Climate Change Alters Zooplankton Community Structure and Biodiversity in Coastal Wetlands

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Intermittent saline intrusions are a common feature of many coastal lakes and wetlands. Such ecosystems are often important sites of biodiversity, biological productivity, and ecosystem services such as sediment, nutrient, and contaminant removal from inflowing rivers. Predicted effects of global climate change and future sea level rise are likely to exacerbate saline intrusions into such ecosystems. In this report, we demonstrate the severe perturbations of zooplankton community structure and biomass caused by saline intrusions of variable magnitude into Lake Waihola, South Island, New Zealand. Our analyses from Lake Waihola and other brackish ecosystems around the world show that even relatively small increases in mean salinity levels can drive such systems to a state of depleted biodiversity and biomass, altering fundamental ecosystem functioning.

Low-lying lakes, wetlands and lagoons are common features of coastal areas of many parts of the world. Such ecosystems are often connected to the sea and may experience tidal water level fluctuations as well as intrusions of saline water that result in a temporary or long-term brackish state. Salinity in such systems may be seasonally variable and can be influenced by variations in sea level, freshwater recharge (precipitation or hydrological flows), and evaporation. Therefore, coastal wetlands are particularly at risk from the predicted effects of global climate change (*1*), as the global mean sea level is projected to rise under various scenarios by 0.09 - 0.88 metres by 2100 (*2*), thereby increasingly salinising brackish and many freshwater coastal aquatic ecosystems. In New Zealand, for example, for every 100 km of coastline, there are, on average, 7.4 lakes, wetlands and lagoons (comprising 260.5 hectares) that are likely to be impacted by salinisation as a result of predicted sea level rise in the next century (*3*).

Salinity affects an aquatic organism's ability to osmoregulate, a biochemical process regulating solute transport and many biochemical reactions. The classification of biological communities in relation to the salinities in which they are found has led to attempts to define salinity thresholds that describe the distributions of taxa and communities along salinity gradients (*4*). The threshold salinity level functionally delimiting freshwater from brackish lake communities has been suggested to occur at 2 ‰ (*5*). Similarly, the salinity threshold between subsaline and hyposaline waters has been defined as 3‰ (*6*). Furthermore, species richness along salinity gradients is generally minimised at salinities between 5 - 7‰ (*4*).

Lake Waihola is a medium sized (surface area = 7.2 km^2), shallow, (mean depth = 1.15 m), tidal (mean tidal range c. 0.40 m) lake, connected to the sea via a 10 km reach of the Taieri River, c. 30 km south west of Dunedin, South Island, New Zealand. The lake has a hydraulic residence time of 153 days, based on non-tidal, freshwater inflows (*7*). A preliminary study indicates that Lake

Waihola was estuarine during the mid-holocene highstand (c. 4000 years before present) because a layer of articulated shells of the estuarine/marine bivalve, *Austrovenus stutchburyii,* is ubiquitous c. 1.15 metres below the surface of the lake bed (M. Schallenberg, unpublished data). Shells have been carbon-dated at 4059 - 4232 years before present (^{14}C calibrated age; 1 sigma interval). *A. stutchburyii* does not inhabit the lake at present, which, is habitat now for a freshwater mussel (*Hyridella menziesi*).

During typical drought conditions, when water levels in the Taieri River are low and when other freshwater inputs are small, significant intrusions of saline water enter the lake, as occurred in the austral summers 1997/98 (*7*) and 1998/99. During this dry period, saline intrusions in Lake Waihola created strong temporal and spatial salinity gradients (*7*). While sea levels around New Zealand are predicted to rise by between 2 cm and 35 cm by the year 2050, meteorological perturbations resulting from global climate change are expected to exacerbate the salinisation of Lake Waihola (*8, 9*).

A variety of zooplankton taxa occur in the Lake Waihola, including species of rotifers, cladocerans, copepods, and one species of amphipod. Canonical correspondence analysis showed that salinity was the factor most strongly related to zooplankton community structure in Lake Waihola and in neighbouring Lake Waipori in the year September 1997 - September 1998 (*7*). The primary canonical axis for Lake Waihola was strongly driven by salinity and explained 41% of the species-environment correlation (*7*). However, because the saline intrusion in 1997/98 was seasonal, occurring in late summer and autumn, the interpretation of the effects of the relationship between zooplankton community structure and the salinity gradient was not conclusive, as other physico-chemical variables also showed similar seasonal patterns in 1997/98 (*7*).

The 1999/2000 austral summer period was locally typified by wetter, north easterly weather patterns. Fortnightly sampling of salinity and zooplankton abundance was undertaken again for December 1999 - October 2000 (*10*). Salinity reached 1.2 psu (specific electrical conductivity = 1.85 mS cm^{-1}) during this year, compared to 4.2 psu (6.80 mS cm^{-1}) in austral summer/autumn 1998 (Fig. 1).

Figure 1 Salinity patterns measured at three sites in Lake Waihola in two non-consecutive years (September 1997 - September 1998; December 1999 - October 2000), measured fortnightly.
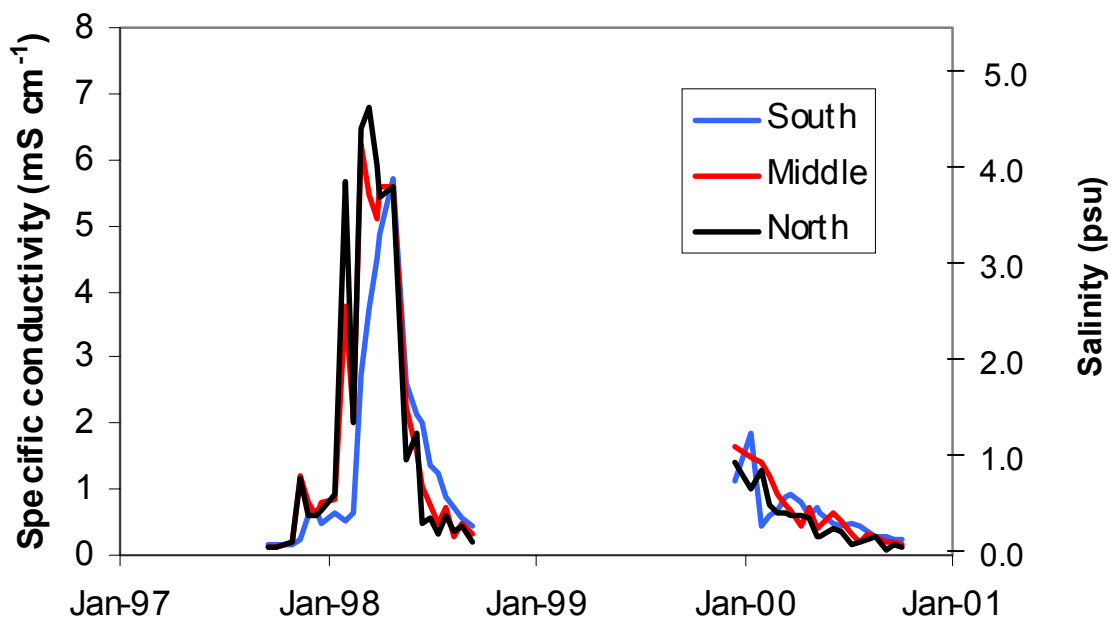
The second year's data allowed us to re-analyse the relationship between salinity and zooplankton community structure using a 2-year data set, in which the pattern of salinity was decoupled from seasonality. In this analysis, the possible confounding effects of seasonal patterns of other environmental variables on zooplankton community structure were effectively "controlled" by the lack of summer saline intrusion in 1999/2000. To determine the relationship between salinity and zooplankton community structure we used a weighted averaging technique that calculated the abundance-weighted, average salinity optima and tolerances for individual zooplankton taxa (*11*).

The zooplankton taxa in Lake Waihola showed a wide variety of salinity tolerances and optima (Fig. 2). Noteworthy are the optima and tolerances of three periodically abundant metazoan taxa, the calanoid copepods *Boeckella hamata* and *Gladioferens pectinatus,* and the cladoceran, *Daphnia carinata*. Whereas *G. pectinatus* showed a wide salinity tolerance, that of *B. hamata* was restricted to salinities of 0 - 0.6 psu, and that of *D. carinata* was restricted to salinities of 0 - 0.3 psu.

Figure 2 Abundance-weighted salinity optima (stars) and tolerances (± 2SD; bars) of 28 zooplankton taxa in Lake Waihola. Colours indicate general taxonomic grouping to which the taxa belong. The coloured square, triangle and circle indicate the taxa used in salinity toxicity experiments (see Fig. 3). Taxa are ranked according to maximum salinity tolerance.
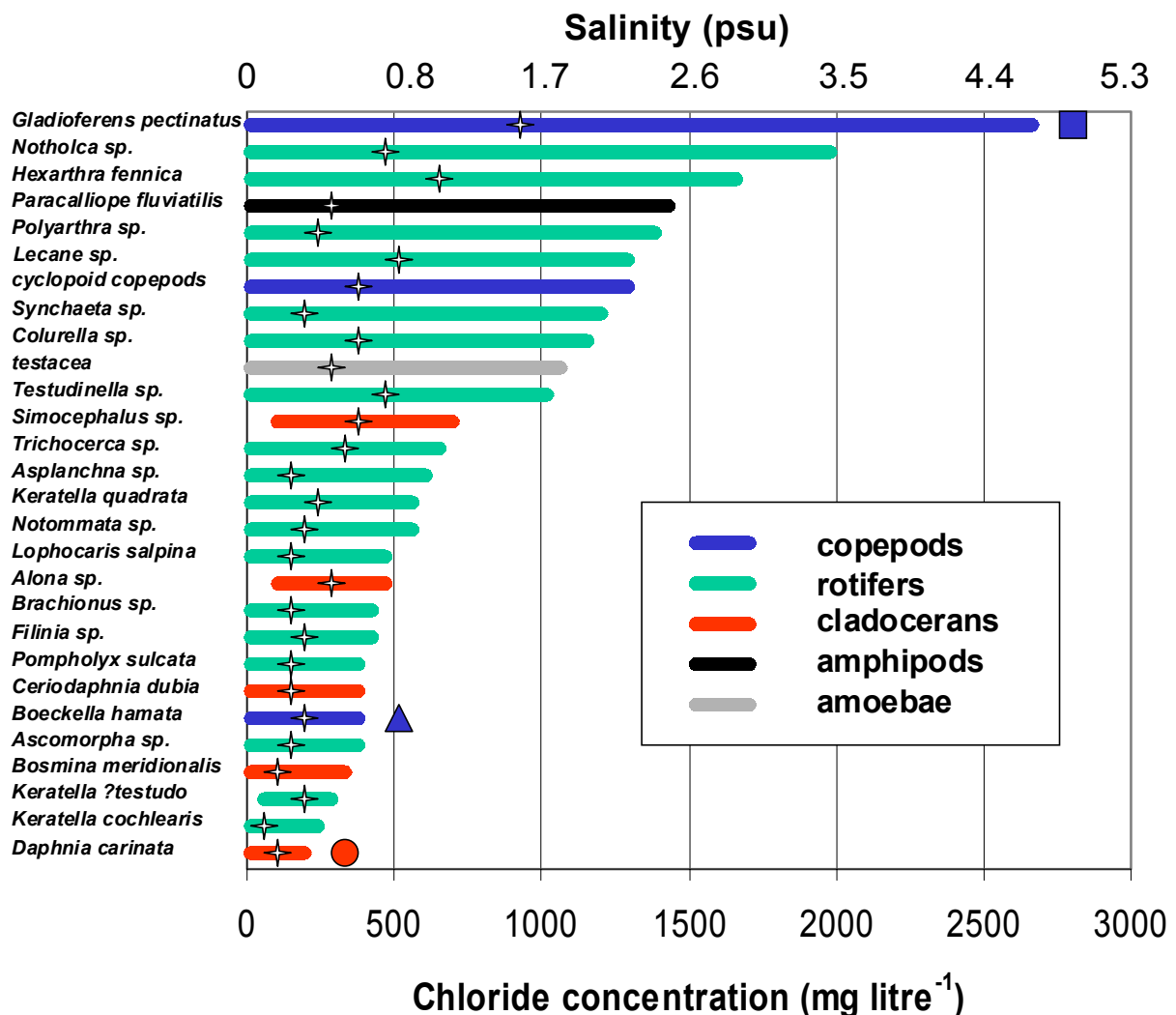
The calculated salinity tolerances of these three species based on the field data, were tested in the laboratory in a series of salinity toxicity tests (*12*). The tests were run at various chloride concentrations but only the results of a survivorship trial run at an intermediate chloride concentration of 1500 mg Cl⁻ litre^{-1} (c. 2.7 psu) are presented here (Fig. 3). *G. pectinatus* was the most tolerant of salinity and *D. carinata* the most sensitive, with *B. hamata* intermediate in tolerance, thereby confirming the pattern of salinity tolerance of these three taxa that is implied by the field data (Fig. 2). From these and other data (*13*; C. Hall unpublished data), the LD50s for chloride (the chloride concentration at which 50% of the zooplankters were killed after 96h at 10°C) for the three taxa were 1780 mg Cl⁻ litre^{-1} (c. 3.2 psu) for *G. pectinatus*, 1500 mg Cl⁻ litre^{-1} (c. 2.7 psu) for *B. hamata*, and 1400 mg Cl⁻ litre^{-1} (c. 2.5 psu) for *D. carinata*.

Figure 3 Toxicity test showing the survival of adults of three crustacean zooplankton taxa in 1500 mg Cl⁻ litre^{-1} at 10°C.
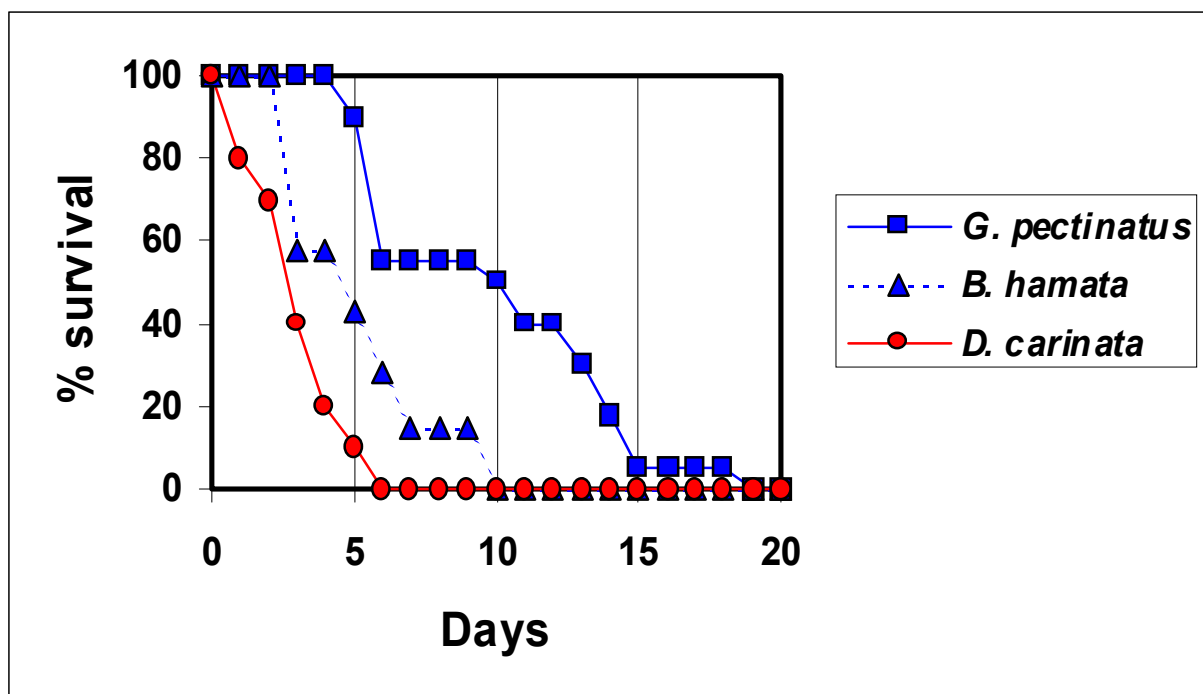

Daphnia is a key conduit between phytoplankton and fish in the food chains of many lakes. Through their effective grazing on algal biomass, *Daphnia* can improve water quality, and they are also important in the diet of many planktivorous fish (*14*). In many lakes, *Daphnia* do not tolerate even low levels of salinity (*5, 15*). Furthermore, cladocerans, in general, are poorly represented in marine environments (*16*). Comparison of the effects of cladocerans and copepods on pelagic food webs of lakes of different trophic condition show that shifts in dominance in the zooplankton from *Daphnia* to copepods could cause significant changes in food web structure, and matter and energy flow (*17*).

The zooplankton taxa in Lake Waihola were ranked by maximum tolerance to salinity and colour-coded by general taxonomic groupings to indicate how the zooplankton community structure changed with increasing salinity (Fig. 2). At salinities > 700 mg Cl⁻ litre^{-1} (c. 1.3 psu), cladocerans were excluded from the lake. Although some rotifer taxa showed low salinity optima and

tolerances, at least some rotifers persisted at all but the highest salinities. The calanoid copepod, *G. pectinatus* was the most tolerant taxon to salinity. As salinity increased in Lake Waihola the zooplankton community changed from one represented by copepods, rotifers, cladocerans, amphipods and amoebae at low salinities to one consisting of only the copepod, *G. pectinatus*, and rotifers above 1500 mg Cl⁻ litre⁻¹ (c. 2.7 psu).

Furthermore, zooplankton diversity and abundance in Lake Waihola decreased strongly with increasing salinity (Fig. 4). The strongest decline in both species richness and diversity occurred at c. 500 mg Cl⁻ litre⁻¹ (corresponding to c. 0.9 psu or 1.4 mS cm⁻¹), and species richness reached a minimum at c.2000 mg Cl⁻ litre⁻¹ (c. 3.6 psu or 5.2 mS cm⁻¹).

Figure 4 (a) The effect of salinity (psu) on zooplankton species richness in Lake Waihola, as calculated from salinity tolerances in Fig. 2, (b) and the effect of salinity (mg Cl⁻ litre⁻¹) on zooplankton density in Lake Waihola. X-axes are similarly scaled.
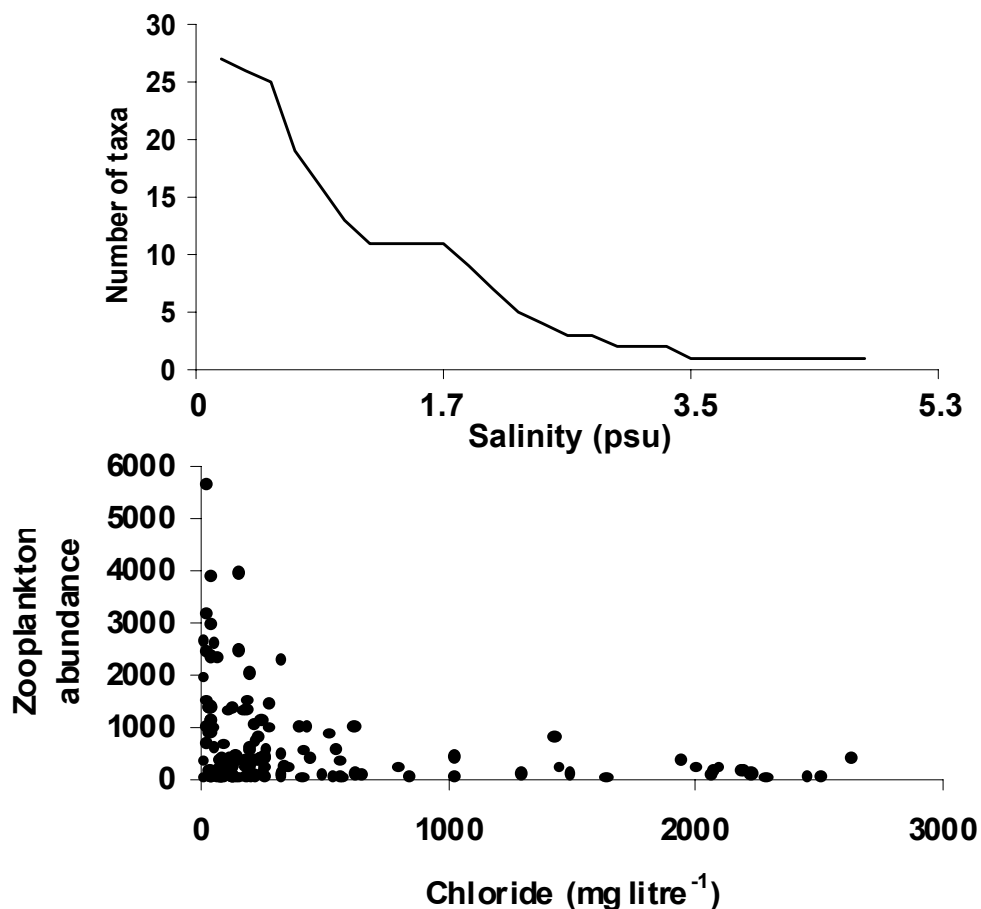
Similar patterns have been reported in other freshwater - brackish ecosystems around the world (Table 1). Results from field surveys, carried out on numerous water bodies within specific geographic regions (survey studies) showed that total zooplankton diversity (*5, 16, 18, 19, 20*), cladoceran diversity (*16, 18*), rotifer diversity (*18, 21*), and copepod diversity (*18*) all decreased with increasing salinity (*22*). Zooplankton density also decreased with increasing salinity in a number of Danish and Canadian brackish and freshwater lakes (*5, 19*). Field studies carried out along salinity gradients in single systems (longitudinal studies) tended to show that zooplankton diversity and density decreased with increasing salinity (*22 24, 25, 26*, this study). This pattern was

not observed in four Brazilian estuaries where the high humic content and low pH of the blackwater rivers possibly contributed to the unusually low abundance and diversity of zooplankton in the rivers discharging into the estuaries (*27*). In a South African estuary zooplankton diversity declined along a salinity gradient from fresh water to c. 2.0 psu, but increased as salinity increased from c. 5 to 10 psu and stabilised at higher salinities (*24*). A pattern similar to this has been proposed as a general model describing species diversity as a function of salinity; however the salinity threshold delimiting the decline of species richness was suggested to occur at c. 5 - 7 psu (*4*).

Table 1 The effect of salinity on zooplankton community diversity and abundance reported for various aquatic ecosystems. The salinity threshold is that corresponding to steepest decline/increase in species richness or abundance along salinity gradients unless otherwise stated. ● indicates athalassic systems. ○ indicates thalassic (marine-influenced) systems.

System	Type of system	Zooplankton species richness	Zooplankton abundance	Salinity threshold	Reference
Survey studies					
Danish lakes	lakes●	decrease	decrease	< c. 2 psu[†]	4
Australian, South African, Canadian, Iranian and German waterbodies	various●○	decrease[1]		c. 3 psu[1‡]	16
East African lakes	inland lakes○	decrease[1,2,3]		1.0 mS cm^{-1}*	18
Canadian prairie lakes	saline lakes○	decrease	decrease	c. 7 psu; c. 30 psu	19
Ethiopian water bodies	water bodies○	decrease[2]		c. 2 psu	21
Longitudinal studies					
Carapebus Lagoon	lagoon●	decrease			23
Brazilian estuaries	estuary●		increase		27
Lake Waihola	tidal lake●	decrease	decrease	0.9 psu	this study
Swartkops Estuary	estuary●	decrease/ increase		c. 1.0 - 2.0 psu/ c. 5 -13 psu	24
Onondaga Lake	ionically polluted lake	decrease			25
Lagos Harbour - Badagry Creek	estuary●	decrease[2]			26
Fuente de Piedra	temporary lake○	decrease			20

[1] cladocerans

[2] rotifers

[3] copepods

[†] threshold delimiting freshwater and brackish communities

[‡] threshold delimiting subsaline from hyposaline waters based on zooplankton communities

* temperature of samples not specified

Our results show that the predominantly freshwater zooplankton community in Lake Waihola is adversely affected by small increases in salinity levels, and that the threshold above which the effects become severe is c. 0.9 psu. This threshold is lower than previously reported thresholds defining minima in zooplankton species richness and abundance in marine-influenced waters and the functionally important loss of *Daphnia* from lakes. Therefore, the predicted meteorological and sea level effects of global climate change in this century (*2, 8, 9*) will have severe negative impacts on zooplankton community structure and abundance in coastal, tidal freshwater and brackish waterbodies unless the rate of evolutionary adaptations can keep pace with the rate of salinisation. Such changes to zooplankton communities may reflect similar impacts on other biotic communities in coastal wetlands, leading to the perturbation of ecological functioning of these valuable and vulnerable ecosystems.

References and Notes

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3. The density and total area of New Zealand (including islands) coastal wetlands likely to be impacted by sea level rise in the next century was calculated using 1:50,000 digital topographic maps using ArcView GIS software. All coastal wetlands (mangroves, lagoons, swamps) in the 1 - 20 m contour band were determined and each was examined with respect to spot height elevations < 2 m asl, distance from the coast, and hydraulic connectivity to tidal or coastal aquatic systems. Based on this analysis a subset of coastal wetlands was defined as those most likely to be affected by a 1m rise in sea level.

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10. Zooplankton was sampled fortnightly from the entire water column using a 10 cm diameter tube sampler. Lake water was passed through a 50 μm-mesh zooplankton net. Specific electrical conductivity was measured in the field using a Hanna model HI 8633 conductivity meter and a YSI (Yellow Springs Instruments) 85 probe/meter unit. Chloride ion concentrations were measured by electrochemical silver titration using an Aminco analytical chloride titrator. Conversions from specific conductivity to chloride ion for the few samples in which chloride was not measured were

carried out using the regression equation generated from both specific conductivity (20°C) and chloride measurements obtained for Lake Waihola:

$$[Cl-] = -34.6 + 0.39 \text{ (specific conductivity), (N= 125, R}^2 = 0.99, P < 0.0001)$$

For marine-influenced waters, the ratio of chloride to total dissolved salts is generally constant, and the coefficient, 1.8066, was used to convert chlorinity to salinity.

11. Calculations of the salinity optima and tolerances of zooplankton taxa were carried out using the following equations:

$$WA_{opt} = \Sigma_i^n (A \times S) / \Sigma_i^n A, \text{ (ref. 28)}$$

where WA_{opt} is the salinity optimum for each taxon, A is the taxon's abundance in sample i and S is the salinity of sample i,

$$WA_{tol} = +/- 2* WA_{sd} ,$$

where WA_{tol} is the salinity tolerance and WA_{sd} (standard deviation of the weighted average) is:

$$(\Sigma_i^n(A \times (S - WA_{opt})) / \Sigma_i^n S)^{0.5}, \text{ (ref. 28)}.$$

12. Zooplankton toxicity experiments involved exposing adult zooplankters to a range of salinities (at 10°C) representative of levels recorded in Lake Waihola. Animals were collected from the lake at least three days before experiments began, and acclimated to a defined culture medium (14). Animals were fed daily 2 mg litre^{-1} dry weight of the alga, *Cryptomonas sp.,* and kept under a day/night cycle (16 h light : 8 h dark). The percentage of animals alive after 96 h in all salinity treatments was used to calculate the intermediate salinity at which 50% mortality would have been expected after 96 h.

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22. For the meta-analysis, we selected studies where effects of salinity on zooplankton diversity and/or abundance were described. Only those studies were included in the analysis in which salinity gradients encompassed oligohaline (or subsaline) waters. Conversions of literature data from specific conductivity to salinity were carried out using the Oceanus 2000 software (29). As salinities have often been reported in the literature as parts per thousand (‰ or ppt) and practical salinity units (psu), which are almost identical, for consistency, all salinity values converted to psu from other units are presented as c. practical salinity units.

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