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SALT LAKE RESEARCH

Dietary flexibility in three representative waterbirds across salinity and depth gradients in salt ponds of San Francisco Bay

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Abstract Salt evaporation ponds have existed in San Francisco Bay, California, for more than a century. In the past decade, most of the salt ponds have been retired from production and purchased for resource conservation with a focus on tidal marsh restoration. However, large numbers of waterbirds are found in salt ponds, especially during migration and wintering periods. The value of these hypersaline wetlands for waterbirds is not well understood, including how different avian foraging guilds use invertebrate prey resources at different salinities and depths. The aim of this study was to investigate the dietary flexibility of waterbirds by examining the population number and diet of three feeding guilds across a salinity and depth gradient in former salt ponds of the Napa-Sonoma Marshes. Although total invertebrate biomass and species richness were greater in low than high salinity salt ponds, waterbirds fed in ponds that ranged from low (20 g l^{-1}) to very high salinities (250 g l^{-1}). American avocets (surface sweeper) foraged in shallow areas at pond edges and consumed a wide range of prey types (8) including seeds at low salinity, but preferred brine flies at mid salinity (40–80 g l^{-1}). Western sandpipers (prober) focused on exposed edges and shoal habitats and consumed only a few prey types (2–4) at both low and mid salinities. Suitable depths for foraging were greatest for ruddy ducks (diving benthivore) that consumed a wide variety of invertebrate taxa (5) at low salinity, but focused on fewer prey (3) at mid salinity. We found few brine shrimp, common in higher salinity waters, in the digestive tracts of any of these species. Dietary flexibility allows different guilds to use ponds across a range of salinities, but their foraging extent is limited by available water depths.

Keywords Salt ponds · Diet · Waterbirds · San Francisco Bay

Introduction

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). San Francisco Bay is recognized as a site of hemispheric importance for shorebirds because it

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supports at least 30% of some populations in the flyway (Harrington & Perry, 1995) and also supports up to 50% of many diving duck populations (Accurso, 1992). Many migratory waterbirds use the baylands, which consist of the area between the historic high and low tide lines, and comprises about 85,830 ha in the estuary (Goals Project, 1999).

Several tidal marsh species are now endangered because more than 90% of historic wetlands have been lost to urbanization, agriculture, and salt production (Josselyn, 1983; Nichols et al., 1986). The 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). Salt ponds have been present in the San Francisco Bay estuary for more than 150 years (Ver Planck, 1958). These 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 simple but productive assemblages of algae and invertebrates (Carpelan, 1957; Lonzarich, 1988; Lonzarich & Smith, 1997). The ponds have become an integral part of the landscape, as well as critical habitats for a large number of waterbirds during migration and the winter (Anderson, 1970; Swarth et al., 1982; Accurso, 1992; Takekawa et al., 2001; Warnock et al., 2002).

Nearly 4,000 ha were purchased in the North Bay and taken out of salt production in 1994. Resource management agencies have proposed converting the salt ponds into tidal marshes to minimize management costs and restore populations of tidal marsh species of concern. Only a few hundred hectares of salt ponds in the estuary will likely remain through the next century (Goals Project, 1999), but the importance of these ponds as foraging areas for migratory birds is not well understood. Little is known about the invertebrate prey in these ponds and their use by migratory birds. Thus, we initiated a study to document the dietary flexibility of three representative waterbirds or their consumption of different invertebrate prey across salinity and depth gradients.

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 (38.17°N, 122.33°W), and comprised about 4,000 ha. They were acquired in 1994 by the California Department of Fish and Game as part of the Napa-Sonoma Marshes Wildlife Area (hereafter Napa-Sonoma Marshes). Although salt production ceased in 1993, the hyperhaline 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 (Miles et al., 2000; Takekawa et al., 2000).

Materials and methods

Three ponds representative of the salinity gradient in the salt pond system were selected for dietary sampling (Fig. 1). Ponds 1 (P1), 3 (P3), and 4 (P4) ranged in size from 127 to 534 ha and varied in mean salinity from 22 to 69 g l^{-1} between August 1999 and April 2000. Pond P2 was not used for diet analyses, because minimal numbers of the representative bird species were found in the pond. Pond P1 was the intake pond from a channel to the North Bay, fed by tidal influence through a one-way gate, and was pumped into Pond 2 (P2) intermittently during the study period (T. Huffman, California Department of Fish and Game, personal communication). Siphons that connect P2 to P3 and P3 to P4 were blocked by salt plugs through the study period, so that P3 and P4 were isolated with little inflow or outflow (Lionberger et al., 2004). We superimposed a 250 × 250 m (6.25 ha) Universal Transverse Mercator (UTM) grid upon the sampled ponds to provide a geographical framework for identifying depths used within ponds (Miles et al., 2000; Takekawa et al., 2000). This gridcell system provided the basis for identifying locations of birds in each pond (Matveev, 1995; Posey et al., 1995).

Water quality

Water quality parameters were measured monthly in P1–P4 in 1999 and 2000 (Lionberger et al., 2004). 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

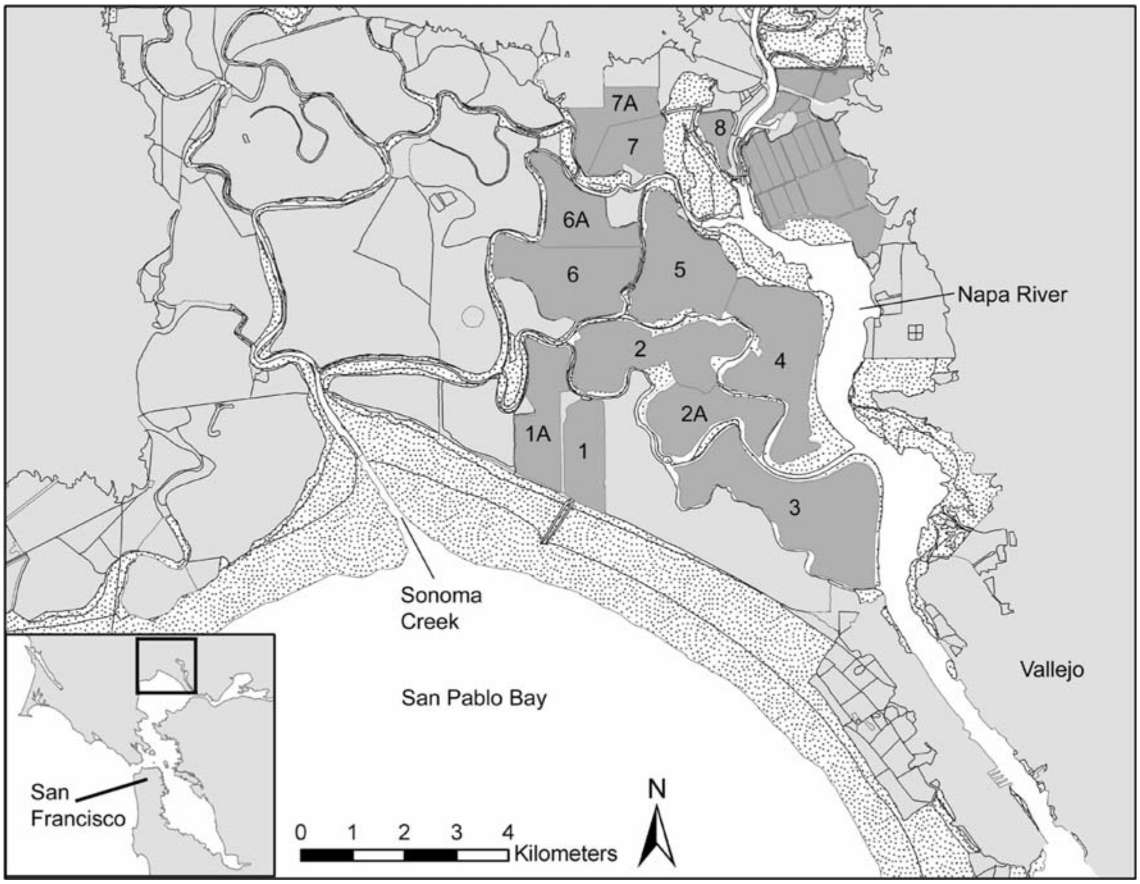

Fig. 1 Former salt evaporation ponds in the Napa-Sonoma Marshes located 5 km northwest of Vallejo, California, USA on the northern edge of San Pablo Bay in the San Francisco Bay estuary. Bold text indicates ponds 1, 3, and 4 sampled in this study

spatial variability in the ponds, and measurements were made on the same day as 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 (Lionberger et al., 2004). The sensors on the sonde 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, New Jersey) scaled for the appropriate range. These data were corrected for temperature and converted to salinity.

Macroinvertebrate availability

Benthic macroinvertebrates were sampled bimonthly in P1–P4 from July 1999 to March 2000. Monthly waterbird surveys were used to identify areas used by birds, and 10 gridcells were randomly selected and located by GPS to sample for benthic macroinvertebrates within each pond. From a 3.5 m flat-bottom boat, we located the center of each sample gridcell with a GPS unit and then collected three cores (about 3 m apart) with a standard Ekman grab sampler (15.2 cm^3; Wildlife Supply Company, Buffalo, NY).

A standard (USA ASTME—11 Number 18) 1.0-mm ATM standard mesh sieve was used to reduce cores to invertebrates and debris that were then preserved in 70% ethanol, glycerin, and rose bengal dye.

Field samples were processed using binocular microscopes (3–10×) 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). For quality control, our identifications were confirmed by an independent invertebrate taxonomist (Hydrozoology Corp., New Castle, CA). Further, an experienced second observer verified identification and numeration of 5–10% of all processed samples. Prey items were grouped into nine categories (categories were based primarily on relative abundance of these taxa in ponds and in bird diets) for analysis: *Heteromastus* and *Polydora* (polychaete worms), *Corophium* and *Grandidierella* (amphipods), Diptera (flies in Ephydridae & Muscidae), Nematoda (free-swimming roundworms), Mollusca (the bivalves *Gemma gemma*, *Macoma balthica*, *Potamocorbula amurensis*), seeds (Asteraceae), and other [mostly Corixidae (water boatman), Capitella, Streblospio, Tubificoides (polychaetes), Cumacea (small crustacean), and Hydrophilidae (beetles)]. 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 and weighed to determine the dry weight. Invertebrate biomass was obtained from 10 sample locations per pond per month. A composite value was obtained for invertebrate availability from the mean of the three samples at each location for Pond 1 ($N = 15$), P3 ($N = 9$), and P4 ($N = 3$).

Bird surveys

We conducted monthly complete counts of the ponds in 1999 and 2000. 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. Waterbirds were separated into seven guilds to examine differences among foraging groups rather than differences among species (Takekawa et al., 2006). In this study, we examined the diet of representative species from three of these foraging guilds: (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); and (3) diving benthivores—fed in deeper water on benthic invertebrates e.g., *Oxyura jamaicensis* (ruddy duck). We recorded whether observed birds exhibited foraging or non-foraging behaviors.

Diet sampling

Diet samples were obtained from 13 American avocets (6 from Pond 1, 7 from Pond 4), 19 Ruddy ducks (10 from Pond 1, 9 from Pond 3), and 18 western sandpipers (10 from Pond 1, 8 from Pond 4) from November 1999 to March 2000. Birds were collected with 12-gauge shotguns and #6 steel shot from flocks that were observed actively foraging. Specimens were measured, weighed, aged, and sexed. The complete digestive tract was removed immediately after collection and placed in 75% ethanol. Invertebrates contained in each esophagus and proventriculus were removed, sorted, and identified with a 20-power dissection microscope before being dried and weighed.

Analyses

Diet was analyzed by unique prey category using three relative measures of prey quantity (RMPQ): percent composition by number (%N), percent composition by mass (%M), and percent frequency of occurrence (%F), defined as samples containing a unique prey category divided by the total samples × 100. To present diet variability, we used the three RMPQ graphically in index of relative importance (IRI) charts. IRI (Pinkas, 1971) was calculated with the formula $\mathrm{IRI} = F\ (N + M)$, where F is the percent frequency of occurrence, N is the percent abundance, and M is the percent biomass, adapted by Risbey et al. (1999).

We conducted multiple regression analyses (SAS Institute, 2000) to identify relationships among

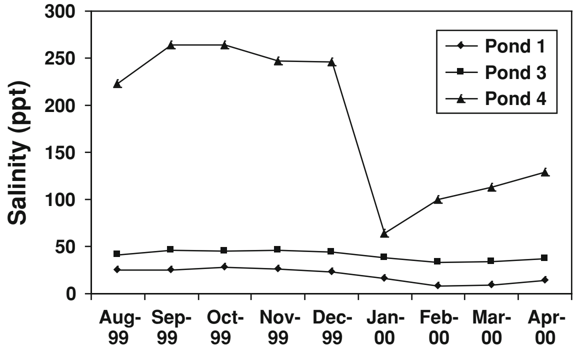

Fig. 2 Monthly salinity ranges for Ponds 1, 3, and 4 in the Napa-Sonoma Marshes, 1999–2000

macroinvertebrates, salinity, and water depth. Salinity was averaged across ponds, while depth was estimated for individual grid cells within ponds. We related the abundance of birds with salinity, depth, dominant macroinvertebrates and total biomass. Bird counts were log-transformed, and zero counts were included. We specified significant findings where $P < 0.05$.

We then used CANOCO 4 (ter Braak & Smilauer, 1998) to perform canonical correspondence analyses (CCA; ter Braak, 1986, 1988) to reveal gradients in species composition and relate log-transformed avian abundance values to environmental variables (salinity, depth, and biomass). The CCA biplot shows the correlation between species and environmental variables. Longer lines indicate stronger relationships than shorter lines. Lines pointing in the same direction indicate correlated variables, in opposite directions are negatively correlated, and at 90° are uncorrelated. Similarly, species near each other are highly correlated.

Mention of trade names does not imply U. S. Government endorsement.

Results

Salinity

The salt production system' control infrastructure deteriorated after purchase in 1994, and salinity varied widely under the compromised water management system (Fig. 2). Pond P4, isolated from flow by an ineffective siphon (Lionberger et al., 2004), showed the widest variation in salinity. Mean salinity ranged from 22 g l^{-1} in P1, 40 g l^{-1} in P3, and 69 g l^{-1} in P4 during the spring months. Salinity was elevated through the early winter, but following late winter rainfall, decreased with a gradual increase through the spring (Fig. 2). The pH of most ponds was alkaline, and 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 (Takekawa et al., 2006). Decreased water levels combined with elevated temperatures resulted in low dissolved oxygen readings in P4 during the summer months.

Table 1 Total dry weight biomass (mg m^{-2}), mean number of individuals (n m^{-2}), and mean weight (mg $item^{-1}$) of individual invertebrates found in benthic samples of three salt ponds ($n = 9$) taken from salt ponds in Napa-Sonoma Marshes Wildlife Area, California (November 1999 to March 2000)

Taxa	Pond 1			Pond 3			Pond 4			All Ponds
	mg m^{-2}	n m^{-2}	mg $item^{-1}$	mg m^{-2}	n m^{-2}	mg $item^{-1}$	mg m^{-2}	n m^{-2}	mg $item^{-1}$	mg m^{-2}
Corophium	261.1	3,125	0.08	4.3	35	0.13	0	0	0	265.5
Diptera	0	0	0	0	0	0	1053.2	3,203	0.33	1053.2
Grandidierella	112.8	984	0.11	0	0	0	0	0	0	112.8
Heteromastus	2265.1	1,405	1.6	0	0	0	0	0	0	2265.1
Bivalves	36966.2	16,384	2.26	0	0	0	0	0	0	36966.2
Nematoda	0.0002	332	0.0001	0	0	0	0	0	0	0.0002
Other	46.16	332	0.14	129.8	398	0.33	304.4	303	1.0	480.4
Polydora	0	0	0	79.6	796	0.1	0	0	0	79.6
Seeds	0	0	0	181.8	208	0.88	0	0	0	181.8
Total	39651.4			395.6			1357.6			41404.7

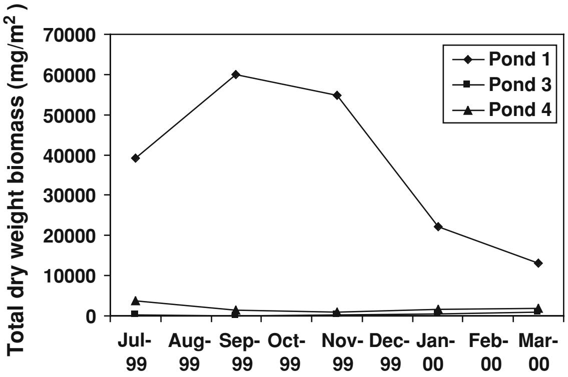

Fig. 3 Total dry biomass of macroinvertebrates in Ponds 1, 3, and 4 of the Napa-Sonoma Marshes, July 1999–March 2000

Macroinvertebrate abundance

Richness and numbers of individual benthic macroinvertebrate prey were higher on P1 compared with P3 and P4 (Table 1). Macroinvertebrate prey on P1 were represented by 50–55 taxa, many of which were uncommon, and high densities of individuals from 3 to 4 taxa (Takekawa et al., 2006). Ponds P3 (25 taxa) and P4 (12 taxa) had lower numbers of taxa, but higher densities relative to P1. Biomass of invertebrates was highest on P1 and much lower in P3 and P4 (Table 1; Fig. 3). *Gemma gemma* (bivalve) dominated the taxa on P1, followed by *Heteromastus* (polychaete) and *Grandidierella* (amphipod). *Polydora* (polychaete) dominated the taxa on P3 followed by other including Streblospio (polychaete), *Corophium* (amphipod), and occasionally Corixidae (water boatman). Seeds were also abundant on P3. On P4, *Artemia* (brine shrimp) and Diptera (mostly the brine fly *Ephydra*) dominated the taxa. We found that abundance of *Corophium* and total biomass was inversely related to salinity, while *Ephydra* was positively linked to salinity (Table 2).

Avian populations

Sixty-five species have been recorded in the ponds representing all seven foraging guilds (see Takekawa et al., 2001). Diving benthivores comprised the majority of birds, followed by shallow probers. P1 and P4 contained the greatest number of birds through the winter, whereas P1 and P3 were substantially lower. P3 was more uniformly deep than the other ponds and supported diving birds almost exclusively. 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) (Takekawa et al., 2006).

Water depths varied spatially in P1, very shallow at the southern end and deeper on the northern end, and temporally in P4, which was deep (0.5–2.0 m) in the winter and much shallower or dry in the summer. Water was not flowing through the siphon pipe to P4 in the summer, and as a result, P4 was more than 50%

Table 2 Regression analyses of macroinvertebrate biomass with salinity and water depth (November 1999–March 2000)

Dependent variable	Independent variable	Coefficient	*F*-value	*P*-level
Corophium sp.*			$F_{2,67} = 4.547$	0.014
	Salinity	−0.178		0.160
	Water depth	−0.234		0.066
Grandidierella sp.			$F_{2,67} = 1.831$	0.168
	Salinity	−0.099		0.450
	Water depth	−0.170		0.196
Ephydra sp.*			$F_{2,67} = 23.009$	0.000
	Salinity*	0.677		0.000
	Water depth	−0.121		0.242
Polydora sp.			$F_{2,67} = 1.168$	0.317
	Salinity	−0.114		0.388
	Water depth	0.197		0.138
Total invert biomass*			$F_{2,67} = 5.496$	0.006
	Salinity	−0.222		0.077
	Water depth	−0.227		0.071

dry during summer months. This caused a decline in diving benthivore numbers and an increase in the number of shorebirds, particularly shallow probers. Diving benthivores were common on the deeper northern end of P1 while avocets used the shallower southern end. P4 had more overlap of these two guilds, 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.

In P1, the three species that we sampled for diet were present with larger numbers of western sandpipers during the spring migration in April (Fig. 4). Ruddy ducks were much more abundant than other species in P3 in the midwinter because the pond provided deeper water preferred by diving birds. Western sandpipers and American avocets were more abundant than ruddy ducks in P4, a pond that was very shallow because of limited inflow.

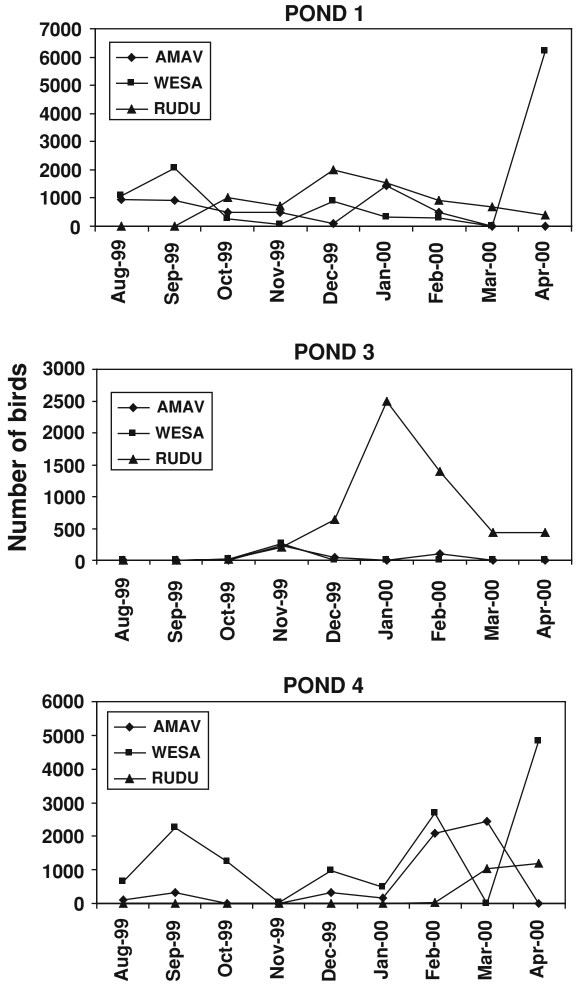

Fig. 4 Numbers of American avocets, western sandpipers, and ruddy ducks counted on Ponds 1, 3, and 4 during monthly surveys in the Napa-Sonoma Marshes, August 1999–April 2000

Diet preferences

Collected samples indicated that birds varied their diets widely with changing salinity (Table 3). The flexibility in diets of American avocets was evident as they switched from six main prey types in P1 to only one Diptera in P4. Ruddy ducks consumed five main prey types in P1, but only two main prey types in P3. Western sandpipers consumed two major prey types in P1, and like American avocets, only Diptera in P4.

American avocets preferred *Heteromastus* in P1; bivalves were consumed, but in lower proportion than abundance would indicate (Fig. 5). In P4, American avocets consumed Diptera in lower proportion than found in samples; however, it was very difficult to obtain representative samples of Diptera adults and larvae that were found along beach ridges rather than in the water. Ruddy ducks had greater proportions of *Corophium*, *Grandidierella*, and bivalves than those, which were available in P1 (Fig. 5), but surprisingly their use of *Polydora* was the only preferred prey in P4. Western sandpipers preferred *Grandidierella* and Nematoda in P1, and *Corophium* in P4.

Overall, the IRI (Fig. 6) indicated a different dietary flexibility for all three species. American avocets changed from consuming several prey items in low salinity P1 to consuming a single prey in high salinity P4. Ruddy ducks consumed several different prey at both low (P1) and high (P3) salinity, while western sandpipers seemed most selective, consuming only a few prey across salinities. Although *Artemia* were often abundant in the water column, few were found in the Ekman samples that were the best for sampling benthic invertebrates; however, we also found few *Artemia* in the digestive tracts of the avian species that we sampled, indicating that they were not often consumed.

Water depth and availability

We found that all species were clustered by depth to some extent (Fig. 7), but ruddy ducks were

Table 3 Percent of gut content samples containing at least one prey item

Bird species	American avocet		Ruddy duck		Western sandpiper	
Prey type	Pond 1 $n = 6$	Pond 4 $n = 7$	Pond 1 $n = 10$	Pond 3 $n = 9$	Pond 1 $n = 10$	Pond 4 $n = 8$
Corophium	8.3	0	23.5	0	0	0.2
Diptera	0	100	0	0	0	95.3
Grandidierella	8.3	0	33.1	0	12.5	0
Heteromastus	0	0	6	0	0	0
Bivalves	16.7	0	27	0	0	0
Nematoda	8.3	0	0	0.2	87.5	0.4
Other	41.7	0	0	2.4	4.3	0
Polydora	8.3	0	0	44.6	0	0
Seeds	8.3	0	10.4	52.7	0	0

Samples taken from wintering American Avocets, Ruddy Ducks, and Western Sandpipers collected while foraging in three salt ponds in the Napa-Sonoma Marshes State Wildlife Area, California

distributed more widely than the other species. Western sandpipers were found in shallow edges of P1 and P3, but water levels were shallow throughout P4, resulting in a wide distribution. Ruddy ducks were limited to deeper waters in the northern end of P1, as well as in much of P3.

We used CCA to examine species–environmental relationships and found that the first axis eigenvalue was 0.53 ($F = 19.35$, $P = 0.003$), and the second eigenvalue was 0.28 ($F = 6.70$, $P = 0.001$), each based on 1,000 Monte Carlo iterations (Fig. 8). The first two axes explained 92% of the species–environment variance and 49.7% of variation among the species. The sum of the unconstrained eigenvalues = 1.63 and canonical eigenvalues = 0.877 and the model explained 54% of the overall variance.

Presence of *Ephydra* was strongly related to salinity, and presence of *Grandidierella* and *Corophium* was highly correlated, but inversely related to water depth (Fig. 8). Biomass was positively correlated with *Polydora*. None of the physical variables was correlated with each other. The species response showed similar responses for non-foraging and foraging American avocets and western sandpipers, but foraging ruddy ducks were related to higher salinity, higher *Ephydra* areas, while non-foraging ruddy ducks were weakly correlated with biomass and not correlated with foraging ruddy ducks.

Relating species presence and behavior to salinity, depth, and macroinvertebrates in multiple regressions (Table 4), we found significant relationships for foraging and non-foraging western sandpipers and foraging American avocets. Ruddy ducks used the widest range of water depths, and their presence was not significantly related to water depth. With the exception of western sandpipers, relationship to *Grandidierella* and total biomass, relationships to specific invertebrates were low for all avian species indicating dietary flexibility across salinity.

Discussion

We compared mixohaline (0.5–30 g l^{-1}) and hyperhaline (>40 g l^{-1}) salt ponds to examine macroinvertebrate communities and avian consumers representing three different foraging guilds. We found that macroinvertebrate abundance varied with salinity and was much higher at lower salinity, but that foraging and non-foraging western sandpipers and foraging American avocets were present within gridcells with appropriate water depths. The availability of macroinvertebrate prey was likely dependent on water depth (Velasquez, 1993), especially for the relatively short-legged western sandpipers. However, the presence of ruddy ducks, a diving benthivore, was not correlated with water depth.

Shorebirds

Most shorebirds have a flexible diet and consume across a considerable breadth of prey. We found that

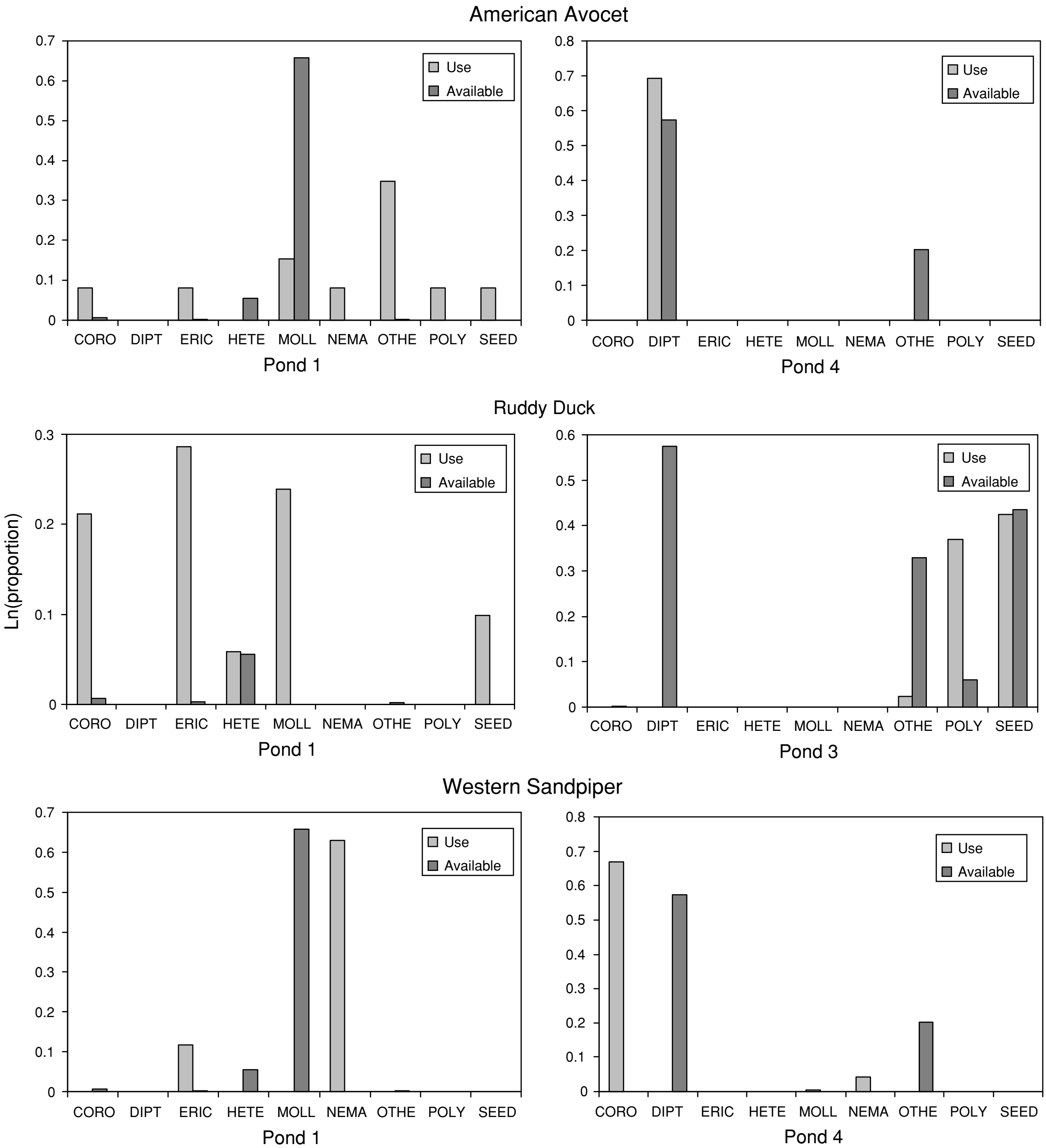

Fig. 5 Log-transformed percent use and availability of macroinvertebrates for American avocets, ruddy ducks, and western sandpipers in Ponds 1,3, and 4 of the Napa-Sonoma Marshes

a flexible diet was supported by the many prey consumed by American avocets and western sandpipers in salt ponds at low salinities, but less so at high salinities. At low salinities in P1, American avocets consumed prey items that were not even represented in availability samples. Although the availability samples were taken in gridcells adjacent to the foraging birds, the patchiness of their invertebrate prey was probably at a finer scale than we measured in our 250 × 250 m grids. Similarly,

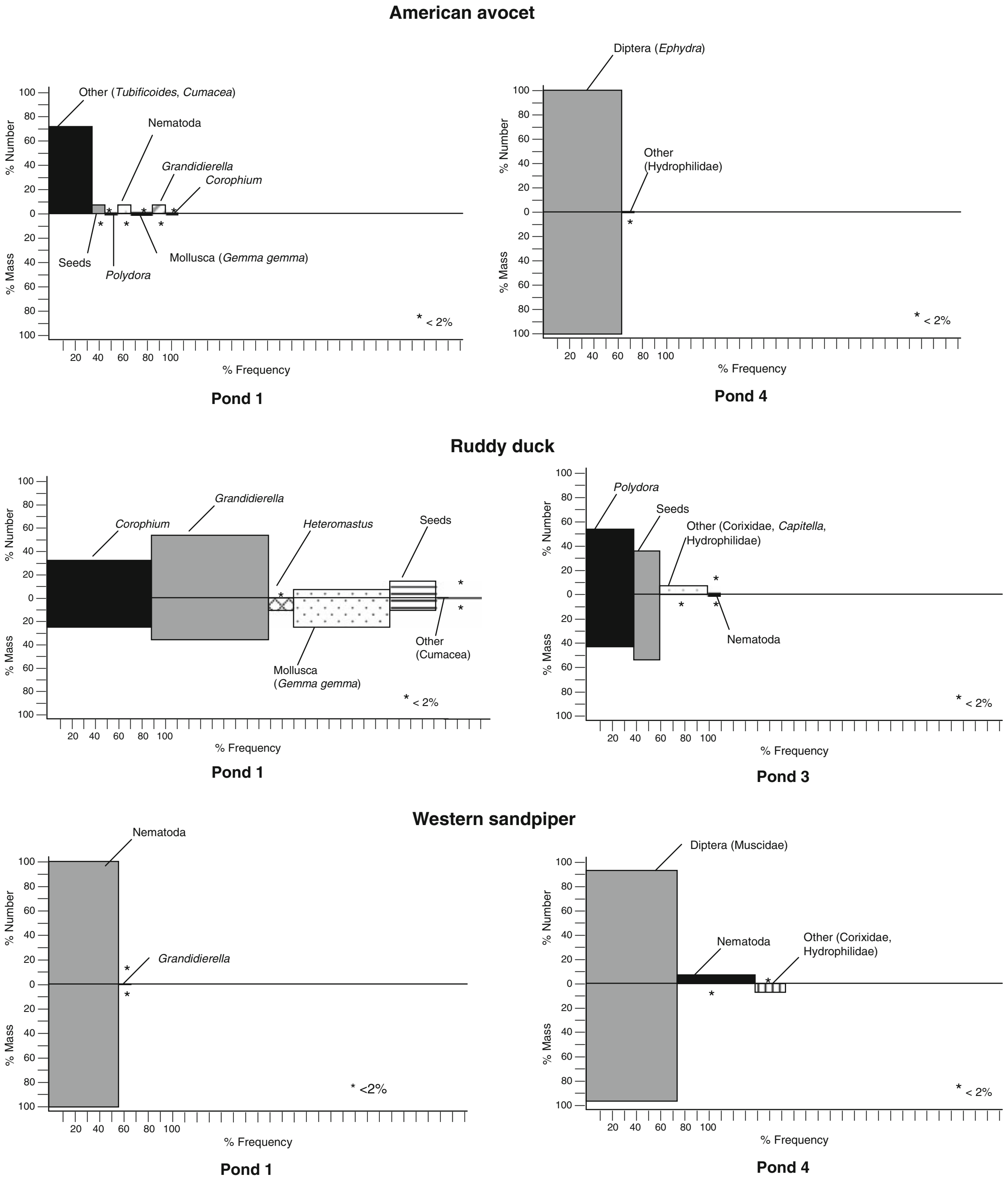

Fig. 6 Index of relative importance including three Relative Measures of Prey Quantity (RMPQ): percent number (%*N*), percent mass (%*M*), and percent frequency (%*F*): area of boxes represent relative importance for American avocets, ruddy ducks, and western sandpipers in the Napa-Sonoma Marshes

western sandpipers consumed prey not represented in availability samples. Although prey risk increases with prey size (Myers et al., 1980), sandpipers avoided mollusks probably because they were too large for easy consumption by this small shorebird. Redshanks (*Tringa tetanus*) passively select prey of a

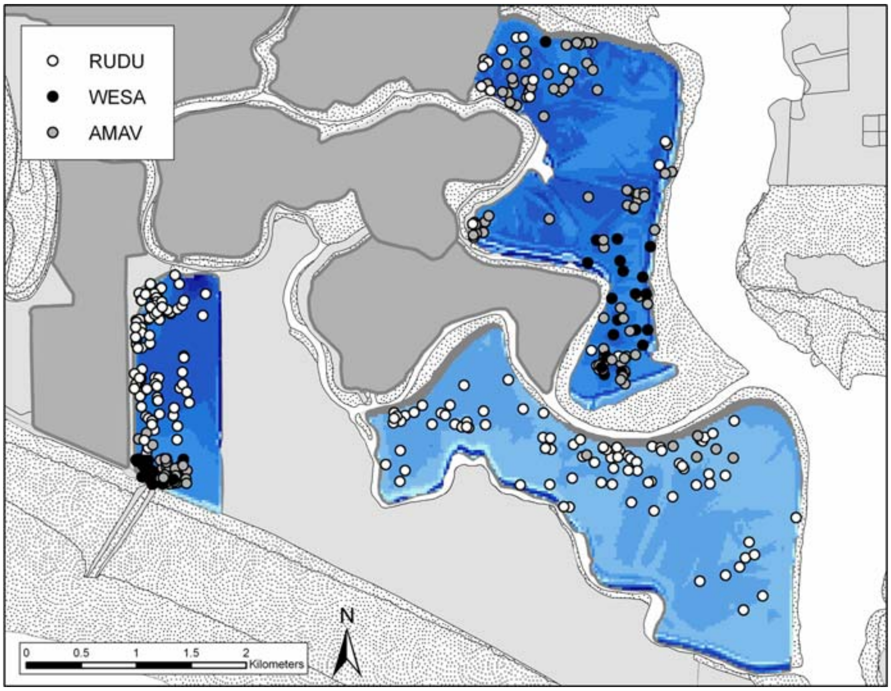

Fig. 7 Distribution of American avocets, ruddy ducks, western sandpipers on salt ponds of the Napa-Sonoma Marshes by water depth. Symbols represent 100 individuals and are located within 250 m × 250 m grid squares representing different water depths ranging from 0 to 5, 5 to 10, 10 to 15, and >15 cm shown with lighter shading for shallower water depth

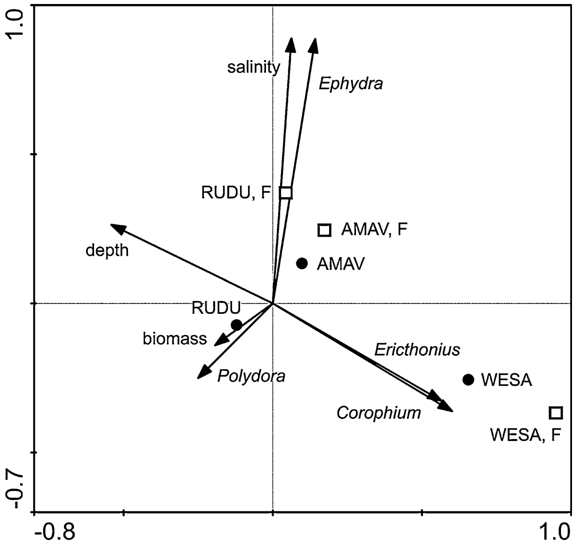

Fig. 8 The canonical correspondence analysis biplot shows the correlation between species and environmental variables. Longer lines are more important than shorter ones. Lines pointing in the same direction indicate correlated variables, lines in opposite directions are negatively correlated, and lines at 90° are uncorrelated. Similarly, species near each other are highly correlated

certain size with low energy intake in the winter, but high energy intake before migration (Masero & Perez-Hurtado, 2001).

At higher salinity in P4, consumption by both shorebirds was primarily of one prey item. When prey such as brine flies and brine shrimp were superabundant, the shorebirds responded by focusing on that readily available resource. Anderson (1970) concluded that shorebirds used salt ponds regardless of salinity, but our canonical correspondence analysis indicated that salinity was a major determinant of use. Although brine shrimp are a dominant invertebrate at higher salinities, we found that salinity was highly correlated with the presence of brine flies and that they were consumed by western sandpipers, a prey preference observed much earlier in higher salinity wetlands (Murie, 1935). Large numbers of brine shrimp were not present in digestive tracts of western sandpipers or American avocets, an indication that they were not an important diet item or that their use of this invertebrate was seasonal, such as during the spring migration (April).

The duration of available prey on mud flats may be related to use of high tide foraging areas in habitats such as salt ponds (Velasquez & Hockey, 1991; Masero et al., 1999). For example, shorebirds migrating northward along the Pacific coast of North America during April and May stage longest in San Francisco Bay (Warnock et al., 2004). In SFB, invertebrates may be available at higher densities

Table 4 Multiple regression analyses of November 1999–March 2000 bird abundance with salinity, depth, and macroinvertebrate biomass among grid cells

	Western sandpiper		Ruddy duck		American avocet	
	Total $F_{7,62} = 5.880$*	Foraging $F_{7,62} = 6.918$*	Total $F_{7,62} = 0.767^{NS}$	Foraging $F_{7,62} = 2.545$**	Total $F_{7,62} = 1.524^{NS}$	Foraging $F_{7,62} = 5.880$*
Salinity	-0.084^{NS}	-0.068^{NS}	-0.038^{NS}	0.591**	0.357**	-0.084^{NS}
Depth	−0.278**	−0.249**	0.031^{NS}	-0.115^{NS}	−0.335**	−0.278**
Corophium sp.	0.373**	0.441**	-0.078^{NS}	-0.023^{NS}	0.067^{NS}	0.373**
Ephydra sp.	0.046^{NS}	0.055^{NS}	-0.136^{NS}	-0.181^{NS}	-0.157^{NS}	0.046^{NS}
Grandidierella sp.	0.527**	0.553*	-0.237^{NS}	-0.051^{NS}	0.098^{NS}	0.527**
Polydora sp.	-0.048^{NS}	-0.020^{NS}	0.000^{NS}	-0.072^{NS}	-0.079^{NS}	-0.048^{NS}
Total invert biomass	−0.790*	−0.804*	0.332^{NS}	0.036^{NS}	-0.211^{NS}	−0.790*

* $P < 0.001$, ** $0.01 \le P < 0.05$, $^{NS}P > 0.05$

for a longer time on mud flats located near salt ponds where shorebirds may forage at high tide (Warnock et al., 2002). Feeding rates of semipalmated sandpipers (*Calidris pusilla*) are determined by a threshold density of prey in eastern North America (Wilson, 1990, 1991), and this may be similar for western sandpipers on the west coast.

With two low tides daily, shorebirds in SFB may only have low tide foraging opportunities for <12 h in a day (Warnock & Takekawa, 1995), with most of the foraging activity along the falling tideline. Preliminary studies in the south SFB have shown that shorebirds interchange between the salt ponds at high tide and adjacent mud flats at low tide (J. Takekawa, unpubl. data). In some areas, the depth gradient may be steeper resulting in even less time for foraging or a greater proportion of sand in the substrates may reduce prey capture (Quammen, 1982). Thus, supplemental food from impoundments may be crucial (Masero et al., 2000).

Diving ducks

A large proportion of the continental population of ruddy ducks winters in this estuary, possibly because of the availability of the pond habitats. We found that when we separated foraging ruddy ducks from birds roosting on open water, they were correlated with higher salinity. Surprisingly, brine flies were a major prey item for this diving species, even though most brine flies and their larvae are found along the shorelines. However, their consumption of seeds at higher salinity suggested that they switch to consuming prey from the water column rather than diving and obtaining benthic prey at lower salinity.

Of species that are most affected by restoration of salt pond habitats, diving ducks may decline with loss of water depths suitable for their foraging. Although the shoals of the estuary provide seemingly large expanses of suitable habitats, the level of disturbance found in the open water is far greater than that seen in salt ponds. For example, diving ducks will respond to disturbance by ferry traffic from a distance of a few hundred meters (J. Takekawa, unpubl. data). However, a much better understanding of invertebrate densities in shoal and mud flat areas is needed to better predict responses of diving ducks to reduced availability of higher salinity ponds.

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