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Effects of increasing salinity on freshwater ecosystems in Australia

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Abstract. Salt is a natural component of the Australian landscape to which a number of biota inhabiting rivers and wetlands are adapted. Under natural flow conditions periods of low flow have resulted in the concentration of salts in wetlands and riverine pools. The organisms of these systems survive these salinities by tolerance or avoidance. Freshwater ecosystems in Australia are now becoming increasingly threatened by salinity because of rising saline groundwater and modification of the water regime reducing the frequency of high-flow (flushing) events, resulting in an accumulation of salt. Available data suggest that aquatic biota will be adversely affected as salinity exceeds 1000 mg L⁻¹ (1500 EC) but there is limited information on how increasing salinity will affect the various life stages of the biota. Salinisation can lead to changes in the physical environment that will affect ecosystem processes. However, we know little about how salinity interacts with the way nutrients and carbon are processed within an ecosystem. This paper updates the knowledge base on how salinity affects the physical and biotic components of aquatic ecosystems and explores the needs for information on how structure and function of aquatic ecosystems change with increasing salinity.

Introduction

Salt is a natural component of the Australia landscape and has been deposited from a variety of sources over millions of years. Salt enters aquatic systems from groundwater, terrestrial material via the weathering of rocks or from the atmosphere, transported by wind and rain (Baldwin 1996*a*; Williams 1987). The relative contributions of these sources depend on factors such as distance inland, climate and geology (Williams 1987).

Under natural flow conditions in many wetlands and rivers, periods of low flow resulted in the concentration of salts in wetlands and riverine pools. Evaporation, combined with intrusions of groundwater often caused natural salinity levels to be high for periods of time (Close 1990; Williams 1999; Kay *et al.* 2001) (Fig. 1*A*). During these periods of low flow/high salinity, biota that could not readily disperse managed to survive either with little or no reproduction and recruitment (Mills and Geddes 1980; Williams 1985; Brock *et al.* 2003). Biota that are unable to tolerate these periods either perish or disperse to recolonise when more favourable conditions occur (Williams 1985).

In many river system such as the River Murray, alteration of flows, through modification of temporal and spatial

patterns, has reduced the periods of high flow/low salinity and low flow/high salinity. The periods in which salt concentrations exceed the critical thresholds of biota now rarely, if ever, occur, but secondary salinisation, caused by run-off from the terrestrial landscape, has increased the amount of salt entering rivers. The reduction in the frequency of high-flow (flushing) events is causing an accumulation of salt in these river systems and a gradual increase in the mean concentration over time (Close 1990; MDBC 1999; DLWC 2000). While the salinity threshold levels for mature biota may no longer be exceeded, the mean salinity thresholds for more sensitive life stages may eventually be surpassed (Fig. 1*B*).

A similar pattern of salt accumulation occurs in wetlands. Prior to the removal of the terrestrial vegetation, most of the water carrying dissolved salts from the surrounding catchments was trapped by vegetation and transpired or evaporated. The salt that did wash into wetlands became concentrated by evaporation, often exceeding tolerance levels of sensitive biota. Once these wetlands dried the salt accumulated in the sediments and was removed by flushing during the next high-flow events. Removal of vegetation has increased the amount of water entering the groundwater and the amount of water and salt that enters wetlands. Many



Fig. 1. The relationship between flow and salinity in (A) non-modified and (B) modified water regimes. Solid line indicates the variation in salinity over time. Dotted line indicates the variation in water level over time. Small-dashed line indicates biotic threshold level above which loss of biota may occur or strategies to either avoid or tolerate increased salinity available. Large-dashed line indicates mean salinity over time.

wetlands are no longer flushed, so the continual input of salt increases concentration of salt in the sediments and this will influence biota such as aquatic plants and benthic animals (Bailey and James 2000). The increase in salt may also affect the long-term viability of dormant eggs of microinvertebrates and seed of aquatic plants. When sediments with raised salt concentration are wetted during subsequent wetland refilling, salt concentrations in the water column again can exceed the tolerance of wetland biota (Fig. 2).

A taskforce on salinity and biodiversity established by the Australian and New Zealand Environment and Conservation Council has predicted that by the year 2050 more than



Fig. 2. The relationship between water regime and accumulation of salts in wetlands. Solid line indicates the variation in salinity over time. Dotted line indicates the variation in water level over time. Small-dashed line indicates biotic threshold level above which loss of taxa will occur. Large-dashed line indicates mean salinity over time. Solid rectangle indicates the accumulation of salts in the sediment as a consequence of reduced flushing.

40000 km of waterways and associated wetlands will have significantly elevated salt concentrations (ANZECC 2001). Management organisations such as the Department of Infrastructure, Planning and Natural Resources (DIPNR) in New South Wales (NSW) and the Murray-Darling Basin Commission (MDBC), have set interim end-of-catchment (or valley) targets for salinity on the basis of existing knowledge. Available data suggest that aquatic biota will be adversely affected as salinity exceeds 1000 mg L^{-1} (1500 EC) (Hart et al. 1991). For many plants and animals there is information available on the threshold levels of salinity on mature life stages. For most of these, there is very little information on threshold levels for earlier developmental stages (Fig. 3). The early stages of development for some biota (i.e. fish) have been shown to be more sensitive to salt than mature stages. For example, Macquarie perch (Macquaria australasica) has been shown to have a salinity tolerance of more than 30000 mg L⁻¹ but if eggs are exposed to salinity of only 4000 mg L⁻¹ egg survivorship is reduced by 100% (O'Brien and Ryan 1997). While some native aquatic biota appear to be tolerant of increase in salinity above 10000 mg L⁻¹ (Williams and Williams 1991), early life forms may be potentially most at risk from gradual increases in salinity. There is even less information about how salinity interacts with processes in aquatic ecosystems, such as carbon and nutrient cycling.

The large spatial and temporal scales of salinity mean that if our current best land-management practices were fully implemented, salinisation would continue to increase in aquatic ecosystems throughout Australia. Although the

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Fig. 3. Changes in life-history traits as a consequence of modifying the delivery of salt. (*A*) Natural delivery. (*B*) Increased delivery. Solid line indicates increasing salinity over time. Dotted lines indicate tolerance levels for each life history phase. The time available for completion of each stage is decreased as the rate of delivery of salt is increased.

effect of increasing salinity on aquatic biota has been extensively reviewed, we do not understand the ecological consequences of salinisation in Australian freshwaters (Hart *et al.* 1991; Bailey and James 2000; Nielsen and Hillman 2000; Clunie *et al.* 2002). The aim of this paper is to review and update the knowledge base on how salinity affects not only aquatic biota but also the physical component of aquatic ecosystems.

Physical and chemical environment

Salinisation of a freshwater body can potentially change both the light climate and the mixing properties, which in turn have an impact on the cycling of energy and nutrients. Salt-induced aggregation and flocculation of suspended matter is recognised as a major factor in the removal of particles from the water column, resulting in an increase in light penetration, and may increase photosynthesis. The rate of clarification is enhanced by the presence of divalent cations (particularly Ca^{2+} and Mg^{2+}) common in saline ground water (Grace *et al.* 1997). Increased water clarity, as a consequence of saline groundwater intrusions has been implicated in the formation of significant blooms of cyanobacteria (Geddes 1988; Donnelly *et al.* 1997). Alternatively, flocculation of colloids may also remove trace elements and nutrients from the water column making them less readily available to pelagic organisms (Donnelly *et al.* 1997).

Salinisation can alter the relative proportions of cations and anions in water that can change chemical equilibria and solubility of some minerals. The major cationic (Na⁺, K⁺, Mg²⁺, and Ca²⁺) and anionic species (Cl⁻, SO₄²⁻, HCO_3^{-}/CO_3^{-}) vary between locations in both abundance and concentration. Freshwater biota are influenced as much by the ionic composition and pH of water as by the total concentration of dissolved substances (Frey 1993). The relative proportions of the main cations and anions modify the way biota respond to high salinities (Bayly 1969; Bailey and James 2000; Radke et al. 2002). Bayly (1969) suggested that the ratio of $(Na^+ + K^+)/(Mg^{2+} + Ca^{2+})$ is important in determining toxicity and suggested that the monovalent ions are more toxic than divalent ions. This offers an explanation as to why many species of copepods have been found across a broad range of salinities in Australia (Hammer 1986). For example, Boekella triarticulata is a freshwater species that has been shown to survive in highly saline waters (Bayly 1969). Bayly (1969) hypothesised that the upper limit of salinity tolerance of freshwater animals is determined by the chloride content in the blood and that the suppression of this by a regime of bicarbonate might permit survival in higher than usual salinities.

Salt-dependent stratification can occur in freshwater systems following groundwater incursions. Establishment of a salt gradient can reduce mixing and solute transport within aquatic ecosystems. The halocline is a barrier for transport of materials between the surface and bottom strata and has important implications for nutrient and carbon cycling. In particular, it may become a barrier for the movement of oxygen from the surface water to the bottom, causing the rate of oxygen consumption in the bottom waters to exceed the rate of replenishment from the surface, which ultimately leads to anoxia and the death of benthic organisms (Legovic et al. 1991). Anoxia can also alter the microbially mediated cycling of nutrients. Anoxia of bottom waters has been reported in rivers where intrusions of saline water occur (Anderson and Morison 1989; McGuckin 1990; Donnelly et al. 1997; Ryan et al. 1999). Salinity of the groundwater intrusion does not need to be substantially higher than the salinity of the surface water to induce stratification and anoxia. Stratification in the Wimmera River has been observed at a salinity gradient between 300 and 700 mg L^{-1} (Anderson and Morison 1989). Gribben et al. (2003) reported the formation of a seasonal salinity gradient in a shallow freshwater wetland of only about 70 mg L^{-1} , which they attribute to a ground-water intrusion during the drier summer months. This gradient, coupled with a corresponding thermal gradient, is sufficient to prevent mixing between the surface and bottom waters, with resultant anoxia in the bottom waters.

Saline ground waters can also lead to elevated levels of sulfate, dissolved iron and nitrate (Nines et al. 1992). Sulfate has been implicated in the cycling of phosphorus (Carraco et al. 1989). Sulfate-reducing bacteria use the sulfate ion for anaerobic respiration. The respiratory end product from sulfate reduction is hydrogen sulfide, which is a reducing agent that can facilitate the dissolving of iron minerals with a release of phosphorus (Boström et al. 1988). It has also been suggested that sulfide can displace P from insoluble Fe^{2+} phases (Roden and Edmonds 1997). On the other hand, if a saline groundwater intrusion has a high level of dissolved iron, oxidation and subsequent precipitation of the iron can lead to the removal of phosphorus from solution (Baldwin 1996b). Similarly, increases in the concentration of calcium can also lead to the loss of phosphorus from solution through precipitation (House 1999).

The increase in ionic strength as a consequence of salinisation can also disrupt chemical equilibria between dissolved and particulate phases, either through changes to ion activity co-efficients or through salt ions blocking mineral surface adsorption sites (Chang 1977; Stumm and Morgan 1996). The activity co-efficient of phosphate decreases with increasing salinity, suggesting that phosphate should be more soluble in saline systems than in freshwater systems. Surface chemistry may also be disrupted with increasing salinity as cations present in salt compete with other ions for adsorption sites on particle surfaces. For example, Seitzinger et al. (1991) have shown that the concentration of exchangeable ammonium in freshwater sediments is significantly greater than in marine sediments. They attributed this difference to cations out-competing ammonium ions for adsorption sites on the sediment.

Biological communities

Some organisms are adapted for living in freshwater, others for living in salt water. In general, freshwater biota do not extend into saline or slightly saline water. Consequently, as salinity increases, the species richness and growth of freshwater biota is reduced (Hart *et al.* 1991). Freshwater is generally defined as water in which salinity is less than 3000 mg L⁻¹ and sea water as 35000 mg L⁻¹. These are the world average values for those systems (Boulton and Brock 1999); 3000 mg L⁻¹ is often considered the lower limit for saline waters (Hart *et al.* 1991). Water between 3000 mg L⁻¹ and 10000 mg L⁻¹ can be defined as saline as biotic effects are well known within this range. Animals are divided on the basis of their ability to regulate their internal osmotic concentrations against the external environment: those that regulate internal salt concentrations well can adapt to a wide range of salinities (euryhaline regulators), whereas those that are poor regulators cannot and are restricted only to a narrow range of salinities (stenohaline regulators). Salt-tolerant plants (halophytes) tend to prefer brackish or saline conditions rather than freshwater, whereas most freshwater plants (non-halophytes) do not tolerate increasing salt concentration.

Changes in salinity can affect biota in freshwater directly or indirectly. Toxic effects as a consequence of increasing salinity cause physiological changes, resulting in a loss (or gain) of species. Indirect changes can occur where increasing salinity modifies community structure and function by removing (or adding) taxa that provide refuge, food or modify predation pressure. Other factors such as water-logging or loss of habitat may interact with salinity or have a more immediate impact on species richness (Savage 1979; Froend *et al.* 1987; Bailey and James 2000; Clunie *et al.* 2002).

Over the past 12 years several reviews on the effects of salinity in freshwater ecosystems have highlighted the paucity of suitable information for making informed predictions on what future aquatic communities will look like as salinity increases (Hart et al. 1991; Metzeling et al. 1995; Gutteridge, Haskins and Davey Pty Ltd 1999; Bailey and James 2000; Nielsen and Hillman 2000; Clunie et al. 2002). In this review, increases in salinity from less that 500 mg L^{-1} up to above 10000 mg L^{-1} are considered. This is the most likely range of salinities that Australian freshwater rivers and wetlands may experience in the next 50 years. Pulses of higher salinity are also likely to be encountered in some rivers and for some wetlands higher levels of salinity may be experienced as they evaporate and dry out. Ecological effects of salinity are likely to be observed within these ranges (Hart et al. 1991).

Microbial function and community structure

Bacteria have a major role in carbon and nutrient cycling. Our understanding of how microbially mediated processes with changing salinity has come change from cross-ecosystem comparisons, in which rates of various processes have been measured in freshwater, estuarine, marine and hypersaline environments. A less common approach has been to examine bacterial populations along a salinity gradient within rivers as they undergo transition from freshwater to brackish at estuaries. Understanding of the function, structure and diversity of microbial community has recently been advanced with the availability of molecular DNA methods to identify the presence and diversity of microbes, and techniques to estimate in situ bacterial production (growth) or the metabolic capacity of microbes. In general, aerobic bacterial heterotrophic production in different aquatic ecosystems has been found to be broadly predictable, with no consistent differences existing between

marine and freshwater systems (Cole *et al.* 1988). Where differences occur, factors such as carbon and nutrient input and temperature are more important in regulating production than salinity (Findlay *et al.* 1991). Similarly, Hobbie (1988) concluded that although marine and freshwater microbes have different physiological methods for tolerating high salt concentrations, the ecology of marine and freshwater microbes is virtually identical. As such, it has been assumed that a process of species replacement will occur in salinised freshwater systems, that is, increased salinisation of freshwater ecosystems will simply select for new physiological types that are able to tolerate given salt levels, but possessing the same metabolic capabilities (Hart *et al.* 1991).

Molecular DNA techniques have established that distinct differences occur in the phylogenetic make up of microbial populations in freshwater and marine ecosystems (Nold and Zwart 1998; Crump *et al.* 1999). Recently it was also shown that shifts in microbial composition occur along fresh to brackish gradients in riverine/estuarine systems (Bouvier and del Giorgio 2002). Metabolic activities of planktonic bacteria also are known to vary in space and time along a riverine/ estuary gradient (Schultz and Ducklow 2000; del Giorgio and Bouvier 2002). In the latter study, salinity was an important determinant in separating bacterial communities.

The sparse information on the response of cyanobacteria to salinity indicates that some members of this group occur at salinities greater than that of seawater (>35000 mg L⁻¹). Freshwater cyanobacteria appear to be inhibited by variations in salinity (Hart *et al.* 1991) but may adapt to gradual increases. Species of *Anabaena* have been found to acclimatise to salinities of 7000 mg L⁻¹ after several days' exposure (Hart *et al.* 1991; Winder and Cheng 1995).

The relationship between salinity and specific bacterial processes has been examined, although not extensively. Nitrogen fixation and nitrification are known to occur in environments with widely differing salt levels. Nitrogen fixation by planktonic organisms generally is greater in freshwater than in marine systems; however, within given ecosystems, the rate of nitrogen fixation generally is regulated by nutrient status and not salinity (Howarth *et al.* 1988). There appears to be no difference in the rate of nitrogen fixation by benthic communities with respect to different salinities. However, nitrifying and nitrogen-fixing communities are known to vary significantly across such systems (Affourtit *et al.* 2001; de Bie *et al.* 2001). Specific linkages between structure and function of nitrifying and nitrogen-fixing organisms have not been made.

A major difference between freshwater and marine systems are the processes in anaerobic degradation of carbon. In marine and estuarine systems sulfate-reduction is the major step, whereas methanogenesis dominates in fresh systems. (Capone and Kiene 1988). This difference is driven by the presence of sulfate ions in sea water stimulating sulfate-reducing bacteria, which in turn are able to out-compete methanogens for substrates (Widdel 1988). Marine and freshwater species of sulfate-reducing bacteria and methanogens are known to exist (Postgate 1984; Oremland 1988).

Denitrification occurs in all aquatic ecosystems; however, it has been suggested that in general terms the range of rates of denitrification in marine systems is greater than in freshwater systems (Seitzinger 1988). Denitrification rates tend to be limited by nitrate concentration, and salinity by itself may not be the underlying regulating factor in nitrate reduction. Molecular studies have been carried out on denitrifying bacteria from freshwater and marine ecosystems (Braker *et al.* 1998; Bothe *et al.* 2000; Scala and Kerkhoff 2000). However, no extensive cross-system comparisons of denitrifying populations have been made.

Studies on rivers and estuaries continue to provide useful insights as to how bacterial populations change across salt gradients. Whether such comparisons can readily be transferred to freshwater ecosystems that undergo long-term increases in salinity remains to be tested.

Algae

There is only sparse information on the sensitivity and tolerance of freshwater algae; however, the majority of taxa do not appear to be tolerant of increasing salinity (Hart *et al.* 1991; Bailey and James 2000; Nielsen and Hillman 2000; Clunie *et al.* 2002).

The majority of algae do not appear to tolerate salinities in excess of 10000 mg L⁻¹ (Bailey and James 2000). Field observations indicate that as salinity increases, diatoms decrease in both abundance and richness (Blinn 1993; Blinn and Bailey 2001). Experimental flooding of sediments has suggested that some phytoplankton emerge in substantial numbers when exposed to saline water but diversity is reduced (Skinner *et al.* 2001; L. Bowling, unpubl. data). Some unicellular algae such as *Dunaliella salina* produce resting cysts that allow them to survive high salinities. Species such as *D. salina* also undergo morphological and physiological changes that allow them to survive across a broad range of salinities (Borowitska 1981; Brock 1986).

Aquatic plants

In general, freshwater aquatic plants are not tolerant of increasing salinity. The majority of data on the response of aquatic plants to increasing salinity come from field observations. The upper limit of salinity tolerated by most freshwater aquatic plants appears to be 4000 mg L⁻¹. Above this, non-halophytes such as *Myriophyllum* are replaced by more tolerant halophytic species such as *Ruppia* spp. and *Lepilaena* spp. which have been recorded in salinities several times that of seawater (Brock 1981, 1985, 1986).

At salinities above 1000 mg L^{-1} , adverse effects on aquatic plants appear, with reduced growth rates and reduced

development of roots and leaves. Both sexual and asexual reproduction become suppressed (James and Hart 1993; Warwick and Bailey 1997, 1998). The development of below-ground tubers, necessary for growth in the following year, and the development of flowers are also prevented (Warwick and Bailey 1996).

Information on sublethal effects of increasing salinity on germination, growth or development of aquatic plants is limited. Salt sensitivity may differ among various life stages of a species, which may reflect exposure to different environmental conditions (Bailey and James 2000). High salinity is usually inhibitory or toxic to seed germination of most freshwater plants (Ungar 1962; Williams and Ungar 1972; Baskin and Baskin 1998). For example, germination of seeds from both *Sagittaria latifolia* and *Ruppia megacarpa* decreases as salinity increases (Brock 1982; Delesalle and Blum 1994). However, there are isolated cases in which germination of a halophytic species has increased under higher salinities (e.g. *Ruppia tuberosa*) (Brock 1982).

Results from the experimental inundation of sediments from seven wetlands across inland New South Wales under five salinities (300, 1000, 2000, 3000 and 5000 mg L⁻¹) indicated that salinity has a significant impact on the germination of seeds of aquatic plants when it exceeds 1000 mg L⁻¹. The greatest impact was on species richness and abundance in communities developing from sediment subjected to shallow flooding. Communities developing from sediment subjected to deeper flooding showed a lesser effect of salinity. This suggests that submerged aquatic plant communities may be buffered from elevated concentrations of salt, whereas those plants that live in the margins of wetlands may be more susceptible to increases in salinity (D. L. Nielsen and M. A. Brock, unpubl. data).

Invertebrates

It has been predicted that salinity exceeding 1000 mg L⁻¹ will have adverse affects on invertebrates (Hart *et al.* 1991). Results from field studies examining salinity gradients in rivers or across wetlands indicate that as salinity increases there is a loss of diversity. Diversity decreases rapidly as salinity increases up to10000 mg L⁻¹, but less rapidly above 10000 mg L⁻¹ (Williams *et al.* 1990).

Invertebrates can be divided into the following two groups: (1) microinvertebrates, comprising protozoan, rotifers and micro-crustaceans (particularly copepods, cladocerans and ostracods) (Shiel 1990) and (2) macroinvertebrates in which the major taxonomic groups are insects, worms, snails and macro-crustaceans (shrimp, yabbies) (Bennison and Suter 1990).

Microinvertebrates

Microinvertebrates are generally considered to be of non-marine origin (De Deckker 1983; Hammer 1986) and as a group they appear not to be tolerant of increasing salinity. As salinity increases, there is a general decrease in abundance and richness of rotifers and microcrustaceans (Brock and Shiel 1983, Campbell 1994). There is little information on salt tolerance in protozoa, although they have been recorded from Lake Gregory, Western Australia, when the lake contains freshwater but not when it is saline (Halse *et al.* 1998).

Field studies have shown that there is a decrease in the number of rotifer species occurring in lakes at salinities above 2000 mg L⁻¹ (Brock and Shiel 1983; Green and Mengestou 1991). In freshwater wetlands in Australia, over 200 taxa have been recorded from individual sites (Boon *et al.* 1990), but at high salinities, taxon richness is substantially reduced, often to as little as one or two taxa (Timms 1981; Brock and Shiel 1983; Halse *et al.* 1998). The rotifers and *Brachionus plicatillis, Hexarthra fennica* and *Trichocerca* spp. have been recorded in saline lakes (Timms 1981, 1987, 1998; Brock and Shiel 1983) and many ostracods also appear to tolerate a broad range of salinities (De Deckker 1983).

Few studies have examined the effect of increasing salinity on the emergence of microfauna from dormant eggs. It has been shown that increases in salinity may inhibit emergence from resting eggs (Skinner et al. 2001). High salinity has been linked to blocking hatching of the rotifer Brachionus plicatilis (Pourriot and Snell 1983), and the microcrustacean Daphniopsis pusilla (Geddes 1976). Ostracods have also been noted as emerging only in saline lakes when salinities are low (De Deckker 1983). In the experimental inundation of sediments from seven wetlands across inland New South Wales under five salinities (300, 1000, 2000, 3000 and 5000 mg L^{-1}), the majority of microinvertebrate taxa had significantly reduced emergence at salinities of 2000 mg L^{-1} and above. For some taxa there was a significant reduction in emergence below 1000 mg L^{-1} (Nielsen et al. 2003; D. L. Nielsen and M. A. Brock, unpubl. data). Increasing salinity may be reducing the viability of the eggs or it may be blocking the required cues to trigger emergence.

Food availability may also influence the ability of animals to tolerate increased salinity. The estuarine copepod *Sulcanus conflictus* has been shown to have lower survival at high salinities when the available food is of poor quality (Rippingale and Hodgkin 1977). However, in the case of rotifers, decreases in numbers have been linked more to specific physiological tolerances rather than food availability (Green and Mengestou 1991). The effects of salinity may also be sex-dependent. Females of the copepods *Boekella hamata* and *Acartia tonsa* are larger than males and exhibit higher survival at increased salinities (Hart *et al.* 1991; Cervetto *et al.* 1999; Hall and Burns 2001).

Macroinvertebrates

A large proportion of Australian macroinvertebrates has a marine ancestry (Hart *et al.* 1991) and as a group they appear

to be more tolerant of increasing salinity than the microinvertebrate group.

There is more information on salinity effects on macroinvertebrates than other biotic groups, as they have been widely used in the monitoring of the health of aquatic system. Data are generally from field surveys comparing taxon presence with conductivity (salinity) collected as an environmental parameter. In some cases, there is limited monitoring of community changes at a site over time so ranges of tolerance for some taxa can be inferred from within-site as well as between-site data. Much of these data have been collated into a database (Boon *et al.* 2002).

In river ecosystems, macroinvertebrate diversity and salinity are not closely correlated. While salinity may cause the loss of some taxa and facilitate the intrusion of estuarine taxa upstream, increasing salinity may not be a catastrophic event. The macroinvertebrate fauna of rivers appear to be tolerant and relatively resilient to increasing salinity (Williams et al. 1991; Metzeling 1993; Metzeling et al. 1995). Data from wetlands confirm this view. Substantial changes in diversity of wetland macroinvertebrates are not likely to occur until salinities exceed 10000 mg L⁻¹, after which substantial loss of diversity and changes in community composition may occur (Suter et al. 1993; Halse et al. 2000). The groups most sensitive to increasing salt are the structurally simple, often soft-bodied animals such as hydra, insect larvae and molluscs (Hart et al. 1991). Data from acute 72-h toxicity tests (LC50) of 59 macroinvertebrate taxa indicate that the salinity tolerance ranged from 5000 up to 50000 mg L⁻¹, with baetid mayflies the least tolerant $(LC_{50} = 5500 \text{ mg } L^{-1})$ and macrocrustaceans the most tolerant ($LC_{50} = 38000 \text{ mg } L^{-1}$) (Kefford *et al.* 2003).

Although the adults and larvae of many macroinvertebrates appear to be tolerant of elevated salinity, there is little information on modifications to egg development or early instar and juvenile development.

Fish

Most adult native and introduced fish are tolerant of increasing salinity, but juveniles and eggs of some species are susceptible (Clunie *et al.* 2002).

The majority of native Australian fish are derived from relatively recent marine ancestors. Only the lung fish (*Neoceratodus forsteri*), spotted barramundi (*Scleropages leichardti* and *S. jardini*) and the Western Australian salamanderfish (*Lepidogalaxias*) have long evolutionary histories in freshwater (Merrick and Schmida 1984). Studies have shown that the majority of native and introduced fish in Australia appear to be tolerant of salinities exceeding 3000 mg L⁻¹ (Chessman and Williams 1974; Hart *et al.* 1991; Williams and Williams 1991; O'Brien and Ryan 1997; Whiterod 2001).

There has been only limited examination of the affect of salinity on juveniles and eggs, although evidence suggests

some are susceptible to increased salinity. Eggs of the native Macquarie perch have only 50% survival when exposed to 3000 mg L⁻¹ and juveniles that hatched in this salinity were smaller than the controls. In a similar experiment, trout cod egg survival was reduced by 50% at 4500 mg L⁻¹ (O'Brien 1995; O'Brien and Ryan 1997). Eggs of silver perch are not affected until salinity exceeds 9000 mg L⁻¹; however, juveniles hatched at 6000 mg L⁻¹ had better survival than those hatched in freshwater, possibly resulting from decreased mortality as a consequence of salt-inhibiting diseases that commonly affect larvae (Guo *et al.* 1993). The Australian grayling, which is found in coastal rivers of south-eastern Australia and spends part of its life cycle in estuaries, produces eggs that are tolerant of salinities up to 5000 mg L⁻¹ (Bacher and O'Brien 1989).

Discussion

There is a general acceptance that freshwater ecosystems undergo little ecological stress when subjected to salinities up to 1000 mg L^{-1} . However, much of our understanding of the effects of salinity on freshwater ecosystems comes from lowland rivers where exposure to significant salt concentrations already occurs; other systems may be more sensitive. Hence, this view could lead to the misinterpretation that freshwater ecosystems below 1000 mg L^{-1} are 'healthy', and there will be no adverse effects on biota or ecosystems. For many taxa, sublethal effects may not be apparent at the community level for many generations. Much of our knowledge of the impacts of salinity on aquatic ecosystems comes from field sampling along a gradient of salinity, from which it is difficult to attribute cause of ecological change. Other underlying factors such as habitat modification, loss of food resources or modification of predation pressure may also be causing changes within these systems (Blinn and Bailey 2001).

Some biotic groups are more tolerant of salinity than others. Communities of adult fish and macroinvertebrates appear to tolerate increasing salinity because they either comprise salt-tolerant remnants left after salt-sensitive species have been eliminated or reflect an evolution from marine ancestors (Williams *et al.* 1991; Bunn and Davies 1990; Mitchell and Richards 1992; Metzeling 1993; Kay *et al.* 2001). The freshwater algae, aquatic plants and microinvertebrates, appear to be less tolerant of increased salt. For these groups the general trend is to reduction of species richness as salinity increases with either a loss (or gain) in abundance. The freshwater taxa in these groups appear restricted to below 3000 mg L⁻¹, which may reflect a non-marine recent ancestry.

Life cycles of aquatic organisms generally are controlled by the presence of water, in association with other triggers (e.g. temperature) that cue the onset of processes such as germination of seeds, hatching of invertebrates from diapausing eggs or spawning of fish. Although specific information on impacts of increasing salinity is limited, we do know that life-history traits related to fitness, such as survival, growth and reproduction, can be reduced by stress (Hoffman and Parsons 1991). Hence, stresses such as long-term exposure to salinity may lead to reduction in reproduction, recruitment and ultimately depletion of biotic reservoirs, reducing the sustainability of communities and their ability to respond when a flush of freshwater occurs.

The current rate of change of salinity in freshwater ecosystems may be much faster than freshwater biota can evolve or adapt. Although lowland river biota may have mechanisms that allow survival during periods of extreme salt concentrations, upland rivers potentially have experienced lower natural variation in salinity and therefore biota in these systems may be less salt-tolerant. Induced changes in salinity in upland systems may be too rapid for taxa to adapt, suggesting that freshwater taxa may be lost and communities will become dominated by salt-tolerant taxa. Pulses of salt into freshwater ecosystems will influence survival of a range of biota and although such increases in salt may be rapid and short-lived, the consequences to the freshwater biota are unknown.

We need to know how salinity changes ecosystem functioning through alteration of biotic and abiotic processes: do changes to ecological processes change community composition? Managers need to know more about the relationship between flow patterns, salt concentrations and environmental damage to predict consequences of management actions. How a combination of changes in flow and salt affect river and wetland communities is also relevant to management predictions. We have many systems that are naturally variable in both salinity and hydrology, yet we do not know how increasing salinity will affect the biota or ecosystem integrity. Linking salinity levels directly to mortality or recruitment potential of aquatic biota is not sufficient to predict the outcome of increasing salinity on freshwater ecosystems. Second- and third-order effects must also be taken into account in describing the full effect of salinity on aquatic ecosystems. Of particular interest are the effects of increasing salinity on primary and secondary production, nutrient dynamics and food-web structure. Once we understand these interactions, links and the flow on consequences, managers and researchers will be in a better position to predict the condition of aquatic ecosystems under modified salinity and move towards focusing on effective rehabilitation. For example, the use of environmental water allocations (environmental flows) could be considered as a tool in managing salinity in aquatic ecosystems, once the relationships between hydrology, salinity and environmental damage are further delineated. Use of this relationship could enhance effective disposal of salt-contaminated water, with minimal damage to the environment.

If ecosystem health and salt can be related, then tools such as water allocations, river operation, engineering intervention and catchment management programs can be designed to manipulate salt loads to increase the health of aquatic ecosystems. Innovative experimental science, together with imaginative predictive management can work together to underpin salinity management issues on both broad and local scales.

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