

## Salinity effects on macroinvertebrate assemblages and waterbird food webs in shallow lakes of the Wyoming High Plains

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### Abstract

We determined the biomass and community structure of macroinvertebrates ( $>500\ \mu\text{m}$ ) associated with macrophytes, sediments, and unvegetated open water in three oligosaline ( $0.8$  to  $8.0\ \text{mS cm}^{-1}$ ) and three mesosaline ( $8.0$  to  $30.0\ \text{mS cm}^{-1}$ ) lakes in the Wyoming High Plains, USA. Total biomass of epiphytic and benthic invertebrates did not change with salinity, but biomass of macroinvertebrate zooplankton in open water was significantly higher in mesosaline lakes. Community composition of invertebrates differed between the two salinity categories: large grazer/detritivores (gastropods and amphipods) were dominant in oligosaline lakes, whereas small planktivores and their insect predators were more prevalent in mesosaline lakes. Both direct physiological effects of salinity, as well as a shift in the form of primary production from macrophytes to phytoplankton, probably explain these changes in community composition. Salinity effects on invertebrate communities appear to be less important to top avian consumers than are costs of osmoregulation.

### Introduction

Saline lakes and wetlands are common in many arid and semiarid regions (Hammer, 1986). These aquatic ecosystems can be extremely productive (Hammer, 1981; Timms, 1981a), and are often used by foraging waterbirds (Vareschi, 1978; Jehl, 1988; Swanson & Duebbert, 1989). However, despite studies in the prairies of north-central North America (Hammer, 1986; van der Valk, 1989), there has been no detailed research on invertebrate communities of saline lakes in the High Plains of the Rocky Mountain region.

Invertebrate community structure often varies substantially among lakes with a gradient of salinities (Hammer, 1986; Hammer *et al.*, 1990). Most studies have examined invertebrate numbers rather than biomass, although biomass is often more relevant to trophic relations. When biomass studies have been conducted, they have usually focused on communities in single habitats such as benthos or zooplankton. For profundal and littoral benthic invertebrates, biomass

declined as salinity increased in Canadian and Australian lakes (Rawson & Moore, 1944; Timms, 1981b; Timms *et al.*, 1986; Hammer *et al.*, 1990). In contrast, the abundance of zooplankton generally increased with greater salinity (Timms, 1981b; Galat & Robinson, 1983). Salinity relations with invertebrate biomass in epiphytic habitats have not been reported. Moreover, the influence of salinity on invertebrate biomass in all three habitats simultaneously has not been studied, even though predators may forage in a variety of habitats and these habitats are highly interconnected ecologically (Gilinsky, 1984).

Scheffer (1990) proposed that shallow aquatic systems can exist in alternative stable states dominated by either phytoplankton or macrophytes. Macrophyte species richness declines as salinity increases (Stewart & Kantrud, 1972; Hammer & Heseltine, 1988), and macrophytes are often absent or insignificant in lakes of high salinities (Williams, 1972; Hammer, 1981; Lancaster & Scudder, 1987; Hammer & Heseltine, 1988). Shifts to phytoplankton production with

increased salinity might result from a combination of higher nutrients in the water column, greater turbidity, and loss of salt-intolerant macrophytes. Because the form of primary production can change with salinity, involving shifts in the relative abundance of open-water and macrophyte/epiphyte habitats, changes in invertebrate communities are also expected (Lancaster & Scudder, 1987).

Availability of invertebrate prey for birds can be high in saline lakes. Saline lakes often lack fish because of salinity intolerance or winterkill from low dissolved oxygen (Hammer, 1986; Peterka, 1989). With minimal competition from aquatic vertebrate predators, a variety of birds are top consumers in these rather simple food webs (Hurlbert *et al.*, 1986; Vareschi, 1987; Jehl, 1988). Because of specialized feeding modes and preferred prey, avian predators might be affected by shifts in stable state and invertebrate communities with changes in salinity.

In this paper, we describe the biomass and community structure of macroinvertebrates in macrophyte, sediment, and open-water habitats in oligosaline (0.8–8 mS cm<sup>-1</sup>) versus mesosaline (8–30 mS cm<sup>-1</sup>) lakes in the Laramie Plains of Wyoming. We then evaluate how these differences might result from shifts in the form of primary production caused by increased salinity and correlated changes. Finally, we assess the importance of shifts in invertebrate community structure to different avian predators, given their various feeding modes and prey preferences.

### Study area

The Laramie Plains of Albany County, Wyoming, USA contain many shallow lakes with a salinity range of at least 0.3 to 250 mS cm<sup>-1</sup>. The Laramie Plains are at about 2200 m elevation between the Laramie Mountains to the east and Medicine Bow Mountains to the west. Saline lakes are common due to low precipitation (25 to 30 cm yr<sup>-1</sup>) relative to evaporation, water diversion for agriculture, and numerous wind-eroded, terminal basins that in some cases receive intermittent stream flow from mountain snowpack.

Six lakes were selected from a survey of shallow lakes in the Laramie Plains (Table 1). By the salinity classification of Cowardin *et al.* (1979), three of the lakes (Caldwell, George, and Nelson) were oligosaline (defined as 0.8 to 8.0 mS cm<sup>-1</sup>) and three (Hoge, Creighton, and Hutton) were mesosaline (defined as 8.0 to 30.0 mS cm<sup>-1</sup>). Conductivities in

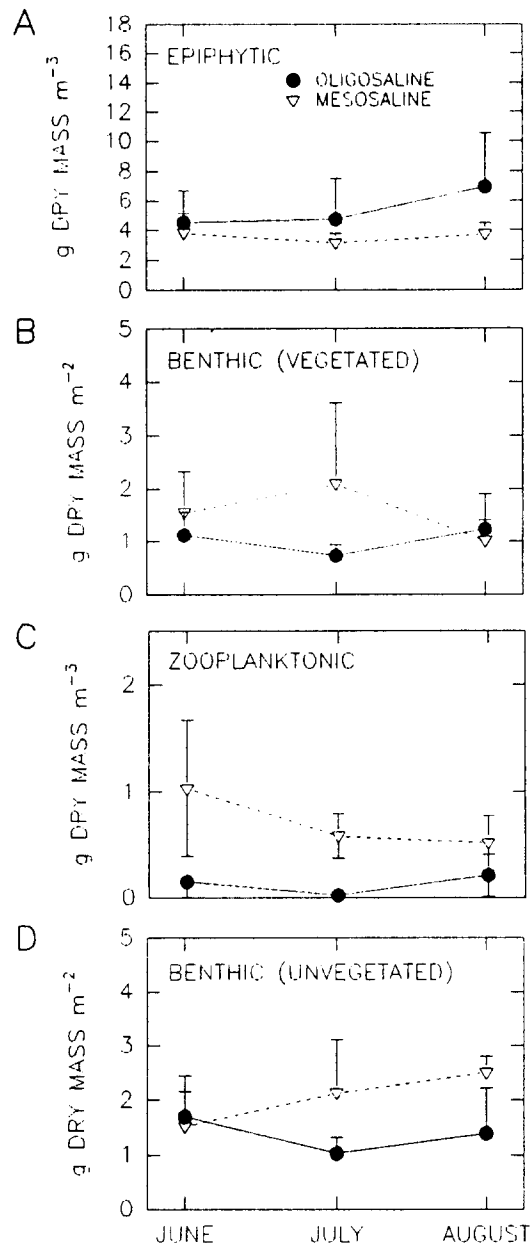


Fig. 1. Mean dry mass ( $\pm 1$  S.E.) of macroinvertebrates (>500  $\mu\text{m}$ ) in (a) macrophytes (including benthic mats of filamentous algae), (b) vegetated sediments, (c) open water without vegetation, and (d) unvegetated sediments in oligosaline ( $n=3$ ) and mesosaline ( $n=3$ ) lakes of the Laramie Plains, Wyoming, 1992.

the mesosaline lakes increased as summer progressed. Oligosaline George and mesosaline Hoge, Creighton, and Hutton are located in the Hutton Lake National Wildlife Refuge (HLNWR) about 15 km southwest of Laramie, Wyoming. Oligosaline Caldwell and Nelson

Table 1. Selected chemical characteristics of study lakes in the Laramie Plains, Wyoming. Conductivity range is from May to August 1992; alkalinity and total phosphate are means of measurements in May and September 1992. Total phosphate was measured with a Hach test kit which did not discriminate values below  $67 \mu\text{g l}^{-1}$ .

Lake	Conductivity range ( $\text{mS cm}^{-1}$ )	Alkalinity Mean ( $\text{mg l}^{-1}$ $\text{CaCO}_3$ )	Total phosphate Mean ( $\mu\text{g l}^{-1}$ )
<b>Oligosaline</b>			
Caldwell	0.8–1.1	118	75
George	2.2–2.4	128	< 67
Nelson	2.9–4.2	168	< 67
<b>Mesosaline</b>			
Hoge	9.3–19.0	1320	500
Creighton	12.9–16.3	355	133
Hutton	18.6–23.5	318	508

are located on private land about 20 km southwest of Laramie.

The mesosaline lakes had salinity-correlated features distinct from those of the oligosaline lakes. The former lacked an emergent fringe of *Scirpus acutus*, and had a less diverse community of submerged aquatic vegetation (SAV) (Table 2). SAV in mesosaline lakes generally included only *Ruppia maritima*, although *Potamogeton pectinatus* can occur in years when the same lakes are at lower salinities. The three mesosaline lakes also had higher alkalinity and higher total phosphate in the water column (Table 1). All the oligosaline lakes receive water annually from creeks and/or irrigation ditches. In contrast, the amount of any surface water entering the mesosaline lakes varies among lakes and years (Table 2); e.g., Lake Hoge had declining water levels through the summer of 1992, and dried up in October after our study was completed.

## Methods

We sampled macroinvertebrates (i.e., retained by a  $500\text{-}\mu\text{m}$  sieve) in epiphytic, benthic, and planktonic habitats during 8–24 June, 15–28 July, and 17–28 August 1992, between 08:30 and 15:00 h. In this paper, we define zooplankton as macroinvertebrates collected in the water column in unvegetated areas. Each lake required one to three days to sample.

Sampling of epiphytic invertebrates was stratified by macrophyte species, and benthic samples by macrophyte species and unvegetated sediment. We categorized macroalgae (*Chara* sp. and benthic mats of filamentous metaphyton) with macrophytes because they both provide habitat structure in the water column. Sample stations were randomly selected from a set of ten stakes placed regularly in the shallows (<2 m) of each lake. Each macrophyte species was sampled at the site nearest each stake at which the macrophyte stand was monospecific (or no stems were present at sites classified as unvegetated), and macrophyte density was representative for that species in the lake at that time (see Wollheim, 1994). In each lake, five epiphytic and five benthic macroinvertebrate samples were collected for each macrophyte species, and five zooplankton and five benthic samples from unvegetated areas.

Epiphytic macroinvertebrates were sampled by lowering a plastic tube (diameter 29.5 cm) over macrophytes. The tube was 50 cm tall, with a cylindrical net ( $100 \mu\text{m}$ -mesh) attached to the top to increase height. Three legs supported the tube 10 to 15 cm above the sediment so that macrophytes could be cut at the sediment-water interface. A  $100\text{-}\mu\text{m}$  net sewn to a flexible aluminum ring was then sealed around the tube bottom to retain severed macrophytes and invertebrates as the sample was brought to the surface. Epiphytic samples included the water column up to the top of the canopy; sample (canopy) height was recorded so samples could be standardized by volume (see below). Invertebrates were later rinsed from macrophytes and preserved in 70% alcohol.

Macroinvertebrate zooplankton were collected over unvegetated sediments with a 19-cm diameter plankton net with  $100\text{-}\mu\text{m}$  mesh. The net was pulled from sediment surface to water surface; water depth was recorded so samples could be standardized by volume. Samples were preserved in 70% alcohol. Benthic invertebrates in the upper 5 cm of sediment were collected directly beneath epiphytic and zooplankton samples with a 5-cm diameter plastic corer, preserved in 70% alcohol, and stained with Rose Bengal.

All macroinvertebrates ( $>500 \mu\text{m}$ ) in benthic samples were counted. For epiphytic macroinvertebrates, all individuals of large or rare taxa (e.g., odonates and gastropods) were completely counted, and other taxa (e.g., chironomids and copepods) were counted in subsamples of known percent volume extracted with a Stempel pipette. Individuals from each sample were pooled by taxa, dried at  $60^\circ\text{C}$ , and weighed.

Table 2. Selected physical and biological characteristics of study lakes in the Laramie Plains, Wyoming, 1992.

Lake	Surface outflow	Surface inflow	Basin area (ha)	Approx. lake area (ha)	Mean depth ( $\pm 1$ S.D.) at sampling sites (m)	Emergent fringe <sup>a</sup>	Aquatic vertebrates present <sup>b</sup>	Dominant macrophytes <sup>c</sup>
<b>Oligosaline</b>								
Caldwell	yes	annual	32.4	32.4	1.16 + 0.21	yes	<i>E. exile</i> <i>A. tigrinum</i>	Po,My,Al,Sc
George	yes	annual	2.8	2.8	1.29 + 0.23	yes	<i>E. exile</i>	Po,My,Ch,Sc
Nelson	no	annual	2.8	2.8	0.58 + 0.14	yes	no	Ch,Sc,Po
<b>Mesosaline</b>								
Hoge	no (most years)	some years	30.0	8.0	0.29 + 0.07	no	no	Ru
Creighton	no	annual	81.0	16.0	1.33 + 0.25	no	no	Ru
Hutton	no	very wet years	89.0	34.0	0.77 + 0.20	no	no	Ru

<sup>a</sup> *Scirpus acutus*

<sup>b</sup> *Etheostoma exile* (Iowa darter), *Ambystoma tigrinum* (tiger salamander)

<sup>c</sup> Po = *Potamogeton pectinatus*, My = *Myriophyllum exalbescens*, Ch = *Chara* sp., Al = benthic mats of filamentous algae, Sc = *Scirpus acutus*, Ru = *Ruppia maritima*

Masses of uncommon or small-bodied taxa of epiphytic macroinvertebrates were obtained by pooling individuals within lake and macrophyte habitat. For each sample, biomass for each taxonomic group was calculated from average masses (for a sample of individuals) and numbers for the taxon from either complete counts or subsample estimates. Biomass estimates for all taxa were then summed to obtain total macroinvertebrate biomass within samples. Biomass of zooplankton >500  $\mu\text{m}$  was calculated by multiplying counts in plankton tows by the average mass of a sample of individuals in each taxonomic group as measured in epiphytic samples.

Biomass of epiphytic and zooplanktonic macroinvertebrates per unit volume of water ( $\text{g m}^{-3}$ ) was obtained by dividing biomass in the sample by the volume of water sampled (calculated from basal area of the sampler and height of the sample). Biomass of benthos per unit area ( $\text{g m}^{-2}$ ) was obtained by dividing biomass in each sample by area sampled. Epiphytic invertebrates are reported per unit volume to account for differences in height between the various macrophyte growth forms within lakes, and between the same growth forms in lakes of varying depth (Table 2). Biomass of invertebrates ( $\text{g m}^{-3}$  of water) in each macrophyte species is reported elsewhere (Wollheim, 1994). Mean biomass was calculated for macroinver-

tebrates in planktonic, benthic (vegetated and unvegetated), and epiphytic habitats in each lake.

To test for effects of salinity category on invertebrates in each habitat, we used nested ANOVA on ranked data with date as a blocking variable and lake nested within salinity category. A significance level of  $\alpha = 0.05$  was used for all tests. In figures, unranked data are presented parametrically for ease of understanding.

Taxa of epiphytic macroinvertebrates were classified as primary and secondary consumers based on the literature (e.g., Merritt & Cummins, 1984). Because we did not identify all organisms to species and did not examine food habits ourselves, we assumed that most members of a given taxa belong in one consumer group and that food habits reported in the literature apply to our study. For example, Chironomidae include herbivores, detritivores, and predators (Merritt & Cummins, 1984), but most are primary consumers (herbivores and detritivores). Two species of *Cenocorixa*, the genus of Corixidae common on the Laramie Plains, were predatory in British Columbia (Reynolds & Scudder, 1987), so we assumed *Cenocorixa* sp. in our study were also predatory. We did not distinguish herbivores from detritivores.

Conductivity was measured with an Orion conductivity meter, and alkalinity and total phosphate in the water column were measured with a Hach test kit (Hach

Table 3. Percentage of total dry mass of epiphytic macroinvertebrates in submerged aquatic vegetation (including benthic mats of filamentous algae) made up of major taxa and consumer levels in oligosaline lakes of the Laramie Plains, Wyoming, 1992.

	Caldwell			George			Nelson		
	June	July	August	June	July	August	June	July	August
<b>2° Consumer</b>									
Mite	1.1	1.0	0.1	0	0	0	3.2	3.5	1.2
Leech	0.8	0.3	0	0	0	0	0	0	0
Hydra	0.5	0.1	0	0	1.0	0.1	0	1.8	0.2
Copepoda (cyclopoid)	0.5	0.9	0.3	1.8	1.2	0	0	0.5	0
Odonata	4.8	2.3	1.1	1.1	2.4	0.3	76.1	30.3	23.6
Corixidae	0.9	1.0	1.6	1.3	11.3	10.1	1.2	3.8	4.4
Coleoptera	1.9	0.4	0.1	11.1	6.1	6.9	0.6	3.1	0
<b>1° Consumer</b>									
Amphipoda	66.8	71.5	60.7	63.2	47.0	38.7	4.7	6.9	24.8
Gastropoda	8.2	13.8	28.4	0	17.4	26.9	2.8	10.3	7.2
Cladocera	1.1	2.8	1.4	7.0	1.4	0	1.3	4.2	0.9
Copepoda (calanoid)	0	0.1	0.2	2.8	0	0	0	0.6	0
Ostracoda	2.7	1.1	0.4	0	0	0	7.3	29.1	18.9
Chironomidae	6.3	4.1	4.3	9.4	11.7	12.7	1.8	4.1	1.8
Diptera pupae	2.6	0.1	0.7	2.0	0.2	0.4	0.1	0.4	0.4
Trichoptera	0.5	0.1	0.2	0.1	0.2	3.8	0.9	1.0	7.5
Ephemeroptera	1.3	0.1	0.2	0	0.3	0	0	0	9.1
<b>Total %</b>									
1° Consumer	89.3	94.2	96.5	84.8	78.3	82.4	18.9	57.1	70.8
2° Consumer	10.7	6.1	3.3	15.2	22.2	17.6	81.1	42.9	29.6
Total mass (g m <sup>-3</sup> )	8.8	10.3	14.1	1.7	2.3	3.5	3.0	1.8	3.2

Co., Loveland, Colorado). The Hach kit could not detect total phosphate concentrations below 67  $\mu\text{g l}^{-1}$  (Table 1).

## Results

### *Epiphytic invertebrates*

Total biomass of epiphytic macroinvertebrates (g m<sup>-3</sup>) did not differ significantly between oligosaline and mesosaline lakes (Fig. 1a). Because of extremely high epiphytic biomass in Caldwell, the mean biomass for the three oligosaline lakes combined was slightly higher than the mean for the mesosaline lakes (Fig. 2a), but biomasses in macrophyte habitats in oligosaline George and Nelson and the three mesosaline lakes were

similar. Vegetation in Caldwell included thick mats of filamentous algae on otherwise unvegetated sediments; these mats were sampled in June and July, but not in August because the algae disappeared. Filamentous algae were absent from oligosaline George and Nelson, and from the mesosaline lakes. Large areas of lake bottom in George and Nelson were covered with *Chara* sp., whereas lake bottom not vegetated by *Ruppia* in mesosaline lakes was bare.

Biomass of grazers and predators did not differ significantly between oligosaline and mesosaline lakes (Fig. 3, Tables 3 and 4). Oligosaline Nelson and the mesosaline lakes had high secondary consumer biomass at least once during the summer (Fig. 3); these four lakes also lacked aquatic vertebrate predators (Table 2).

Table 4. Percentage of total dry mass of epiphytic macroinvertebrates in submerged aquatic vegetation (including benthic mats of filamentous algae) made up of major taxa and consumer levels in mesosaline lakes of the Laramie Plains, Wyoming, 1992.

	Hoge			Creighton			Hutton		
	June	July	August	June	July	August	June	July	August
<b>2° consumer</b>									
Copepod (cyclopoid)	0	0.8	0	1.5	1.2	0	0	0	0
Odonata	2.0	3.2	5.3	28.8	3.3	2.3	69.0	58.2	57.5
Corixidae	5.0	63.7	24.2	2.3	11.0	22.6	1.5	22.1	24.3
Coleoptera	0.1	0	0	1.1	1.7	0	0.3	0.2	0.5
Other <sup>a</sup>	1.6	0	0	0	0	0	0	0	0
<b>1° consumer</b>									
Amphipoda	0	0.6	5.9	0	0.1	0.1	11.3	7.0	1.8
Gastropoda	0	0	0	0	0	0	0	0	0
Cladocera	75.4	5.9	0	1.1	17.2	0	0	0	0
Copepoda (calanoid)	6.6	5.3	0	1.9	18.3	14.9	13.4	9.4	13.1
Ostracoda	0	3.0	23.2	0	0	5.5	0	0	0
Chironomidae	9.4	17.1	38.3	55.7	44.8	54.0	5.1	1.8	2.4
Diptera pupae	0.8	0.2	3.1	7.4	0.8	0.6	0	3.0	0
Other <sup>b</sup>	0	0	0	0	0.2	0	0	0	0
<b>Total %</b>									
1° Consumer	91.4	32.2	70.3	65.9	81.4	75.3	29.6	19.7	17.4
2° Consumer	8.6	67.8	29.5	33.8	18.6	24.7	70.4	80.3	82.6
Total mass (g m <sup>-3</sup> )	6.1	4.4	5.1	3.9	2.9	2.4	1.4	2.1	3.7

<sup>a</sup> Includes mites, leeches, and hydras.

<sup>b</sup> Includes Trichoptera and Ephemeroptera.

For primary consumers in epiphytic habitats, higher salinity corresponded to a shift in dominant taxa (Tables 3 and 4). In oligosaline lakes, primary consumer biomass in George and Caldwell was dominated by amphipods (both *Hyaella azteca* and *Gammarus lacustris*) and gastropods; in Nelson, ostracods were the dominant primary consumers, whereas amphipods (*H. azteca*) and gastropods were common but less important (Table 3). In contrast, in mesosaline lakes gastropods were absent and amphipods rare; primary consumer biomass was dominated by cladocerans and calanoid copepods, as well as chironomids (Table 4). Amphipods (*H. azteca*) were of some significance in mesosaline Lake Hutton only in early summer.

For epiphytic secondary consumers, higher salinity corresponded to greater biomass, especially of corixids (*Cenocorixa* sp.) and odonates (*Enallagma* sp.). However, the importance of secondary consumers to total invertebrate biomass varied with lake and season (Fig. 3, Table 4). Corixids increased in

all lakes as summer progressed; they were the dominant invertebrate predator in Hoge, and were common in Creighton and Hutton. Patterns of odonate biomass varied more by lake; in Nelson and Creighton, odonates declined in July with mass emergence of late instars, but increased steadily in Hutton through the summer. Predator biomass was consistently much higher than primary consumer biomass in mesosaline Hutton (Fig. 3).

Richness of the recognized taxa declined as salinity increased. All taxa were found in oligosaline lakes, but many taxa were not represented in mesosaline lakes, including gastropods, *Gammarus lacustris*, flatworms, *Hydra* sp., and leeches. Some other taxa still occurred in mesosaline lakes but with reduced importance, such as *Hyaella azteca*, cyclopoid copepods, mites, ephemeropterans, and trichopterans (Table 4).

Table 5. Percentage of total dry mass of benthic macroinvertebrates made up of major taxa in oligosaline and mesosaline lakes in the Laramie Plains, Wyoming, 1992. Data for benthos beneath submerged aquatic vegetation (including benthic mats of filamentous algae) and in unvegetated sediments are combined.

Oligosaline									
	Caldwell			George			Nelson		
	June	July	August	June	July	August	June	July	August
Chironomidae	0	47.2	61.1	39.4	41.4	56.6	51.9	40.4	19.1
Diptera pupae	0	0	1.0	4.4	0	0	4.7	4.4	1.1
Ostracoda	0	0	0	34.2	56.7	43.4	29.2	51.8	54.3
Oligochaeta	56.5	13.0	15.1	8.6	0.3	0	0	0	0
Amphipoda	36.9	39.5	22.7	3.2	1.7	0	14.3	3.3	25.7
Total mass (g m <sup>-2</sup> )	0.27	0.75	2.68	1.49	1.14	0.22	2.03	0.51	0.95
Mesosaline									
	Hoge			Creighton			Hutton		
	June	July	August	June	July	August	June	July	August
Chironomidae	68.6	55.8	67.9	87.1	100.0	85.4	89.1	71.7	100.0
Diptera pupae	0.9	2.2	4.6	12.9	0	14.6	0	8.4	0
Ostracoda	28.8	40.5	27.4	0	0	0	10.9	12.0	0
Oligochaeta	0	0	0	0	0	0	0	7.1	0
Amphipoda	0	1.5	0	0	0	0	0	0.8	0
Total mass (g m <sup>-2</sup> )	2.80	4.50	2.55	0.31	0.37	1.26	1.53	1.45	1.61

### Benthic invertebrates

As in epiphytic habitats, total biomass of benthic macroinvertebrates did not differ significantly between mesosaline and oligosaline lakes in either vegetated or unvegetated areas (Fig. 1b, d). Benthic biomass was more variable from month to month in different lakes than was epiphytic biomass (Fig. 2). Biomass of invertebrates was significantly greater in unvegetated than in vegetated sediments in Creighton, but the two habitats did not differ significantly in the remaining lakes (Fig. 1b, d).

Also as in epiphytic habitats, benthic community structure changed as salinity increased (Table 5). Oligochaetes and amphipods had larger relative biomass in oligosaline than mesosaline lakes, but their contribution was variable. Chironomids were more abundant in the mesosaline lakes, and were the only important benthic taxa in Creighton and Hutton (Table 5).

### Zooplankton

For zooplankton (macroinvertebrates in the water column in unvegetated areas), total biomass was significantly greater in mesosaline than oligosaline lakes (Fig. 1c). Zooplankton biomass was highest in Hoge in June, but declined steadily to almost zero in August along with water depth (Fig. 2c). Taxonomic composition of zooplankton biomass responded less strongly to salinity, being dominated by cladocerans or calanoid copepods in all lakes (Table 6). The high biomass of zooplankton in Hoge in June and July was comprised mainly of large cladocerans carrying ephippia. In general, cyclopoid copepods were somewhat common only in oligosaline ponds, and contributed appreciably to biomass only in Lake George in July.

### Salinity effects on invertebrate community structure

Overall, invertebrate community structure differed between salinity categories (Fig. 4). In the epiphytic community, amphipods and gastropods dominat-

Table 6. Percentage of total dry mass of macroinvertebrate zooplankton made up of major taxa in oligosaline and mesosaline lakes in the Laramie Plains, Wyoming, 1992.

Oligosaline									
	Caldwell			George			Nelson		
	June	July	August	June	July	August	June	July	August
Copepoda									
Calanoid	13.0	17.6	15.1	47.9	21.8	0	24.2	71.2	0
Cyclopoid	2.9	3.9	1.5	0.9	54.0	0	0.9	1.0	0
Cladocera	46.4	49.0	63.2	45.3	0	0	69.4	24.9	13.8
Chironomidae	7.2	3.9	0	0.3	24.2	100.0	0.1	2.9	9.7
Amphipoda	13.5	25.3	20.1	5.1	0	0	0	0	10.4
Mite	0	0	0	0	0	0	5.4	0	66.0
Total mass (g m <sup>-3</sup> )	0.069	0.051	0.601	0.267	0.002	0.0003	0.109	0.016	0.022
Mesosaline									
	Hoge			Creighton			Hutton		
	June	July	August	June	July	August	June	July	August
Copepoda									
Calanoid	14.1	43.2	0	87.9	49.4	87.0	100.0	100.0	99.6
Cyclopoid	0	0.5	0	0.6	0.2	0	0	0	0
Cladocera	85.4	54.5	0	6.3	48.3	11.9	0	0	0
Chironomidae	0.6	0.4	100.0	5.1	2.3	1.1	0	0	0.3
Amphipoda	0	1.3	0	0	0	0	0	0	0
Total mass (g m <sup>-3</sup> )	2.3	0.985	0.015	0.371	0.464	0.840	0.424	0.286	0.692

ed in oligosaline lakes, but were rare or absent in mesosaline lakes. In contrast, the epiphytic community of mesosaline lakes was dominated by planktivorous calanoid copepods and cladocerans, as well as predatory odonates and hemipterans. Calanoid copepods and cladocerans also dominated unvegetated open water in mesosaline lakes, but were unimportant in oligosaline lakes. Chironomids and ostracods were abundant in both salinity categories in both benthic and epiphytic communities.

## Discussion

### *Salinity effects on total invertebrate biomass*

We recognized three macroinvertebrate habitats in our study lakes: macrophytes (including *Chara* sp. and benthic mats of filamentous algae), sediments (vegetated and unvegetated), and unvegetated open water. We categorized *Chara* sp. and benthic mats of filamen-

tous algae with macrophytes because they both provide habitat structure in the water column. Macrophytes supported the greatest macroinvertebrate biomass, followed by sediments and then open water. Salinity categories did not differ in total biomass of epiphytic and benthic macroinvertebrates, but did differ in biomass of macrozooplankton. Taxonomic composition generally changed in all habitats as salinity increased, beyond variation within salinity categories.

### *Footnote to Table 7*

1: Afton & Hier, 1991. 2: Afton *et al.*, 1991. 3: Austin *et al.*, 1990. 4: Baldassarre & Fischer, 1984. 5: Bartonek, 1972. 6: Bartonek & Hickey, 1969. 7: Dirschl, 1969. 8: DuBow, 1985. 9: Gammonley & Heitmeyer, 1990. 10: Hughes & Young, 1982. 11: Jarvis & Noyes, 1986. 12: Krapu, 1974a. 13: Krapu, 1974b. 14: Krapu & Swanson, 1977. 15: Serie & Swanson, 1976. 16: Siegfried, 1973. 17: Swanson *et al.*, 1974. 18: Swanson *et al.*, 1979. 19: Swanson *et al.*, 1984. 20: Swanson *et al.*, 1985. 21: Taylor, 1978. 22: Wetmore, 1924. 23: Wetmore, 1925. 24: Woodin & Swanson, 1989.



Table 7. Consumption of invertebrates reported for waterfowl and shorebirds occurring in our High Plains study area. Data include male, female, and juvenile birds during breeding and migration. Consumption (percent mass or volume of total diet) is reported when a given invertebrate taxon makes up  $\geq 10\%$  of a bird's diet.

Prey taxon	Bird species	Range of consumption	Reference
Diptera	Ruddy duck ( <i>Oxyura jamaicensis</i> )	48–85	16, 24
	Wilson's phalarope ( <i>Phalaropus tricolor</i> )	71	4
	American avocet ( <i>Recurvirostra americana</i> )	24–70	4, 23
	Redhead ( <i>Aythya americana</i> )	1–63	6, 11, 24
	Lesser scaup ( <i>Aythya affinis</i> )	0–63	1, 2, 6, 9
	Northern pintail ( <i>Anas acuta</i> )	7–41	12, 13, 14, 18
	Gadwall ( <i>Anas strepera</i> )	6–26	15, 18
	Blue-winged teal ( <i>Anas discors</i> )	0–20	7, 9, 18, 21
	Bufflehead ( <i>Bucephala albeola</i> )	12–18	9
	Mallard ( <i>Anas platyrhynchos</i> )	6–13	20
	Hemiptera	Lesser yellowlegs ( <i>Tringa flavipes</i> )	52
Eared grebe ( <i>Colymbus nigricollis</i> )		40	22
Bufflehead		14–29	9
Wilson's phalarope		24	23
Redhead		1–19	11
Odonata	Mallard	0–20	20
	Canvasback ( <i>Aythya valisineria</i> )	1–20	6, 11
	Lesser scaup	0–24	1
Ephemeroptera	American wigeon ( <i>Anas americana</i> )	24	5
	Canvasback	1–14	6
Trichoptera	Redhead	18–80	6
	Canvasback	0–59	3, 6, 11
	Mallard	9–20	20
	Lesser scaup	2–16	1, 6
	American wigeon	12	5
Coleoptera	Wilson's phalarope	20	23
	Gadwall	4–16	18
	Lesser yellowlegs	14	4
	American avocet	10–11	4, 23
Amphipoda	Lesser scaup	8–85	1, 2, 6, 7
	Ruddy duck	1–12	24
Cladocera	Northern shoveler ( <i>Anas clypeata</i> )	33–69	8, 18
	Mallard	0–11	20
	Gadwall	4–11	15, 18
Copepoda	No reports found		
Ostracoda	Lesser scaup	1–20	9
	Green-winged teal ( <i>Anas crecca</i> )	11	10
Gastropoda	Canvasback	18–66	6, 11
	Northern pintail	0–49	12, 13, 14, 18
	Blue-winged teal	20–48	7, 8, 17, 18, 21
	Northern shoveler	40	18
	Lesser scaup	0–39	2, 6, 7, 9
	Bufflehead	15–26	9
	Mallard	5–25	18

Footnote: see p. 214.

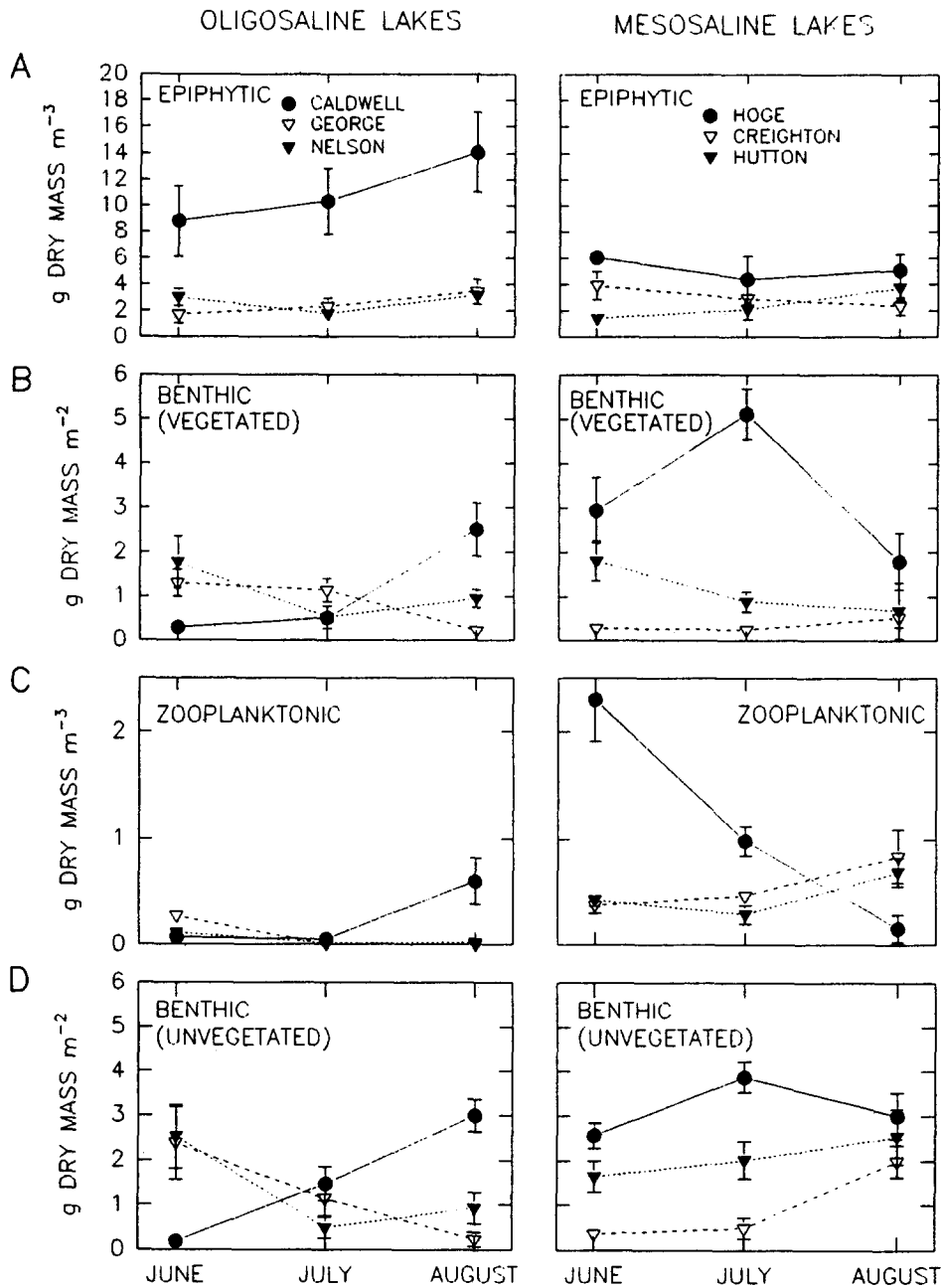


Fig. 2. Mean dry mass ( $\pm 1$  S.E.) of macroinvertebrates ( $>500 \mu\text{m}$ ) in a) macrophytes (including benthic mats of filamentous algae), b) vegetated sediments, c) open water without vegetation, and d) unvegetated sediments in individual oligosaline and mesosaline lakes of the Laramie Plains, Wyoming, 1992.

#### Benthic invertebrates

Benthic biomass in both vegetated and unvegetated sediments showed no obvious trends as salinity increased from oligosaline to mesosaline (Figs 1 and 2). In other studies, biomass of both littoral and profundal benthos declined as salinity increased over broader

ranges than we investigated (Timms, 1981b, 1983; Timms *et al.*, 1986; Hammer *et al.*, 1990). Peaks in benthic biomass occurred when Total Dissolved Solids (TDS) were between 10 and 20 g l<sup>-1</sup> in the littoral zone of Saskatchewan Lakes (Hammer *et al.*, 1990), and between 5 and 15 g l<sup>-1</sup> in shallow Australian

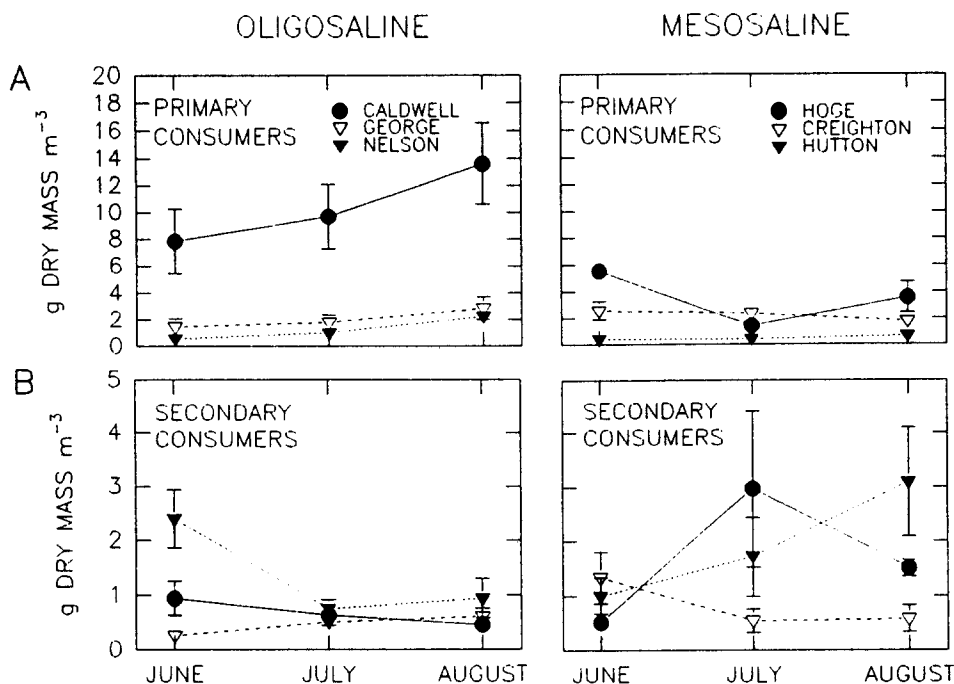


Fig. 3. Mean dry mass ( $\pm 1$  S.E.) of epiphytic macroinvertebrates ( $>500 \mu\text{m}$ ) classified as a) primary consumers and b) secondary consumers in individual oligosaline and mesosaline lakes of the Laramie Plains, Wyoming, 1992.

lakes (Timms, 1983). Although mesosaline lakes in our study were in the range of 10 to 25  $\text{mS cm}^{-1}$ , biomass of benthos was not consistently higher than in oligosaline lakes of  $<5 \text{mS cm}^{-1}$ . Benthic biomass in mesosaline lakes was highest in Hoge (conductivity range of 9.3 to 19  $\text{mS cm}^{-1}$ ), lowest in Creighton (12.9 to 16.3  $\text{mS cm}^{-1}$ ), and intermediate in Hutton, the most saline lake studied (18.6 to 23.5  $\text{mS cm}^{-1}$ ). Benthic biomass in oligosaline lakes was similar to that of mesosaline Hutton and Creighton, especially when seasonal variation is considered (Fig. 2). Salinity alone cannot explain these patterns.

#### Zooplankton

Mean biomass of zooplankton (macroinvertebrates in the water column in unvegetated areas) was considerably higher in mesosaline lakes (Fig. 1). Open-water zooplankton populations are often higher in lakes of greater salinity (Timms, 1981b; Galat & Robinson, 1983). One explanation is that saline lakes often lack planktivorous aquatic vertebrates (Hammer, 1986; Swanson *et al.*, 1988; Peterka, 1989), as is true of mesosaline lakes on the Laramie Plains (Table 2). Peruvian lakes without fish (salinity range 0.1 to 251  $\text{g l}^{-1}$ ) had higher zooplankton biomass than lakes with fish (salinity range 0.2 to 16  $\text{g l}^{-1}$ ) (Hurlbert *et al.*, 1986). In

a series of three Australian lakes of increasing salinity, Timms (1981b) found the highest zooplankton abundance in the most saline lake (58  $\text{g l}^{-1}$  TDS) which was devoid of fish; zooplankton abundance was the same in fresh (0.4  $\text{g l}^{-1}$ ) and mesosaline (8  $\text{g l}^{-1}$ ) lakes containing fish, despite elevated phytoplankton production in the mesosaline lake that might otherwise result in increased zooplankton (Timms, 1981a). However, in our study, oligosaline Nelson had extremely low zooplankton populations despite lack of fish (Nelson also had low total phosphate, Table 1) (Fig. 2c).

A second possible cause of higher zooplankton abundance in saline lakes is increased food resources. Phytoplankton production can be high in saline lakes (Wetzel, 1964; Vareschi, 1987), with greatest production occurring in lakes with high phosphorus levels and salinity from 3 to 50  $\text{g l}^{-1}$  TDS (Hammer, 1981; Timms, 1981a). These conditions occurred in our mesosaline lakes (Table 1), so phytoplankton and thus food for zooplankton was probably high.

Of interest was the lack of Anostracans (fairy shrimp) in our samples. Pennak (1989: 354) noted that phyllopods are almost defenseless, and are not often abundant in ponds containing carnivorous insects and are rarely present along with carnivorous fishes. Our study ponds all had insect predators and some had

## RELATIVE BIOMASS

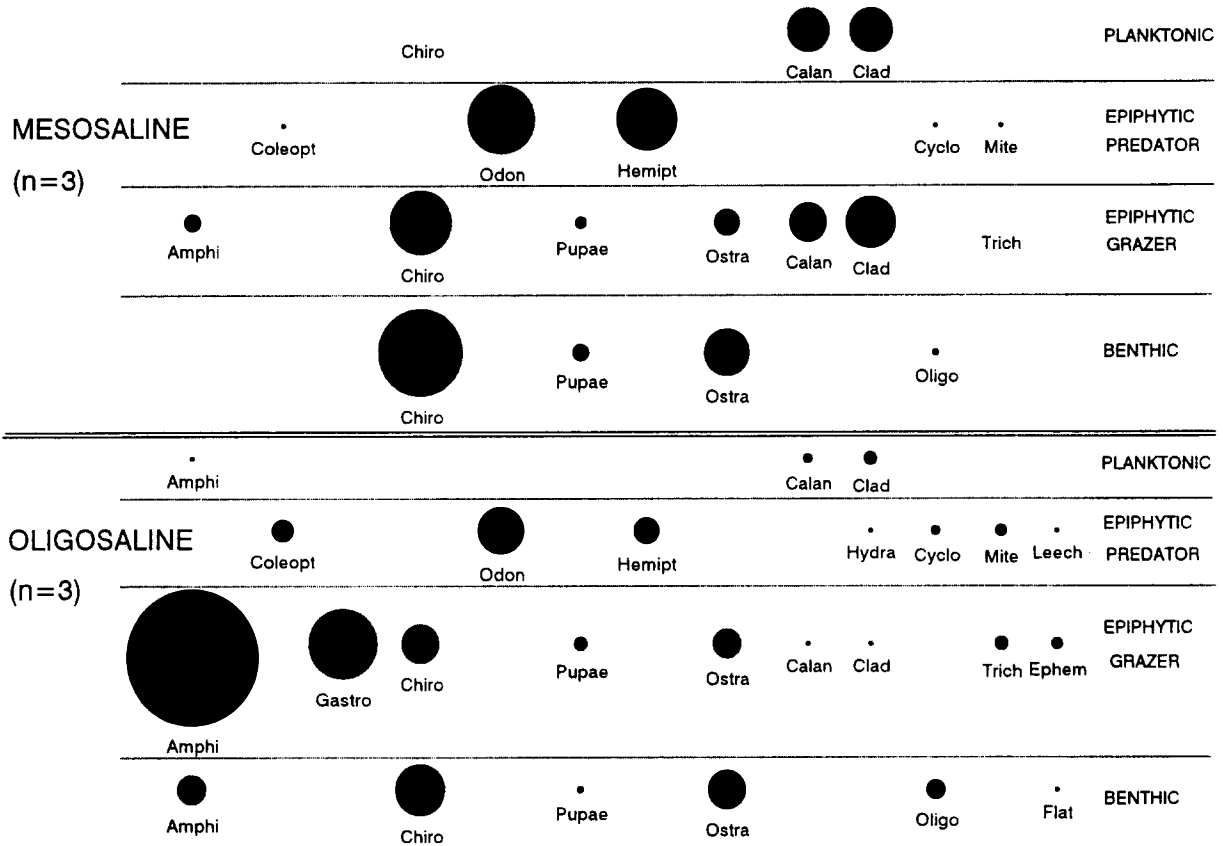


Fig. 4. Relative dry mass of major macroinvertebrate taxa ( $>500 \mu\text{m}$ ) in oligosaline and mesosaline lakes of the Laramie Plains, Wyoming, June–August 1992. Planktonic, epiphytic predator, epiphytic grazer (all  $\text{g m}^{-3}$ ), and benthic ( $\text{g m}^{-2}$  for vegetated and unvegetated sediments combined) communities are shown. Relative biomass within each salinity category is combined over lake and month. Amphi = Amphipoda, Coleopt = Coleoptera, Gastro = Gastropoda, Chiro = Chironomidae, Odon = Odonata, Pupae = insect pupae (mainly Chironomidae), Hemipt = Hemiptera, Ostra = Ostracoda, Calan = Calanoid Copepoda, Clad = Cladocera, Cyclo = Cyclopoid Copepoda, Oligo = Oligochaeta, Trich = Trichoptera, Ephem = Ephemeroptera, Flat = flatworms (see Tables 3–6).

carnivorous fish or salamanders (Table 2), but other factors might be involved.

#### Epiphytic invertebrates

As for benthic invertebrates but not zooplankton, the total biomass of epiphytic invertebrates showed no obvious relationship with salinity. Highest biomass occurred in Caldwell, the freshest lake studied, probably because of superabundant filamentous algae which were likely used as food by invertebrates (Kornijow *et al.*, 1990). In our study, biomass of epiphytic invertebrates appeared to be affected less by salinity than by habitat structure and other lake characteristics (Wollheim, 1994).

Unlike for zooplankton, biomass of epiphytic invertebrates did not correspond with the higher phos-

phate levels (see Table 1) in mesosaline than in oligosaline lakes. This pattern differed from that in fresh water, where epiphytic algal production usually increases with higher nutrient levels (Cattaneo & Kalff, 1980) resulting in more epiphytic invertebrates (Mason & Bryant, 1975; Cattaneo, 1983). In our study, lack of difference in epiphytic biomass resulted from variation among macrophyte growth forms within lakes. Our calculations of epiphytic biomass for oligosaline George and Nelson include *Chara* habitat, which supported significantly greater biomass of invertebrates than other habitats (Wollheim, 1994). When only similar growth forms of vegetation (erect angiosperms) were compared, these low-phosphate oligosaline lakes supported less biomass of epiphytic invertebrates than mesosaline lakes (Wollheim, 1994). Thus, changes in

nutrient levels combined with loss of certain growth forms (e.g., *Chara*) as salinity increases might impact biomass of invertebrates. Epiphytic invertebrates as a unique community in saline lakes are relatively unstudied, so there are insufficient comparative data for evaluating salinity effects. Timms (1981b) recorded species but not numbers or biomass of epiphytic invertebrates in a series of three saline lakes, and sampling by Hammer *et al.* (1990) did not distinguish epiphytic from benthic invertebrates.

Macrophyte habitats (especially benthic mats of filamentous algae) supported the greatest invertebrate biomass regardless of salinity (Figs 1 and 2). In fresh water, epiphytic invertebrates are usually much more abundant than littoral macrobenthos (Cyr & Downing, 1988b). Greater abundance of epiphytic invertebrates occurs because macrophytes provide support structures (Rosine, 1955; Rooke, 1984), high quality foods such as epiphytic algae (Carpenter & Lodge, 1986; Cattaneo, 1983), and cover from vertebrate predators (Crowder & Cooper, 1982).

Thus, in shallow lakes, reduced area of macrophyte habitat with increased salinity corresponds to a major reduction of invertebrate biomass. However, loss of epiphytic invertebrate biomass is somewhat offset in saline lakes by increased biomass of open-water zooplankton, and possibly increased biomass of benthic invertebrates in unvegetated sediments (Figs 1 and 2). The impact of salinity on lake-wide secondary production must consider total volume or area occupied by each habitat type, as well as the concentration of invertebrates in those habitats.

#### *Potential shifts in stable state with elevated salinity*

Scheffer (1990) proposed that two stable equilibria occur in shallow lakes: a state with clear water dominated by macrophytes, and a state with turbid water dominated by phytoplankton [see Hanson & Butler (1994) and references therein for empirical evidence of these equilibria]. Shifts in stable state will affect relative habitat availability for benthic, epiphytic, and zooplanktonic invertebrates. Either stable state may occur in saline lakes. Macrophytes are rare or of little importance in some saline lakes (Wetzel, 1964; Tones, 1976; Hammer, 1981; Vareschi, 1987; Hammer & Heseltine, 1988), but remain abundant in others of comparable salinities (Tones, 1976; Hammer & Heseltine, 1988). Alternative stable states may explain this contradictory evidence.

Equilibria dominated by phytoplankton may be more frequent at higher salinities because nutrient levels, especially phosphorus, tend to be higher in saline lakes (Hammer, 1986; Bierhuizen & Prepas, 1985; Wood & Talling, 1988; Table 1). Higher total phosphorus levels enhanced phytoplankton biomass in saline lakes with comparable ionic composition and high total nitrogen (Bierhuizen & Prepas, 1985); but these conditions occurred only in lakes up to  $6.5 \text{ mS cm}^{-1}$ , so the relationship may not hold at higher salinities. Wood & Talling (1988) also found that higher soluble phosphorus levels in saline lakes corresponded with increased chlorophyll *a*. Phosphorus may be high in saline lakes because the lack of water outflow and high evapotranspiration which concentrate salts in terminal basins may also concentrate phosphorus. Also, phosphate release from sediments to the water column might increase with higher salinity (Clavero *et al.*, 1990), thereby increasing turbidity of biotic origin.

A second reason that phytoplankton-dominated systems are favored at higher salinities is the loss of salt-intolerant macrophytes (Stewart & Kantrud, 1972; Hammer & Heseltine, 1988), with resulting positive feedback from vegetation loss. Macrophytes reduce turbidity by damping water movements and sediment resuspension (Scheffer, 1990; Hanson & Butler, 1994) and, along with attached epiphytic algae, by removing nutrients from the water column during the growing season (Carpenter & Lodge, 1986; Hammer, 1986; Scheffer, 1990). Loss of salt-intolerant macrophytes, combined with shallow water depths, high winds, and unconsolidated sediments (conditions found on the Laramie Plains), will add considerably to abiotic turbidity (Wetzel, 1964; Hanson & Butler, 1994). Because salinity often increases as water depth declines through evaporation, higher salinity is often correlated with shallower depths, which favor mixing of sediments and associated nutrients into the water column. Therefore, declines of salt-intolerant macrophytes could contribute to declines of salt-tolerant macrophytes because of enhanced turbidity. In our study, increased salinity resulted not only in decreased abundance and diversity of submerged vegetation, but also in loss of emergent plants which supported additional invertebrate community components (Wollheim, 1994).

Unlike in mesosaline lakes, elevated nutrients in shallow oligosaline lakes do not necessarily result in phytoplankton stable states. Instead, metaphytic algae can maintain habitat characteristics of macrophyte stable states, while enhancing invertebrate production (e.g., in Caldwell). Although water-column phosphate

levels were lower in oligosaline Caldwell than in the mesosaline lakes (Table 1), abundant metaphyton indicated eutrophic conditions (Crumpton, 1989). Phosphorus stored in metaphytic algae was probably substantial, possibly explaining the lower water-column phosphate measurements. Thus, elevated nutrient levels in oligosaline lakes resulted in a very different form of primary production (metaphyton) than in mesosaline lakes (phytoplankton). This metaphyton, because it may be a good food source (Kornijow *et al.*, 1990), was probably responsible for the high epiphytic invertebrate biomass in Caldwell.

#### *Salinity effects on invertebrate community structure*

In our study, richness of the recognized taxa declined as salinity increased from oligosaline to mesosaline (Tables 3–6). Amphipods and gastropods were dominant components of oligosaline communities, but were rare or disappeared entirely in mesosaline lakes (Fig. 4). At higher salinities, chironomids became more prevalent in benthic and epiphytic habitats, cladocerans and copepods more prevalent in macrophytes and open water, and predators (odonates and hemipterans) on cladocerans, copepods, and chironomids more prevalent in macrophytes. These changes in trophic structure probably resulted from both direct effects of salinity and indirect effects through changes in stable state (*sensu* Scheffer, 1990).

Direct effects of salinity were probably important for gastropods and amphipods. No gastropods were found in any of our mesosaline lakes, despite the presence of macrophyte habitat (*cf.*, Tables 1 and 2; Fig. 4). In Saskatchewan, gastropods were rare in lakes with over  $3 \text{ g l}^{-1}$  TDS (Rawson & Moore, 1944). In North Dakota, the gastropod *Lymnaea stagnalis* was restricted to lakes of  $<5 \text{ mS cm}^{-1}$ , and *Stagnicola* spp. to  $<10 \text{ mS cm}^{-1}$ ; the amphipod *Gammarus lacustris* lost dominance to fairy shrimp (Anostraca) at 3 to  $8 \text{ mS cm}^{-1}$  (Swanson *et al.*, 1988). In our study, *Gammarus lacustris* was abundant in George and common in Caldwell (both oligosaline), but was absent from all other lakes; *Hyaella azteca* was abundant in all oligosaline lakes, but rare in mesosaline lakes. In mesocosms, *H. azteca* densities were lower in water with 8 and  $11 \text{ g l}^{-1}$  TDS than in water with  $5.6 \text{ g l}^{-1}$  (Galat *et al.*, 1988). In our study, direct effects of salinity on other taxa could not be adequately evaluated because we did not identify most taxa to species. For example, chironomids were abundant in all lakes (Tables 3–6,

Fig. 4), but the species composition probably changed with salinity (Cannings & Scudder, 1978). Nevertheless, decline of gastropods and amphipods indicates that important shifts in community structure occurred at the low end of the salinity range (*cf.*, Williams *et al.*, 1990).

Indirect effects of salinity through shifting stable states could explain certain trends in invertebrate communities (Tables 3–6, Fig. 4). Stable states affect both the form of primary production as food and the availability of macrophyte habitat (including mats of filamentous algae). Oligosaline lakes with more diverse and abundant macrophytes (Table 2) have greater and more varied inputs of litter and coarse detritus, and more plant surface area for epiphytic algae. Thus, invertebrate communities in oligosaline lakes are expected to be dominated by scrapers, shredders, and coarse detritivores such as gastropods and amphipods. In a Minnesota lake undergoing biomanipulation, *Hyaella azteca* increased dramatically as macrophytes returned (Hanson & Butler, 1994). In contrast, mesosaline lakes tend to have higher phytoplankton production and often reduced macrophyte production. Invertebrate communities in such systems are generally dominated by planktivores such as calanoid copepods and other crustacean zooplankton (Vareschi, 1987; Hanson & Butler, 1994; Fig. 4). As the invertebrate grazer community shifts to smaller planktivores, invertebrate predators might also increase because smaller prey are more available (de Bernardi *et al.*, 1987). In British Columbia, predatory hemipterans increased, and herbivorous coleopterans were replaced by predatory coleopterans, as salinity increased and macrophytes declined (Lancaster & Scudder, 1987).

#### *Salinity and food-web effects on higher trophic levels*

As guild structure of primary consumers changes, one might also expect changes in guilds of their avian predators. Based on literature for birds that commonly occurred in our study area (Table 7), only two species, both diving ducks, include amphipods as over 10% of their diet. Despite high digestibility (Swanson & Bartonek, 1970) and high abundance in oligosaline lakes (Fig. 4), epiphytic and epibenthic amphipods may be less available to most avian predators than other taxa. Gastropods are eaten by a wide variety of dabbling (Anatini) and diving (Aythyini) ducks, but these birds also exploit other foods such as chironomids

that are abundant at higher salinities. Phalaropes, avocets, and yellowlegs generally do not take gastropods or amphipods found at lower salinities, and consume many predatory invertebrates more common at higher salinities (diving beetles, corixids). However, these shorebirds can exploit other prey such as chironomids which are abundant in oligosaline lakes (Table 7).

Thus, although avian predators in shallow lakes may be roughly classified into foraging guilds such as pelagic surface siezers (phalaropes), littoral siezers (avocet, yellowlegs), filter-feeding zooplanktivores (shoveler), benthivores (canvasback, ruddy duck), or divers that feed epibenthically or in the water column (lesser scaup, eared grebes), these species can potentially exploit different guilds of primary consumers in either oligosaline or mesosaline lakes (Fig. 4). Given that total invertebrate biomass did not change between these salinity classes, any trends in bird species composition or food intake at upper mesosaline conductivities (Swanson, 1986) might reflect avian limits to avoiding salt toxicity rather than changes in prey community structure.

American avocets, Wilson's phalaropes, eared grebes, and California gulls (*Larus californicus*) limit salt loading by eating hypoosmotic prey and avoiding intake of salt water, and can forage in hypersaline environments unavailable to other species (Mahoney & Jehl, 1985a, b, c). In contrast, depending on ion ratios, ducklings experience sublethal toxicity and retarded growth at salinities of only 3–9 g l<sup>-1</sup> TDS, and mortality at >12 g l<sup>-1</sup> (Mitcham & Wobeser, 1988a, b; Barnes & Nudds, 1991; Moorman *et al.*, 1991). Nestling white ibises (*Eudocimus albus*) lost weight when fed brackish-water crabs containing 1.08 osm kg<sup>-1</sup> (≈ 31.6 g kg<sup>-1</sup>) salt instead of freshwater crayfish containing 5.35 osm kg<sup>-1</sup> (≈ 15.6 g kg<sup>-1</sup>), explaining why adults flew up to 25 km away to obtain freshwater prey for nestlings despite local abundance of crabs eaten by adults and recently fledged ibises (Johnston & Bildstein, 1990). Food consumption by captive adult sanderlings (*Calidris alba*) and knots (*C. canutus*) declined substantially at salinities above 20 g l<sup>-1</sup> (Klaassen & Ens, 1990). Adult ducks feeding in water with salinities of upper mesosaline and higher may require fresh water for drinking to avoid high energy costs of osmoregulation (Nystrom & Pehrsson, 1988; Mitchell *et al.*, 1992) or even mortality (Windingstad *et al.*, 1987). Because waterbirds in our area appear capable of exploiting prey in both oligosaline and mesosaline lakes (Table 7), but can experience salt toxicity in mesosaline waters, it is likely that salinity

effects on prey communities are less important to them than costs of osmoregulation. It should be noted, however, that surface or ground water inflow can cause spatial variations in salinity within the same lake. Access to fresher water in such localized flows or in nearby fresher ponds can in some cases allow birds to tolerate water or foods with salt content higher than would otherwise be acceptable (Swanson, 1986; Swanson *et al.*, 1988).

As salinity is often a critical issue in creating and managing wetlands and lakes in arid regions, mechanisms by which salinity affects diversity of both prey and predator populations need to be investigated. Adequate understanding and predictive capabilities will require laboratory tests of tolerance to salt in both water and food, together with field data and modeling of indirect salinity effects on food web structure (Galat & Robinson, 1983; Vareschi, 1987; Galat *et al.*, 1988; Gulley *et al.*, 1992).

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