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Trophic structure and avian communities across a salinity gradient in evaporation ponds of the San Francisco Bay estuary

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Abstract

Commercial salt evaporation ponds comprise a large proportion of baylands adjacent to the San Francisco Bay, a highly urbanized estuary. In the past two centuries, more than 79% of the historic tidal wetlands in this estuary have been lost. Resource management agencies have acquired more than 10 000 ha of commercial salt ponds with plans to undertake one of the largest wetland restoration projects in North America. However, these plans have created debate about the ecological importance of salt ponds for migratory bird communities in western North America. Salt ponds are unique mesohaline (5–18 g l^{-1}) to hyperhaline (>40 g l^{-1}) wetlands, but little is known of their ecological structure or value. Thus, we studied decommissioned salt ponds in the North Bay of the San Francisco Bay estuary from January 1999 through November 2001. We measured water quality parameters (salinity, DO, pH, temperature), nutrient concentrations, primary productivity, zooplankton, macroinvertebrates, fish, and birds across a range of salinities from 24 to 264 g l^{-1}. Our studies documented how unique limnological characteristics of salt ponds were related to nutrient levels, primary productivity rates, invertebrate biomass and taxa richness, prey fish, and avian predator numbers. Salt ponds were shown to have unique trophic and physical attributes that supported large numbers of migratory birds. Therefore, managers should carefully weigh the benefits of increasing habitat for native tidal marsh species with the costs of losing these unique hypersaline systems.

Introduction

Several tidal marsh species are now endangered because more than 79% of historic tidal wetlands have been lost to urbanization, agriculture, and salt production (Goals Project, 1999). The San Francisco baylands comprise a fragmented landscape of non-tidal salt, brackish and freshwater wetlands; agricultural lands; seasonal ponds; vernal pools; riparian scrub; and commercial salt ponds (Goals Project, 1999). Although salt ponds were not a natural feature of the landscape, they have existed in the San Francisco Bay estuary for more than 150 years (Ver Planck, 1958). These

non-tidal hyperhaline ponds vary seasonally in salt content from brackish to saturated, range from a few centimeters to a few meters in depth, and are composed of relatively simple but productive assemblages of algae and invertebrates (Carpelan, 1957; Lonzarich & Smith, 1997).

The San Francisco Bay ecosystem is an important staging and wintering area for migratory waterfowl and shorebirds in the Pacific Flyway (Harvey et al., 1992). It is recognized as a site of hemispheric importance for shorebirds because it supports at least 30% of some populations in the flyway (Page et al., 1999), and also up to 50% of many diving duck populations (Accurso, 1992). Many migratory waterbirds use the baylands, which consists of the area between the historic high and low tide lines and comprises about 85 830 ha in the estuary (Goals Project, 1999). The ponds have become an integral part of the landscape, as well as essential habitats for large numbers of waterbirds during migration and winter (Anderson, 1970; Accurso, 1992; Takekawa et al., 2001; Warnock et al., 2002).

A large proportion of the salt ponds was purchased and taken out of salt production in 1994 (North Bay: 4045 of 4610 ha) and 2002 (South Bay: 6110 of 10 520 ha, North Bay: the remaining 565 ha). Resource management agencies have proposed converting the salt ponds into tidal marshes to restore populations of tidal marsh species of concern and to minimize management costs. A planning report for the future of wetlands in the estuary (Goals Project, 1999) suggested that only a few hundred ha of more than 10 000 ha of salt ponds in the estuary would likely remain through the next century. However, it is not well understood how these ponds support such large numbers of wintering and migratory birds, and it is unknown whether sufficient alternative habitats remain in this highly urbanized estuary. Thus, we initiated a study to document the limnological character of salt ponds in the estuary. We examined water quality, nutrient concentrations, primary productivity, zooplankton, macroinvertebrates, fish, and birds across a salinity gradient to examine the ecological character and trophic structure of salt ponds in the estuary and to determine the relationship between salinity and community structure.

Study area

We examined salt ponds in the North Bay subregion (37.90° N–38.25° N; 122.25° W–122.50° W) of the San Francisco Bay estuary (Fig. 1). The salt ponds were located 5 km northwest of Vallejo, California (38° 10′ W, 122° 20′ N) and comprised about 4000 ha. They were acquired in 1994 by the California Department of Fish and Game as part of the Napa-Sonoma Marshes Wildlife Area. Although salt production ceased in 1993, the system remained intact with lower salinities and muted tidal flow in primary ponds and higher salinity and very little tidal flow in ponds farther inland (Takekawa et al., 2000; Lionberger et al., 2004).

Methods

A sub-sample of five ponds was selected for study, representative of the salinity gradient in the salt pond system (Fig. 1). Ponds 1 (P1), 2 (P2), 3 (P3), 4 (P4), and 7 (P7) ranged in size from 127 to 534 ha and varied in mean salinity from 23 to 224 g l^{-1} (Table 1), similar to the salinity range found in commercial salt production systems. Originally, P1 was the intake pond from a channel to the North Bay, whereas ponds with higher numbers had increasing salinity. Water entered P1, primarily by tidal influence through a one-way gate and was pumped into P2 intermittently during the study period (T. Huffman, California Department of Fish and Game, personal communication). Increased water elevation in P2 supplied water into P3 via an inverted siphon except when density differences and small hydraulic head prevented flow (Lionberger et al., 2004). Density differences and small hydraulic head usually prevented flow through an inverted siphon between P3 and P4 (Lionberger et al., 2004). During salt production, the supernate was removed from the brine and stored in P7, the bittern pond.

We superimposed a 250×250 m (6.25 ha) Universal Transverse Mercator (UTM) grid upon the sampled ponds to provide a framework for integrated sampling (Takekawa et al., 2000). This grid system provided the basis for identifying sampling locations in each pond (Matveev, 1995; Posey et al., 1995). Individual gridcells where birds were located

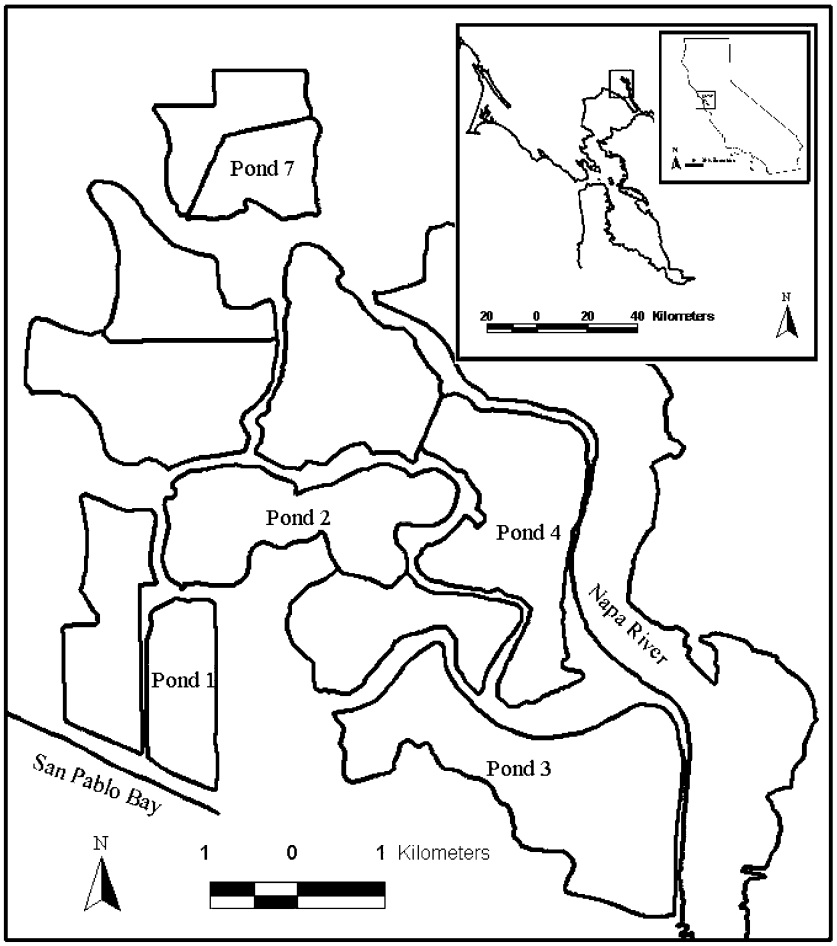

Figure 1. Former salt evaporation ponds in the Napa-Sonoma Wildlife Area located 5 km northwest of Vallejo, California, USA on the northern edge of San Pablo Bay in the San Francisco Bay estuary.

in monthly surveys were identified and selected as sampling locations in each pond to facilitate the study of trophic level relationships. Beginning in March 1999, 10 gridcells in which birds were observed during monthly surveys were randomly selected from each pond for nutrient, primary productivity, invertebrate and fish sampling. If <10 gridcells were used by birds within a pond, additional gridcells were selected randomly.

Water quality

From February 1999 until November 2001, water quality parameters were measured monthly in P1,

Table 1. Average water quality values ± SD in milligrams per liter for Napa-Sonoma Ponds 1, 2, 3, 4 and 7 during 1999, 2000 and 2001

Pond	Salinity (PPT)	D.O. mg l^{-1}	pH	Turbidity (NTU)	Temp. (°C)
1	23.1 ± 9.4	8.7 ± 1.5	8.1 ± 0.3	253.9 ± 227.0	18.2 ± 4.8
2	23.1 ± 8.2	8.5 ± 1.5	8.6 ± 0.3	82.0 ± 44.1	16.8 ± 4.3
3	47.6 ± 16.1	8.3 ± 2.2	8.4 ± 0.2	198.4 ± 94.8	18.0 ± 4.7
4	169.7 ± 70.6	6.0 ± 4.6	7.7 ± 0.5	96.8 ± 97.1	19.6 ± 5.8
7	224.3 ± 66.4	3.6 ± 1.8	5.9 ± 0.8	163.4 ± 74.4	20.5 ± 5.4

P2, P3, P4 and P7. Four or five sampling locations were established for each salt pond with measurements taken at the corners of the ponds. Water quality sampling locations were chosen to maximize the detection of spatial variability in the ponds, and measurements were timed to occur within a week of the bird surveys. Sample locations were referenced to the 250×250 m UTM grid.

A Hydrolab Minisonde® (Hydrolab-Hach Company, Loveland, CO) was used to measure conductivity (internally converted to salinity with the 1978 Practical Salinity Scale), pH, turbidity, temperature, and dissolved oxygen at each location. The sensors on the Hydrolab were calibrated prior to each use and a calibration check was performed after sampling. Because the salt ponds are known to stratify under certain conditions, readings from near-surface and near-bottom of the water column were collected at sampling locations where water depth exceeded 60 cm. When salinity in the ponds exceeded 70 g l^{-1}, specific gravity was measured with a hydrometer (Ertco, West Paterson, NJ) scaled for the appropriate range. These data were corrected for temperature and converted to salinity.

Chlorophyll and nutrients

We collected a sub-surface sample of water from each of the sampled gridcells on each survey date. Water samples were immediately placed on ice in a cooler and frozen within 8 h. Water samples were subsequently divided for analyses of chlorophyll *a* (chl *a*) and nutrients. Chl *a* concentration was determined with the monochromatic method described by Wetzel & Likens (1991). Each sample was passed through a 0.45 μm filter, and the filter was immediately ground in a tissue grinder with 3–4 ml of 90% alkaline acetone. Contents were transferred to a 20-dram vial, capped and placed in a darkened refrigerator. After 12 h, supernatant in vials was decanted into a glass cuvet (light path 2.0 cm) and absorption measured at 750 and 665 nm on a spectrophotometer with maximum spectral bandpass width of 8 nm and wavelength accuracy of ±2 nm (Model 401, Spectronic Instruments, Inc., Rochester, NY). For each sample, we then added 0.1 ml of 1 N HCl ml^{-1} extract, mixed the solution and repeated absorption measurements at the same wavelengths. Chl *a* was then calculated (Wetzel & Likens, 1991).

The remainder of the water sample was analyzed for concentrations of nitrogen and phosphorus. Nitrate was measured with an ultraviolet screening method, and ammonia nitrogen was determined following the Nesslerization method (American Public Health Association, 1989). Soluble reactive phosphorus concentration was determined with persulfate digestion after filtering the sample through a 0.45 μm filter, and total phosphorus concentration was determined with persulfate digestion on unfiltered samples (APHA, 1989).

Zooplankton

Zooplankton samples were collected with a Miller high-speed plankton sampler fitted with a 149 mm mesh net and flow meter. Samples were collected by pulling the sampler about 10 m off the side of a small boat at a depth of about 0.25 m. Zooplankton samples were immediately concentrated with a 149 mm mesh screen and preserved in 5% formalin, then later transferred to 70% alcohol. Zooplankton in samples were identified and enumerated under a stereo-zoom microscope with 10–100× magnification. When the number of individuals was >1000, sub-sampling was performed (Wetzel & Likens, 1991). In sub-sampling, we first enumerated all *Ephydra* (brine flies) and *Artemia* (brine shrimp) in the sample. We then diluted the remainder of the sample to 200 ml, mixed it on a magnetic stirrer and withdrew five 1 ml subsamples in a Hansen-Stempel volumetric pipet.

Sub-samples were transferred to a grid-lined petri dish and zooplankton were enumerated. Nauplii (larvae) and juvenile stages of *Artemia* were distinguished by the presence and length of filtering appendages. Individual organisms within each sample were categorized as adults or as 1st, 2nd or 3rd instar larvae. In addition, larvae were measured and separated into 1 mm size classes ranging from 1 to 7 mm. Adult males were distinguished by the presence of claspers, whereas females were distinguished by the presence of extended ovisacs. Larval instars of *Ephydra* were determined by size and by the presence of respiratory siphons and appendages. *Ephydra* larvae were also measured and separated into 1 mm size classes. Other taxa were identified to a practical taxonomic level and counted.

Biomass of *Artemia* and *Ephydra* was calculated from length to weight relationships and abundance. Length–weight regressions were determined from 60 *Artemia* and 32 *Ephydra*. We recorded lengths (nearest 0.01 mm) under the stereomicroscope fitted with an ocular micrometer and preserved weight of individuals (nearest 1.0 μg) on a Mettler model M1 microbalance (Mettler-Toledo, Inc., Columbus, OH). We determined fresh weight from preserved weight with a conversion of 0.8, and dry weight from fresh weight with a conversion of 1.1 (Wetzel, 1983).

Macroinvertebrate surveys

Benthic macroinvertebrates were sampled in P1, P2, P3 and P4. P7 was sampled on three occasions, but sampling was discontinued because invertebrates were rare or not found at such high salinities. Monthly waterbird surveys were used to randomly select 10 gridcells identified by GPS location to sample for benthic macroinvertebrates within each pond. P1–P4 were sampled every other month beginning April 1999 to November 2000, and then in February, June and November 2001 (sample frequency changed with very low water levels in some ponds in summer or during inclement weather conditions in winter).

Within each gridcell, we located the center with a GPS unit, allowed the boat to drift, and then collected three cores (about 3 m apart) with a standard Ekman grab sampler (15.2 cm^3). A standard (USA ASTME-11 Number 18) 1.0 mm mesh sieve was used to reduce cores to invertebrates and debris that were preserved in 70% ethanol and Rose Bengal dye. The qualitative procedure for estimating the texture of the substrate was developed by a single observer, who trained others in this characterization. Substrate was characterized as soft, medium, or hard in penetrability, and as primarily clay, sandy, or silty in appearance. We noted outstanding features, such as abundant shell fragments, large organic debris, or encrusted crystalline salt.

Field samples were processed using binocular microscopes (3–10× power) by sorting individual invertebrates from debris and residual sediment. Invertebrates were identified and enumerated to genus or species (when common) or family (when uncommon) with appropriate keys (e.g., Smith & Carlton, 1975; Morris et al., 1980). As a quality control measure, a second observer verified the identification of 5–10% of these samples. Blotted wet weight biomass of organisms was determined with an Ohaus, Model 3130 scale (Pine Brook, NJ). Samples were dried in a Precision convection oven (Winchester, VA) at 15.5 °C for 24 h to determine dry weight.

Fish surveys

Fish species assemblages were surveyed bimonthly from July 1999 until December 2000 in P1–P3 (sampling in P4, which ranged to salinity 100, was discontinued after no fish were detected in initial samples; P7, with salinity >250, was presumed not to support fish life). We used bag seines to sample shallow areas near shore and gill nets to sample deeper areas offshore to assess the distribution and relative abundance of both juvenile and adult fishes. Fishing effort for each gear type was standardized and replicated to allow for statistical comparisons of fish catch among dates and sites. A 5.5 m bag seine with 6.4 mm mesh in the bag and 12.7 mm mesh in the wings was used along shorelines in water < 1.5 m deep. Six sites were sampled with five hauls of a bag seine at each site by manually dragging the seine about 8 m perpendicular or parallel to shore.

In addition, six 38.1 m long (1.8 m deep) variable-mesh monofilament gill nets with 12.7, 15.4, 38.1, 50.8 and 63.5 mm square mesh panels were fished for a maximum of 6 h, checking them every 1–2 h to release protected fish species such as Sacramento splittail (*Hypomesus transpacificus*) and delta smelt (*Pogonichthys macrolepidothus*). Individuals were identified to species in the field with taxonomic keys (Miller & Lea, 1972; Moyle, 1976; Eschmeyer et al., 1983; McGinnis, 1984). Fish that were not reliably identified in the field were preserved and later identified by taxonomic specialists. The first 25 individuals of each species were measured for standard length (to the nearest mm) and weighed (blotted wet weight biomass to the nearest 0.1 g).

Bird surveys

We conducted monthly complete counts of the five ponds from January 1999 to June 2001, and then

bimonthly counts thereafter through November 2001. Observers conducted counts of species with binoculars and spotting scopes from vantage points at the edge of ponds during the first week of each month, and locations of waterbirds were placed within the gridcells of each pond. Surveys were conducted during the day within 3 h of the highest high tide when the largest number of waterbirds was roosting in the salt ponds.

Identified waterbirds were separated into guilds to examine differences among foraging groups rather than differences among species. These foraging guilds included: (1) sweepers – obtained prey from the surface, e.g., *Recurvirostra americana* (American avocet); (2) shallow probers – foraged in the top layer (< 3 cm) of sediments, e.g., *Calidris mauri* (western sandpiper); (3) deep probers – reached deeper into the substratum than shallow probers, e.g., *Limosa fedoa* (marbled godwit); (4) dabblers – fed in the upper water column, e.g., *Anas acuta* (northern pintail); (5) diving benthivores – fed in deeper water on benthic invertebrates, e.g., *Aythya affinis* (lesser scaup); (6) piscivores – fish consumers, e.g., *Pelecanus erythrorhynchos* (American white pelican); and (7) other – omnivores and incidental species including gulls.

Statistical analyses

We examined differences in salt ponds during the winter (Dec–Feb), spring (Mar–May), summer (June–Aug), and fall (Sep–Nov) seasons, 1999–2001. Months were assigned to seasons to encompass the major bird migration chronology in spring and fall. We computed means from repeated monthly water quality measurements but did not make statistical comparisons, because sampling locations were fixed and non-random. We computed means from repeated monthly or bimonthly nutrient measurements for each pond and examined between-pond differences with univariate analysis of variance (ANOVA) or multivariate (MANOVA) tests (SAS Institute, 1990). We tested for equal variances using Levene's test and then used the multiple variance mixed procedure (SAS Institute, 1990) if data violated the equal variance assumption. Because sample sizes often differed among ponds, significant ANOVA results were investigated with the Tukey–Kramer procedure (SAS Institute, 1990) to make multiple comparisons among pairs of means (Sokal & Rohlf, 1995).

Sampling effort for chl *a*, zooplankton, invertebrates, and fish was standardized and replicated to allow for statistical comparisons among ponds. The results of fish sampling methods were not directly comparable because species composition, numbers, and biomass differed strongly between gear types. However, samples were standardized for sample size and then combined for biomass and species diversity comparisons. To ensure equal representation of sampling methods in comparisons of fish species composition between ponds, catch data were converted to proportions of the total catch for each gear type and then combined. Complete counts of birds were standardized by conversion to density (birds ha^{-1}) because salt ponds varied in size. We used the Shannon–Weiner index (Krebs, 1999) to assess species diversity for birds, fish, and invertebrates for each independent sampling event. For invertebrates, we used a MANOVA model to compare diversity indices over time by pond (model effect) with least squares and mean response design. ANOVA was then used to compare individual differences among ponds or time.

We elaborated on the between-pond comparisons by directly examining the relationship between salinity and other parameters. We independently examined chl *a* concentrations and zooplankton biomass in addition to invertebrate, fish, and bird concentrations and diversity by applying a best-fit quadratic function to the relationship with salinity. Non-metric Multidimensional Scaling (NMDS), a distance-based ordination method that displays multi-dimensional data by maximizing rank–order correlation, was used to present similarity matrix distances and distance in ordination space on two-dimensional plots (Clarke & Warwick, 2001). We used the PRIMER program (Plymouth Routines in Multivariate Ecological Research, Plymouth, England) to perform NMDS on transformed data based on a Bray–Curtis similarity matrix (Bray & Curtis, 1957), and visually compare species composition among samples in two dimensions. We averaged sample values by season to simplify the display and associated larger diameter circles with increased salinity to accentuate the relationship

between salinity and species composition (Clarke & Warwick, 2001). We used analysis of similarities (ANOSIM, PRIMER) to further investigate community differences among ponds with 5000 permutations to compare overall and pair-wise effects of pond differences on species composition. PRIMER provides Global *R* and pairwise *R* statistics that provide a measure of the difference between rank dissimilarities within and among groups (Sommerfield et al., 2002). Stress values represent how well the multi-dimensional relationship between variables is represented in the two-dimensional plot; although stress parameters change according to quantity of data as well as the number of dimensions, Clarke & Warwick (2001) suggest that stress <0.05 is excellent but stress <0.10 is a good ordination, whereas stress >0.3 suggests that the ordination plot is not interpretable. For all analyses, results were deemed significant when $p \leq 0.05$.

Results

Water quality

Salinity varied widely throughout the study, ranging from 23.1 to 224.3 g l^{-1} (Table 1, Fig. 2). The intake pond (P1) and an interior pond (P4) showed the greatest temporal variation in salinity. Ponds varied more seasonally than they did annually, especially in the higher salinity ponds (Fig. 2). Salinity was lowest following late winter rainfall and increased to peak concentrations in the late summer. The pH of the system was alkaline, but the water in P7, a bittern pond that was often very shallow with few areas to sample, was acidic throughout the year (Table 1). Turbidity was generally high in P3, coincident with seasonal winds. Water temperature ranged from 9 to 30 °C, with greatest extremes in P1 and P4, ponds that also had the greatest changes in water levels. Decreased water levels combined with elevated temperatures resulted in low dissolved oxygen readings in P4 during the summer months.

Nutrients

Nutrient concentrations varied among ponds and seasons (Table 2). Nitrate (NO_3–N) concentration ranged from 0.306 to 8.05 mg l^{-1} (Fig. 3). Nitrate was greater in P4 than in P1 and P2 ($F_{3,25} = 3.89$, $p < 0.021$). Ammonia (NH_3–N) concentrations ranged from 0.409 to 18.2 mg l^{-1} (Fig. 3). Ammonia was greater in P4 than in P1–P3 ($F_{3,24} = 25.23$, $p < 0.0001$). Average soluble reactive phosphorus (SRP) concentration ranged from 0.151 to 3.21 mg l^{-1} (Fig. 3). Overall, SRP concentration was lower in P4 than in P2 or P3 ($F_{3,25} = 3.33$, $p = 0.036$). Average total phosphorus (TP) concentration ranged from 0.29 to 4.88 mg l^{-1} (Fig. 3). TP concentration was greater in P2 and P3 than in P4 ($F_{3,25} = 4.72$, $p = 0.0096$). Nitrogen to phosphorus (N:P) ratios ranged from 0.3 to 3.2 in P1, from 0.7 to 3.4 in P2, from 0.9 to 7.5 in P3 and from 2.3 to 30.3 in P4. N:P ratios in P4 were >10.0 on 4 of 7 dates, but <10.0 in the other ponds on all dates.

Primary productivity

Mean annual chl *a* concentration was higher in P3 and P4 than in P1 (Table 3). Seasonal change in chl *a* concentration was most pronounced in P4, and least pronounced in P1 and P2 (Fig. 4a). Chl *a* concentration was greater in P3 and P4 than in P1. However, the mean annual concentration in P4 reflected exceptionally high chl *a* concentrations (130.0 mg m^{-3}) measured in the winter (Fig. 4a). Overall, chl *a* generally increased with salinity, but only P1 was significantly lower than the other ponds (Table 3; $F_{3,164} = 4.46$, $p = 0.0048$). Patterns in phaeophyton concentrations by pond were similar to chl *a* ($F_{3,164} = 4.46$, $p = 0.0049$) and were higher in P2, P3, and P4 than in P1 (Table 3).

Among all ponds, chl *a* concentration was negatively correlated with total zooplankton biomass (intercept = 1.2266, slope = −0.4547, adjusted $r^2 = 0.17$, $p < 0.0001$). Similarly, chl *a* concentration in P4 was negatively correlated with *Artemia* biomass (intercept = 12.333, slope = −0.7689, adjusted $r^2 = 0.331$, $p < 0.0001$).

Zooplankton

Twenty zooplankton taxa were identified in the salt ponds. Eight taxa were recorded in lower salinity ponds (P1 and P2), seven were recorded in P3 and only five taxa were recorded in P4 and P7. Seasonally, more taxa were recorded during

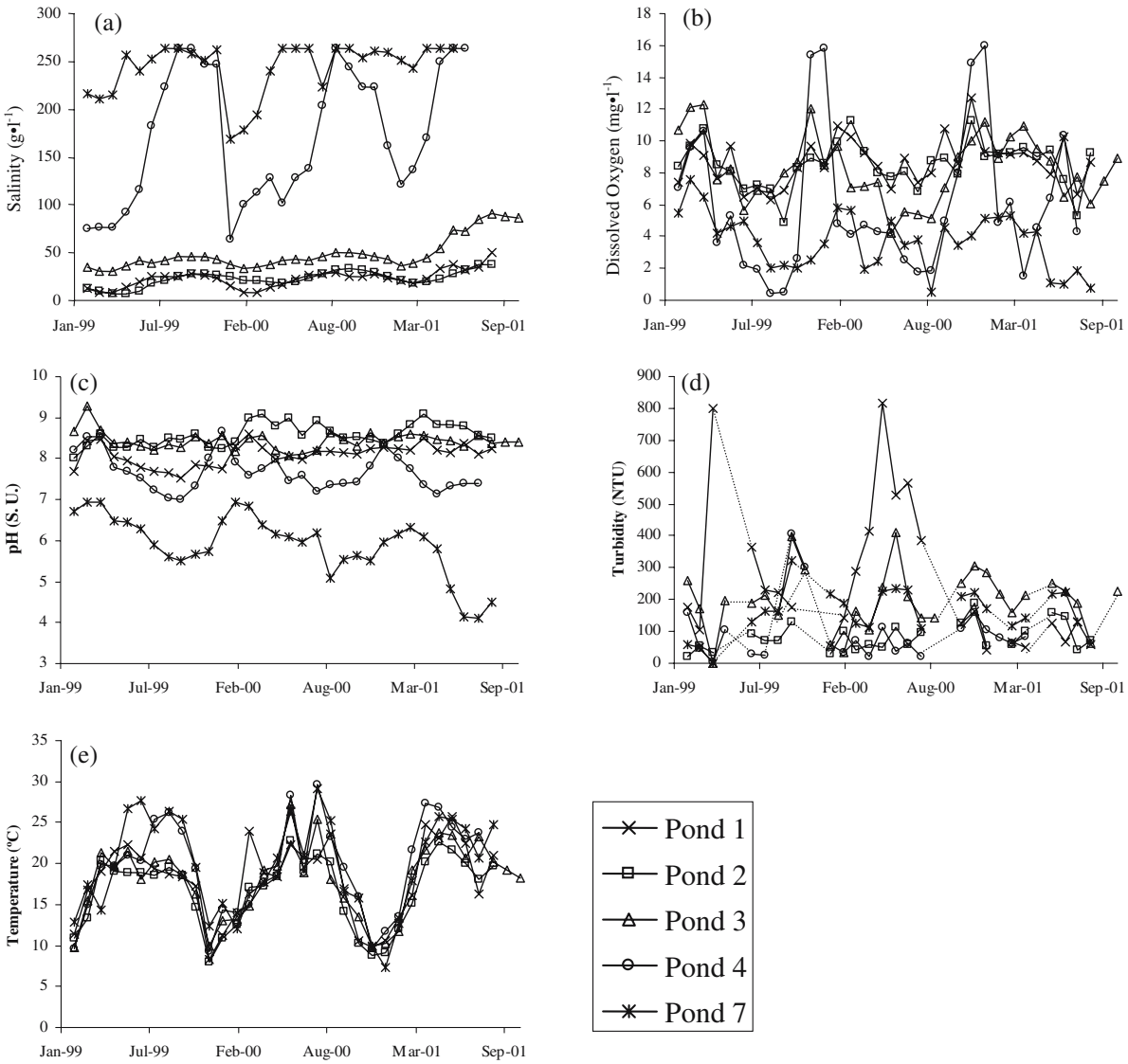

Figure 2. Salinity (g l^{-1}), dissolved oxygen (mg l^{-1}), pH (SU), turbidity (NTU), temperature (°C) for Ponds 1, 2, 3, 4 and 7 in the Napa-Sonoma Marshes from 4 to 5 sampling locations per pond, Feb 1999–Nov 2001.

Table 2. Average dissolved nutrient concentrations ± SD (μg l^{-1}) for Napa-Sonoma Ponds 1–4 during 1999 and 2000. Means that are not significantly different (Tukey–Kramer) are indicated by similar superscripts

Pond	NO_3 mg l^{-1}	NH_3–N mg l^{-1}	SRP mg l^{-1}	TP mg l^{-1}
1	$1.57^{a} \pm 1.1$	$5.56^{a} \pm 2.8$	$2.18^{ab} \pm 0.8$	$2.17^{ab} \pm 0.8$
2	$1.47^{a} \pm 1.7$	$6.24^{a} \pm 1.1$	$3.21^{b} \pm 1.3$	$3.34^{b} \pm 1.4$
3	$3.30^{ab} \pm 2.6$	$7.21^{a} \pm 3.0$	$2.57^{b} \pm 0.9$	$2.71^{b} \pm 1.2$
4	$4.02^{b} \pm 1.3$	$15.42^{b} \pm 2.2$	$1.25^{a} \pm 1.7$	$1.16^{a} \pm 1.2$

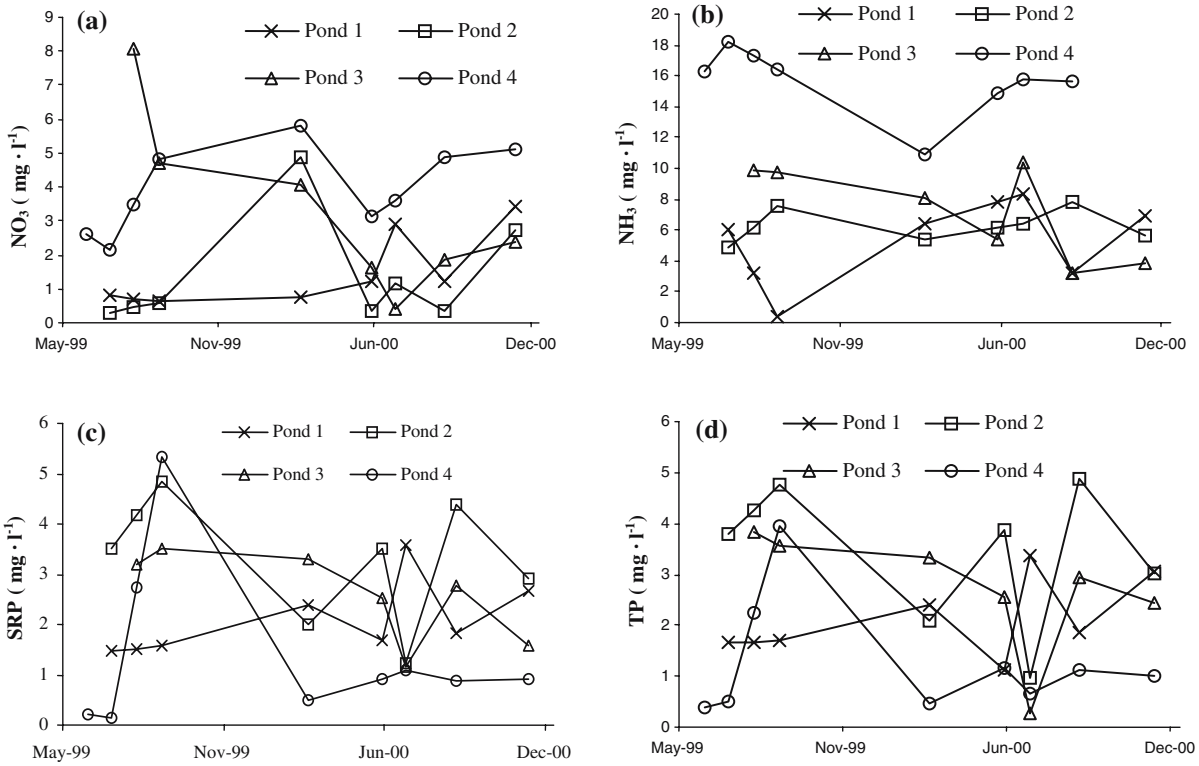

Figure 3. Nutrients (mg l^{-1}) including nitrate (NO_3–N), ammonium (NH_4–N), soluble reactive phosphorus (SRP) and total phosphorus (TP) in Ponds 1–4 of the Napa-Sonoma Marshes during May 1999–Sep 2000.

Table 3. Average chlorophyll *a* and phaeophyton values ± SD (mg m^{-3}) for Napa-Sonoma Ponds 1–4 during 1999, 2000 and 2001. Means that are not significantly different (Tukey–Kramer) are indicated by similar superscripts

Pond	Chl *a* mg m^{-3}	Phaeophyton mg m^{-3}
1	$25.5^{a} \pm 24.9$	$43.4^{a} \pm 42.3$
2	$37.9^{ab} \pm 26.3$	$64.4^{ab} \pm 44.8$
3	$47.9^{b} \pm 33.7$	$81.5^{b} \pm 57.2$
4	$52.4^{b} \pm 61.9$	$89.1^{b} \pm 105.2$

May–Jun and fewest during Sep–Mar. Two taxa comprised 94.3% of the zooplankton counted: copepods comprised 66.1% and *Artemia* 28.2%. Copepod abundance differed among ponds ($F_{3,465}$ 13.80, $p < 0.001$) and were more abundant in P3 than in P2 or P4 (T–K, $p < 0.001$). Average number of copepods during the entire sampling period ranged from 82 to 301 m^{-3} in P1–P3, but was < 1.0 m^{-3} in P4. Copepods were not found in P7. *Artemia* comprised $< 0.05\%$ of organisms in P1–P3, but comprised $> 98\%$ of organisms in P4. The single other taxon considered common was *Ephydra*. Like *Artemia*, *Ephydra* appeared to be incidental in P1–P3 (0–0.1%), but was more common in P4 (1.5%). Average abundance of zooplankton in P2 (87 m^{-3}) was less than in other ponds (range: 236–323 m^{-3}) ($F_{3,465} = 6.00$, $p = 0.0005$; T–K, $p = 0.012$). Seasonally, total zooplankton abundance was greatest in spring and early summer with peak biomass 3–5 magnitudes higher in P4 than in all other ponds (Fig. 4b).

Zooplankton biomass in ponds reflected the numerical distribution of taxa. Copepods comprised 73–90% of the zooplankton biomass in P1–P3, but almost none of the biomass in P4. Average copepod biomass in P1–P4 was 0.23, 0.09, 0.32 and < 0.01 mg m^{-3}, respectively. Copepod biomass differed among ponds ($F_{3,465} = 13.77$, $p < 0.001$) and was greater in P3 than in either P2 or P4 (T–K, $p < 0.001$). Biomass of total zooplankton in P4 (96.0 mg m^{-3}) was greater than in any other pond (range 0.1–0.3 mg m^{-3}). In P4, *Artemia* comprised 99% and *Ephydra* 1% of the

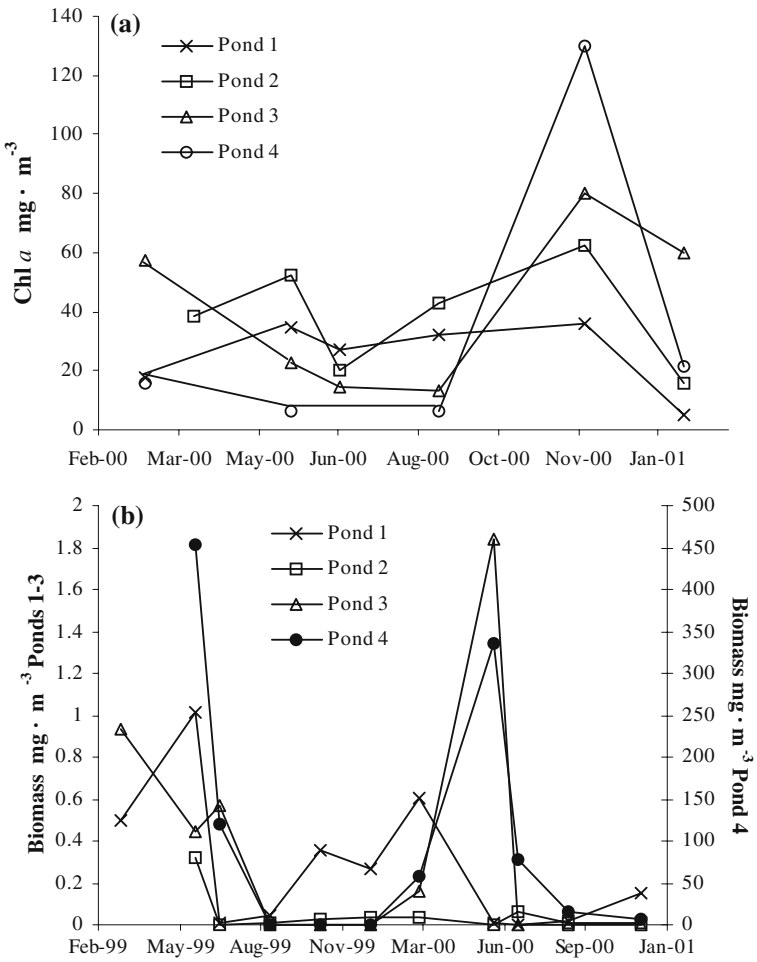

Figure 4. (a) Chlorophyll *a* (mg m^{-3}) and (b) zooplankton (mg m^{-3}) in Ponds 1–4 of the Napa-Sonoma Marshes, May 1999–Sep 2000.

biomass. Seasonally, total zooplankton biomass was greatest in spring and summer, except in P2 where it was low on most dates.

Macroinvertebrates

Species diversity (Shannon–Wiener) of benthic macroinvertebrates among ponds and time periods sampled (approximately bimonthly) differed significantly (MANOVA, $F_{36,299} = 23.90$, Wilk's $\lambda = 0.02$, $p < 0.0001$). Mean overall diversity differed significantly among ponds ($F_{3,48} = 17.80$, $p < 0.001$). P1 and P2 were different from P3 and P4 (T–K $p = 0.0002$; Table 4). Diversity was generally higher and similar in P1 and P2 relative to P3 and P4. One-way ANOVA and Tukey–Kramer tests indicated that diversity in P1 and P2 did not differ significantly in 1999 and early 2000 ($F_{3,116} = 10.99$–205.51, $p < 0.0001$) but were significantly higher in P1 than P2 in May 2000 ($F_{3,116} = 34.30$, $p < 0.0001$) and higher in P2 after May 2000

Table 4. Mean Shannon–Wiener diversity indices ± SD from 1999 to 2001. Fish were not detected in Napa-Sonoma Ponds 4 and 7. Invertebrates were collected too infrequently in Pond 7 for comparison. Means that are not significantly different (Tukey–Kramer) are indicated by similar superscripts

Pond	Mean bird H'	Mean fish H'	Mean invert H'
1	$1.75^{c} \pm 0.5$	$1.31^{b} \pm 0.5$	$0.96^{b} \pm 0.3$
2	$1.40^{b} \pm 0.7$	$0.53^{a} \pm 0.3$	$1.12^{b} \pm 0.3$
3	$1.58^{bc} \pm 0.4$	$0.84^{a} \pm 0.2$	$0.54^{a} \pm 0.3$
4	$1.83^{c} \pm 0.8$	–	$0.51^{a} \pm 0.2$
7	$0.60^{a} \pm 0.9$	–	–

($F_{3,116} = 57.11–139.05$, $p < 0.0001$). Mean separation tests indicated that diversity in P3 and P4 was similar on 6 of 10 intervals sampled in 1999 and 2000, but like P1 and P2, differed significantly in 2001. Diversity in P1 and P4 were similar (Jul 1999, Jan and Mar 2000) until 2001 when all ponds were dissimilar during all sampling intervals.

Diversity in P1 and P2 was represented by 50–55 taxa, many of which were uncommon, and high densities of individuals from just 3–4 taxa. P3 (25 taxa) and P4 (12 taxa) usually had lower numbers of taxa and similarly high densities in 2–4 taxa. *Heteromastus* sp. (polychaete), *Gemma* sp. (bivalve), *Corophium* sp. and *Ericthonius* sp. (amphipods) dominated taxa in P1 and P2, *Polydora* sp., *Capitella* sp. (polychaetes), *Corophium* sp., and occasionally *Streblospio* sp. (polychaete) and Corixidae (waterboatman insect) dominated P3, and *Artemia* and *Ephydra* dominated P4.

Fish

From July 1999 to December 2000, a total of 4334 fish representing 16 species was captured from P1 to P3. Gill netting yielded 730 fish (16.8%), whereas bag seining yielded 3604 fish (83.2%). Fish abundance from gill nets was high in both P1 (343 fish) and P2 (368 fish), with far fewer fish captured in P3 (19 fish). No fish were captured in P4. By comparison, bag seines indicated that fish abundance was highest in P1 (2694 fish), followed by P3 (779 fish), and P2 (131 fish). Combined biomass was greatest in P1 and P2, and much lower in P3.

Gill netting and bag seining sampled different segments of the fish species assemblage in each pond. In P1, American shad (*Alosa sapidissima*, 37.3%), striped bass (*Morone saxatilis*, 42.9%), and striped mullet (*Mugil cephalus*, 8.5%) were captured in gill nets, whereas Pacific staghorn sculpin (*Leptocottus armatus*, 51.4%) and yellowfin goby (*Acanthogobius flavimanus*, 41.6%) were captured in bag seines. In P2, gill net catches consisted almost exclusively of striped bass (94.3%), while bag seine catches consisted mostly of inland silverside (*Menidia beryllina*, 42.0%) and striped bass (32.8%). In P3, striped bass (47.4%), longjaw mudsucker (*Gillichthys mirabilis*, 36.8%), and yellowfin goby (15.8%) were caught in gill nets, and longjaw mudsucker (45.3%), Shimofuri goby (*Tridentiger bifasciatus*, 28.6%), and inland silverside (20.9%) were captured in bag seines. Shannon–Wiener diversity differed significantly among ponds ($F_{2,\ 22} = 10.40$, $p = 0.0007$). P1 had the highest overall diversity, significantly higher than P2 and P3 ($p = 0.0005$), which did not differ ($p = 0.318$; Table 4).

Birds

Mean diversity differed significantly among ponds ($F_{4,146} = 4.84$, $P = 0.0011$). P7 had the lowest diversity and differed significantly from all other ponds. Sixty-five species were recorded in all ponds, comprising several foraging guilds (see Takekawa et al., 2001). Diving benthivores comprised the majority of birds in all ponds followed by shallow probers. Surface feeders, dabblers, piscivores, and deep probers made up the remainder. P4 contained the greatest density of birds, whereas P1–P3 and P7 contained substantially less.

P1–P4 supported the majority of diving benthivores, primarily diving duck species. P2 supported almost exclusively diving ducks, representing over 95% of the birds counted in the pond. In P3, diving ducks comprised 70% of the birds counted in the pond. P7 had very few birds present year-round. Density of non-piscivorous birds was highest in Pond 1, and lowest in Pond 3. Piscivorous birds were much higher in Pond 1 compared with other ponds.

Waterbirds were most diverse and abundant on P1 (48 species and 23% of the total birds) and P4 (46 species and 46% of the total birds), but diversity on these ponds did not differ significantly from P3 ($T–K_{P3,P4}$, $p = 0.1293$; Table 4). In summer, P4 contained few diving benthivores relative to shorebirds, particularly shallow probers.

Trophic variation and the salinity gradient

The relationship between salinity and chl *a* (Fig. 5a) fit a quadratic equation with lowest concentrations at mid salinity ($r^2 = 0.4201$, $p = 0.0499$). Conversely, the relationship between salinity and zooplankton (Fig. 5b) was inverse, with highest concentrations of zooplankton at mid-salinities ($r^2 = 0.3661$, $p = 0.0002$). A test of the relationship between invertebrate biomass and

salinity (Fig. 5c) showed that salinity explained 16.8% of the variation in biomass ($p = 0.0176$) and 27.8% of the variation in invertebrate diversity ($p = 0.0008$). Macroinvertebrate biomass and diversity fit a quadratic curve similar to chl *a* (Fig. 5c), but with much higher levels at low salinities. Biomass of fishes decreased with salinity ($r^2 = 0.5667$, $p = 0.0002$; Fig. 5d), but the relationship between salinity and diversity was not significant ($r^2 = 0.0895$, $p = 0.3913$). Finally, bird density and diversity fit quadratic equations with highest levels at mid-salinities (Fig. 5e); density was not well explained by salinity ($r^2 = 0.0501$, $p = 0.0312$), whereas and bird diversity (Fig. 5e) fit a quadratic equation with highest levels at mid-salinities ($r^2 = 0.2308$, $p < 0.0001$).

Trophic similarity by season and salinity

The NMDS ordination showed that macroinvertebrate community composition was consistent within ponds across seasons and varied with salinity (Fig. 6a). Each pond had a cluster in Figure 6a, indicating that macroinvertebrate community composition was consistent within ponds for all seasons. Composition also varied with salinity, as indicated by left to right increase in salinity (bubble size) in Figure 6a. The macroinvertebrate ordination had a fairly good relationship with a low stress value of 0.12. P1 and P2 had comparable composition of taxa, but abundances of these common taxa differed over time. P3 had a distinct invertebrate community that differed from P1, P2 and P4, and the community of P4 vastly differed from P1, P2 and P3, reflecting the much higher salinity in P4 (Table 1).

Seasonal differences in invertebrate communities were not consistent, but spring was most often represented on the perimeter of pond groupings in ordination space (Fig. 6a). ANOSIM determined that the composition of invertebrate communities differed significantly among ponds (Global $R = 0.779$, $p < 0.0001$; Clarke & Warwick, 2001). In pairwise tests of the ponds, P1 and P2 community composition differed significantly but at a lower level of significance ($p = 0.001$) than all other pond pairs ($p < 0.0001$).

Fish community composition differed significantly among ponds overall (Global $R = 0.313$, $p < 0.0001$) and across pairwise comparisons ($p < 0.0001$). The excellent fit for the NMDS relating fish communities across ponds (stress = 0.07) suggests that seasonal variation in species composition may be closely related to salinity. Samples with similar salinity values had dissimilar species composition, whereas samples with dissimilar salinities had similar species composition, but within-pond samples were most similar across seasons (Fig. 6b). During summer and fall, the fish ordination plot suggested that P3 had the most dissimilar fish species composition from other ponds, and its community composition was closer to P3 in winter and spring than to any other pond (Fig. 6b).

Although species composition within ponds was less clearly delineated for birds than other taxa (except P7), community composition differed significantly among ponds overall (Global $R = 0.398$, $p < 0.0001$) and across pair-wise comparisons ($p < 0.0001$). The NMDS analysis (stress = 0.13) suggested a strong influence of salinity on avian species composition in P7 and in P4 (Fig. 6c), but P4 values were more similar to P1–P3. P7 in the spring was most dissimilar to all other pond and season combinations.

Discussion

The wetland classification system for the United States (Cowardin et al., 1979) recognizes estuarine wetlands modified by salinity, but poorly distinguishes the hyperhaline (haline is used to indicate an ocean salt source, but salinity is used interchangeably here unless referring to a specific wetland type) communities that we studied in the San Francisco Bay salt ponds. For example, P1 and P2 had very similar salinity, dissolved oxygen, and pH patterns, but they would be separated into mixohaline (0.5–30 g l^{-1}) and euhaline (30–40 g l^{-1}) classes. P3, P4 and P7 would be classified under the single modifier of hyperhaline (>40 g l^{-1}), despite great differences in their ecological communities. Inland saline classification systems also were inappropriate for classifying the ecological communities we studied. Javor (1989) used microorganisms to describe four hyperhaline classes characterized by macroalgae and fish (60–100 g l^{-1}), halophilic species (100–140 g l^{-1}), *Dunaliella* and *Artemia* (140–300 g l^{-1}), and low

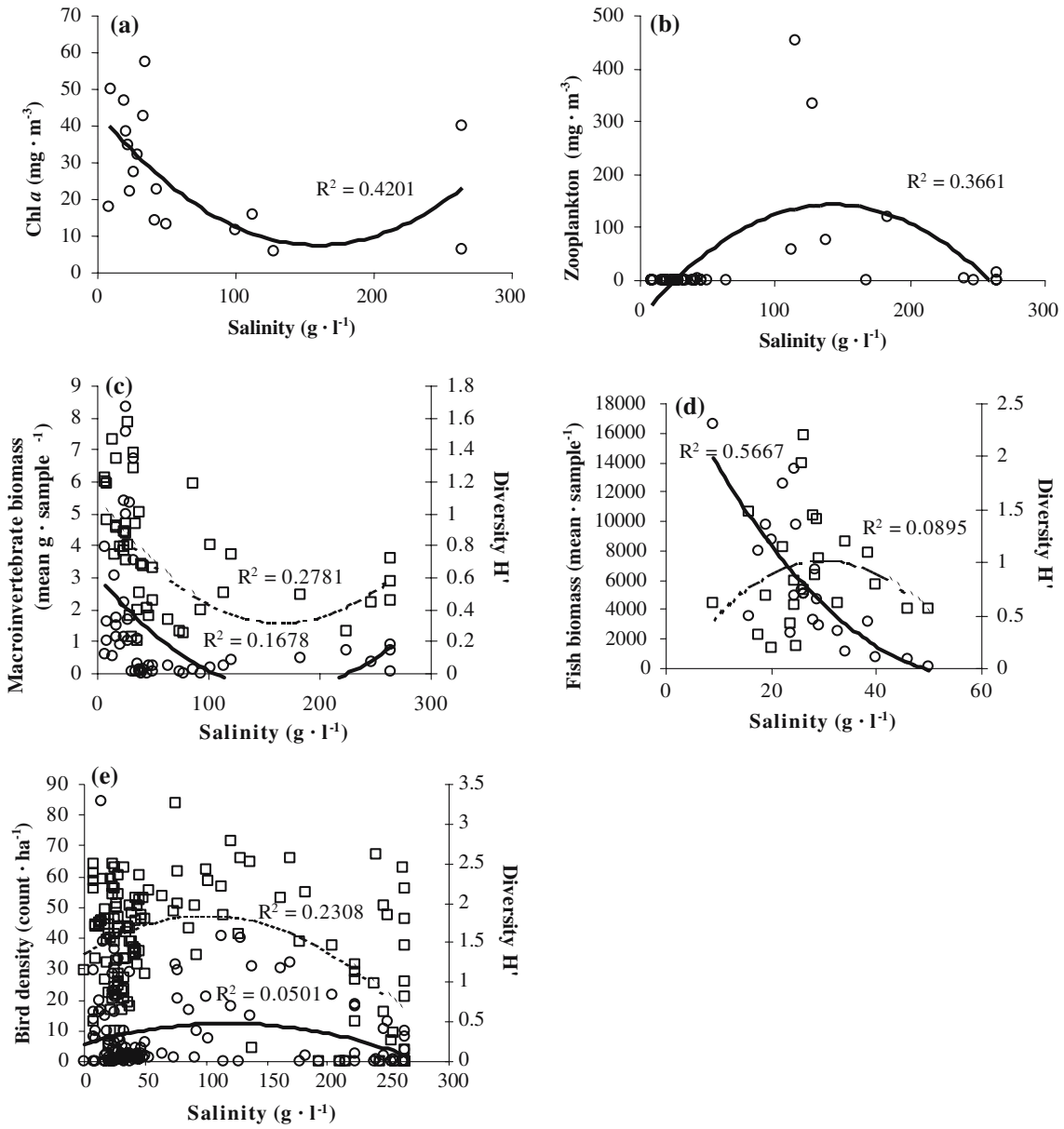

Figure 5. (a) Chlorophyll *a* (mg m^{-3}); (b) zooplankton (mg m^{-3}); (c) macroinvertebrate biomass (mg m^{-3}) and diversity (H'); (d) fish biomass (mg m^{-3}) and diversity (H'); and (e) avian counts (birds ha^{-1}) and diversity (H') across salinities in Ponds 1–4 of the Napa-Sonoma Marshes. Biomass (circles; solid line) and Shannon–Weiner species diversity (H': squares; broken line) are shown for (c) macroinvertebrates, (d) fish and (e) birds along with the best-fitting curves and regression coefficients for each. All relationships were significant ($p < 0.05$) except for fish species diversity ($p = 0.3913$).

productivity *Dunaliella* and bacteria (300–360 g l^{-1}), but higher trophic levels were not considered in his definitions. Thus, we used mixohaline (0.5–30 g l^{-1}), and low (31–80 g l^{-1}), mid (81–150 g l^{-1}), and high (>150 g l^{-1}) hyperhaline classes to better represent the distinctive trophic communities we observed.

Most studies of hypersaline systems have been conducted in interior salt lakes where species richness decreases steeply from freshwater to

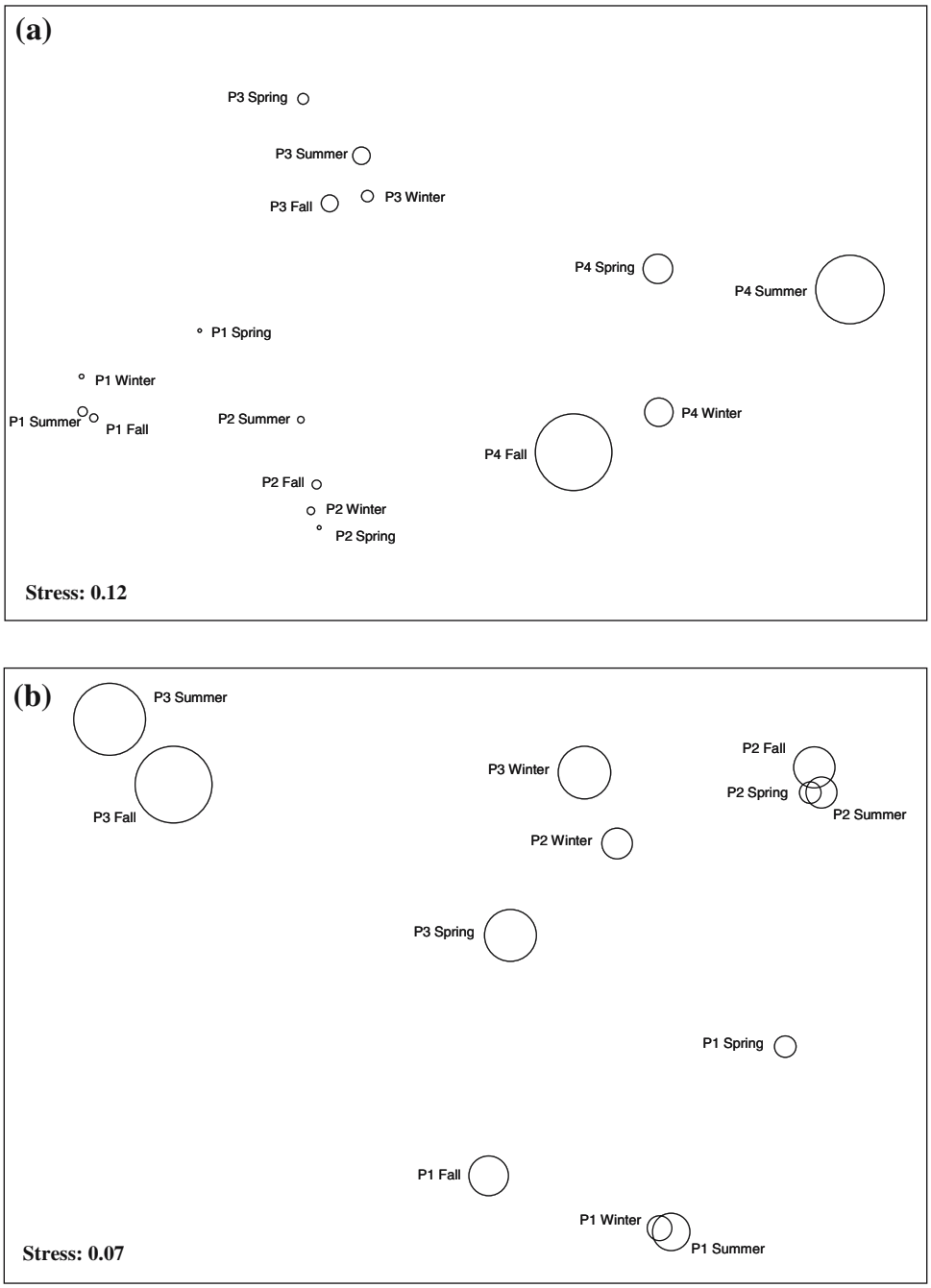

Figure 6. a and b

10 g l^{-1} and then gradually at higher salinity levels (Hammer, 1986). Our studies were conducted where salinities generally exceed mesohaline levels (5–18 g l^{-1}), and range as high as 224 g l^{-1}. Although hypersaline waters have been characterized as having low biological diversity determined by increasing salinity (Velasquez, 1992), we found that quadratic curves rather than inverse linearity

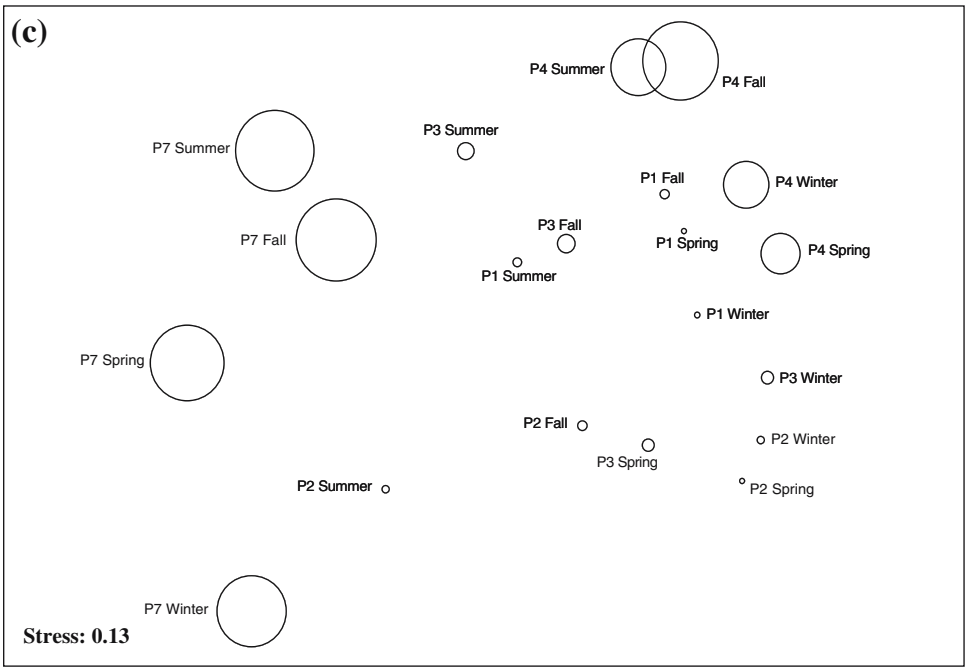

Figure 6. Non-metric Dimensional Scaling (NMDS) bubble plots across salinities (increasing diameter bubble with higher salinity) and seasons in Ponds 1–4 of the Napa-Sonoma Marshes, 1999–2001 for (a) macroinvertebrates (stress = 0.12), (b) fishes (stress = 0.07), and (c) birds (stress = 0.13). Low stress (excellent < 0.05; good < 0.010; uninterpretable > 0.3; Clark & Warwick, 2001) indicates a close representation of species composition differences in ordination space.

best described the relationship of biomass to salinity in salt ponds of the San Francisco Bay estuary (Fig. 5). A large proportion of the variation in biomass was explained by salinity for primary producers and primary consumers, and this relationship changed at higher salinities. Primary productivity biomass was highest under mid and high salinity conditions, whereas zooplankton biomass was highest under mid-salinity conditions. Changing biomass at higher salinities was likely often preceded by a shift in species composition. Copepods predominated in mid-salinity ponds P1–P2, but were replaced by *Artemia* and *Ephydra* in P4. Average zooplankton biomass in P4 was several orders of magnitude greater than in less saline ponds, due primarily to large concentrations of *Artemia* in this hyperhaline system.

Our analyses showed that salinity explained less of the variation in biomass for higher trophic levels than for lower ones. Macroinvertebrate biomass was highest in mixohaline P1, but the biomass of hypersaline ponds (P4, and also P3 toward the end of the study) was only slightly lower because they included large numbers of *Artemia* and *Ephydra*. Invertebrates underwent a change in community composition that resulted in an increase in biomass of *Artemia* following a decline in biomass of copepods, but fish as a group exhibit less variability in salinity tolerance and cannot survive > 80 g l^{-1}; thus, they cannot shift species composition. Although the relationship between fish biomass and salinity was strong ($r^2 = 0.5667$), this was an exception to the quadratic relationships because no fish were found above the low hyperhaline ponds. The relationship between bird density (as an index of biomass) and salinity was weak ($r^2 = 0.0360$), but the highest density of birds was found in the low to mid hyperhaline ponds (Fig 5e). Bird density and salinity followed a similar quadratic model at South Bay salt ponds (Warnock et al., 2002). Warnock et al. (2002) found a poorer fit for piscivorous than for non-piscivorous birds, possibly reflecting the greater numbers of fish in mixohaline ponds.

Descriptions of hypersaline systems suggest that as a general rule, species diversity decreases with salinity (Hammer, 1986; Williams et al., 1990; Williams, 1998). However, we found that similar to biomass, the relationship of salinity and species diversity in upper trophic levels followed quadratic curves (Fig. 5c–e). This was probably due to shifts in species composition, following salinity regimes, within these larger taxonomic groups. However, macroinvertebrates and fish did not respond to salinity changes as quickly as birds because community composition inside the ponds was dependent upon the source populations within the ponds and the opportunistic immigration of organisms into the ponds.

Diversity in the mid hyperhaline was lowest for macroinvertebrates and highest for fishes and birds. Similar to our findings, Britton & Johnson (1987) found highest biodiversity at mid hyperhalinity salt ponds in the Camargue estuary in southern France, but decreasing species richness with increasing salinity.

Seasonal variation

Britton & Johnson (1987) found that the regular seasonal cycle of salinity in salt ponds resulted in a predictable food supply and abundant avifauna. We found cyclical patterns of physical and biological variables with salinity, but the regularity of these patterns was obscured by changes in water management during our studies. Water quality (Fig. 2) generally followed annual weather patterns. The lowest salinity levels were recorded in winter (February) and highest in late summer (August), but salinities gradually increased overall during the study (Fig. 2a). Dissolved oxygen was inversely related to salinity and temperature and reached anoxic levels (<2 mg ml^{-1}) in P4 and P7.

The limited inflow to the pond system created greater dependence on nutrient recycling through remineralization and N-fixation in higher salinity ponds. Intake water accounted for the primary input of nutrients into P1 available for transformation by microbial organisms. Allochthonous nutrient sources also increased in importance as water was moved through the ponds and nutrients were transformed and depleted. Bacterial N-fixation and transformation of phytoplankton may have influenced the gradual increase in nitrate in higher salinity ponds.

Effects of salinity and evaporation were greatest on P4 with the lowest influx of water, contributing to the higher concentrations of both measured forms of nitrogen. Ammonia gradually increased from P1 to P3, but doubled from P3 (7.21 mg l^{-1}) to P4 (15.42 mg l^{-1}). This may be attributed to animal waste (i.e., zooplankton, birds) or decomposition of *Artemia* that exceeded bacterial oxidation and phytoplankton uptake. A simple feedback loop in the form of primary producers, grazers, higher consumers, and decomposers may be occurring in P4. Also, phosphorus was slightly higher in P2 than in other ponds; this pond was managed to attract waterfowl for hunting and stocked with fish, which may explain the elevated phosphorus.

Seasonal maximum macroinvertebrate biomass was recorded in mid hyperhaline P4 during spring and coincided with the largest number of foraging birds at the ponds. Salinity changes in the ponds followed a seasonal pattern, but changes in macroinvertebrate diversity did not. The water regime on P1 was muted tidal flow influenced largely by changes in adjacent estuarine waters, and the diversity of taxa in this pond was generally similar to that found in the North Bay sub-region (Miles, unpublished data). Water quality and diversity in P2 was similar to that in P1, except in September 2000; water management on P2 may have been altered around that sampling interval. The temporal pattern of species diversity was similar in P3 and P4, but changes in P3 were followed by changes in P4 at subsequent sampling intervals, e.g., peaks in diversity in P3 during Jul 1999, Mar 2000, and Feb 2001 were followed by peaks in P4 during Sep 1999, May 2000 and after Jun 2001.

The largest densities of waterbirds were seen in spring, with the next largest number of birds observed in winter (Takekawa et al., 2001). Most migratory bird species were not present in the estuary during summer, and we counted fewer birds in fall compared with spring when the largest number of waterbirds was counted. Although species composition did exhibit some seasonal variability, there was a greater degree of similarity within ponds than within seasons, even when salinity levels were similar (Fig. 6). Thus, factors

other than salinity seemingly influenced species composition in ponds.

Factors other than salinity

We measured seasonal variation in biomass and diversity among trophic levels across a salinity gradient, but we did not control for differences among or within ponds because we lacked replication in this single system. Factors other than salinity may have greatly influenced the system, such as hydrologic patterns, ionic composition, oxygen content, biological interactions, and water depth that might affect community structure (Carpelan, 1957; Anderson, 1970; Williams et al., 1990; Velasquez, 1992; Williams, 1998).

Hydrologic patterns

In northern San Francisco Bay, salinities may become diluted to oligohaline levels (0.5–5 g l^{-1}) in late winter, but average salinities in the salt ponds typically remained above mesohaline levels and were influenced by rainfall and evaporative loss. Fauna in even the mixohaline salt ponds differed from euryhaline estuarine species in salt ponds of southern France (Britton & Johnson, 1987) and impoverished fauna at hypersalinity was attributed to lagoon-type confinement. Similarly, Carpelan (1957) described South Bay salt ponds as more similar to littoral lagoons than estuarine wetlands.

Ionic composition and nutrients

Species diversity quickly decreases in low hyperhaline ponds when carbonates precipitate (70 g l^{-1}), remains constant in mid hyperhaline ponds when $CaSO_4$ precipitates (150 g l^{-1}), and declines in high hyperhaline ponds where few species of invertebrates survive (300 g l^{-1}; Britton & Johnson, 1987). Fish are absent above the low hyperhaline, but *Artemia* and *Ephydra* reach maximum density at high hyperhaline, although they may survive across a much wider range of salinities (Maffei, 2000). Molluscan species with carbonate shells tend to disappear above low hypersalinity, and our collections indicated few clams in P3 and P4. Salt ponds typically have low N and P, restricting plant growth (Britton & Johnson, 1987) and increasing nitrate with salinity, although our results showed nitrates were highly variable (Fig. 3). P1–P2 had beds of *Ruppia maritima*, but hyperhaline ponds lacked any submergent macrophytes.

Dissolved oxygen

Sherwood et al. (1992) reported an inverse relationship between oxygen content and salinity ranging from 8.85 mg l^{-1} at 5 g l^{-1} to 1.7 mg l^{-1} at 260 g l^{-1}. Williams (1998) suggested that respiratory breakdown occurs at ~2 mg l^{-1}. In the mid and high hyperhaline ponds, oxygen dropped below the respiratory threshold in summer months. The lack of oxygen in those ponds may have influenced the biomass of invertebrates.

Biological interactions

Our chl *a* and zooplankton data illustrate food web interactions at several trophic levels. First, we found a weak negative correlation of zooplankton biomass with chl *a*. The negative relationship between biomass of *Artemia* and chl *a* was stronger in P4. Grazing by *Artemia* probably reduced algal densities, resulting in low chl *a* concentrations during summer. In turn, increased chl *a* concentrations in winter were probably influenced by decomposition of *Artemia* and subsequent increased ammonia that benefited phytoplankton. *Artemia* was the key taxon in the simple food web of P4. In this fishless pond, high densities and biomass of *Artemia* likely contributed to the high use by foraging birds.

Replacement of copepods in the hyperhaline ponds by *Artemia* is likely the result of both salinity and food web effects. Although *Artemia* may tolerate salinities near sea-water (35 g l^{-1}) (Persoone & Sorgeloos, 1980), *Artemia* predators occupy lower salinity environments (Wurtsbaugh, 1992). When salinity in the Great Salt Lake, Utah, declined from >100 to ~50 g l^{-1}, Wurtsbaugh (1992) reported that the predaceous insect *Trichorixa verticalis* became abundant in the open waters of the lake and *Artemia* declined dramatically. Wurtsbaugh (1992) subsequently reported corixids attacking adult *Artemia*, but more importantly preying on nauplii or other juvenile stages of *Artemia*, therefore limiting the development of the population. In a similar study, Herbst (2001) observed *Artemia* and *Ephydra* were restricted to moderate to high salinity

salt ponds located in the Mojave Desert, California, while *Trichorixa* adults occupied lower salinity ponds.

Soluble and total P concentrations seemed to be higher in mixohaline P2 than elsewhere, chl *a* concentration was intermediate, and copepod abundance and biomass was low. P2 has been the subject of manipulations for sport fishery purposes and had higher densities of potentially zooplanktivorous fishes than any other pond. Thus, it appears that fish predation on zooplankton may have contributed to a trophic imbalance in P2 (Carpenter, 1988), where reduced zooplankton biomass resulted in greater algal growth than in P1, and algal growth in P2 reduced nitrogen, the limiting nutrient in these ponds.

Water depth

Velasquez (1992) noted that while bird abundance was related to salinity, availability of habitat to birds depended on depth. Ponds that contained islands and were more spatially variable in depth overall contained a wider variety of foraging guilds, particularly shorebirds. P2 and P3 were more homogenous and invariant in depth than the other ponds and supported diving birds almost exclusively in 1999–2001. P2, which contained few islands, supported almost exclusively diving ducks whereas P3, which had more islands and exhibited more variability in depth overall, contained fewer relative to other guilds. Dabblers and diving benthivores were present in P1–P3, but the two guilds were mostly spatially separated within the ponds. Water depths varied spatially in P1, which was very shallow at the southern end and deeper on the northern end. Diving benthivores were more common on the deep northern end of P1 while dabbling ducks used the shallower southern end. Water depth varied temporally in P4, which was deep (0.5–2.0 m) in the winter and much shallower or dry in the summer. P4 had more overlap of dabblers and diving benthivores, in part explained by the water fluctuation in this pond throughout the year. The water depth was more variable and there may have been times when the water level was acceptable for both guilds. Water was not flowing through the siphon pipe to P4 in the summer, and as a result, P4 was more than 50% dry during summer months. This caused a decline in diving benthivores numbers and an increase in the number of shorebirds, particularly shallow probers.

Anderson (1970) noted that birds such as diving ducks, grebes, phalaropes, and Bonaparte's gulls (*Larus philadelphia*) in the South Bay salt ponds used high hyperhaline ponds, and shorebirds seemed to use ponds of suitable water depth regardless of the salinity. Other researchers have suggested that shorebirds require water depths of <8 cm (Collazo et al., 1995; Davis & Smith, 1998). However, shallow water depths may also indicate warmer temperatures and less DO, reducing populations of macroinvertebrate and fish prey species.

Optimizing salt ponds for waterbirds

Salt ponds are synonymous with large populations of migratory waterbirds (Takekawa et al., 2001; Paracuellos et al., 2002; Warnock et al., 2002), yet the unique ecology of these hyperhaline systems has not been well described, especially within estuaries. Artificial salt ponds have existed in the estuary since the mid-1800s (Ver Planck, 1958). Our study indicated that salinity was a major driver in the system for lower trophic levels, but it was more variable at higher trophic levels. Seasons and salinity were more similar than pond for macroinvertebrates (Fig. 6a), but for fish (Fig. 6b), salinity was a major driver. In contrast, mixohaline and high hyperhaline avian communities were distinct, while mid hyperhaline ponds were similar (Fig. 6c). Most birds were found in the mid hyperhaline (Fig. 5e). We found that the density of benthivores was four times greater in the salt ponds compared with the baylands in the winter and spring (Takekawa et al., 2001).

Salt ponds were heavily used during migration, and populations of waterbirds were higher in spring than in fall, possibly because invertebrate populations tended to increase during winter and into spring. Studies of western sandpipers (*Calidris mauri*; Warnock & Takekawa, 1996) confirmed that this species used salt ponds more during spring. Shallow probers were found to be denser in spring, primarily because of the migration of large numbers of western and least sandpipers. Salt ponds provided these species with multiple advantages. The large expanses of water facilitated

taking flight, and predator avoidance without human disturbance and the shallow, sheltered impoundments likely created a favorable microclimate for roosting and foraging.

The salt ponds generally decreased in depth and increased in salinity from summer through fall, which may have reduced invertebrate biomass and foraging value for many waterbirds. In salt ponds, the largest densities of waterbirds were seen in spring, with the next largest number of birds observed in winter. Most migratory bird species were not present in the estuary during summer, and we counted fewer birds in fall than in spring.

Historic wetland habitats that were converted to agriculture or urban development now have limited value for waterbird species, with the exception of areas inundated seasonally during winter and spring. Restoring or rehabilitating these agricultural and urban areas is likely beneficial for waterbirds. However, converting from one wetland habitat type to another, such as converting salt ponds to tidal marsh, will likely benefit some species at the expense of others. Most shorebirds prefer more open habitats rather than tidal marsh plain habitats (Warnock & Takekawa, 1995). Development of coastal zones and interior valley wetlands have resulted in fewer areas available for migratory waterbirds in the flyway, and alternative wetlands may not exist outside of the San Francisco Bay estuary to compensate for loss of waterbird habitats in the ecosystem.

Our results suggest that the Napa salt ponds provide a unique habitat for waterbirds. *Artemia* represents an important food resource in mid hypersaline ponds, with biomass exceeding the combined biomass of other ponds by several orders of magnitude. Because *Artemia* was so abundant in the diversity-poor mid hypersaline ponds, its demise probably would substantially affect upper trophic level organisms. Although zooplankton species richness decreased with increased salinity, the ability of the larger bodied *Artemia* to successfully occupy hypersaline waters allows it to escape predators and competitors found in lower salinity ponds (Herbst, 2001; Wurtsbaugh, 2002). Changes that reduce salinity will eradicate *Artemia*, as well as *Ephydra*, and result in a dramatically different food web. Proper management of hyperhaline salt ponds must include water depth and hypersalinity as elements important for waterbirds. Eliminating artificial salt ponds without providing alternative habitats may reduce or extirpate avian species from the ecosystem.

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