

SALINITY CONTROLS ON TROPHIC INTERACTIONS AMONG INVERTEBRATES AND ALGAE OF SOLAR EVAPORATION PONDS IN THE MOJAVE DESERT AND RELATION TO SHOREBIRD FORAGING AND SELENIUM RISK

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Abstract: Three saline evaporation ponds formed by wastewater from a solar energy-generating facility near Harper Dry Lake in the Mojave Desert of California, USA were compared for differences in the communities of benthic and planktonic invertebrates and algae present along with avian visitation and foraging activity. Salinity of the ponds ranged from near 90 to over 200 g L⁻¹ total dissolved solids. During the period of study (1997–1999), the lowest salinity pond averaged 98 g L⁻¹, the intermediate salinity pond 112 g L⁻¹, and the high salinity pond 173 g L⁻¹. Differences in the biological communities, abundance of invertebrates and algae, and avian foraging were examined in relation to these differences in salinity. Only three aquatic invertebrate species were present in substantial numbers, a water boatman (*Trichocorixa reticulata*), a brine shrimp (*Artemia franciscana*), and a brine fly (*Ephydra gracilis*). An abundance of the predator *Trichocorixa* under low salinity conditions appeared to reduce algae-grazing *Artemia*, and so released phytoplankton growth, but this was observed only in surveys later in the growth season when populations were mature and had greatest potential for efficient consumption of resources. Brine fly larvae were also fed upon by *Trichocorixa* and were least abundant in the low salinity pond. At highest salinities where *Trichocorixa* could not survive, *Artemia* were abundant and waters were usually clear, becoming dense with phytoplankton only during the winter dormancy of brine shrimp. Intermediate salinity levels supported some water boatmen, often coexisting with dense brine shrimp and phytoplankton populations, and the greatest dry mass of benthic brine fly larvae and pupae. The high salinity pond produced abundant but small *Ephydra* larvae and pupae, accompanied by reduced emergence success of adult flies. Birds appeared to forage primarily on benthic brine fly larvae and were most successful in the intermediate salinity pond, possibly because lower salinity resulted in loss of this preferred prey to water boatman predation, and high salinity produced prey of poor quality. These observations suggest that reduced salinity may at times mediate a trophic cascade within a simple food chain, where an invertebrate predator may reduce primary consumers and permit enhanced algal density, but the predation control becomes uncoupled as salinity increases. In the case of the ponds studied here, there appeared to be minimal risk associated with selenium poisoning of water birds because Se was not detected in brine fly larvae or pupae and was found only occasionally in low content in the brine shrimp and corixids and mostly in locales where few birds were found feeding.

Key Words: *Artemia*, *Ephydra*, evaporation ponds, predation, risk assessment, saline wetlands, salinity, selenium, shorebird foraging, *Trichocorixa*, trophic cascade, wastewater

INTRODUCTION

Harsh environments exert a controlling influence on the composition and interactions in biological communities—often evident in the simple and productive ecosystems of saline lakes (Hammer 1986). The low species richness of many salt lakes may be due both to severe chemical stress and to high population growth rates of specialist species such as brine shrimp and brine flies, exploiting productive algae to the exclusion of other grazers. Simple and productive aquatic

ecosystems have also been thought to foster trophic cascades, where predators enhance plant biomass through control of herbivore grazing (Power 1992, Strong 1992). While trophic cascades and the conditions that produce this effect have been of considerable interest to ecologists, the extent to which stress gradients may modulate cascade strength has received less attention than other explanations (Borer et al. 2005) but might profitably be investigated in ecosystems such as salt lakes. Indeed, observations made over a period of years at Great Salt Lake, Utah, USA provide

circumstantial evidence that when salinities were high, densities of brine shrimp were high and grazed phytoplankton chlorophyll to low levels, but when salinity was reduced, a less salt-tolerant corixid predator on brine shrimp appeared, and brine shrimp became scarce while chlorophyll increased (Wurtsbaugh 1992).

Saline managed wetlands and evaporation ponds are biologically productive aquatic habitats, attracting large numbers of migrating and breeding waterfowl and shorebird populations throughout the interior west of North America (Euliss et al. 1991a, 1991b, Jehl 1994, Cox and Kadlec 1995, Wollheim and Lovvorn 1995). While invertebrate food sources for birds are often dense in salt ponds, it is not clear what salinity conditions make these habitats most favorable for feeding (Anderson 1970, Lonzarich and Smith 1997, Takekawa et al. 2001, Warnock et al. 2002) or create the risk for consumption of toxic trace elements such as selenium that may disrupt avian development and increase mortality (Ohlendorf et al. 1986, Saiki and Lowe 1987, Besser et al. 1989). Gathering examples from different settings can help inform these questions, and an opportunity to collect such information was afforded through studies of constructed saline evaporation ponds in the Mojave Desert near Harper Dry Lake, California, USA. These ponds contained dissolved salts in varied levels of concentration, formed by wastewater received from solar energy generating facilities. Sampling surveys of aquatic invertebrates and algae were conducted in these ponds at seasonal intervals between September 1997 and March 1999. The purpose of these studies was to determine the composition and changes in the biological communities established in these differing saline water impoundments. The type, density, size, and Se content of invertebrates in the ponds were examined to evaluate food availability to birds feeding at these ponds and potential selenium contamination. This study took advantage of a group of three adjacent ponds that encompassed a wide range of salinity conditions, were comprised of simple communities, and involved interactions of multiple trophic levels. The main goal of these studies was to determine under what conditions there was evidence for an aquatic trophic cascade and how bird foraging responded to differences in invertebrate communities between ponds.

Evaporation ponds in agricultural areas containing selenium-rich soils may concentrate this potentially toxic trace element. Ground water and industrial wastewaters may also contain selenium. This element may move through aquatic food webs through a bioaccumulation process from initial incorporation into phytoplankton and algal-microbial mats in contact with sediments, which are fed upon by invertebrates

(especially salt-tolerant forms). Birds then feed upon these often abundant invertebrates, and accumulated selenium may then produce physiological disruption of growth and reproduction of birds (Skorupa and Ohlendorf 1991). Dissolved sources of selenium may also become incorporated into the tissues of aquatic organisms (Luoma et al. 1992). A further objective of this study was to evaluate the potential sources of selenium in bird diets, and so provide risk assessment for wastewater management at the solar energy generating facilities.

ENVIRONMENTAL SETTING

The solar evaporation ponds were located near Harper Dry Lake, about 25 miles west of Barstow, California. The climate is often hot and arid, resulting in rapid evaporation of surface water and few natural perennial aquatic habitats (June to September monthly maximum temperature = 36.4 °C, annual monthly precipitation = 11.8 cm; Western Regional Climate Center). This region is within the Mojave Desert and is part of the hydrological Great Basin (Grayson 1993). At the Harper Dry Lake facilities, ground water containing selenium is pumped from wells that supply water to solar energy steam turbines. When conductivity becomes too high for the water to be recycled within the power plant, it is delivered as wastewater to the evaporation ponds. Water at the times of collection was in the range of 2–6 times the salinity of seawater and formed lower, moderate, and high salinity ponds (Figure 1). Chemistry was dominated by sodium (35% by weight), chloride (45–50% by weight), and sulfate (15–20% by weight), with calcium and magnesium also present (0.5–1.0 g L⁻¹ range each). The type of water chemistry (solutes and salinities) and geographic location may be prime determinants of what species will be successful in colonizing these ponds (Herbst 2001). The chemistry of the ponds also appears to favor the formation of tufa deposits on the bottoms of some of the ponds (the middle salinity pond had well-developed formations). These formations serve as an important habitat feature for the attachment of benthic organisms such as brine fly larvae and pupae. Pond bottoms otherwise had sand deposits over plastic liners. Although the average depths of the ponds were similar, the middle and high salinity ponds often were shallow near the margins, while the low salinity pond was usually deeper along most edges (except at one corner where most bird feeding was observed) but had a smaller surface area (Table 1). Ponds were first constructed and filled in 1989–90, built within concrete basins separated from one another by no more than 25 meters horizontal distance. Ponds are not interconnected and have undergone irregular variations in level

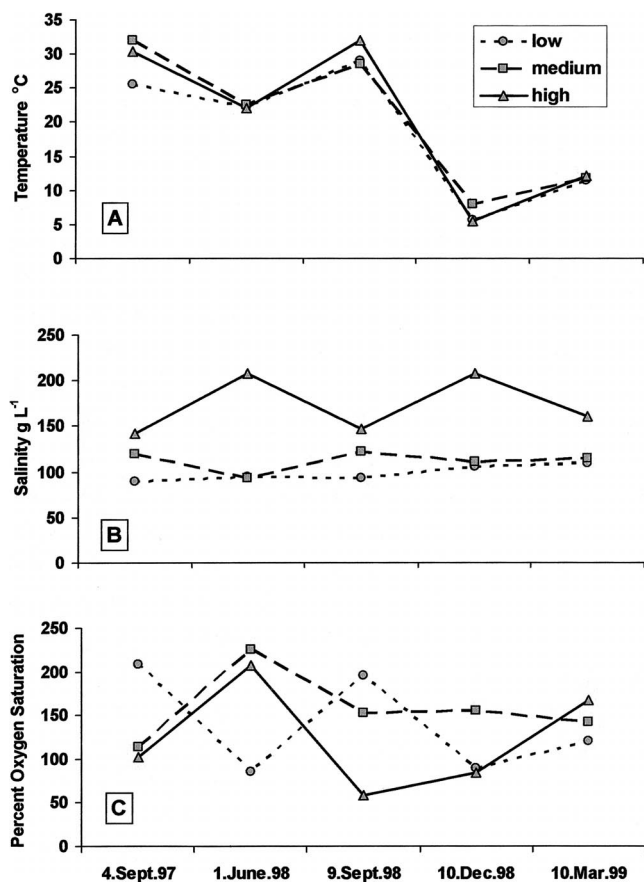


Figure 1. Temperature (A), salinity (B), and percent oxygen saturation (C) in salt ponds from September 1997 to March 1999. Percent saturation was calculated from the ratio of measured to predicted dissolved oxygen corrected for salinity and temperature using a nomogram for sodium chloride dominated water chemistry (Sherwood et al. 1992).

and volume, as wastewater “blow-down” is not equally distributed, and as they have sometimes been drained for repairs. The middle and high salinity ponds were constructed earlier and typically contained more dissolved salts than the low salinity pond.

There were three primary invertebrate species present in the ponds. Brine shrimp are (Artemiidae: *Artemia franciscana* Kellogg) filter-feeders of suspended algae (phytoplankton), water boatman (Corixidae: *Trichocorixa reticulata*) (Guerin-Meneville) are predators

feeding in open water and benthic habitats, and brine flies (Ephydriidae: *Ephydra gracilis* Packard and *E. hians* Say) feed in their aquatic larval stage on algae that grow attached to the pond bottom (benthic algae). Phytoplankton consisted primarily of the salt-tolerant flagellated green alga *Dunaliella* sp. (present in all ponds but dominant in the high salinity pond), along with some diatoms in the low and middle salinity ponds. Benthic algal mats formed during parts of the year (in low and middle salinity ponds) and were composed of diatoms and filamentous cyanobacteria.

METHODS

Five seasonal surveys of invertebrate fauna were conducted, on 3 September 1997, 1 June, 9 September, 10 December 1998, and 10 March 1999, and included benthic or bottom-dwelling organisms, planktonic or free-swimming organisms, and adult insects around the margins of the ponds. Collections of benthic insects were made using a D-frame aquatic net (30 cm wide, 250-micron mesh) as triplicate standing kick samples over approximately 500 cm² areas of pond bottom that represented a mix of near-margin substrate variety. The standard benthic samples were taken in 25–50 cm water depth, each consisting of two net sweeps, back and forth above an approximately 25 cm × 20 cm area of substrates stirred into the water column by the action of foot-shuffling over the sample area. Duplicate plankton samples were collected using a 20-cm-diameter plankton net of 150-micron mesh towed horizontally over a 5-m distance at a depth of 10–25 cm below the surface. Qualitative collections of adult shore insects were also made during several surveys to determine species and food value by dry mass. Preserved invertebrate samples were returned to the laboratory for sorting, identifications, counts, and measures of body size and dry mass. Dry mass conversions from organism densities were based on weighing of counted groups of each invertebrate species and life stage from each pond, dried at 60 °C to constant mass. Separate collections of the dominant organisms were made for analysis of tissue selenium content (after rinsing with distilled water). Dissolved total selenium

Table 1. Solar salt pond habitat characteristics at Harper Dry Lake, California, USA.

Pond Salinity	Salinity Range g L ⁻¹	Mean Depth Range (m)	Substrate	Area (hectares)
Low	89–110	2.26–3.15 deeper margins	Mud sediments, some gravel/tufa	3.0
Medium	94–122	2.03–3.30 shallow margins	Sand/mud and tufa fragments	4.8
High	142–208	1.65–2.79 shallow margins	Sand and tufa fragments	4.8

was also periodically determined in unfiltered water column samples from the ponds. Selenium content of frozen samples of pooled organisms and pond water was determined at an analytical laboratory (Del Mar Analytical; Colton, California) using the inductively coupled plasma method (reported detection limit 0.5 mg kg⁻¹).

The density of benthic and planktonic algae were characterized by measuring the chlorophyll content of benthic algae in cores taken with a 10 cm² coring tube (2 cm deep), and in 50 ml of pond water filtered to remove phytoplankton (using A/E glass fiber filters, 1.0-micron pore size). Benthic cores and plankton filters were stored on ice, ground and extracted in 90% acetone, and chlorophyll determined using a fluorometer standardized with a known chlorophyll dilution curve (Wetzel and Likens 1991). Conductivity, temperature, and dissolved oxygen were also measured in each pond at mid-day using calibrated electronic meters (Oakton and YSI). Percent saturation was calculated from the ratio of measured to predicted dissolved oxygen corrected for salinity and temperature using a nomogram for sodium chloride dominated water chemistry (Sherwood et al. 1992).

Differences in foraging rates and diets between ponds were based on spotting scope observations of individual birds over 5-minute time trials, taken either in the early morning or late afternoon, and attempting to balance observations across those species present and active. Since only three prey species were present, each mainly occupying benthic shallows, margins, or open water locations, and bird feeding behavior and location could be coded, a contingency table of behavior, foraging habitat, and known prey availability in a pond was used to assign the most likely prey items taken during a particular time trial (capture success inferred from head-jerk movements). The inferred probable food consumption by each bird species observed was then calculated as the product of average capture rates (assuming one prey item captured per successful attempt) and the measured dry mass of the prey type consumed (determined for each prey type from each pond, using an average where prey had equal probability of being taken, and assuming adult mass for *Artemia* and *Trichocorixa*). Over 70% of all feeding observations made (75 of 105) were for only five common birds species at the ponds—Least Sandpiper (*Calidris minutilla*) (Vieillot), Western Sandpiper (*Calidris mauri*) (Cabanis), American Avocet (*Recurvirostra americana* J.F. Gmelin), Black-necked Stilt (*Himantopus mexicanus*) (Muller), and Red-necked Phalarope (*Phalaropus lobatus*) (Linnaeus). These species form the basis of the foraging analysis presented here. Although observations were attempted in all seasons during 1998, feeding occurred almost

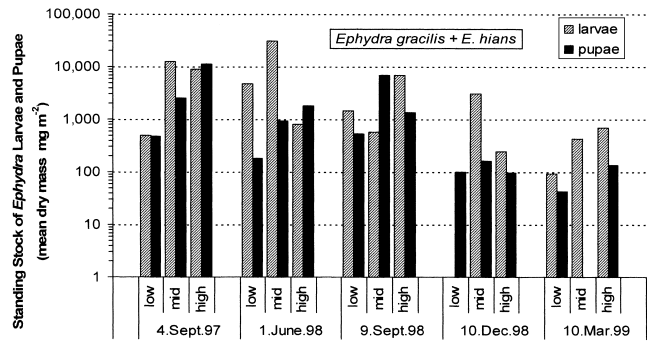


Figure 2. Standing stock dry mass density of *Ephydra* larvae and pupae in solar salt evaporation ponds 1997–1999. Coefficient of variation averaged 80–100% for three benthic kick samples per density estimate. Values are zero where no bars appear. *Ephydra hians* included in these measures along with *E. gracilis* but comprised no more than 10–15% of total (larvae only in June, pupae mostly in September, otherwise rare), and never occurred at high salinity.

exclusively in the June through September period, and birds appeared to be using the ponds for resting during the remainder of the year. The pond contrasts presented here represent feeding trials taken over nine days during the summer 1998 season.

RESULTS

Water temperatures of the ponds were similar over all periods, ranging from lows of 5 to 12 °C during the late fall and winter surveys of December and March to 22 °C in early June, and were highest in both September samplings at 29 to 32 °C (Figure 1A). Salinity of the ponds (converted from conductivity as $TDS = 0.77 \text{ (mS cm}^{-1}) + 36.46$; D. Galat, unpublished data) was 89 to 110 g L⁻¹ in the low salinity pond, 94 to 122 g L⁻¹ in the middle salinity pond, and 142 to 208 g L⁻¹ TDS in the high salinity pond over the study period (Figure 1B). Levels of oxygen saturation during the daytime samplings varied between ponds but were always supersaturated (>100%) in the medium salinity pond and exceeded saturation in the other ponds when phytoplankton were dense (Figure 1C).

The evaporation ponds usually held the greatest standing stock mass of invertebrates and algae in June and September. The combined mass of larvae and pupae of the brine flies *Ephydra gracilis* and *E. hians* was at a maximum in the medium salinity pond in June 1998 at about 31.8 g m⁻² dry mass (mostly as larvae), decreasing to about 7.6 g m⁻² by September (15.2 in September 1997), with an increased fraction of the population maturing to the pupa stage in September of both years in both low and medium salinity ponds (Figure 2). During the colder winter months, standing

Table 2. Contingency table for inferred diet data for most likely prey type(s) taken for a given foraging habitat and behavior at each pond, and associated food values (prey mass). Letters refer to prey type code. When mixed prey were possible, food value was calculated as the mean of those types.

Foraging Habitat	Foraging Behavior	Pond Salinity g L ⁻¹		
		Low 89–110	Medium 94–122	High 142–208
Onshore	Pick at margin	F	F	F
Shallow Water	Spin-pick	L, P	L, P	L, P
	Paddle-pick	L, P	L, P	L, P
	Probe bottom	L, P	L, P	L, P
	Below surface	T	A, T	A
Open Water	Surface-pick	F, P	F, P	F, P
	Surface-pick	F, P, T	F, P, A, T	F, P, A
	Below surface	T	A, T	A
Prey type average food value as mg dry mass individual ⁻¹				
	Code			
<i>Ephydra gracilis</i> larvae	L	3.47	2.72	0.29
<i>Ephydra gracilis</i> pupae	P	2.01	2.80	1.22
<i>Ephydra gracilis</i> adult flies	F	1.51	2.1	0.92
<i>Artemia franciscana</i> juveniles	—	0.184	0.17	0.088
<i>Artemia franciscana</i> adults	A	NA*	0.73	0.297
<i>Trichocorixa reticulata</i> nymphs	—	0.195	0.094	NA
<i>Trichocorixa reticulata</i> adults	T	0.476	0.571	0.617

* NA = not available, rare observation.

stock decreased to 3.2 g m⁻² in December and 0.4 g m⁻² by March. Brine fly larvae and pupae were at peak abundance in the high salinity pond in September surveys (at 20.1 g m⁻² in 1997, 8.4 in 1998) compared to 2.6 in June 1998, falling to 0.3 to 0.8 g m⁻² in December and March. Larvae and pupae were least dense in the low salinity pond, ranging from 5.0 g m⁻² in June to only 1.0 to 2.0 g m⁻² in September surveys and 0.1 g m⁻² or less in December through March. Although data for the two species of brine flies were combined here, *Ephydra hians* never comprised more than about 15% of the total abundance, and were found only in the low and medium salinity ponds. This species is commonly known as the alkali fly for its preference of alkaline carbonate waters. Under conditions where chloride-dominated salt water habitat is not hypersaline, this species has been predicted to co-occur with *E. gracilis* but in lower numbers (Herbst 1999), consistent with observations in the chloride-rich evaporation ponds of this study. In confined culture dishes, I also observed that *T. reticulata* adults fed upon early instar *E. gracilis* larvae gathered from the Harper Dry Lake salt ponds.

Although densities of *E. gracilis* in the high salinity pond were at times somewhat greater than in the low or medium salinity ponds (September surveys), individual size of larvae (Table 2) and pupae (Figure 3A) were significantly smaller (t-test for pupae, $p \ll 0.001$). Collections of pupae showed a higher fraction of emp-

ty cases (from which adults had emerged) among the larger puparia found in the medium salinity pond compared to the small pupae from high salinity (Figure 3B), where dissections revealed that many had ceased development and died. In addition, adult flies collected from the high salinity pond were, on average, only two-thirds to half the mass of adults from the other ponds (Table 2).

The brine shrimp *Artemia franciscana* was most abundant in the high salinity pond in September 1997, at 5.7 g m⁻³, while the medium salinity pond held 1.3 g m⁻³ but were absent from the low salinity pond (Figure 4). In September 1998, the high salinity pond averaged just 0.3 g m⁻³, but *Artemia* was absent from both the low and medium salinity ponds. During the colder December-to-March period, *Artemia* was absent from the high salinity pond but began recruitment into the medium salinity pond and then to a lesser extent in the low salinity pond. The late spring sampling in June 1998 showed similar mass in medium and high salinity at 1.8 and 1.4 g m⁻³, and 0.4 in low salinity. This smaller dry mass of *Artemia* in the low salinity pond compared to the high and medium salinities coincided with high relative density of the predatory water boatman *Trichocorixa reticulata*. *Trichocorixa* was usually most abundant in low salinity (86.1 g m⁻³ or 200 individuals per liter maximum in September 1998), absent or very rare in high salinity, and moderately abundant at medium salinity (Figure 5). The

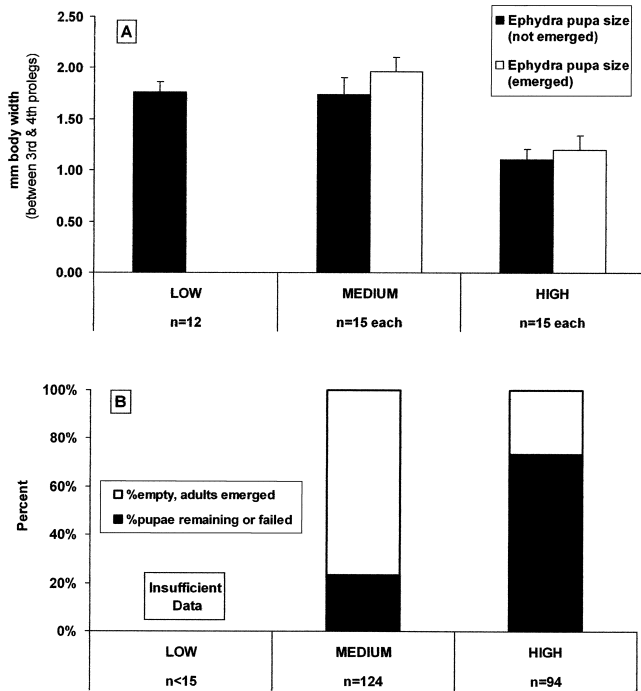


Figure 3. Body size at maturity of *Ephydra gracilis* pupae (empty cases from which flies have emerged and full cases with pupa still within) from three evaporation ponds of increasing salinity (A), and success of adult brine fly emergence judged from the frequency of empty pupa cases (B) collected in September 1997. Few pupae were found at low salinity and so emergence was not scored. Error bars in A = standard deviation (pupae smaller at high salinity, $p < 0.001$).

general seasonal pattern of *Trichocorixa* went from absent or rare in March (late winter), followed by a period of population dominance by nymphs in June (late spring, from egg hatching earlier in the spring), and becoming mostly adults during the summer and into the fall (September and December). In the high salinity

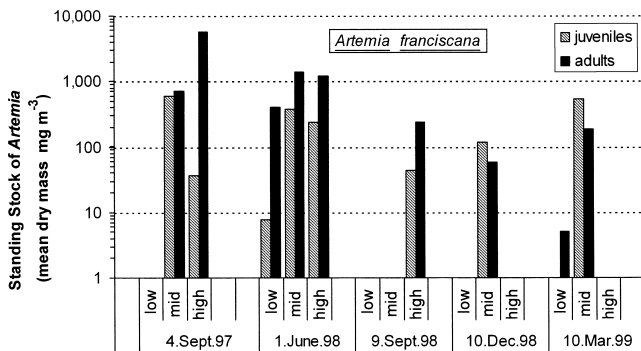


Figure 4. Seasonal abundance of the brine shrimp *Artemia franciscana* in solar salt evaporation ponds 1997–1999. Coefficient of variation averaged 80–100% for two plankton tow samples per density estimate. Values are zero where no bars appear.

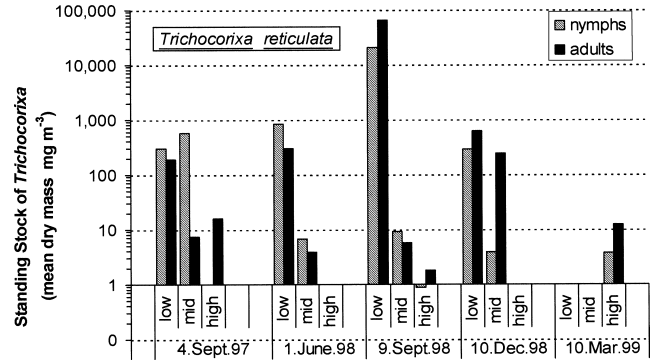


Figure 5. Seasonal abundance of the water boatman *Trichocorixa reticulata* in solar salt evaporation ponds 1998–1999. Coefficient of variation averaged 80–100% for two plankton tow samples per density estimate. Values are zero where no bars appear.

pond, *Trichocorixa* was mostly excluded—found only in September samples and March when salinities were reduced to near 150 g L⁻¹. September samples showed an abundance of *Artemia* at high salinity where *Trichocorixa* was least abundant, while brine shrimp were less dense or absent in low and medium salinity ponds where *Trichocorixa* were more abundant. Although tolerant of high salinity, *Artemia* (like *Ephydra gracilis*) growth may have been reduced by salinity stress or food limitation, with an adult dry mass of 0.30 mg individual⁻¹ in high salinity compared to 0.73 in the medium salinity pond (Table 2). In contrast, *Trichocorixa* adult body mass increased with salinity (though few in number), suggesting possible food limitation in the crowded low salinity.

Phytoplankton (*Dunaliella* sp.) were typically found in very low densities in the high salinity pond, judging by the low chlorophyll content of the water (Figure 6), except in March when brine shrimp were absent and phytoplankton reached high levels of chlorophyll

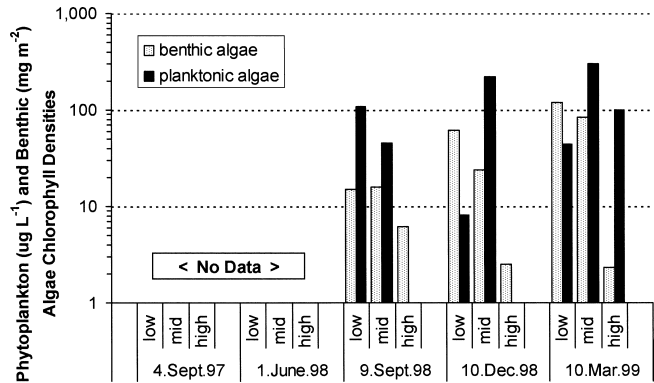


Figure 6. Standing crop of algae (planktonic and benthic) in 1998 and 1999. Coefficient of variation averages 30% for three replicate samples each. Values are zero where no bars appear.

Table 3. Selenium detections for invertebrate tissue samples collected from salt evaporation ponds, maximum selenium concentrations ($\mu\text{g L}^{-1}$) of pond water, and predicted egg selenium levels for black-necked stilts (as $\text{Log} [\text{egg Se}] = 0.44 + 0.434 \text{ Log} [\text{water Se}]$, $r^2 = 0.81$; from Skorupa 1998b), from seasonal samples taken from September 1997 to March 1999.

	Pond Salinity Level			Range of [Se] mg kg^{-1} where detected
	Low	Medium	High	
<i>Ephydra</i> larvae or pupae	0/2	0/9	0/6	None detected
<i>Artemia</i> juveniles and adults	none	none	2/3	5–15
<i>Trichocorixa</i> nymphs and adults	3/5	2/4	0/1	3–12
Maximum pond water dissolved [Se] $\mu\text{g L}^{-1}$	24	37	55	
Predicted stilt egg Se content mg kg^{-1}	10.9	13.2	15.7	

without grazing (100 g L^{-1}). Although high density of phytoplankton in the medium salinity pond in December–March coincided with the presence of brine shrimp, these were mostly early instars, and grazing rates may have been low under these colder conditions. While no phytoplankton chlorophyll data were available for June, the percent oxygen saturation data suggest that phytoplankton were dense in medium and high salinity ponds even in the presence of abundant *Artemia* and were less abundant in the lower salinity pond where brine shrimp were moderately abundant. When and where *Artemia* grazing was minimized (in the presence of *Trichocorixa* and during winter) phytoplankton photosynthesis also generated oxygen supersaturation (Figure 1). Conditions in the high salinity pond appeared to restrict benthic mat standing crop even as dense mats were growing on the bottoms of low and medium salinity ponds (Figure 6).

In September surveys, conditions existed that were consistent with the presence of a trophic cascade—abundant *Trichocorixa* predators in low salinity were coupled with the absence of grazing *Artemia* and dense phytoplankton (shown by both chlorophyll and oxygen saturation), while at high salinity *Trichocorixa* was nearly absent, *Artemia* were abundant, and phytoplankton were reduced. This pattern was also displayed by brine fly larvae and benthic algae. This coupling was not evident in the medium salinity ponds where predator-prey-algae populations coexisted at intermediate densities. In December and March, benthic algae became more dense in low and medium salinity ponds, providing a renewed food base for resumed production of *Ephydra* during the summer. During these colder winter months, phytoplankton in medium and high salinity ponds also increased but were somewhat reduced in low salinity relative to the high ungrazed chlorophyll present in September. Neither these surveys from the colder months nor the samples taken in June showed patterns consistent with a trophic cascade. The high phytoplankton chlorophyll densities of December and March in the medium salinity pond were associated with a growing *Artemia* population,

and although *Trichocorixa* may have reduced *Artemia* in the low salinity pond in June, oxygen saturation suggested no increase in algae here, but instead, high saturation levels occurred in the other ponds where *Artemia* was more abundant.

Tissue analysis of selenium in invertebrates yielded detectable amounts in 7 of 30 samples from fall 1997 to spring 1999 as available from all ponds (Table 3) —5 to 15 mg kg^{-1} dry mass in two of three *Artemia* samples from high salinity, 3 to 12 mg kg^{-1} in five of 10 *Trichocorixa* samples from low and medium salinity, and none of 17 *Ephydra gracilis* samples from any pond. These analyses were based on pooled samples by pond and life stage and so represent averaged content over large numbers of specimens (usually 50–100+ individuals).

The accordance of avian foraging observations among the five most common species (all shorebirds) with location, behavior, and prey available suggested that nearly 90% of all feeding was on brine flies (66 of 75 time trials), and this occurred mostly along the onshore margins of the medium salinity pond, in shallow water of the high salinity pond, or shallows and open water of the low salinity pond. Weekly counts of bird visitation (recorded by facility staff only as shorebirds or waterfowl) during the June through September period when all foraging was observed tallied about 68% at the medium salinity pond, 21% at high salinity, and 11% at low salinity (for over 2000 counts).

Comparisons of shorebird foraging between ponds for (a) the most frequently observed species at each pond (different at each pond) and (b) among red-necked phalaropes, the most common bird seen across all ponds, showed the greatest rates of food consumption at the low and medium salinity ponds (Figure 7). Although the rate of food capture was similar across salinities (no significant differences among red-necked phalaropes feeding at the different ponds, and only black-necked stilts at low salinity fed slightly faster than least sandpipers in the medium salinity ponds), the amount of return per capture at high salinity was lower, being limited by the small prey sizes available

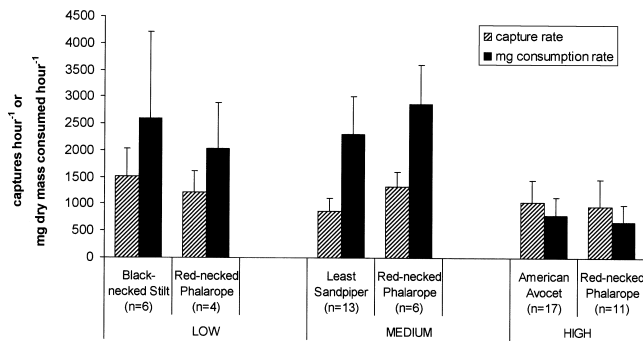


Figure 7. Foraging and consumption rates for the most commonly observed birds and for red-necked phalaropes in each evaporation pond. Error bars are the SD for n 5-minute time trial observations at each pond (for observations on 1–3 June, 3–5 August, 8–10 September 1998).

(Table 2). In the high salinity pond, american avocets consumed significantly less invertebrate mass than least sandpipers in medium salinity ($p \ll 0.001$, 2-tailed unequal variance t-test) or black-necked stilts at low salinity ($p = 0.04$), and red-necked phalaropes likewise had lower consumption rates at high salinity than they achieved in the low ($p = 0.05$) or medium ($p = 0.004$) salinity ponds.

DISCUSSION

Salinity of the evaporation ponds studied here appears to control an intermittent trophic cascade. While high salinity may place physiological limitations on the abundance of the predator *Trichocorixa*, which under low salinity conditions appeared to reduce algae-grazing *Artemia* and so released phytoplankton growth, this was observed only in late summer (September surveys) when populations were mature and had greatest potential for efficient top-down consumption of resources. As salinity increases, corixid predation is reduced or eliminated, permitting herbivore prey to feed on algae and become abundant. Further increases in salt concentration limit the growth of algae and invertebrates, diminishing the value of such habitats as a food source area to birds. These salinity-dependent alterations in community structure and food web organization are also consistent with changes observed in the plankton of Great Salt Lake over a time period when salinity was reduced and then increased again (Wurtsbaugh 1992) and involved the same inverse relation between *Trichocorixa* (*T. verticalis*) and *Artemia* and increased phytoplankton density at low salinity. Although *T. reticulata* was observed here in low numbers at salinities as high as 150 g L^{-1} , the limit for growth of abundant populations of nymphs and adults appears to be in the range of $80\text{--}100 \text{ g L}^{-1}$, consistent with observations at the Alviso salt ponds

near San Francisco Bay (Carpelan 1957). Here too, *Artemia* thrived in salinities in excess of the concentrations where *T. reticulata* was abundant but were scarce in the presence of the predator. The results found in the present study lend further support to the intermediate salinity hypothesis (Herbst 1988, 2001), where production has been postulated to be optimized between the ecological losses imposed by predation and competition at low salinity and the physiological limits of high salinity stress. It is most likely that the reduced abundance of *Artemia* and *Ephydra* at low salinity can be attributed to predation rather than salinity *per se* because these more dilute conditions should actually promote growth and survival of these osmoregulators. The potential for *Trichocorixa reticulata* to act as a predator has been established in laboratory studies where adults have been shown to prey upon brine shrimp nauplii and juveniles (Hammer and Hurlbert 1992). Corixids of saline and alkaline lakes, including *Trichocorixa verticalis interiores* Sailer, have also been shown to be predators on benthic chironomid fly larvae (Scudder 1976). The small size of *Ephydra* observed at high salinity (Figure 3) may have resulted from slower growth due to the developmental cost of osmoregulation (Nemanz 1960, Herbst 1992, Herbst 1999), limitations on benthic algae food resources (Collins 1980, Herbst and Blinn 1998), or competition within the sometimes dense population of larvae. The reduction of *Dunaliella* algae at high salinity was most likely due to brine shrimp grazing because these algae did become abundant in winter in the absence of *Artemia*, and it is also renowned as a halotolerant alga that survives in high salt concentrations through production of the osmotic counter-solute glycerol (Javor 1989).

Birds foraged primarily on the benthic brine fly *Ephydra gracilis* at moderate salinity in shallow water. Water boatman predation on brine fly larvae in the low salinity pond, and the limited shallow water habitat present, likely combined to reduce the favorability of this pond for feeding by birds. *Trichocorixa* may in effect be competing with birds for prey at the lower salinity pond and may themselves be difficult for birds to feed on because they are such active and fast swimmers and are often able to avoid capture. As such, shorebirds do not add another trophic level, in that they feed mostly on the same prey as the corixids, so they operate more as competitors on the same trophic level. The high salinity pond was a poor foraging ground for birds, probably because salinity stress resulted in small prey size and low productivity. Amount of food captured per time trial was greatest in the moderate salinity pond—where brine fly prey were often most dense, larger in body size, and easily accessed along shallow margins. High salinity would be ex-

pected to limit larval growth rate, resulting in reduced body size and emergence success (Herbst 1986). Body size of brine shrimp was also lower in high salinity (Table 2) and have previously been shown to suffer loss in growth rate and size with increased salinity (Gilchrist 1960, Dana et al. 1993). As a food resource to birds then, individual prey (flies and shrimp) from the high salinity pond were therefore of more limited nutritional value, although greater densities of individual prey could have at times (winter and spring) compensated for this reduced food value per prey captured. Moderate salinities not only supported high abundance of *Ephydra* and *Artemia* but also permitted coexistence with *Trichocorixa*, possibly because these salinities are near the survival limit of *T. reticulata*, impeding efficient consumption of prey. At low salinity, *Artemia* and *Trichocorixa* apparently may coexist for a brief period of time when the brine shrimp population is recruiting from resting eggs (spring into June) and before high densities of adult water boatmen have developed.

The seasonal variations in the timing of algal growth, brine shrimp hatching, and colonization by corixids and brine flies over a gradient of salinity may give rise to an alternating temporal sequence between bottom-up and top-down influences in dominating trophic dynamics. Cascade strength may vary according to system-specific heterogeneity in growth, recruitment, resource availability, and physico-chemical conditions (Carpenter and Kitchell 1988, Hunter and Price 1992, Borer et al. 2005) and when measurements are made during the dynamic turnover of predator, herbivore, and plant populations. Results are consistent with the meta-analysis conclusion (Borer et al. 2005) that aquatic herbivores produce the strongest cascades (*Artemia* on fast-growing palatable *Dunaliella*, *Ephydra* larvae on benthic mats with rapid turnover), although invertebrate predators are usually associated with weak cascades. While the meta-analysis also indicated that high resource availability and linear food chains (simple productive ecosystems) did not support the strongest cascades, the intermittent nature of the cascade observed here conforms to the generality that only when populations of predators and herbivores can form efficient conversion (consumption) linkages does a strong trophic cascade develop. An explicit statement in this case would be that, for these simple salt pond ecosystems, a cascade forms under low-to-moderate salinity conditions only later in the growth season when mature populations of corixids, brine shrimp, and brine fly larvae establish strong food consumption linkages, but that this relationship becomes uncoupled as salinity is increased.

The finding that moderate salinities provide optimum foraging habitat for waterbird populations has

been observed elsewhere. Surveys of shorebirds in ponds of varied salinity on the southern margins of San Francisco Bay have shown that abundance and diversity were greatest within an intermediate range of salt concentrations (120–140 ppt, Warnock et al. 2002). Here again, the high salinity habitats (>180 ppt) attracted fewer birds, and low salinity ponds contained fish that may have been consuming much of the invertebrate biomass that was not then available to birds. Ephydriids (brine flies) in these saline water habitats form dense and accessible food sources to shorebirds because larvae and pupae are often abundant in shallow water, pupae may float or be washed by waves into onshore windrows, and adults aggregate in great numbers along shorelines. Red-necked phalaropes have also shown preferential feeding on brine flies at Mono Lake, California and an inability to grow on brine shrimp as an alternative, probably because they have lower individual food value (Rubega and Inouye 1994).

Foraging behavior indicated that birds consumed more of selenium-free benthic *Ephydra* than of planktonic *Artemia* and *Trichocorixa*, which sometimes contained selenium. The potential for selenium toxicity to birds from these prey is unknown, but some context may be provided relative to Se content of water and prey from other studies of saline waters in southern California. Agricultural drainwater ponds in the San Joaquin Valley, where selenium toxicity produced high egg mortalities or birth defects in birds including avocets, stilts, and waterfowl, showed dissolved selenium levels ranging from 15 to 350 $\mu\text{g L}^{-1}$ in 12 ponds at Kesterson National Wildlife Refuge and 0.5 to 1,014 $\mu\text{g L}^{-1}$ in 25 ponds in the Tulare Basin. The invertebrates sampled averaged a selenium range of 20 to 210 mg kg^{-1} at Kesterson and 1 to 250 mg kg^{-1} in Tulare Basin (Saiki and Lowe 1987, Skorupa 1998a) compared to 0 to 15 mg kg^{-1} found in this study. In contrast, at Salton Sea where only low toxicity effects were observed in stilts, dissolved Se was measured at 1.5 $\mu\text{g L}^{-1}$ and 2 to 13 mg kg^{-1} in invertebrate tissue. There is a narrow range between dietary selenium levels that are considered nutritionally optimal (0.1 to 0.3 mg kg^{-1}) and those that are potentially harmful to bird reproduction (3–8 mg kg^{-1}) or toxic to non-breeding adults (10–15 mg kg^{-1}) (Heinz 1996). Typical background values of selenium in uncontaminated waters range from 0.1 to 0.4 g L^{-1} and from 0.4 to 4.5 mg kg^{-1} dry mass in aquatic invertebrates. The risk of selenium producing impaired reproduction in birds at the Harper Dry Lake evaporation ponds can be estimated from the relationship between pond water selenium concentration and egg selenium content known to produce embryonic defects in Black-necked stilts that was developed from studies in the Tulare

Basin (Skorupa 1998b). The threshold level for increased inviability of eggs above background is at egg Se concentrations over 6 mg kg^{-1} , with about 25% of eggs becoming inviable at 9 mg kg^{-1} . In contrast, avocets are more tolerant of Se, with the hatchability threshold between $61\text{--}80 \text{ mg kg}^{-1}$. The three ponds of this study had maximum dissolved Se of 24, 37, and 55 g L^{-1} (low, medium, and high salinity, respectively), giving predicted egg Se of 10.9 to 15.7 mg kg^{-1} (Table 3). Although selenium levels in pond water were above the threshold for producing inviable stilt eggs, there are several reasons to believe that these may not be poisoning risks for birds feeding at the Harper Dry Lake ponds. (1) A food chain link for transfer of selenium to birds from pond food sources was absent—there was no selenium detected in brine flies, the primary food organism identified for foraging birds. (2) The occurrence of selenium in brine shrimp and water boatman was sporadic and at low levels (similar to Salton Sea) relative to the range documented for invertebrate foods from sites where selenium poisoning was severe (Tulare and Kesterson). (3) Local breeding and nesting activity of birds feeding at the ponds has not been documented and may not be occurring (i.e., all birds may be migrants or short-term residents). In similar saline industrial wastewater ponds in Arizona with dissolved and brine shrimp tissue Se levels in the same range as those observed here, selenium contamination could not be linked to bird mortality and did not produce toxicity in fish-feeding trials (Tanner et al. 1999). Other desert wastewater ponds have also been shown to provide abundant invertebrate food resources to migratory birds with low risk of metals contamination (Cieminski and Flake 1995).

The absence of Se in brine fly larvae and pupae, and low levels found in shrimp and water boatmen, may be due to the high sulfate content of pond water. Sulfate is known to compete with the similar selenate ion and has been shown to reduce uptake, toxicity, and bioavailability of Se for brine shrimp (Forsythe and Klaine 1994), midge larvae (Hansen et al. 1993), and a variety of other aquatic animals (Brix et al. 2001). Exposures of *E. gracilis* larvae to selenate related to industrial waste at Great Salt Lake (Brix et al. 2004) showed very high acute tolerance (96 hr LC-50 of nearly 500 mg L^{-1} selenate), attributed to high sulfate content of lake water (5.8 g L^{-1}). Sulfate in the ponds studied here contained even more sulfate, in the range of 10 to 32 g L^{-1} . Selenium bioassays of *E. gracilis* larvae in high sulfate water have shown bioaccumulation from food (Rosetta and Knight 1995), but this occurred to an appreciable extent only at concentrations far higher than those found in the present study, and primarily for organic selenomethionine. Although

sulfate content of water does not always seem predictive of toxicity and potential for Se bioaccumulation of birds in nature (Skorupa 1998b), it is conceivable that high sulfate may prevent or reduce sediment-associated microbial/algal Se uptake and conversion to more toxic organo-selenium compounds. Benthic algal-microbial feeding brine fly larvae may not then be consuming much selenium where high sulfate inhibits incorporation into bioavailable forms.

The low risk of selenium contamination in the Harper Dry Lake ponds should be weighed against the benefits of wastewater creating productive saline water habitat for migratory birds. Salinity management would provide the most effective means for providing favorable bird foraging habitat. Moderate salinity provides the best conditions for brine fly production and availability to water birds with a preference for this food source. Increased salinity could be used to eliminate water boatman, if these were deemed undesirable, and/or decrease attraction to the more tolerant brine shrimp and brine flies that lose food value as they become salt-stressed. Combined with alterations providing shallow water along shorelines (for wading shorebirds) and rocky substrates (gravel habitat for brine fly larvae and pupae), saline evaporation ponds could be managed as an ecological benefit of the solar energy generating process and mitigation for the historical loss (to agricultural irrigation and development) of natural saline wetland habitats.

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