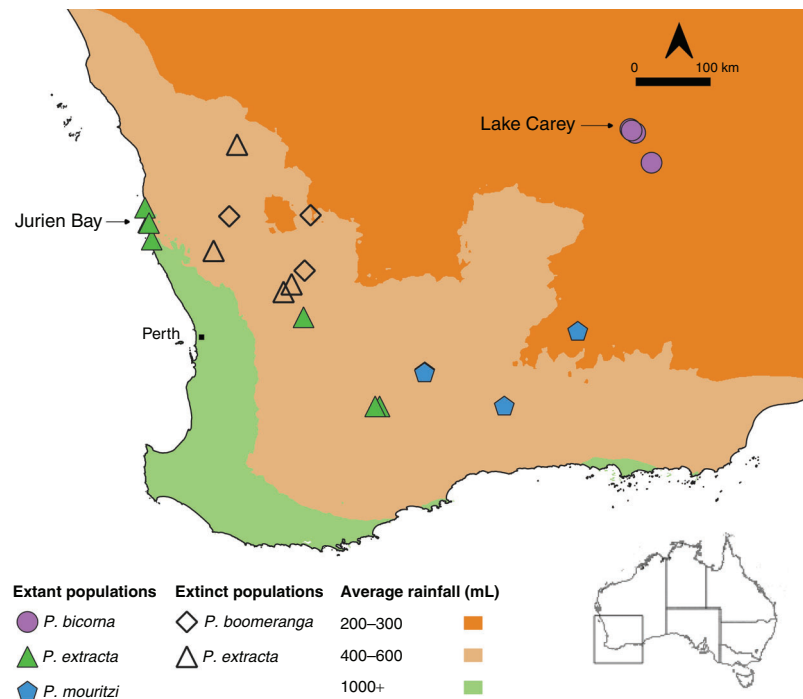
Fig. 1. Reported distributions of four species of *Parartemia* from Western Australia that have been identified as of conservation concern. Likely extinct populations of *P. boomeranga* and *P. extracta* are displayed as open symbols. Data from Timms *et al.* (2009).

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 2015*a*, 2015*b*). Many species have only recently been described (Timms

2015*b*), with cryptic lineages identified using genetic data (Pinceel *et al.* 2013*b*). Only two species, *Branchinella buchananensis* 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.* 2013*a*; 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.* 2013*b*).

B. buchananensis occurs, usually at salinities of $\sim$15 g L^{-1} (limit 42 g L^{-1}; Timms 2009*c*), 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 g L^{-1} (limit 62 g L^{-1}; Timms 2015*b*), 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.* 2013*b*). *B. buchananensis* 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.* 2013*a*).

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 2009*c*). Until recently, *Triops* was

thought to be represented in Australia by a single, widespread and morphologically variable species (*Triops australiensis* Spencer & Hall; Timms 2012*a*). 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 2009*b*), 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 1990*a*, 1990*b*; Hebert and Wilson 2000). Furthermore, one of six ephippia 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 2009*a*). 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 daphnids (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.* 2010*a*, 2011*a*; 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. 2*a*). *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. 2*b*).

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.* 2010*a*), 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.* 2011*b*). *D. australis* experienced significant mortality at temperatures above 28°C (Ismail *et al.* 2010*a*), which is consistent with field observations that it occurs
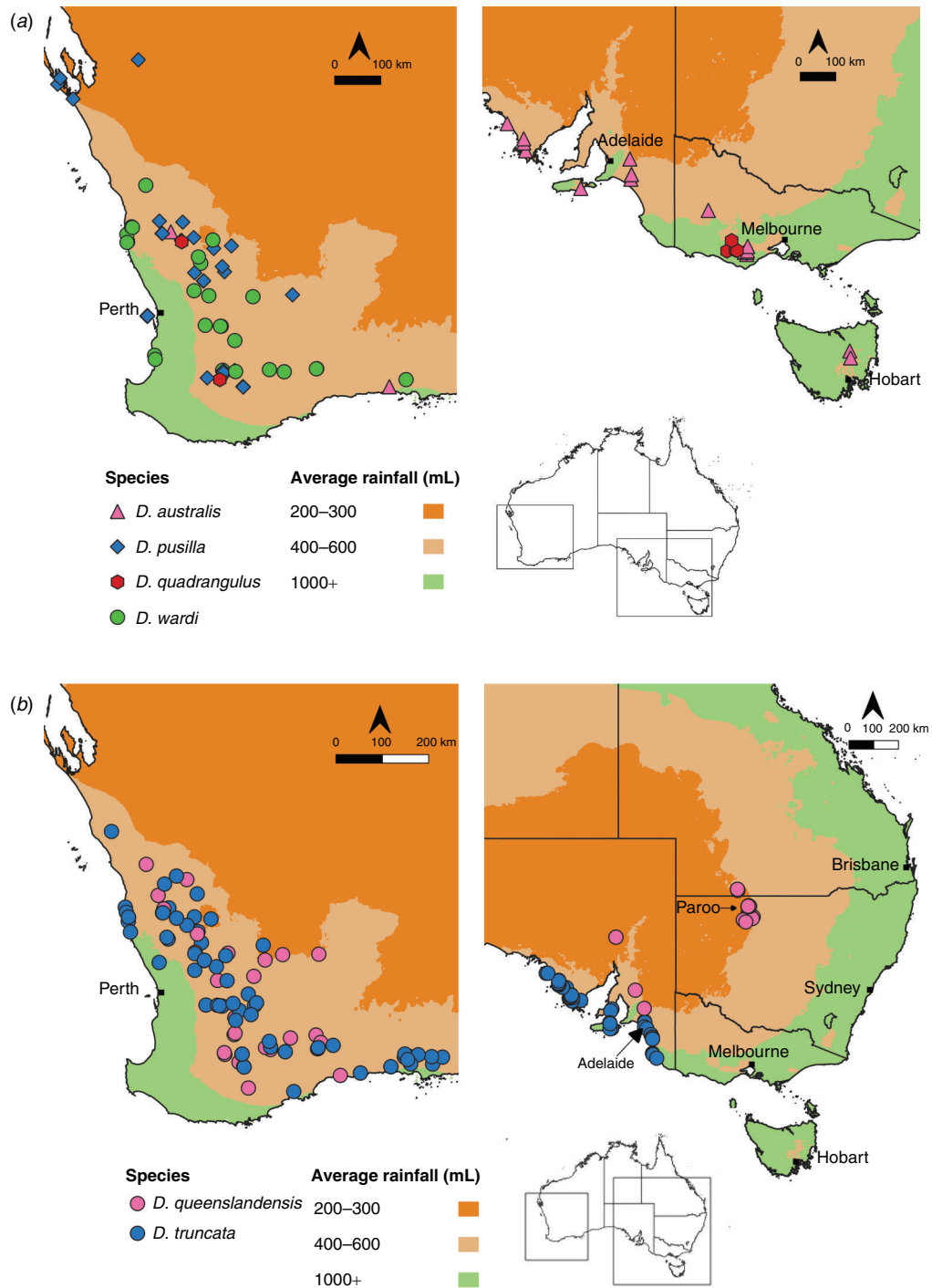
Fig. 2. Recent reported distributions of *Daphniopsis* in Australia. (*a*) *D. australis*, *D. pusilla*, *D. quadrangulus* and *D. wardi*; (*b*) *D. queenslandensis* and *D. truncata*. Data are from Edward (1983), Sergeev and Williams (1985), Sergeev (1990*a*, 1990*b*), Timms (1993, 1998, 2001, 2009*a*, 2009*b*, 2018), Williams *et al.* (1998), Halse *et al.* (2000*a*, 2000*b*), 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.* (2000*a*); 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 (2009*a*); 11, Timms (2009*b*); 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	
Daphniopsis			
australis	17.2 (4–154.1)	16	4, 6, 10, 12
pusilla	29.7 (0.6–77.3)	42	1–4, 12
quadrangulus	22.7 (7.6–37.8)	2	4, 12
queenslandensis	20 (1–145.6)	45	1, 4, 7–9, 12, 13
truncata	24.1 (0.04–109.2)	60	1, 4, 5, 10–12
wardi	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, 2009*b*, 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 trigged 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.* 2010*b*). Detailed lifecycle data are available only for *D. australis* under laboratory conditions, as described by Ismail *et al.* (2010*b*). 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.* (2011*a*) 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.* 2000*a*). 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 2009*b*).

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, 1981*a*) 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*
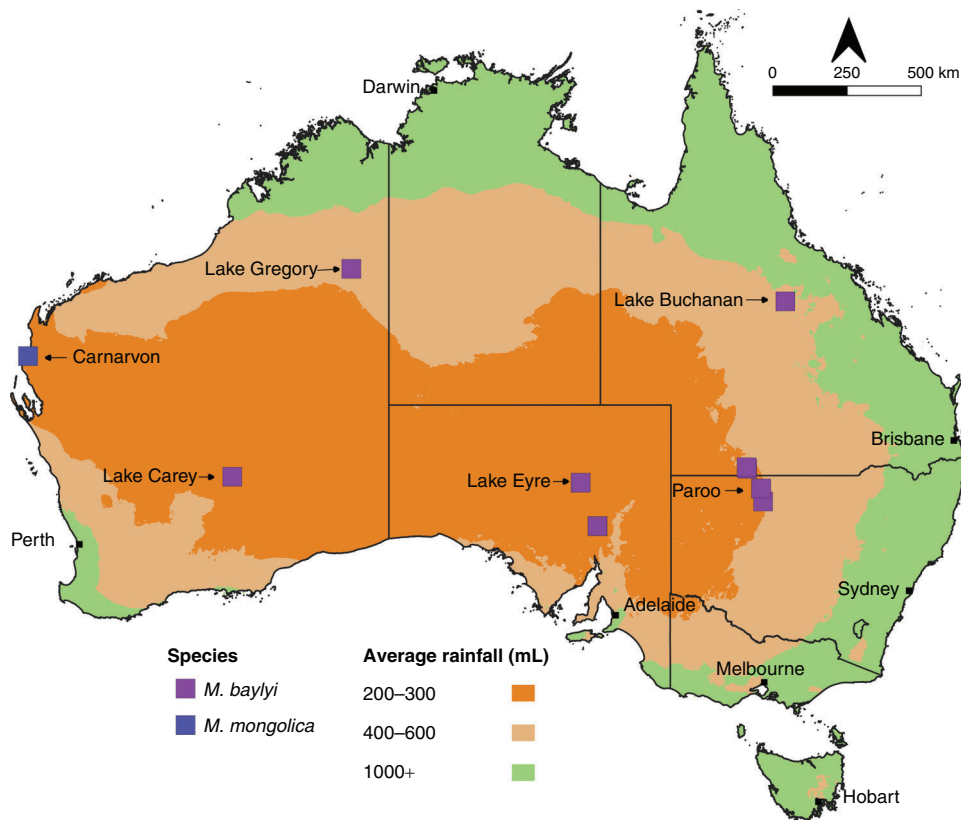
Fig. 3. Reported distributions of halophilic species of *Moina* in Australia. Data are from Timms (1987, 1993, 1998, 2001, 2018), Williams and Kokkinn (1988), Halse *et al.* (1998), Williams *et al.* (1998), Timms *et al.* (2006) and unpublished records from the Western Australian Department of Biodiversity 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 southeastern 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 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 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
Australocypris		
beaumonti	40.9–73.7	South-western WA
bennetti	25–282.1	South-western WA, central WA
dispar	3.1–128	South-western WA, south-eastern SA
insularis	2–200.2	South-western WA, central WA, south-eastern SA, central SA, Vic.
mongerensis	11	Central-west WA
rectangularis	45.2–198.9	South-western WA[A], south-eastern SA, Vic.
robusta	4.4–288	South-western WA[A], central WA[A], south-eastern SA, central SA, Vic., Tas.
Mytilocypris		
ambiguosa	1.3–64.6	South-western WA, south-eastern SA, Vic.
henricae	1.5–20	South-western WA[A], south-eastern SA, Vic., south-eastern NSW
mytiloides	1.3–172.9	South-western WA, central WA, south-eastern SA, Vic., Tas.
splendida	0.3–77.3	South-western WA, south-eastern SA, central SA, Vic., north-western NSW, south-eastern NSW, south-eastern Qld, central Qld
praenuncia	4–51.1	South-eastern SA, Vic., Tas.
tasmanica	4–9	South-eastern SA, Vic., Tas.
Repandocypris		
austinensis	40–117	Central WA
gleneagles	42–51	Central SA
Trigonocypris		
globulosa	0.7–122	South-western WA, central WA, north-western WA, central SA, north-west NSW, south-eastern Qld, central Qld

[A]Recorded 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 2009*b*). 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, 1983*a*). 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 1983*a*). 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 1983*a*). 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 *Diacypris* in microcosm experiments (Campbell 1995).

Small ostracods

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

Australia, and have no known recent freshwater or marine ancestors (De Deckker 1981*b*). The taxonomy of Diacypridinae has not been addressed since De Deckker (1981*a*, 1981*c*), and the extent to which it captures the biodiversity of this group is not clear. There are reports of multiple undescribed species of *Diacypris* and *Reticypris*, 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 1981*c* for *Diacypris*). Some characters, such as variation in the carapace shape and size, are ecophenotypic at least in several *Diacypris* and *Reticypris* species (De Deckker 1981*c*, 1981*d*).

Other small halophilic ostracods from Australian salt lakes are the endemic *Platycypris baueri* (Herbst), *Patcypris outback* Halse & Martens and *Trilocypris horwitzi* Halse & Martens, which are all in the cosmopolitan subfamily Cyprinotinae (De Deckker and Geddes 1980; De Deckker 1981*b*; 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 1983*a*; 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
Diacypris							
compacta	X	X	X		X		1, 3, 10, 15, 17, 18, 20–26
dictyote	X	X		X			1, 5, 15, 19–23, 26
dietzi	X	X	X	X		X	3, 7, 11, 19, 22, 24, 25
fodiens	X	X					3, 10, 15, 20, 22, 23
phoxe	X	X					5, 15, 22
spinosa	X	X	X			X	1, 5, 7, 8, 9, 12, 15–17, 20–24
whitei	X	X					3, 10, 15, 20–23, 26
Reticypris							
clava	X	X	X				1, 6, 10, 15, 17, 22–24, 26
herbsti		X	X	X			3, 19, 24
kurdimurka	X	X					6, 22, 27
pinguis	X			X			4, 11, 15, 22
walbu	X	X		X	X		1, 2, 6, 15, 18, 19, 26
Platycypris							
baueri	X	X	X				1, 3, 10, 15, 17, 20–24, 26
Patcypris							
outback	X						14
Trilocypris							
horwitzi	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 *Reticypris* 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 *Reticypris* 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 *Reticypris herbsti* McKenzie (known from South Australia but not Western Australia) and *Reticypris 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*, *Reticypris kurdimurka* De Deckker, *R. pinguis* and *Reticypris 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 *Reticypris* 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 Harpaticoida (i.e. *Mesochra baylyi* Hamond), represented.
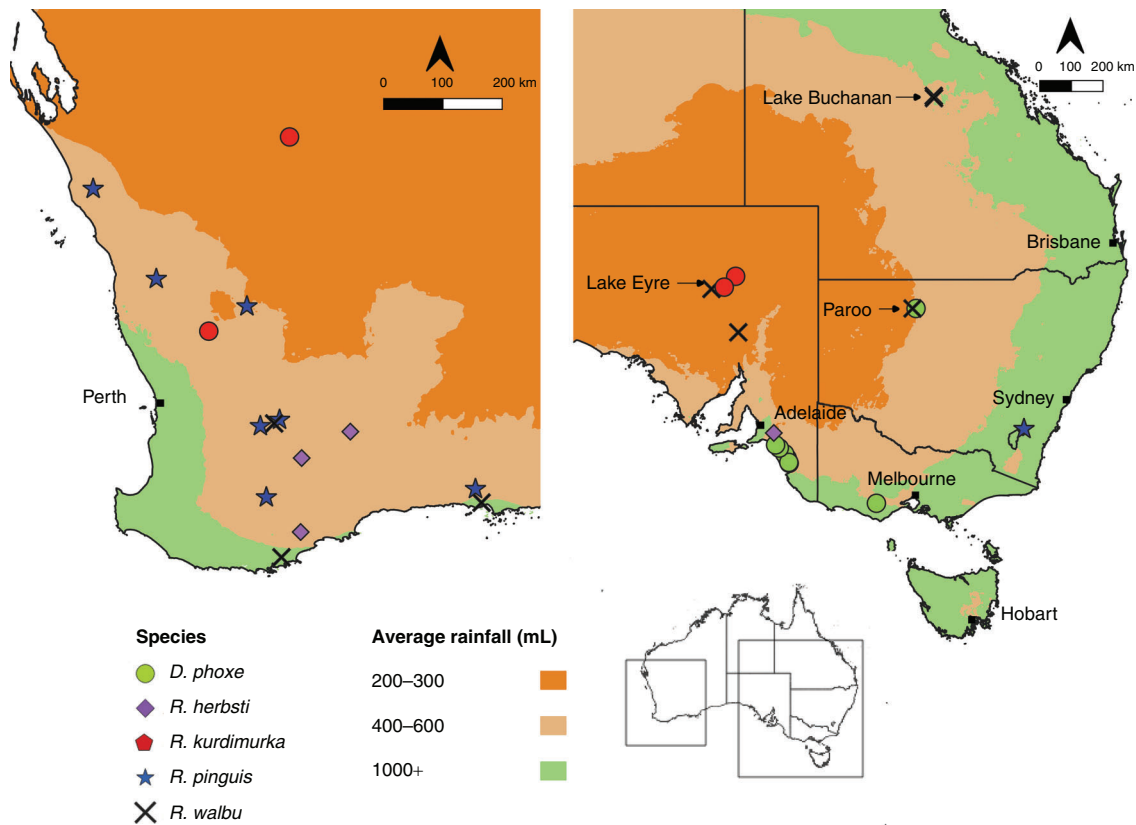
Fig. 4.   Reported distributions of four species of *Reticypris* and *Diacypris phoxe* to illustrate the patchy occurrence of small ostracods. Data are from De Deckker (1979, 1981*a*, 1981*c*, 1981*d*), De Deckker and Geddes (1980), Timms (1987, 1993), Williams and Kokkinn (1988), Williams *et al.* (1990, 1998), Halse *et al.* (2000*a*) and unpublished records from the Western Australian Department of Biodiversity Conservation and Attractions.
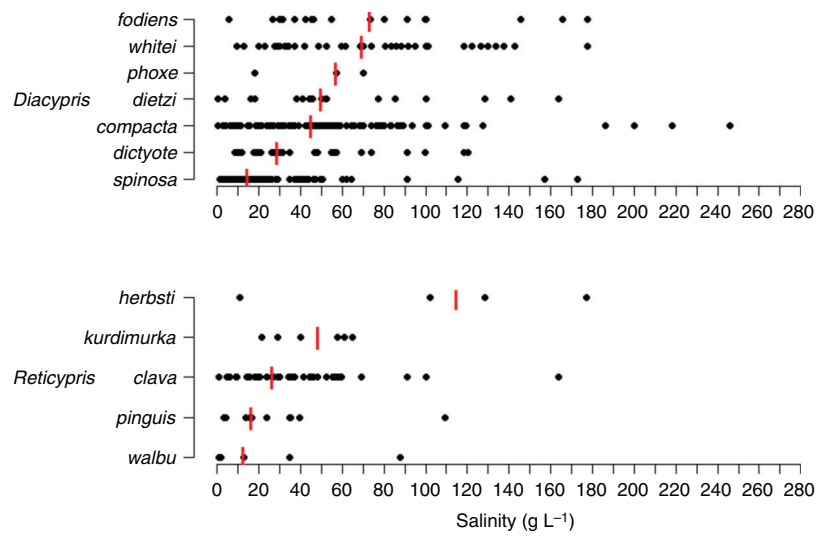

Fig. 5.   Salinity distributions of *Diacypris* and *Reticypris* species from field data. The red lines indicate median values. Data are from De Deckker and Geddes (1980), De Deckker (1981*a*, 1981*c*, 1981*d*), Geddes *et al.* (1981), De Deckker and Williams (1982), Edward (1983), Williams (1984, 1995),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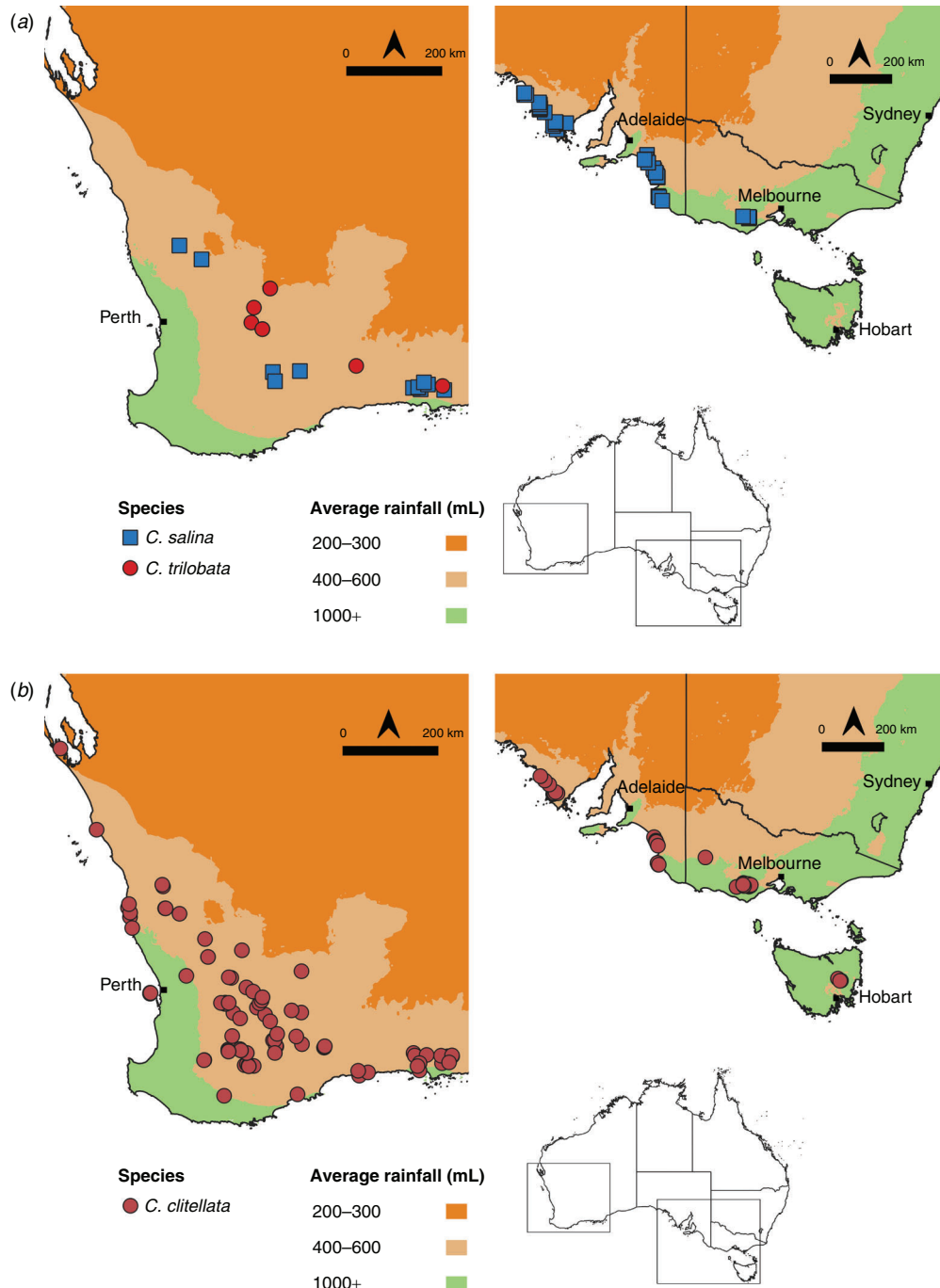

Fig. 6. Reported distribution of *Calamoecia* in Australia: (*a*) *C. salina* and *C. trilobata* and (*b*) *C. clitellata*. Data are from Bayly and Williams (1966), Bayly (1970), Geddes (1976), De Deckker and Geddes (1980), Geddes *et al.* (1981), De Deckker and Williams (1982), Edward (1983), Williams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

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 2009*b*). 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 2009*b*). 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 *Pescecyclops arnaudi* (Sars) (Anufriieva 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.

Harpacticoidea

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, 2009*b*; 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 *Pescecyclops* and *Meridiecyclops*
For further details see Fiers (2001), Tang and Knott (2009) and Karanovic *et al.* (2011).

Current nomenclature	Names used
Pescecyclops arnaudi (Sars)	*Microcyclops arnaudi* in Geddes (1976), Morton and Bayly (1977), Geddes *et al.* (1981) and Williams *et al.* (1990)
	Metacyclops arnaudi (Sars) in Halse *et al.* (2000*a*) and Timms (2009*a*)
Meridiecyclops baylyi Fiers	*Microcyclops arnaudi* in Bayly and Williams (1966)
	Metacyclops arnaudi sensu Kiefer in Halse *et al.* (2000*a*) and Pinder *et al.* (2002).
	Meridiecyclops baylyi in Pinder *et al.* (2005) and Pinder and Quinlan (2015).
Meridiecyclops platypus Fiers	*Microcyclops platypus* in Geddes *et al.* (1981) and Williams and Kokkinn (1988)
	Metacyclops platypus in Timms (1993) and Timms (2001)
	Meridiecyclops platypus 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 2009*b*). 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 2009*b*). 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 waterbody, although there are reports of *C. striata* and *C. glauerti* co-occurring in lakes on the Eyre Peninsula (Timms 2009*a*). 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
Coxiella		
exposita	Iredale (1943)	Endemic to south-western WA
glabra	Macpherson (1957)	Endemic to south-western WA
striatula	Menke (1843)	Endemic to south-western WA[A]
pyrrhostoma	Cox (1868)	Endemic to south-western WA
glauerti	Macpherson (1957)	South-western WA and Eyre Peninsula
striata	Reeve (1842)	South-eastern Australia including the Eyre Peninsula and Tas.
Coxielladda		
gilesi	Angas (1877)	Central WA and SA, central and south-eastern Qld[B]

[A]Reported from fossil deposits in Streaky Bay, South Australia (see Cotton 1942).
[B]Reported 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 LD$_{50}$ 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* (Krefft); 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 (Diacypridinae and Mytilocypridinae), 11 genera (*Parartemia*, *Extremalona*, *Australocypris*, *Repandocypris*, *Diacypris*, *Reticypris*, *Platy-cypris*, *Patcypris*, *Trilocypris*, *Meridiecyclops* 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 Savatenalinton 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 2012*b*). 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 ($35\text{–}{>}50$ g L^{-1}) to one of higher salinity ($50\text{–}100$ 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 1998*a*). 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.* 2011*b*). 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 1983*b*).

Competitive exclusion (Timms 2012*a*) 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 outcompeted 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 2012*b*) 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 physicochemical 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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