

Responses of freshwater biota to rising salinity levels and implications for saline water management: a review

Kimberley R. James^{A,C}, Belinda Cant^B and Tom Ryan^B

^ADeakin University, School of Ecology and Environment, Burwood, Vic. 3125, Australia.

^BDepartment of Sustainability and Environment, PO Box 137, Heidelberg, Vic. 3084, Australia.

^CCorresponding author; email: kimjames@deakin.edu.au

Abstract. All of the plants and animals that make up freshwater aquatic communities are affected by salinity. Many taxa possess morphological, physiological and life-history characteristics that provide some capacity for tolerance, acclimatisation or avoidance. These characteristics impart a level of resilience to freshwater communities.

To maintain biodiversity in aquatic systems it is important to manage the rate, timing, pattern, frequency and duration of increases in salinity in terms of lethal and sublethal effects, sensitive life stages, the capacity of freshwater biota to acclimatise to salinity and long-term impacts on community structure.

We have limited understanding of the impacts of saline water management on species interactions, food-web structures and how elevated salinity levels affect the integrity of communities. Little is known about the effect of salinity on complex ecosystem processes involving microbes and microalgae, or the salinity thresholds that prevent semi-aquatic and terrestrial species from using aquatic resources. Compounding effects of salinity and other stressors are also poorly understood.

Our current understanding needs to be reinterpreted in a form that is accessible and useful for water managers. Because of their complexity, many of the remaining knowledge gaps can only be addressed through a multidisciplinary approach carried out in an adaptive management framework, utilising decision-making and ecological risk assessment tools.

Introduction

Secondary salinisation is arguably the greatest cause of degradation in freshwater aquatic systems in Australia. Rivers, wetlands, floodplains and riparian zones are the systems most at risk from the salinisation as they occupy the lowest points in the landscape where saline water tends to accumulate via groundwater intrusion and surface runoff from surrounding saline landscapes. These systems may be further affected when saline water is transported downstream to accumulate in pools and terminal basins. It is estimated that up to 41300 km of streams and lake perimeter in Australia could be at risk from shallow water tables or have a high salinity hazard by the year 2050 (National Land and Water Resources Audit 2001).

There are a multitude of potential impacts of secondary salinisation on aquatic systems, including direct toxic effects, changed chemical processes and loss of habitat in the water, riparian zones and adjacent floodplains. It is predicted that these impacts will be transmitted to the wider landscape and affect biodiversity through degradation of the remaining

natural habitat and fragmentation of wildlife corridors provided by aquatic systems in many agricultural areas (Clunie *et al.* 2002).

It appears that the native species of Australian lowland rivers have a level of tolerance and resilience to salinity increases resulting from the selective pressure of the climatic history of the continent which has produced higher salt levels than the current natural level (Williams *et al.* 1991). However, the present rate of change is unprecedented, and is likely to be much too fast for most biota to adapt. The nature of change is also different. Rather than the steady, slow selective pressure of salinisation associated with climate change, biota are subjected to sudden and extreme changes in salinity levels at sites of saline ground- and surface-water incursion or disposal, and to repeated pulses as saline water is transported downstream or through wetland systems. Communities we observe now are possibly the most tolerant vestiges of the once more naturally diverse fauna (Williams *et al.* 1991).

Our challenge for saline water management is to understand the morphological, physiological and life-history

characteristics that provide some capacity for tolerance, acclimatisation or avoidance of elevated salinity levels and impart a level of resilience to the biota of freshwater communities. This review discusses what is known of the impacts of secondary salinisation on Australian freshwater biota and the resilience of communities within salinising landscapes. The discussion is based primarily on information available on the effect of salinisation on macrophytes, invertebrates and fish, with supplementary information on semi-aquatic biota, such as riparian vegetation and waterbirds.

Mechanisms for surviving in an increasingly saline environment

Past reviews have described a great deal of evidence for the decline of aquatic biodiversity in response to salinisation (Hart *et al.* 1991; Bailey and James 2000; Clunie *et al.* 2002). However, some groups of taxa have evolved strategies that allow them to survive in salinising landscapes. In order to conserve biodiversity in salinising rivers and landscapes we must understand these strategies and manage the environment to facilitate their function.

Many plants and animals associated with aquatic systems have evolved morphological, physiological and life-history traits that impart resilience in salinising landscapes. These traits help organisms tolerate or acclimatise to increasing salt concentrations, or allow organisms to persist in an area by avoiding microhabitats where the salt concentrations in soil or water has become elevated. Acclimatisation (an aspect of tolerance) and avoidance are two strategies identified in general ecological theories of species' responses to disturbance (Lavorel and Garnier 2002). Avoidance involves preferential habitat selection, growth into less saline microhabitats or dormancy. For non-sessile species or those that have a mobile life-history stage, avoidance also encompasses dispersal and recolonisation, allowing species to re-establish in areas during periods of sufficiently low salinity. Sessile species or adult life-history stages on the other hand rely on highly developed osmoregulatory structures, which increase an organism's ability to tolerate or acclimatise to increased concentrations of salt by facilitating salt excretion, excluding salt or decreasing osmotic potential by accumulating compatible solutes. Aquatic systems that contain species which exhibit tolerance, acclimatisation or avoidance strategies, may be capable of maintaining functional integrity. These systems are also likely to be more resilient, providing salinities remain below the threshold levels of their constituent species or functional groups.

Tolerance

Salt tolerance in plants and animals depends on their ability to maintain defined conditions in the cytoplasm of their cells over a range of external salt concentrations (Greenway and Osmond 1972; Yeo 1998). Elevated salinity can result in

reduced growth or death in plants, as a result of either the toxic effect of excess ions in the cells and/or water deficiency caused by the difficulty of extracting water from the saline external medium (Greenway and Munns 1980). Plants may cope with high internal ionic concentration by compartmentalisation of ions into vacuoles and by the production of organic solutes in the cytoplasm to maintain osmotic balance within root cells. This compartmentalisation of ions also prevents osmotic withdrawal of water from the cell, low cell turgor and consequent water deficiency. Plants may avoid excess ion concentration by controlling the uptake of ions and their transport to the shoot (Greenway and Munns 1980; Yeo 1998).

Submerged and semi-emergent aquatic macrophytes differ from riparian and terrestrial species as saline water is in contact with the leaf and stem tissue as well as the root tissue. Ion-exclusion mechanisms that operate effectively in the root may be ineffective in the leaf and stem as the capability to absorb nutrients through leaves and stems may prevent exclusion of ions as leaves do not have a well developed epidermis to protect these structures (Warwick and Bailey 1997).

In plants, salt-tolerant and salt-intolerant species differ in the degree to which ion concentration can be regulated within cellular compartments to maintain defined conditions in the cytoplasm, rather than in the mechanisms available for regulation (Greenway and Osmond 1972; Yeo 1998). An exception are those species that possess salt-excreting glands.

Most freshwater macroinvertebrates have internal ionic concentrations of 1000–15000 mg L⁻¹ (Hart *et al.* 1991). They can maintain constant internal ionic concentrations in freshwater via passive mechanisms; however, as salinity increases, so does ion intake (Beadle 1969). An osmotic gradient across the cell wall results in loss of water from cells by osmosis. Loss of cell function resulting from this water loss eventually causes mortality. The variation in tolerance among species is thus in part a function of normal blood ionic concentration; the higher the internal ionic concentration, the higher the tolerance (Hart *et al.* 1991). Generally, osmoregulatory functions fail at salt concentrations of 9000 mg L⁻¹ (Hart *et al.* 1991), but mortality and sublethal effects such as physiological and behavioural changes have been found to occur at far lower concentrations of about 800 mg L⁻¹ (Bailey and James 2000).

While invertebrates use passive osmoregulatory mechanisms to maintain constant internal ionic concentration, many fish species control ion exchange via active transport of ions against external osmotic gradients. Most freshwater fish maintain their blood salt concentration at 7000–13000 mg L⁻¹ (Bacher and Garnham 1992) and have adapted to external salt concentrations well below their

Table 1. Compilation of information on the salt tolerance of freshwater fish of the Murray–Darling Basin and south-eastern Australia (modified from Clunie *et al.* 2002)

Where salinity was measured as electrical conductivity, the conversion used was total soluble salts (mg L^{-1}) = $0.68 \times$ electrical conductivity ($\mu\text{S cm}^{-1}$) (Hart *et al.* 1991). LD50 is the concentration of salts at which 50% of the sample population dies. For references, see the following: (1) Chessman and Williams (1975), (2) Jackson and Pierce (1992), (3) O'Brien and Ryan (1999), (4) Guo *et al.* (1995), (5) Williams and Williams (1991), (6) Bacher and Garnham (1992), (7) Williams (1987), (8) Hart *et al.* (1991), (9) Hogan and Nicholson (1987), (10) Merrick and Schimda (1984), (11) Guo *et al.* (1993), (12) Beumer (1979) in Hart *et al.* (1991), (13) Bacher and O'Brien (1989), (14) Alderman *et al.* (1976), (15) Geddes (1979), (16) Chessman and Williams (1974), (17) Karimov and Keyser (1998), (18) Jasim (1988), (19) Cadwallader and Backhouse (1983), (20) Nordlie and Mirandi (1996)

Species	Common name	Direct (acute) LD50 (mg L^{-1})	Slow (chronic) LD50 (mg L^{-1})	Early life stage LD50 (mg L^{-1})
Native fish				
<i>Bidyanus bidyanus</i>	Silver perch	13700 (2)	16000 (2)	15000 (4)
<i>Bidyanus bidyanus</i>	Silver perch			18000 ^A (4)
<i>Bidyanus bidyanus</i>	Silver perch			6000 ^B (11)
<i>Craterocephalus sterc. fulvus</i>	Unspecked hardyhead	43700 (5)		
<i>Gadopsis marmoratus</i>	River blackfish			6000 (6)
<i>Galaxias maculatus</i>	Common galaxias	45000 (1)	62000 (1)	6000 (6)
<i>Hephaestus fuliginosus</i>	Sooty grunter			8000 (9)
<i>Hypseleotris klunzingeri</i>	Western carp gudgeon	38000 (7)	50000 (7)	
<i>Leiopotherapon unicolor</i>	Spangled perch	22000 (2)	35500 (2)	
<i>Maccullochella peelii peelii</i>	Murray cod	13200 (2)	15700 (2)	9410 (3)
<i>Maccullochella macquariensis</i>	Trout cod			4470 (3)
<i>Maccullochella macquariensis</i>	Trout cod			8100 (3)
<i>Macquaria ambigua</i>	Golden perch	14400 (2)	31000 (2)	8270 (3)
<i>Macquaria australasica</i>	Macquarie perch			2060 ^C (3)
<i>Macquaria australasica</i>	Macquarie perch			13430 (3)
<i>Macquaria novemaculeata</i>	Australian bass			20000 ^D (10)
<i>Melanotaenia fluviatilis</i>	Crimson-spotted rainbow fish	21100 (7)	29800 (13)	12000 ^E (7)
<i>Melanotaenia fluviatilis</i>	Crimson-spotted rainbow fish	30000 (7)		
<i>Melanotaenia splendida splendida</i>	East Queensland rainbowfish		17800 (14)	
<i>Melanotaenia splendida splendida</i>	East Queensland rainbowfish	9000 (12)		17000 (7)
<i>Mogurnda adspersa</i>	Purple-spotted gudgeon	14800 (2)	17100 (2)	
<i>Philypnodan grandiceps</i>	Flat-headed gudgeon	23700 (2)	40000 (2)	
<i>Prototroctes maraena</i>	Australian grayling	30000 (2)		5000 ^A (6)
<i>Pseudaphritus urvilli</i>	Tupong/congoli	17000 (6)		
<i>Retropinna semoni</i>	Australian smelt	59000 (5)		
<i>Tandanus tandanus</i>	Freshwater catfish	13600 (2)	17800 (2)	
Introduced fish				
<i>Carassius auratus</i>	Goldfish	7300 (14)		
<i>Carassius auratus</i>	Goldfish	12800 (15)		
<i>Carassius auratus</i>	Goldfish	13056 (18)	19176 (18)	
<i>Cyprinus carpio</i>	European carp	7300 (14)		
<i>Cyprinus carpio</i>	European carp	12800 (19)		
<i>Cyprinus carpio</i>	European carp			9000 ^F (17)
<i>Gambusia holbrooki</i>	Mosquito fish	19500 (16)		
<i>Gambusia holbrooki</i>	Mosquito fish	25000 ^G (20)		
<i>Perca fluviatilis</i>	Redfin	8000 (15)		
<i>Salmo gairdneri</i>	Rainbow trout		35000 (8)	3000 (8)
<i>Salmo trutta</i>	Brown trout		35000 (8)	3000 (8)

^ALimit of egg development. ^BEgg LD50 tolerance before cleavage. ^CEgg LD50 tolerance before hardening. ^DSpawning requirement. ^EFry LD50 tolerance. ^FLimit to sperm motility. ^GLimit to osmotic ability.

internal concentrations. Nevertheless, when external salinity exceeds the internal concentration, osmoregulatory mechanisms begin to fail, leading to lower fitness and eventually, mortality (Bacher and Garnham 1992).

The variability in the salt tolerance of different fish species can be attributed to long-term and short-term

ancestral and/or life-history acclimatisation (Williams *et al.* 1991). Most inland Australian fish have a diadromous (migrating between freshwater and the sea as part of their life cycle) ancestry (Merrick and Schimda 1984); however, many species have evolved to complete their life cycles completely within freshwater. While not exclusively the case, it appears

that groups such as Atherinids (hardyheads), Eleotids (gudgeons), Gobiids (gobies) and Ariids and Plotosis (catfishes), which may have more recent marine divergence, are more tolerant to saline conditions (Hart *et al.* 1991). For example, unspecked hardyhead (*Craterocephalus stercusmuscarum fulvus*) and smelt (*Retropinna semoni*), within the Hardyhead family, have tested salinity tolerances (LD 50, the concentration of salts at which 50% of the sample population dies) of 43700 and 59000 mg L⁻¹, respectively (Table 1) (Williams and Williams 1991). High salinity tolerance can also exist in other groups such as *Galaxias maculatus* (common galaxias) (Pollard 1971a, 1971b), which is able to tolerate both fresh and saline environments by changing osmoregulation from hypo- to hyper-osmotic when required (Chessman and Williams 1975).

The degree of tolerance to elevated salt concentrations observed in many freshwater taxa may be a legacy of ancestral association with the sea or previously saline inland environments (Williams *et al.* 1991). Many aquatic organisms exhibit physiological and morphological adaptations to saline conditions. Organisms that lack these traits are likely to be intolerant to increases in salinity. For example, Hart *et al.* (1991) suggested that toxic effects would be expected to occur in the simple multicellular organisms (e.g. *Hydra* spp., and flatworms) with quite small increases in salinity, given their lack of complex osmoregulatory structures and small size. Similarly, freshwater macroinvertebrates that have less recent ancestral associations with saline environments also have less advanced osmoregulatory structures and expend large amounts of energy maintaining ionic balance (Sutcliffe 1974).

Variability in the salinity of aquatic systems across catchments can also influence the salt tolerance of populations of the same species, differentially selecting for salt tolerance and resulting in different sensitivities for geographically separated populations (Davis 1975). For example, geographically isolated populations of unspecked hardyhead, smelt, crimson-spotted rainbowfish (*Melanotaenia fluviatilis*) and western carp gudgeon (*Hypseleotris klunzingeri*) were observed to have significantly different salinity tolerances (Williams 1987). A similar finding was reported in the salt tolerance of seedlings of 31 species of *Eucalyptus* and *Melaleuca* from different provenances (Van der Moezel *et al.* 1991).

Within Australia's salinising landscapes, there are likely to be aquatic systems with a comparable diversity of species, but differing in their responses to salinisation. Some will contain highly sensitive species, while others contain species with a level of resilience. Furthermore, the degree to which individual organisms or populations can acclimatise to salinity over a range of time scales may give us some insight into the patterns of responses observed in different aquatic systems. Knowledge of the historical salinity exposure of

biota within a catchment will be important for setting upper limits to the salt content of managed water.

Acclimitisation

The ability of organisms to acclimatise to salinity depends not only on inherent morphological and life-history strategies but also on the nature of the disturbance. The rate, duration, periodicity and seasonality of salinisation have a profound effect on the responses of biota. When salinity increases slowly in a system, some organisms are able to acclimatise and tolerate incremental increases in salt concentration (between 10 and 50% of initial concentration). On the other hand, sudden large increases in salinity (100–200% of initial concentration) may cause significant increases in mortality. For example, *Azolla pinnata* is a salt-sensitive plant and normally cannot tolerate salt concentration above ~1800 mg L⁻¹ NaCl in experiments that test for acute reactions to sudden exposure to significantly elevated salt concentrations. Plants exhibited sublethal effects such as suppressed growth, yellowing and degeneration as this concentration was approached (Rai and Rai 1999). The threshold level of *A. pinnata* rose to 3600 mg L⁻¹ NaCl when plants were incubated at 1200 mg L⁻¹ for 18 days and then subjected to incremental increases of ~600 mg L⁻¹ per day. In contrast to the acute tests, in these incremental tests there were no sublethal effects as the new salinity threshold was approached. Furthermore, a critical period of time is required for acclimatisation as plants preincubated for less than 18 days were killed by the stepwise transfer to ~3600 mg L⁻¹ (Rai and Rai 1999).

Acclimatisation characteristics of freshwater biota have implications for saline water management. Pulsed release of saline water into freshwater systems should be avoided as it is likely to cause higher mortality and loss of biodiversity in a system than does a slow build-up to the same level. Examples of saline pulses include the transport of saline waste water along reaches of natural rivers to disposal sites and, the arrival of the initial 'slug' of highly saline surface-water runoff from the surrounding salt-affected catchment after rain.

Avoidance

Some species may maintain a presence in a salinising environment by using a range of strategies to avoid elevated salt concentrations. These strategies may involve the following: microhabitat selection or utilisation of less saline microhabitats within a salinising habitat patch; dispersing to less saline habitat patches; or remaining in a salinising area in a dormant phase until conditions become less saline usually via a freshening flow or flood. Utilisation of less saline microhabitats has been observed in riparian species such as *Eucalyptus camaldulensis* and *Melaleuca halmaturorum* which have extensive root systems in contact with several

sources of subterranean water of varying salt concentration. Differences in osmotic pressure are thought to lead to differential water uptake from different parts of the root zone, with greater uptake of water by roots in contact with low salt concentration than those in contact with high salt concentration (Mensforth *et al.* 1994; Thorburn *et al.* 1994; Mensforth and Walker 1996).

Similarly, highly mobile and semi-aquatic animals are able to obtain necessary resources from often very productive saline systems while using fresher systems nearby for drinking and breeding. Many waterbirds for example, have been found to move between waterbodies, feeding in saline waterbodies and utilising fresher systems nearby for drinking, nesting or shelter (Hart *et al.* 1991). We have almost no information on the salinity thresholds that prevent semi-aquatic and terrestrial species from utilising the resources they need within an aquatic system.

Where salinity levels vary significantly, plants and animals may avoid the highest salinity events as dormant propagules, seed or eggs in the sediment and then re-emerge following stimulus characteristic of a less saline environment (Skinner *et al.* 2001). Fresher conditions may occur annually, only during particularly wet years or when an environmental flow is allocated to the system. Where biota are dependent on environmental flows to provide suitable conditions for emergence, it is critical that we understand the longevity of dormant propagules so that fresh water is delivered at a frequency and volume that ensures the persistence of the community.

The maintenance of biodiversity over time in variable systems depends in part on the spatial and temporal nature of the mosaic of saline and non-saline aquatic habitat patches and the characteristics of microhabitat selection and dormancy and dispersal exhibited by species within those systems. Although populations may suffer lethal salinity levels in a system during saline periods, they may survive over time by dispersing to refugia and then recolonising during less saline periods. Recolonisation by macroinvertebrates has been observed by Timms (1998a) who found that a decrease in salinity from 17600 mg L⁻¹ to 8300 mg L⁻¹ over 6 years was concomitant with finding eight extra invertebrate species.

While information exists regarding the dispersal capacity of many terrestrial plants and animals, there are significant knowledge gaps relating to aquatic and semi-aquatic biota. Ideally, freshwater systems should be maintained in close proximity to salinising systems to enable dispersal of biota back to the saline system when salinity levels drop and to enable biota to obtain the resources they require from fresh and saline systems.

Determination of salinity thresholds

Analysis of data derived from observations of the presence/absence of species in the field and laboratory-

based ecotoxicological studies reveals large variation in salinity thresholds both within and among taxonomic groups at all levels of the taxonomic hierarchy. Nevertheless, some generalisations about salinity thresholds for freshwater biota can be made.

Most microinvertebrates are not tolerant of saline conditions, although some species of microinvertebrates within the phyla Rotifera and Arthropoda (Class: Crustacea; Order: Copepoda and Class: Insecta; Family: Chironomidae) are saline-water specialists (Halse *et al.* 1998; Timms 1998b; Williams *et al.* 1998). In general, species richness of microfauna is negatively correlated with salinity levels in lakes (Brock and Shiel 1983; Halse *et al.* 1998). This relationship may be driven by one particularly diverse or dominant taxonomic group which constitutes a significant proportion of the species in a system. Declines in that group in response to salinity result in the measurement of decline in species richness for the entire system. For example, 10 species of Ostracod, which constitute a large proportion of macroinvertebrate species in saline lakes, were found in fresh lakes while only one species was found in saline lakes of north-western Australia (Halse *et al.* 1998).

The threshold levels for some species of microinvertebrates have been placed at less than 2000 mg L⁻¹ (Table 2) (Nielsen *et al.* 2003). The majority of macroinvertebrate species are thought to be intolerant of saline conditions. Acute LC50 tests of freshwater invertebrates confirm the general finding of presence/absence data that some species of invertebrates are adversely affected by salinity levels of about 2000 mg L⁻¹ (Table 2) (Bacher and Garnham 1992). Small, multicellular organisms (such as *Hydra* spp., flatworms and leaches) with a distinct lack of osmoregulatory capacity and macroinvertebrates without impermeable exoskeletons (e.g. pulmonate snails) are likely to be the least tolerant to saline conditions (Table 2) (Hart *et al.* 1991).

Within insects, some taxonomic groups (e.g. water bugs, beetles and dipteran flies) appear to be relatively tolerant of salinity increases, while others (e.g. stone flies, some mayflies, some caddisflies, some dragon flies and certain water bugs) are sensitive to even minor increases in salinity (Hart *et al.* 1991). Dipteran flies such as chironomids are often thought of as quite tolerant; however, there are species within this family that exhibit some of the greatest sensitivities observed in macroinvertebrates, with thresholds between 5000 and 10000 mg L⁻¹ (Hart *et al.* 1991; Short *et al.* 1991; Kefford 2000).

Research by Timms (1993, 1998a, 1998b) demonstrates that invertebrates are possibly found at the greatest range of salinity levels of all the taxa investigated. This finding is exemplified by Copepods (Cl. Crustacea) and Dipterans (Cl. Insecta). Within Copepoda, which represents only one of many subclasses of Crustacea, upper-level tolerances (as measured by the presence of species) range from intolerant

Table 2. Generalisations about salinity thresholds for freshwater biota

Taxa	Threshold (mg L ⁻¹)	Effect
Small, multicellular organisms (e.g. hydra, leeches, flatworms)	Not tolerant to elevated salinity levels	Lethal effects
Macroinvertebrates without impermeable exoskeletons (e.g. pulmonate gastropods)		
Microinvertebrates	<2000	Lethal effects
Majority of macroinvertebrates	2000	Adverse effects
Most submerged macrophytes	1000–2000	Sublethal effects, lethal effects for some species
<i>Chara</i> spp. (Charophyta)	1000–3000	Disappeared from wetlands
<i>Nitella</i> spp. (Charophyta)	1000–5000	Disappeared from wetlands
Widespread macrophytes	4000	Disappeared from wetlands
Riparian trees	>2000	Adverse effects
Adult fish	8800	Most are tolerant up to this level
Juvenile fish: pre-hardened eggs	2000–4500	Adverse affects
Juvenile fish: growth rate, survivorship, sperm motility	3000–5000	Optimal between these values
Waterbird broods	15300	Majority found below this level

Table 3. Salt tolerance ranges for charophytes from south-western South Australia and south-eastern Victoria (Garcia 1999)

Species	Tolerance (mg L ⁻¹)
<i>Chara globularis</i> var. <i>globularis</i>	1000–3000
<i>Chara globularis</i> var. <i>virgata</i>	1000–2000
<i>Chara hookeri</i>	1000–2000
<i>Chara fibrosa</i>	1000–2000
<i>Chara fibrosa</i> var. <i>fibrosa</i>	2000
<i>Chara fibrosa</i> var. <i>acanthophytis</i>	1000–3000
<i>Chara preissii</i>	2000–3000
<i>Lamprothamnium macropogon</i>	2000–58000
<i>Nitella congesta</i>	1000–3000
<i>Nitella ignescens</i>	1000
<i>Nitella lhotzkyi</i>	1000
<i>Nitella</i> aff. <i>lhotzkyi</i>	1000–4000
<i>Nitella ungula</i>	2000–3000
<i>Nitella</i> sp. 1	2000–4000
<i>Nitella</i> sp. 2	0–5000

at 670 mg L⁻¹ (*Microcylops* spp.) to highly tolerant at 177 500 mg L⁻¹ (*Schizopera* spp.). Similarly, upper-level tolerances in one family of Dipterans (Chironomidae) ranged from 1900 mg L⁻¹ (*Procladius paludicola*) to 255 000 mg L⁻¹ (*Tanytarsus barbitarsus*).

Most freshwater fish are capable of tolerating at least 7000–13 000 mg L⁻¹, which corresponds to the range of their internal salt concentration (Bacher and Garnham 1992). While data is lacking on many species, the direct LD50 results (Table 2) indicate that a large group of fish are incapable of tolerating rapid salinity changes greater than this range (including *Bidyanus bidyanus*, *Maccullochella peelii peelii*, *Macquaria ambigua*, *Melanotaenia splendida*, *Mogurnda adspersa*, *Tandanus tandanus*, *Carassius auratus*, *Cyprinus carpio*, *Perca fluviatilis*). Others appear to be more tolerant, with some species capable of tolerating salt

concentrations in excess of 40 000 mg L⁻¹ (*Craterocephalus sterc. fulvus*, *Galaxias maculatus*, *Retropinna semoni*) (Table 2).

As expected, the slow or chronic LD50 results indicate that most species of fish are able to acclimatize and can be exposed to higher salt concentrations before suffering adverse effects. The early life stages of freshwater fish are, however, much less tolerant. For example, for eggs and larvae, LD50 tolerance can be as low as 2060 mg L⁻¹, and 4470 mg L⁻¹ for species such as *Macquaria australasica* and *Maccullochella macquariensis* (Table 2).

Many of the submergent macrophytes found in south-eastern Australia are extremely sensitive, with increases in salt concentrations to between 1000 and 2000 mg L⁻¹ likely to result in lethal effects for some species (Table 2) (Bailey and James 2000). This is probably a result of plants being entirely submersed in saline water, with all parts of their structure subjected to ion toxicity and osmotic stress (Warwick and Bailey 1997). Extensive field surveys have demonstrated that once salinity levels have reached 4000 mg L⁻¹, normally widespread freshwater aquatic macrophytes have disappeared from wetlands (Brock 1981).

Considerable variability in salt tolerance is also seen within taxonomic groups of macrophytes. For example, charophyte (green macroscopic algae) taxa, on the whole, are intolerant of the marked changes in water level and salinity experienced in Australia's ephemeral wetlands (Garcia 1999). *Chara* species are found over a range of 0–3000 mg L⁻¹ and *Nitella* species are found over a range 0–5000 mg L⁻¹ (Tables 2, 3) (Garcia 1999). However, *Lamprothamnium macropogon* is an exception as it is found over a range of 2000–58000 mg L⁻¹ (Table 3).

Most of the research on the salt tolerance of riparian plants has been carried out on species from the genera *Eucalyptus*, *Melaleuca* and *Casuarina* and has shown that

many species are salt-sensitive and that adverse effects will occur at salinity levels above 2000 mg L⁻¹ (Table 2) (Hart *et al.* 1991).

Broad generalisations can be made about categories of freshwater biota such as macrophytes, invertebrates and fish. For example, on the whole, adult freshwater fish are more salt-tolerant than macrophytes or macroinvertebrates, which are more tolerant than microinvertebrates. However, taxonomic groups such as Charophyta, Insecta and Crustacea are generally not useful in predicting salt tolerance as each of these groups contains species with differences in salinity tolerances of up to three orders of magnitude. Even tested tolerance levels at the species level may vary with populations from provenances with different histories of salinisation.

Whilst it is useful to be able to identify salinity thresholds for groups of biota, salinity tolerance needs to be considered in terms of community tolerance. Within the taxa making up a freshwater community, there is a wide range of thresholds from relatively high (for fish) to very low (for microinvertebrates). Bearing in mind the trophic and habitat interrelationships of the biota of such a community, the salinity of water should be managed at a level that protects key species within the community.

Sensitive life stages

The majority of research into tolerance and thresholds of aquatic flora and fauna has focused on adult life-history stages. This does not account for the fact that juveniles of higher-order taxonomic groups are generally far more intolerant than adults, although there may be a correlation between the degree of juvenile and adult tolerance. Greater juvenile sensitivity obviously has important management implications. Managing for adult thresholds will lead to an inevitable decline in populations over the long-term as recruitment is reduced. The key to preventing biodiversity loss in salinising landscapes may well be found by investigating the tolerances of early life-history stages and the degree to which increasing salinity disrupts reproductive and recruitment processes.

Interactions between life-history stages and salinity have been studied more thoroughly for fish than for other taxonomic groups. Although most adult fish appear to be tolerant to salinity levels of at least between 7000 and 13 000 mg L⁻¹, during early life stages they are particularly vulnerable (Hogan and Nicholson 1987; Williams 1987; Hart *et al.* 1991; Bacher and Garnham 1992; Guo *et al.* 1993, 1995; O'Brien and Ryan 1999). Juvenile growth rate and survivorship, and sperm motility were optimal between 3000 and 5000 mg L⁻¹ but deteriorated rapidly above this level (Tables 1, 2). Poor egg-hatching and fry-survival rates, resulting from moderate increases in salinity, are likely to lead to a slow decline in fish populations (Tables 1, 2). Pre-hardened eggs were affected by salt concentrations of 2000–4500 mg L⁻¹ (Tables 1, 2).

Semi-aquatic animals such as waterbird chicks may also be more vulnerable than adults because of reduced mobility. If the salinity of the nesting site increases to a critical level before the chicks are fledged, they will not survive. As the adults are highly mobile, they can take advantage of resources in saline wetlands and seek drinking water from surrounding, fresher sources. The utilisation of wetlands by brooding waterbirds was demonstrated to occur most in those systems with salinity levels less than 15 300 mg L⁻¹ (Goodsell 1990) (Table 2).

It is important to be aware of the tolerance of earlier life stages as instantaneous measurements of the occurrence of adults at a site may not necessarily indicate a viable population. If the processes of reproduction and recruitment are disrupted, the persistence of the population is threatened. During the time of year when these processes are occurring, saline water must be managed so that salinity levels remain below the thresholds of zygotes and juveniles.

Community structure

While the lethal and sublethal effects have been used extensively to identify salinity thresholds for individual species, there is now an increasing focus on community-level and indirect effects of salinity on aquatic biota. As salinity levels rise, biotic communities respond in two fundamental ways. First, the most intolerant species within the community are lost from the system. Second, tolerant species begin to competitively dominate (Hart *et al.* 1991; Halse *et al.* 1998). These two responses can be seen at all scales from landscape level to individual wetlands and rivers.

Changes in community structure at the landscape scale were demonstrated by Garcia's (1999) survey of charophytes in wetlands of south-eastern Australia. At the lowest salinity levels, the salt-tolerant *Lamprothamnium macropogon* was found in association with several other taxa of charophytes. However, once salinity levels rose above 5000 mg L⁻¹ the communities became monospecific, consisting of just *Lamprothamnium macropogon* (Table 3).

Several studies of mosaics of saline and fresher wetlands in arid regions of Australia have reported a significant decrease in the diversity of species of waterbirds in saline wetlands compared with freshwater wetlands, along with a concomitant increase in abundance of individuals of tolerant species. (Kingsford and Porter 1994; Chapman and Lane 1997). It is evident that before saline wetlands become hypersaline, they may become highly productive providing both breeding habitat for waterfowl and abundant food resources to sustain large breeding populations (Kingsford and Porter 1994; Chapman and Lane 1997).

Detailed studies at the scale of single or a few systems have revealed more subtle community responses to increasing salinity. Skinner *et al.* (2001) compared hatching rate and mortality of the taxa that emerged from the seedbank under different salinity treatments. Greatest

mortality occurred when salinity conditions diverged, either higher or lower, from natural conditions. There was a shift in community structure whereby algae and protists dominated over invertebrates as salinity levels rose from 1100 to 11 500 mg L⁻¹. They also found that increased salinity levels were associated with lower diversity but higher total abundance of emergent organisms.

As the threshold for salinity tolerance is approached, the abundance of a taxon decreases. In a wetland community, the abundance of some cladoceran (microinvertebrate crustaceans) species that are sensitive to small increases in salinity, was reduced by 77% by the time the salinity level had risen to just 1250 mg L⁻¹ (Bailey and James 2000). Conversely, increasing salinity favoured some of the more salt-tolerant taxonomic groups, such as tolerant species of chironomids, resulting in significant increases in abundance by 90–400% (Bailey and James 2000). It is likely that the combination of salinity stress, ion toxicity and competition will have a compounding impact on species surviving close to their salinity thresholds, causing a further decline in species abundance.

There is also evidence to suggest that there will be a shift in balance between species within a community even at slightly elevated salinity levels. James and Hart (1993) demonstrated different levels of impact of sublethal effects in four macrophyte species from the same freshwater community when subjected to elevated salinity. There was a progressive reduction in growth rate and plant size with increasing salinity in all species, although not to the same extent. Also, asexual and sexual reproduction was blocked in one species. The differential nature of these sublethal effects implies that community structure will change as some species are more detrimentally affected than others at elevated but sublethal salinity levels.

At an even more subtle level of community function, Bailey and James (2000) pointed out that representatives from all biological communities are salt-sensitive and any deleterious effects to particular taxa are likely to translate into broader ecosystem processes, including primary productivity, decomposition, nutrient spiralling/recycling, and the flow of energy and material through trophic webs.

With increasing salinity, there is a transition from freshwater systems dominated by diverse communities of macrophytes to systems dominated by phytoplankton or a few species of submerged macrophytes. This is one of the most striking and characteristic effects of increasing salinity in aquatic systems. With further increases in salinity, a second transition has also been described whereby these phytoplankton/macrophyte-dominated systems may change to systems dominated by microbial mats composed mostly of cyanobacteria and halophilic bacteria (Davis 2002). Alternative-states models are emerging as a powerful method of describing this stepped rather than linear relationship between biodiversity loss and salinity in

salinising wetlands. These models predict that shifts between these states are probably difficult to reverse, which has important implications for the management and rehabilitation of salinising systems.

Whilst it is generally accepted that biodiversity decreases with increasing salinity, community-level research reveals that the relationship between salinity and biodiversity is not a simple negative correlation. Species number may decrease while population size increases. Intolerant species may be lost and tolerant species may take their place. Loss of intolerant species or the appearance of tolerant species is likely to result in indirect effects through the system, either through trophic or habitat pathways. To conserve biodiversity, it is essential that ecosystems are treated as complex systems and management of saline water accounts for the interdependence of different species within communities. One management implication is that flushes of fresh water to saline systems at inappropriate times may have a negative impact on biodiversity, just as saline-water discharges to naturally fresh lotic and lentic systems do.

Compounding interactions and indirect effects

The release of saline water into freshwater systems as a result of secondary salinisation and, more importantly, saline-water disposal often alters more than just the ionic concentration. There will be associated waterlogging, increases in nutrients, sedimentation and other long-term impacts associated with land-use change. In the case of saline-water disposal it is far more likely that nutrients and other toxins will also increase, which may have an even greater impact on aquatic fauna than salinity (Kefford 1998, 2000). Furthermore, compounding effects are likely to occur with increasing salinity when associated with other stressors such as acidity, low levels of dissolved oxygen, waterlogging, pH, temperature and altered hydrology.

Several studies have described the interaction between various water-quality parameters that compound the impact of salinity on freshwater biota. At very high salinity levels (20000 mg L⁻¹) the concentration of dissolved oxygen is less than the critical oxygen tension at which respiratory regulation breaks down for most aquatic invertebrates (dissolved oxygen = 2 mg L⁻¹) (Williams 1998). Furthermore, ionic composition (i.e. proportion of NaCl with respect to CO₃, SO₄ and HCO₃) may determine the distributions of certain copepods and the presence of some ions may actually confound the effects of salinity. For example the copepod, *Boeckella triarticulata*, has been found to withstand salinity levels of 22000 mg L⁻¹ when in the presence of high concentrations of bicarbonate, but in the absence of bicarbonate, *B. triarticulata* was restricted to waters of much lower salinity (Bayly 1969).

Vegetation communities affected by increasing salinity are often also affected by an altered hydrological regime. Van

der Moezel *et al.* (1991) and Marcar (1993) examined the combined effect of salinity and waterlogging on seedlings and saplings of *Eucalyptus* and *Melaleuca* species. The combined effect of salinity and waterlogging had a greater detrimental impact on growth and survival of the young plants than did either salinity or waterlogging alone.

Floodplain vegetation communities have been found to suffer combined impacts of increasing salinity and decreased flooding due to river regulation (Taylor *et al.* 1996). The health of *Eucalyptus largiflorens* woodland on the saline floodplain of the Murray River at Chowilla was found to be poor when associated with shallow, saline groundwater and reduced frequency of flooding. Modelling of the response of this salt-stressed *E. largiflorens* woodland to increased frequency of large floods suggested that very large floods (e.g. inundation for 205 days) are needed to sustain tree cover by periodically leaching accumulated salts out of the root zone, reducing the salinity of the soil water and making groundwater more available to the plants (Slavich *et al.* 1999). Such research can have direct implications for management. Recent changes to diversion entitlements and a focus on flows for the environment may mean there is some potential for this type of management action to occur in the short to medium term.

Indirect effects may be important in determining the integrity of freshwater communities. Whilst a species may be fairly tolerant of salinisation, it may be vulnerable because of flow-on effects from another species or taxonomic group's intolerance. Indirect effects are most likely to occur with predator-prey and plant-animal interactions. They may also occur in the epiphytic relationships of bacteria, fungi and plants or the host substrate. Waterbirds are directly dependent on macrophytes (for food, nesting and cover) and invertebrates (for food). However, these taxonomic groups are likely to be adversely affected at salinity levels well below those causing direct effects on waterbirds (Stolley *et al.* 1999).

Water management needs to take account of the compounding effect of salinity in conjunction with other stressors and also the flow-on effects of elevated salinity levels through trophic and habitat pathways. Positive synergistic reactions (such as the combined benefits of flood and associated reductions in salinity levels) can be used to advantage when managing freshening flows.

Discussion and comments

Resilience in freshwater aquatic communities resides in the capacity for tolerance and acclimatisation and avoidance of elevated salinity levels exhibited by many species. Despite this resilience, any increase in salinity levels will be detrimental to biodiversity as even small increases in salinity will lead to loss of sensitive species. It is important to bear in mind that freshwater aquatic biota are salt-sensitive to varying degrees and all will be further compromised by

elevated salinity levels during sensitive life stages and the compounding effects of other stressors. Freshwater biota occur in complex communities made up of taxa ranging from extremely sensitive to quite tolerant. Extreme care must be taken in the management of saline water not to exceed the resilience of freshwater communities and cause a shift from one stable state to less diverse, more saline, stable states from which recovery may be difficult.

Our understanding of the resilience of freshwater biota is limited. The information summarised in this review is based on relatively few taxa, predominantly aquatic macrophytes, invertebrates and fish. There are large gaps in our understanding of the saline water management requirements of microbes, microalgae, riparian vegetation, amphibians, reptiles, mammals and waterbirds. There is a need for cooperative efforts by researchers from different disciplines to address the very complex questions, such as the impact of saline water on community structure, plant-animal interactions and ecosystem processes.

In order to minimise the impact of salinity on freshwater biota in an increasingly saline environment, managers need information in a form that will aid their decision-making. Unfortunately, the information to support these decisions is inadequate at present and our management of available data is poor. Data have not been systematically collected, or collated into a dedicated and accessible database, and the interpretation of data is rudimentary (Clunie *et al.* 2002). A large body of data in the form of salinity-tolerance database is needed. Detailed analysis of such a database should enable us to identify relationships such as groupings of taxa based on their resilience, ecotypes with different levels of resilience and information on sensitive life stages and sublethal effects. Further refinement of the techniques required to assess such data together with targeted field experimentation will ultimately provide the tools to effectively manage salinity within an adaptive management framework.

Acknowledgments

This review was supported by The Murray-Darling Basin Commission, Strategic Investigations and Education Riverine Program Project R2003 and National Action Plan Non-regional Foundation Funding.

References

- Alderman IR, Smith LL, Siesennop GD (1976) Acute toxicity of sodium chloride to flathead minnows *Pimephales promelas* and goldfish *Carassius auratus*. *Journal of the Fisheries Research Board of Canada* **33**, 203–208.
- Bacher GJ, Garnham JS (1992) The effect of salinity to several freshwater aquatic species of southern Victoria. Freshwater Ecology Section, Flora and Fauna Division, Department of Conservation and Environment, EPA Report SRS 92/003, Melbourne.
- Bacher GJ, O'Brien TA (1989) Salinity tolerance of the eggs and larvae of the Australian Grayling, *Prototroctes maraena* Gunther

- (Salmoniformes: Prototroctidae). *Australian Journal of Marine and Freshwater Research* **40**, 227–230.
- Bailey PC, James KR (2000) Riverine and wetland salinity impacts—Assessment of R & D needs. Land and Water Resources Research and Development Corporation, Occasional Paper No. 25/99.
- Bayly IAE (1969) The occurrence of calanoid copepods in athalassic saline waters in relation to salinity and anionic proportions. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* **17**, 449–455.
- Beadle LC (1969) Osmotic regulation and the adaptation of freshwater animals to saline inland waters. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* **17**, 421–429.
- Beumer JP (1979) Temperature and salinity tolerance of the spangled perch *Therapon unicolor* (Gunther, 1959) and the East Queensland rainbowfish *Nematocentris splendida* (Peters, 1866). *Proceedings of the Royal Society of Queensland* **90**, 85–91.
- Brock MA (1981) The ecology of halophytes in the southeast of South Australia. *Hydrobiologia* **81**, 23–32.
- Brock MA, Shiel RJ (1983) The composition of aquatic communities in saline wetlands in Western Australia. *Hydrobiologia* **105**, 77–84.
- Cadwallader PL, Backhouse GN (1983) 'A guide to the freshwater fish of Victoria.' (Government Printer: Melbourne)
- Chapman A, Lane JAK (1997) Waterfowl usage of wetlands in the south east arid interior of Western Australia. *Emu* **97**, 51–59.
- Chessman BC, Williams WD (1974) The distribution of fish in inland saline waters of Victoria, Australia. *Australian Journal of Marine and Freshwater Research* **25** 167–172.
- Chessman BC, Williams WD (1975) Salinity tolerance and osmoregulatory ability of *Galaxias maculatus* (Pisces, Salmoniformes, Galaxiidae). *Freshwater Biology* **5**, 135–140.
- Clunie P, Ryan T, James K, Cant B (2002) 'Implications for rivers from salinity hazards: scoping study.' Department of Natural Resources and Environment, Arthur Rylah Institute, Heidelberg. ISBN 0 7311 5022 8. <http://www.nre.vic.gov.au/ari/salinityhazards/>
- Davis JC (1975) Minimal dissolved oxygen requirements of aquatic life with emphasis on Canadian species: a review. *Journal of the Fisheries Research Board of Canada* **32**, 2295–2332.
- Davis J (2002) Alternative ecological states: a potential paradigm for managing salinised ecosystems. *Riprap* **20**, 11.
- Garcia A (1999) Charophyte flora of southeastern South Australia and southwestern Victoria, Australia: systematics, distribution and ecology. *Australian Journal of Botany* **47**, 407–426.
- Geddes MC (1979) Salinity tolerance and osmotic behaviour of European carp (*Cyprinus carpio* L.) from the River Murray, Australia. *Royal Society of South Australia* **103**, 185–189.
- Goodsell JT (1990) Distribution of waterfowl broods relative to salinity and pH in south-western Australia. *Australian Wildlife Research* **17**, 219–230.
- Greenway H, Munns R (1980) Mechanisms of salt tolerance in halophytes. *Annual Review of Plant Physiology* **31**, 149–190. doi:10.1146/ANNUREV.PP.31.060180.001053
- Greenway H, Osmond CB (1972) Salt responses of enzymes from species differing in salt tolerance. *Plant Physiology* **49**, 256–259.
- Guo R, Mather P, Capra MF (1993) Effect of salinity on the development of silver perch (*Bidyanus bidyanus*) eggs and larvae. *Comparative Biochemistry and Physiology* **104A**, 531–535.
- Guo R, Mather PB, Capra MF (1995) Salinity tolerance and osmoregulation in the silver perch, *Bidyanus bidyanus* Mitchell (Teraponidae), an endemic Australian freshwater teleost. *Marine and Freshwater Research* **46**, 947–952.
- Halse SA, Shiel RJ, Williams WD (1998) Aquatic invertebrates of Lake Gregory, northwestern Australia, in relation to salinity and ionic composition. *Hydrobiologia* **381**, 15–29. doi:10.1023/A:1003263 105122
- Hart BT, Bailey P, Edwards R, Hortle K, James K, McMahon A, Meredith C, Swadling K (1991) A review of the salt sensitivity of the Australian freshwater biota. *Hydrobiologia* **210**, 105–144.
- Hogan AE, Nicholson JC (1987) Sperm motility of sooty grunter, *Hephaestus fuliginosus* (Macleay), and jungle perch, *Kuhlia rupestris* (Lacepede), in different salinities. *Australian Journal of Marine and Freshwater Research* **38**, 523–528.
- Jackson G, Pierce B (1992) Salinity tolerance of selected adult Murray–Darling Basin fishes. *Newsletter of the Australian Society for Fish Biology* **22**, 35.
- James KR, Hart BTH (1993) Effect of salinity on four freshwater macrophytes. *Australian Journal of Marine and Freshwater Research* **44**, 769–777.
- Karimov BK, Keyser D (1998) The effect of salt composition on the salinity tolerance of mirror carp (*Cyprinus carpio* L.) during early ontogeny. *Archive of Fishery and Marine Research* **48**, 225–239.
- Kefford BJ (1998) The relationship between electrical conductivity and selected macroinvertebrate communities in four river systems of south-west Victoria, Australia. *International Journal of Salt Lake Research* **7**, 153–170. doi:10.1023/A:1009019404720
- Kefford BJ (2000) The effect of saline water disposal: implications for monitoring programs and management. *Environmental Monitoring and Assessment* **63**, 313–327. doi:10.1023/A:1006201512469
- Kingsford RT, Porter JL (1994) Waterbirds on an adjacent freshwater lake and salt lake in arid Australia. *Biological Conservation* **69**, 219–228. doi:10.1016/0006-3207(94)90063-9
- Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* **16**, 545–556. doi:10.1046/J.1365-2435.2002.00664.X
- Marcar NE (1993) Watterlogging modifies growth, water use and ion concentrations in seedlings of salt-treated *Eucalyptus camaldulensis*, *E. tereticornis*, *E. robusta*, and *E. globulus*. *Australian Journal of Plant Physiology* **2**, 1–13.
- Mensforth LJ, Thorburn PJ, Tyerman SD, Walker GR (1994) Sources of water used by riparian *Eucalyptus camaldulensis* overlying highly saline groundwater. *Oecologia* **100**, 21–28.
- Mensforth LJ, Walker GR (1996) Root dynamics of *Melaleuca halmaturorum* in response to fluctuating saline groundwater. *Plant and Soil* **184**, 75–84.
- Merrick JR, Schimda EG (1984) 'Australian freshwater fishes, biology and management.' (Griffin Press: Netley, SA)
- National Land and Water Resources Audit (2001) 'Australian dryland salinity assessment 2000.' National Land and Water Resources Audit, Canberra.
- Nielsen DL, Brock MA, Rees GN, Baldwin DS (2003) Effects of increasing salinity of freshwater ecosystems in Australia. *Australian Journal of Botany* **51**, 656–666.
- Nordlie FG, Mirandi A (1996) Salinity relationships in a freshwater population of eastern mosquitofish. *Journal of Fish Biology* **49**, 1226–1232. doi:10.1006/JFBI.1996.0249
- O'Brien T, Ryan T (1999) Impact of saline drainage on key Murray–Darling Basin fish species: final report to the Murray–Darling Basin Commission. NRMS Project R5004.
- Pollard DA (1971a) The biology of a landlocked form of the normally catadromous salmoniform fish *Galaxias maculatus* (Jenyns). I. Life cycle and origin. *Australian Journal of Marine and Freshwater Research* **22**, 91–123.
- Pollard DA (1971b) Faunistic and environmental studies on Lake Modewarre, a slightly saline athalassic lake in South-Western Victoria. *Australian Society for Limnology* **4**, 25–42.

- Rai V, Rai AK (1998) Growth behaviour of *Azolla pinnata* at various salinity levels and induction of high salt tolerance. *Plant and Soil* **206**, 79–84. doi:10.1023/A:1004340005693
- Short TM, Black JA, Birge WJ (1991) Ecology of a saline stream: community responses to spatial gradients of environmental conditions. *Hydrobiologia* **226**, 167–178.
- Skinner R, Sheldon F, Walker KF (2001) Propagules in dry wetland sediments as indicators of ecological health: effects of salinity. *Regulated Rivers: Research and Management* **17**, 191–197. doi:10.1002/RRR.616
- Slavich RG, Walker GR, Jolly ID, Thorburn P (1999) A flood history weighted index of average root-zone salinity for assessing flood impacts on health of vegetation on a saline floodplain. *Agricultural Water Management* **39**, 135–151. doi:10.1016/S0378-3774(98)00075-4
- Stolley DS, Bissonette JA, Kadlec JA, Coster D (1999) Effects of saline water on early gosling development. *The Journal of Wildlife Management* **63**, 990–996.
- Sutcliffe DW (1974) Sodium regulation and adaptation to freshwater in the isopods genus *Asellus*. *The Journal of Experimental Biology* **61**, 719–736.
- Taylor PJ, Walker GR, Hodgson G, Hatton TJ (1996) Testing of a GIS model of *Eucalyptus largiflorens* health on a semi arid, saline floodplain. *Environmental Management* **20**, 553–564.
- Thorburn PJ, Mensforth LJ, Walker GR (1994) Reliance of creek-side river red gums on creek water. *Australian Journal of Marine and Freshwater Research* **45**, 1439–1443.
- Timms BV (1993) Saline lakes of the Paroo, inland New South Wales, Australia. *Hydrobiologia* **267**, 269–289.
- Timms BV (1998a) Further studies on the saline lakes of the eastern Paroo, inland New South Wales, Australia. *Hydrobiologia* **381**, 31–42. doi:10.1023/A:1003267221960
- Timms BV (1998b) A study of Lake Wyara, an episodically filled saline lake in southwest Queensland, Australia. *International Journal of Salt Lake Research* **7**, 113–132. doi:10.1023/A:1009053217612
- Van der Moezel PG, Pearce-Pinto GVN, Bell DT (1991) Screening for salt and waterlogging tolerance in *Eucalyptus* and *Melaleuca* species. *Forest Ecology and Management* **40**, 27–37. doi:10.1016/0378-1127(91)90089-E
- Warwick NW, Bailey PC (1997) The effect of increasing salinity on the growth and ion content of three non-halophytic wetland macrophytes. *Aquatic Botany* **58**, 73–88. doi:10.1016/S0304-3770(96)01104-7
- Williams MD (1987) Salinity tolerance of small fishes from the Murray Darling river system. BSc (Hons), Department of Zoology, University of Adelaide.
- Williams MD, Williams WD (1991) Salinity tolerances of four species of fish from the Murray–Darling River system. *Hydrobiologia* **210**, 145–150.
- Williams WD (1998) Salinity as a determinant of the structure of biological communities in salt lakes. *Hydrobiologia* **381**, 191–201. doi:10.1023/A:1003287826503
- Williams W, Taaffe R, Boulton A (1991) Longitudinal distribution of macroinvertebrates in two rivers subject to salinisation. *Hydrobiologia* **210**, 151–160.
- Williams WD, De Deckker P, Shiel RJ (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
- Yeo A (1998) Molecular biology of salt tolerance in the context of whole-plant physiology. *The Journal of Experimental Biology* **49**, 915–929. doi:10.1093/JEXBOT/49.323.915

Manuscript received 16 December 2002, accepted 4 September 2003