Management and Conservation of San Francisco Bay Salt Ponds: Effects of Pond Salinity, Area, Tide, and Season on Pacific Flyway Waterbirds

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Abstract.—Throughout the world, coastal salt ponds provide habitat for large numbers and diversities of waterbirds. San Francisco Bay contains the most important coastal salt pond complexes for waterbirds in the United States, supporting more than a million waterbirds through the year. As an initial step in attempting to understand how the anticipated conversion of salt ponds to tidal marsh might affect the Bay's bird populations, the number of birds using salt ponds on high and low tides was counted during the winter months of 1999/00 and 2000/01. Behavior and habitat use of birds in these ponds were assessed, and the effects of tide cycle, pond salinity, and pond area on bird use were examined. We recorded 75 species of waterbirds in surveys of salt ponds in the South Bay from September 1999 to February 2001, totaling over a million bird use days on high tide. Shorebirds and dabbling ducks were the most abundant groups of birds using the salt ponds. Waterbird numbers and diversity were significantly affected by the salinity of ponds in a non-linear fashion with lower numbers and diversity on the highest salinity ponds. With the exception of ducks and Eared Grebe (*Podiceps nigricollis*), tide height at the Bay significantly affected bird numbers in the salt ponds with ponds at high tides having higher numbers of birds than the same ponds on low tides. Considerable numbers of birds fed in the salt ponds on high and low tides, although this varied greatly by species. Habitat use varied by tide. Management recommendations include maintaining ponds of varying salinities and depths. Restoring salt ponds to tidal marsh should proceed with caution to avoid loss of waterbird diversity and numbers in San Francisco Bay.

Key words.—Salinas, solar ponds, waterfowl, shorebirds, waders, salinity.

Waterbirds 25(Special Publication 2): 79-92, 2002

Coastal salt ponds (solar ponds, or salinas), areas where salt is extracted from salt water through solar evaporation, provide important nesting, foraging, and roosting habitat to waterbirds world-wide (Rufino *et al.* 1984; Sampath and Krishnamurthy 1989; Velasquez 1993; Masero and Pérez-Hurtado 2001). For instance, in Australia, three of the ten most important areas for shorebirds encompass commercial salt ponds (Lane 1987), while in Puerto Rico, the Cabo Rojo salt complex holds more shorebirds than any other site on the island and is one of the most important shorebird areas in the Caribbean (Collazo *et al.* 1995). Along the Pacific coast of North America, salt pond habitat supports significant numbers of waterbirds as recorded at critical Pacific Coast sites such as Laguna Ojo de Liebre, Baja California del Sur, Mexico (Page *et al.* 1997); San Diego Bay, California (Terp 1998); and San Francisco Bay, California (Page *et al.* 1999).

San Francisco Bay contains the most important salt pond complexes for waterbirds in the United States, supporting more than a million waterbirds through the year (Accurso 1992; Page *et al.* 1999; Takekawa *et al.* 2001). Single day counts of waterbirds in the salt ponds during winter months can exceed 200,000 individuals (Harvey *et al.* 1992), and single day counts during peak spring migration have exceeded 200,000 shorebirds in a single salt evaporation pond (Stenzel and Page 1988). The Bay and its surrounding salt ponds are significant habitat for waterbirds including Canvasback (*Aythya valisineria*) (Takekawa and Marn 2000), Ruddy Duck (*Oxyura jamaicensis*) (Miles 2000) and a number of shorebird species (Stenzel and Page 1988), including the Pacific Coast population of

Snowy Plover (*Charadrius alexandrinus*) which is considered threatened by the U.S. Fish and Wildlife Service (Page *et al.* 1991).

Commercial salt ponds in San Francisco Bay have existed for over a century (Ver Planck 1958). Prior to European settlement, perhaps 800 ha of natural salt crystallizing ponds were found primarily in southern reaches of the Bay. A series of these ponds of about 400 ha were farmed for salt by the native Yrgin tribe (Goals Project 1999). Beginning with European colonization around the mid 1800s, extensive diking of tidal wetlands occurred to create salt ponds (Josselyn 1983), with accelerated conversion of tidal marsh to salt ponds from the 1930s through the 1950s (Goals Project 1999). Presently, there are over 12,000 ha of salt ponds in San Francisco Bay (Goals Project 1999), most in the south region of the Bay where this study is focused.

Despite the documented occurrence of large numbers of waterbirds in San Francisco Bay salt ponds, comprehensive published studies of the role salt ponds play in maintaining waterbird diversity and numbers in San Francisco Bay are lacking. Presently, there is considerable interest in turning over the commercially operated salt ponds to state and federal wildlife agencies for restoration to tidal marsh, a habitat that has decreased by 80% in the Bay during the past 150 years (Goals Project 1999). We believe that part of this restoration emphasis is driven by a public misconception of salt pond habitat as being less valuable to wildlife since it is "man-made". As an initial step in understanding the effect of restoring salt pond habitat to tidal marsh habitat on the Bay's waterbirds, we evaluate the importance of salt ponds as roosting and feeding sites for migrant and wintering waterbirds, and examine the effects of abiotic variables, such as tide cycle, pond salinity, and pond area, on bird use of salt ponds.

METHODS

Study Area

We surveyed 22 salt ponds in the South Bay, the area of San Francisco Bay south of the San Mateo Bridge (Fig. 1). Nine salt ponds were surveyed during the 1999-2000 season (hereafter called the 1999 season) and 19 during the 2000-2001 season (hereafter called the 2000 season, six of these ponds were also surveyed the previous year, Table 1). Cargill Salt Company managed almost all evaporation ponds we surveyed for salt production. Ponds ranged from 17 ha (Pond N4S) to 175 ha (Pond N3), and from mean salinities (parts per thousand, ppt) of 25 ppt (Pond A9) to 259 ppt (Pond PP1, Table 1).

Study Period and Census Technique

Although salt ponds are non-tidal, ponds were surveyed twice in a day; once on a high tide greater than 1.2 m and once on a low tide less than 0.8 m. This was done since there is an exchange of some birds with the nearby bay, driven by the tidal cycle.

The 1999 survey season extended from late October 1999 through February 2000. Each pond was surveyed at high and low tide during this period, including three times from late October through December and three times January through February.

During the 2000 season, from September 2000 through February 2001, ponds were also surveyed twice in a day on high and low tide. However, on 13 occasions inclement weather prevented the completion of one of the paired censuses, and they were completed within three days of the first census. We attempted to survey each of these ponds twice per month with at least one tide cycle passing between censuses of the same pond. On five occasions, we were unable to complete the planned surveys due to inclement weather during surveys of ponds A4, A16, and A9. An additional five ponds were selected to be surveyed once a month only during high tide to increase our survey efforts (Table 1).

Spotting scopes with 20 × 60 zoom lenses and 8 × 35 binoculars were used to identify birds to species with the exception of Long-billed and Short-billed Dowitcher (*Limnodromus scolopaceus* and *L. griseus*), which were grouped as dowitchers because of the difficulty in distinguishing these species during winter. Rarely, if birds were too distant to identify to species, they were recorded as unidentified shorebird, gull, duck, or other bird group (see below for list). For most analyses, species were grouped into either: 1) dabbling ducks; 2) diving ducks that are not fish-eaters (including Pied-billed Grebe, *Podilymbus podiceps*); 3) Eared Grebe (*Podiceps nigricollis*); 4) fish-eating birds including all herons, egrets, mergansers and *Aechmophorus* grebes; gulls and terns; 5) shorebirds; or 6) landbirds (including raptors). Birds that could not be assigned to a group were not used in analyses. During each census, complete counts were made of all birds using each pond. Large ponds or ponds with a large number of birds were surveyed by at least two people. Each bird was counted individually when possible; however, large flocks were estimated by counting in groups of 5, 10, 20, 50 or 100.

For a particular pond, data recorded for birds included species, behavior, microhabitat, and number of individuals if more than one individual was exhibiting the same behavior in the same habitat at the same time. For analyses, behavior was characterized as either Foraging (feeding, swimming, and diving behaviors) or Non-foraging (all other behaviors). Micro-habitats were defined as 1) Island: island of dry substrate which could not be covered by water in a strong wind; 2) Man-made: structure such as dikes, roads, pilings, boardwalks etc.; 3) Mud: mudflat (dry or wet) or shallow water less than

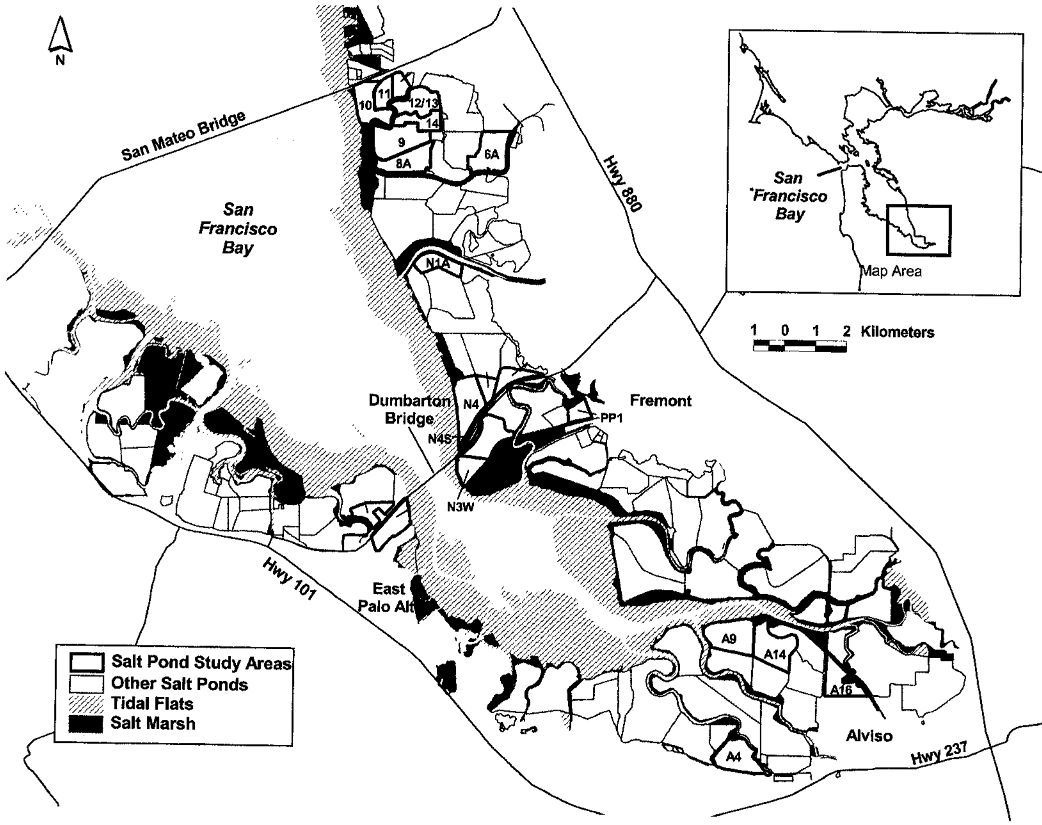

Figure 1. Map of south San Francisco Bay including salt ponds. For more information on ponds see Table 1.

10 cm deep; and, 4) Water: open water greater than 10 cm. The date, tide, pond number, observer, start and end time were also recorded for each census.

On each day that a pond was surveyed, 2-4 salinity measurements spread around the pond were recorded (see Table 1 for total number of salinity measurements taken per pond during the study period). A telescoping pole with a small jar on the end was used to sample water from the surface of the pond. To generate salinity measurements, we took the temperature of our water sample with a digital thermometer, and we measured the specific gravity of the sample with one of four hydrometers ranging from a specific gravity of 1.00 for the freshest water to a specific gravity of 1.25 for the most saline water; these were then converted to ppt. All samples were measured in the field at the time of collection. Because of fluctuations in pond salinities that occurred after heavy rain, extra measurements were taken during those periods.

Statistical Analyses

Frequencies of foraging and non-foraging of birds (grouped by foraging style) in salt pond habitats on high and low tides were analyzed using the χ^2 test (Snedecor and Cochran 1967). Linear models were used to test for effects on total number of birds, as well as number of waterbird species (species richness), using salt ponds. We fitted the same models to all birds and to each of the seven species groups of birds. Effects included year (1999, 2000); month (September-February); area of pond (ha); tide (high and low); salinity (average salinity of pond, ppt) and pond. The dependent variable, number of birds, was log transformed, and the other dependent variable, species richness, was square root transformed in order to conform with assumptions of linear models (normality and homoscedasticity). Species richness was calculated as the number (or mean number in cases where two surveys were done on the same pond in the same month and tide) of waterbird species counted at the same pond in the same year, month, and tide. Salinity, area, and month were treated as quantitative variables. Salinity and month were fitted as quadratic functions since there was evidence that they were non-linear effects. Species richness analyses were weighted by the number of censuses (N = 1 or 2) that were conducted at a given pond in the same year, month, and tide. We tested for unequal variances among groups (heteroscedasticity; Sokal and Rohlf 1981) with the Cook-Weisberg test (test hettest, StataCorp. 1999. Release 6.0, College Station, TX) using fitted values of the variable representing number of birds or species richness. When there was evidence of heteroscedasticity, violating models were rerun using ordinal logistic regression (test ologit, StataCorp. 1999). To run this model, number of birds was grouped into four categories representing the 0-25%, 26-50%, 51-75%, and 76-100% quartiles of the total number of birds.

Table 1. Waterbird surveys of San Francisco Bay saltponds, 1999-2001. Given are pond identification, pond area, number of surveys conducted at high and low tides, and mean pond salinity (ppt ± SD (N subsamples)). See Fig. 1 for location of ponds. Areas of ponds calculated from version 1.50b4 of EcoAtlas (San Francisco Estuary Institute 2000).

Salt pond	Area (ha)	Oct. 1999-Feb. 2000			Sept. 2000-Feb. 2001		
		High tide	Low tide	Salinity	High tide	Low tide	Salinity
10	105				6		31 ± 4 (24)
11	49				12	12	40 ± 10 (47)
12/13	98				12	12	47 ± 8 (49)
14	65				6		64 ± 12 (27)
6A	133				6		68 ± 8 (25)
8A	109				12	12	137 ± 35 (62)
9	151				12	12	108 ± 20 (54)
A14	142				11	11	83 ± 10 (44)
A16	97				12	11	71 ± 6 (44)
A4	124				12	11	39 ± 4 ± (42)
A9	150				11	11	25 ± 3 (44)
B1	38				5		49 ± 23 (18)
N1A	70	6	6	58 ± 5 (26)	12	12	69 ± 6(44)
N3	175				6		216 ± 16 (26)
N3W[a]	58	6	6	155 ± 17[b] (25)			
N4	137	6	6	73 ± 9 (33)	12	12	149 ± 12 (54)
N4S	17	6	6	80 ± 10[b] (29)			
N6	38	6	6	57 ± 5 (25)	12	12	112 ± 5 (48)
N9	55	6	6	54 ± 28 (28)	9	9	108 ± 3 (36)
PP1	40	6	6	186 ± 27 (29)	12	12	259 ± 15 (48)
R2	57	6	6	199 ± 40 (37)			
SF2	98	6	6	171 ± 29 (35)	12	12	257 ± 14 (51)

[a]west side of Pond N3, area of his pond included in the area of N3.
[b]salinity not measured in October.

RESULTS

Abundance and Diversity

We recorded 75 species of waterbirds in surveys of salt ponds in the South Bay from September 1999 to February 2001. In 1999, 51 species of waterbirds totaling 136,900 birds were recorded on 54 high tide counts, and 44 species totaling 49,600 birds were recorded on 54 low tide counts. In 2001, 69 species of waterbirds totaling 919,900 birds were recorded on 192 high tide counts, and 65 species totaling 283,700 birds were recorded on 161 low tide counts. A significant difference in the total number of birds counted in the different groups of waterbirds was found between high and low tides (χ^2_7 = 33,645, P < 0.001; Fig. 2). Shorebirds were the dominant group on the high tide, followed by dabbling ducks. This order was reversed on the low tide with no change in order among the other groups of birds. In both years, on high and low tides, the ten most numerous species accounted for over 85% of all birds counted (Table 2). In both years, the five most numerous waterbird species on the high tide stayed the same and consisted mainly of shorebirds, while the order and species varied between years for the most numerous waterbird species on the low tide (Table 2).

Dunlin (*Calidris alpina*) and Western Sandpiper (*C. mauri*) were the most abundant shorebird species (35% of all the birds counted) found in the salt ponds, followed by Willet (*Catoptrophorus semipalmatus*), American Avocet (*Recurvirostra americana*), and Black-bellied Plover (*Pluvialis squatarola*). Northern Shoveler (*Anas clypeata*) accounted for 18% of all the ducks and grebes counted.

All models examining factors potentially affecting numbers of birds using salt ponds

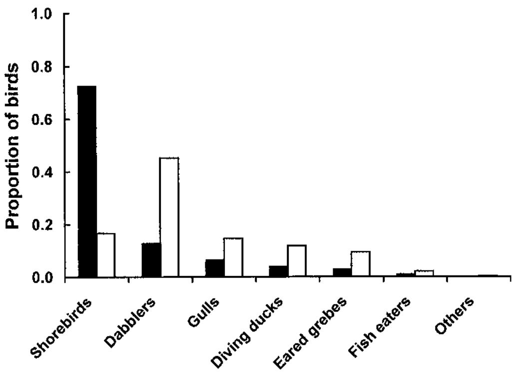

Figure 2. Proportion of all birds counted in south San Francisco Bay salt ponds by bird group and tide. Numbers combined for 1999/00 and 2000/01. Bird groups include: Shorebirds; Dabbling ducks; Gulls (include gulls and terns); Diving ducks; Eared Grebes; Fish eating birds (including waders, mergansers and grebes other than Eared Grebes); and Others (landbirds and raptors). Dark column = high tide, white column = low tide.

in the South Bay were highly significant (Table 3). Four models, including all birds combined, fish eating birds, landbirds, and shorebirds, violated assumptions of equal variances. However, patterns of significance stayed the same for those models using the alternative ordinal logistic regression model with the following exceptions: fish-eating birds—the effect of area went from non-significant ($P = 0.09$) to significant; shorebirds - the effect of area went from significant ($P < 0.001$) to non-significant; and, landbirds—the effect of tide went from non-significant ($P = 0.14$) to significant (Table 3). The individual salt pond where birds were counted explained significant amounts of variation, and this was the only variable that was significant for all models. Pond salinity, modeled as a quadratic function, explained significant amounts of variation in all bird groups with the exception of the landbird group. Models examining the numbers of dabbling ducks, diving ducks, and Eared Grebe all were similar in that month of study, pond salinity, and pond explained significant amounts of variation, while tide, pond area, and year of study (with the exception of the Eared Grebe model) did not. Significant year effects were found only for the Eared Grebe and gull models. All predictor variables were significant in explaining gull and tern numbers while none of the selected variables explained significant amounts of variation in landbird numbers, except tide and pond. For shorebirds, numbers decreased on low tides (high tide: mean number census^{-1} = 3136 birds ± 6810 SD, N = 246 censuses; low tide: mean number census^{-1} = 259 birds ± 580 SD, N = 215 censuses). For all birds combined, year of study did not affect numbers of birds. Combining years, mean number of birds (using only high tide counts) grew from September (mean = 2229 ± 2236 SD birds, N = 17 ponds) into October, peaked in October (mean = 6093 ± 10,620 SD birds, N = 20 ponds), fell slightly in November (mean = 5233 ± 6556 SD birds, N = 28 ponds) and remained relatively stable December through February (means ranged from 4044-4532 birds per month in this period, 28 ponds surveyed per month). High tide counts held significantly more birds than those at low tide (high tide: mean number census^{-1} = 4300 birds ± 6780 SD, N = 246 censuses; low tide: mean number census^{-1} = 1556 birds ± 2362 SD, N = 215 censuses). Holding the effects of pond, year, month, tide, and pond area constant, the largest number of waterbirds occurred at 140 ppt salinity as estimated by the fitted quadratic equation (Fig. 3).

Species richness of waterbirds showed similar patterns of significance as overall bird numbers (Table 4), with the one exception that species richness also showed a significant year effect. Species richness of waterbirds was significantly related to non-linear effects of month and salinity. Mean number of species, combining years (using only high tide counts), grew from September (mean = 12.6 ± 4.9 SD species, N = 17 ponds surveyed) and leveled off from October through February (means ranged from 14.9-16.3 species per month in this period, 20-28 ponds surveyed per month). Holding the effects of pond, year, month, tide, and pond area constant, the largest number of waterbird species occurred at 126 ppt salinity as estimated by the fitted quadratic equation (Fig. 4).

Species richness was positively related to pond area, was higher in the second year of study, and was greater on high tides than low

Table 2. Ten most abundant waterbird species recorded in salt ponds of south San Francisco Bay during autumn and winter on high and low tides. Percent total = (number of particular species/total number of birds) × 100.

	1999/2000		2000/2001	
	Species	Percent total	Species	Percent total
High Tide	Dunlin	26	Dunlin	31
	Western Sandpiper	16	Western Sandpiper	24
	Northern Shoveler	16	Northern Shoveler	13
	Willet	14	Willet	7
	American Avocet	8	American Avocet	6
	Black-necked Stilt	5	Black-bellied Plover	5
	California Gull[a]	4	Herring Gull[b]	4
	Black-bellied Plover	4	Marbled Godwit	4
	Least Sandpiper	4	Ruddy Duck	3
	Marbled Godwit	4	Eared Grebe	3
Total number		118,300		788,900
Low Tide				
	Northern Shoveler	41	Northern Shoveler	46
	American Avocet	12	Eared Grebe	11
	Bonaparte's Gull	11	Ruddy Duck	9
	Black-necked Stilt	10	Herring Gull	8
	Eared Grebe	7	American Avocet	7
	Ruddy Duck	6	Black-necked Stilt	5
	California Gull	5	Bonaparte's Gull[c]	5
	Bufflehead[d]	4	American Wigeon[e]	4
	Dunlin	2	Canvasback	3
	Least Sandpiper	2	California Gull[b]	3
Total number		47,200		249,100

[a]Herring Gull (*Larus argentatus*); [b]California Gull (*L. californicus*); [c]Bonaparte's Gull (*L. philadelphia*); [d]Bufflehead (*Bucephala clangula*); [e]American Wigeon (*Anas americana*).

tides (species richness, mean ± SD; 1999, high tide, 13.7 ± 6.3 species; 1999, low tide, 9.3 ± 4.6 species; 2000, high tide, 15.9 ± 7.0 species; 2000, low tide, 10.5 ± 6.9 species).

Behavior

Major behavioral patterns exhibited by birds using salt ponds in south San Francisco Bay consisted of foraging and roosting (Table 5, see Methods for list of other behaviors recorded). Combining roosting and other behaviors for all birds, the frequency of foraging behavior varied significantly between 1999 and 2000 on high and low tides (high tide, $\chi^2_1 = 70.9$, $P < 0.001$; low tide, $\chi^2_1 = 33.2$, $P < 0.001$; Table 5). There was no significant difference in the frequency of feeding behavior vs. roosting and other behaviors (combined) between tides in either year (1999, $\chi^2_1 = 0.1$, n.s.; 2000, $\chi^2_1 = 0.24$, n.s.; Table 5). However, considerable variation exists in the frequency of foraging behavior in salt ponds between tides within different groups of waterbirds (Fig. 5). For instance, within shorebirds, Marbled Godwit (*Limosa fedoa*), Black-bellied Plover, and Long-billed Curlew (*Numenius americanus*) were rarely observed foraging in the salt ponds on high tides, while other species such as Least Sandpiper (*Calidris minutilla*), Black-necked Stilt (*Himantopus mexicanus*), and American Avocet commonly foraged. At low tide, the majority of shorebirds found in the salt ponds were feeding (Fig. 5).

Effects of Microhabitat

Use of habitats within salt ponds varied for foraging and roosting birds (Fig. 6). In general, foraging birds were found most on moist to wet soils and on the water, and least on islands and other man-made structures. Roosting birds made more use of islands and

Table 3. Results of linear models examining effects on numbers of birds using salt ponds in south San Francisco Bay. Models include all birds; dabbling ducks; diving ducks that are not fish eaters including Pied-billed Grebes; Eared Grebes; fish eating birds including all herons, egrets, mergansers, and *Aechmophorus* grebes; gulls and terns; shorebirds; and landbirds including raptors. Response variable is number of birds counted (log transformed). Effects are year (1999/00, 2000/01), month (September-February analyzed as a quadratic), area = area of pond (ha), tide (high and low), salinity (average salinity of pond per month analyzed as a quadratic), and pond. Salinity, area, and month were treated as quantitative variables. N = 457 surveys.

	df	All birds	Dabbling ducks	Diving ducks	Eared Grebes	Fish-eating birds	Gulls and terns	Shore-birds	Landbirds[a]
Model	27	P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001
Year	1	n.s.	n.s.	n.s.	P < 0.001	-[b]	P < 0.001	n.s.	-[b]
Month[c]	1	P < 0.001	P < 0.01	P < 0.001	P < 0.001	n.s.	P < 0.001	n.s.	n.s.
(Month)[2d]	1	P < 0.001	P < 0.001	P < 0.001	P < 0.001	n.s.	P < 0.001	n.s.	n.s.
Area	1	P < 0.001	n.s.	n.s.	n.s	P < 0.001	P < 0.001	n.s.	n.s.
Tide	1	P < 0.001	n.s.	n.s.	n.s.	P < 0.001	P < 0.01	P < 0.001	P < 0.01
Salinity[c]	1	P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001	n.s.
(Salinity)[2d]	1	P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001	n.s.
Pond	20	P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001
R^2		0.29	0.69	0.70	0.75	0.46	0.59	0.34	0.11

[a]Models for which Cook-Weisberg test scores for heteroscedasticity of linear models at P < 0.05; models rerun using ordinal logistic regression (test Ologit, StataCorp. 1999) and Ologit test values reported. Pseudo R^2 reported for these models.

[b]Convergence of the model not achieved with year included, so model run without year as a variable.

[c]Linear term in the presence of a quadratic term.

[d]Quadratic term in the presence of a linear term.

man-made structures although many birds still roosted on moist-wet soils and on the water (Fig. 6). Of the birds that were foraging and roosting, the frequency of birds using different habitats on the high tide differed significantly from that on low tide (high tide, χ^2_3 = 237, P < 0.001; low tide, χ^2_3 = 219, P < 0.001). For birds observed foraging at high tide, 58% of the birds were seen using mud habitat and 38% water, while on the low tide 41% used the mud habitat and 56% used the water (Fig. 6). For roosting birds, while mud was the most frequently used habitat (38%) on the high tide, man-made structures were the most frequently used habitats (31%) on the low tide.

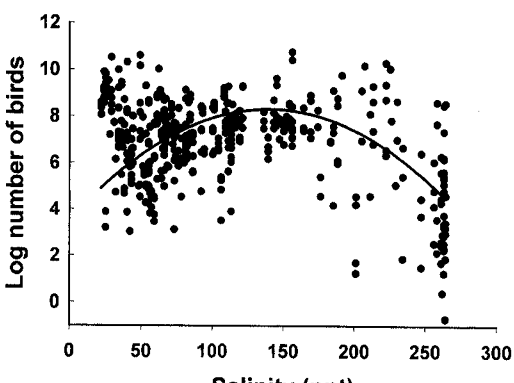

Figure 3. Relationship of bird numbers to salinity (ppt) in south San Francisco Bay salt ponds, 1999 and 2000. Number of birds log transformed. Best-fit quadratic function of numbers of birds depicted, controlling for effects of month, year, tide, pond, and pond area (see Table 3).

DISCUSSION

Abundance and Diversity

This study confirms the importance of San Francisco Bay salt ponds as foraging and roosting habitat to a large number and high diversity of migrant and wintering birds, especially shorebirds, ducks, gulls, and grebes (over 98% of all birds counted), and as such, supports the findings of others who have examined bird use of San Francisco Bay salt ponds (Anderson 1970; Swarth *et al.* 1982; Harvey *et al.* 1992; Takekawa *et al.* 2001). Annual bird use of salt ponds during this study period (calculated in bird days) numbered in the millions, supporting the existing designation of San Francisco Bay as a site of Hemispheric importance to shorebirds (a

Table 4. Results of linear model examining effects on numbers of species of waterbirds (species richness) using salt ponds in south San Francisco Bay, California. Waterbirds include dabbling ducks, diving ducks, grebes, herons, egrets, mergansers, gulls, terns, and shorebirds. Species richness square root transformed. See Table 3 for description of effects. df = numerator df of F test; residual df = denominator df of F test. Adjusted R^2 of model = 0.81.

Source	df	F	P
Model	27	42.6	P < 0.001
Year	1	8.6	P < 0.01
Tide	1	159.0	P < 0.001
Area	1	40.1	P < 0.001
Month[a]	1	15.0	P < 0.001
$(\text{Month})^2$	1	12.7	P < 0.001
Salinity[a]	1	23.1	P < 0.001
$(\text{Salinity})^2$	1	61.0	P < 0.001
Pond	20	18.6	P < 0.001
Residual	238		

[a]Effect of linear term in the presence of a quadratic term.

site supporting >500,000 shorebirds in a given year, Harrington and Perry 1995), as well as a major Pacific Flyway wintering and stopover site for ducks (Accurso 1992), grebes, and gulls (Harvey *et al.* 1992). During two years of salt pond surveys, we recorded 75 species of waterbirds, compared to 55 species found by Anderson (1970) in five salt ponds, and 70 species found by Swarth *et al.* (1982) in approximately 14 salt ponds. This difference probably reflects the greater number of ponds that we surveyed. In other parts of the world, high species diversity of waterbirds in coastal salt ponds has been recorded as well, ranging from 35 to 56 species (Britton and Johnson 1987; Martin and Randall 1987; Sampath and Krishnamurthy 1989; Velasquez 1993).

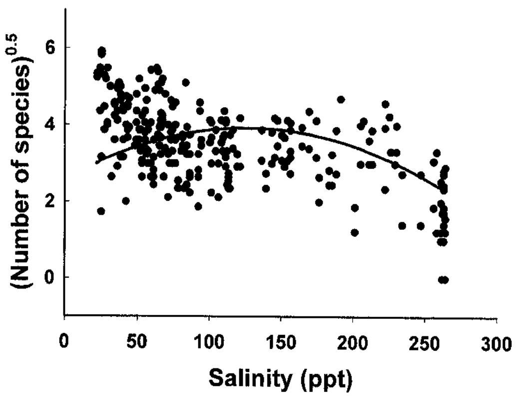

Figure 4. Relationship of waterbird diversity to salinity (ppt) in south San Francisco Bay salt ponds, 1999 and 2000. Number of waterbird species square-root transformed. Best-fit quadratic function of waterbird species number depicted, controlling for effects of month, year, tide, pond, and pond area (see Table 4).

Shorebirds were the most abundant group of waterbird in the salt ponds, as has been documented in other habitats of the Bay (Stenzel and Page 1988), and along the Pacific Coast of the United States (Page *et al.* 1999). Of the shorebirds using South Bay salt ponds, calidrid sandpipers were most abundant, a pattern similar to other parts of the world (Velasquez and Hockey 1992; Collazo *et al.* 1995). Next to shorebirds, dabbling ducks dominated, especially Northern Shoveler, followed by diving ducks and Eared Grebe. This corroborates the findings of Accurso (1992) who found the Northern Shoveler to be the most abundant dabbling duck in San Francisco Bay with 89% of them counted in the salt ponds of the South Bay.

We found a significant non-linear effect of month on numbers of birds and species richness with mean highest numbers and diversity for our autumn and winter study period in October and November. Waterbird species are still migrating through San Francisco Bay from September through November (Swarth *et al.* 1982; Accurso 1992), the early months of this study. Dunlin, the most abundant shorebird species in this study, are the latest autumn migrants, first occurring in any numbers in October (Shuford *et al.* 1989; Warnock and Gill 1996). Using our overall model, year differences were not

Table 5. Proportion of feeding, roosting, and other behavior of birds seen during salt pond surveys in south San Francisco Bay. N is the number of groups of birds observed engaged in a behavior in a pond at the same time (see Methods for more details).

	High tide		Low tide	
	1999	2000	1999	2000
Feed	0.53	0.44	0.54	0.44
Roost	0.43	0.46	0.37	0.39
Other	0.04	0.09	0.09	0.17
N	2,945	9,315	1,082	4,273

detected in numbers of birds, but we did find significant year differences in species richness. This may be partly due to our increased survey effort in the second year of the study resulting in finding more species not commonly found at salt ponds.

Tidal differences accounted for significant variation in numbers and species richness of waterbirds using San Francisco Bay salt ponds, contrary to Anderson's (1970) observations based on a limited number of ponds. Shorebirds, in particular, responded to the tide cycle, with high numbers using the ponds on high tide and lower numbers on the low tide. This fits similar patterns found at San Francisco Bay within species of shorebirds (i.e., Western Sandpiper; Warnock and Takekawa 1995, 1996) and among species (Swarth *et al.* 1982) where birds moved from salt ponds to adjacent tidal mudflats in great numbers to feed (Stenzel *et al.* 2002). In other parts of the world, similar patterns are seen with most shorebird species moving from salt ponds to tidal flats to feed (Velasquez *et al.* 1991; Masero *et al.* 2000). There are a few exceptions to this pattern within the shorebirds, notably the American Avocet and Black-necked Stilt. These species, especially the Black-necked Stilt, often stay in the salt ponds through the tide cycle, a pattern clearly seen during recent radiotelemetry studies in San Francisco Bay (PRBO, unpubl. data), and also observed in salt ponds of San Diego, California (Terp 1998). During winter months in South Africa, the shorebirds showing a positive affinity to salt ponds through the tide cycle included the Pied Avocet (*Recurvirostra avosetta*) and the Black-winged Stilt (*Himantopus himantopus*) (Velasquez *et al.* 1991). While fish-eating birds and gulls responded to the tide cycle in a similar way to shorebirds, duck and Eared Grebe numbers changed little between high and low tide, indicating that they stayed in the ponds through the tide cycle.

Undoubtedly, changes in bird use of salt ponds in response to tidal height are related, in part, to differing prey communities among different types of habitats and densities of birds. Masero and Pérez-Hurtado (2001), suggest wintering Redshank (*Tringa totanus*) in Spain move from salt ponds to tidal areas to feed not because food supplies are better, but because densities of foraging competitors are lower. Studies comparing food resources available to birds on tidal mud flats vs. in salt ponds are needed in San Francisco Bay.

In South Africa, Velasquez (1993) found that highest foraging densities of waterbirds were in salt ponds of 25-70 ppt salinity and 170-220 ppt salinity. Combining all waterbird species and controlling for various effects, we found highest numbers of birds in salinities around 140 ppt and highest species diversity in salinities around 126 ppt. This non-linear effect of salinity on numbers and diversity of waterbirds undoubtedly relates to prey diversity. For invertebrates, species richness declines with increasing salinity (Britton and Johnson 1987; Williams *et al.* 1990), but for invertebrate biomass, this is not a linear effect. Highest densities of important waterbird prey species in San Francisco Bay, the Franciscan Brine Shrimp (*Artemia franciscana,* often called *A. salina;* Larsson 2000), the Reticulated Water Boatman (*Trichocorixa reticulata*) and brine flies (*Ephydra* spp. and *Lipochaeta slossonae*), occur in salinities of 60-200 ppt (Carpelan 1957; Larsson 2000; Maffei 2000a, b). These invertebrate species are targeted by

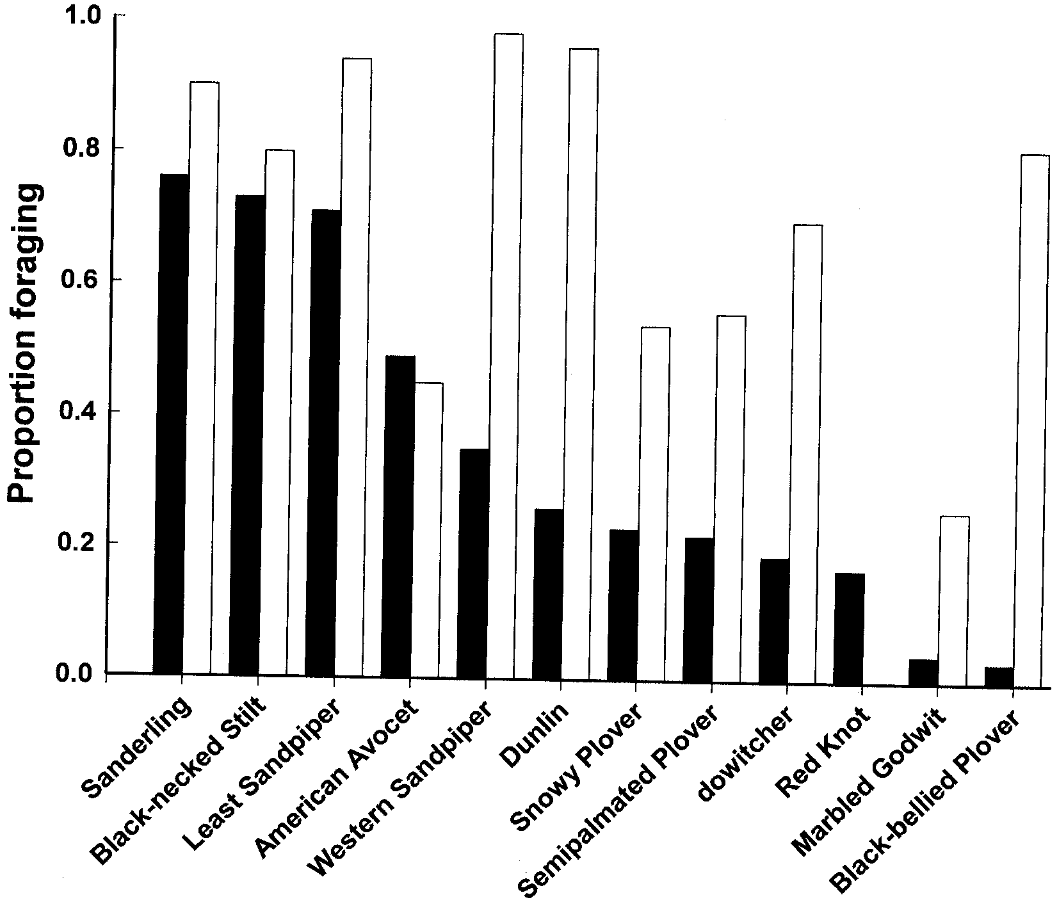

Figure 5. Proportion of most abundant shorebirds seen foraging on high and low tides in salt ponds of south San Francisco Bay. Numbers combined for 1999 and 2000. Dark column = high tide, white column = low tide. Semipalmated Plover (*Charadrius semipalmatus*), Red Knot (*Calidris canutus*), Sanderling (*C. alba*).

many waterbird species, especially the numerically abundant shorebirds and waterfowl (Anderson 1970). Swarth *et al.* (1982) found a strong positive correlation between numbers of Eared Grebe and invertebrate biomass in eleven South Bay salt ponds. This positive relationship of bird numbers (or density) to prey density has been found for other species of waterbirds in other habitats (Yates *et al.* 1993) and in salt pans around the world, although the predictive ability of this relationship tends to be poor (Velasquez 1993; Terp 1998; Grear and Collazo 1999).

It should be emphasized that our graphs depicting the relationship between salinity and all waterbird numbers and diversity obscure important species-specific relationships with salinity. In San Francisco Bay salt ponds, fish cannot tolerate salinities much over 70-80 ppt, with salinity tolerances of most fish in the 20-40 ppt range (Carpelan 1957; Lonzarich 1989 in Harvey *et al.* 1992), so fish-eating birds tend to concentrate in ponds with mean salinities <100 ppt (Anderson 1970; Swarth *et al.* 1982). Plant-eating waterbirds (like some of the dabbling ducks) concentrate at lower salinity ponds (Accurso 1992). Thus, maintaining ponds of different salinity ranges will be critical in maintaining the widest suite of waterbird species using salt pond complexes. A consistent pattern is that at high pond salinities, where salt begins to crystallize, little, if any, invertebrate biomass is found, and fewer waterbirds use these areas (Takekawa *et al.* 2000). Aside from having no prey, birds may avoid these highest sa-

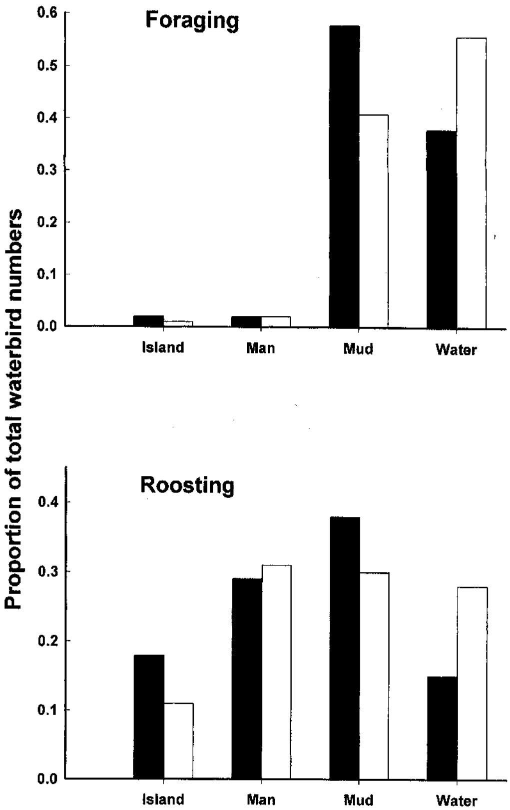

Figure 6. Proportion of waterbird use of different habitats within south San Francisco Bay salt ponds for foraging and roosting during high and low tides. Numbers combined for 1999 and 2000. Island = island of dry substrate which could not be covered by water in a strong wind; Man = man-made structure such as dikes, roads, pilings, boardwalks etc.; Mud = mudflat (dry or wet) or shallow water less than 10 cm deep; Water = open water greater than 10 cm. Dark column = high tide, white column = low tide.

linity salt ponds even for roosting because increasing water salinity negatively affects the waterproofing of waterbird feathers which increases the thermoregulatory costs to the birds (Rubega and Robinson 1997), as well as potentially having other negative effects (Purdue and Haines 1977; Euliss *et al.* 1989).

Other factors may affect numbers and diversity of birds using salt ponds. Area of ponds emerged as a significant effect in our all bird model as well as the fish-eating birds and gull models. There was a tendency for larger ponds to support larger numbers of birds and a higher diversity of species, but the predictive power of these tests was low. Accurso (1992) found different species of diving ducks preferred different size salt ponds in the Bay, but in this study, pond size was not significantly related to numbers of dabbling or diving ducks. Further research on the relationship between pond size and species number and diversity is desirable.

Swarth *et al.* (1982) noted that disturbance affected dabbling ducks in the South Bay salt ponds, causing them to use ponds farthest from points of contact with people. They attributed this wariness of the dabbling ducks to hunting. Ducks were hunted in parts of our study area and this may be the cause of some of the unexplained variation in our predictive models. Additionally, avian predators of birds, including Peregrine Falcon (*Falco peregrinus*), Merlin (*F. columbarius*), accipiters, Northern Harrier (*Circus cyaneus*), and owls were frequently observed during the course of our study. Predator attacks periodically caused birds to move to different ponds.

Habitat characteristics within ponds also affected where birds would concentrate for different activities. While we did not incorporate water depth into our predictive models due to the extreme variability in water depth of the South Bay salt ponds (PRBO, unpubl. data), it has been well demonstrated that water depth can be predictive of waterbird species (Velasquez 1992, 1993; Elphick and Oring 1998). Shorebirds generally do not feed in water at depths much greater than about 10-15 cm, and most prefer water depths under about 4 cm (Isola *et al.* 2000), except for those that swim such as the phalaropes. Dabbling ducks were often observed foraging in the same areas as shorebirds, while grebes and other diving birds typically use ponds <2m in depth (Accurso 1992; J. Takekawa unpubl. data). Over half of all the birds we observed foraging in the salt ponds were either on mudflats or in water we classified as being less than about 10 cm deep, while roosting birds made greater use of islands and dikes.

Conservation and Management Implications

During the past century, salt ponds in south San Francisco Bay have been used by great numbers and a high diversity of birds. In the breeding season, the salt ponds are breeding habitat for a number of waterbirds (Gill 1977), including the Snowy Plover—a species protected under the U.S. Endangered Species Act (Page *et al.* 1991), the Black-necked Stilt, the American Avocet, and a number of gull and tern species (Harvey *et al.* 1992). As this study has shown, each year on high and low tides, salt ponds in San Francisco Bay are used by hundreds of thousands of waterbirds representing over 70 species. This habitat provides valuable roosting habitat to birds that have lost enormous amounts of traditional roosting sites to development around San Francisco Bay, especially super high tide, seasonal roost sites used during winter storms, similar to what has been noted for other man-made wetland types (Davidson and Evans 1986). These ponds also serve as refuges for waterbirds in a disturbance-prone urban environment (Swarth *et al.* 1982). Additionally, we have shown that this habitat provides foraging areas to many species of waterbirds that traditionally feed on tidal mudflats. This open foraging habitat may compensate, in part, for the roughly 40% of tidal mudflats lost in San Francisco Bay to landfills and dredging in the past 200 years (Goals Project 1999). Further research into what waterbirds actually gain in energetic terms from salt ponds relative to tidal marshes and mudflats would be valuable for managing for a suitable mixture of habitats.

The management implications of this study are complex yet several recommendations stand out. For attracting maximum numbers and diversity of migrating and wintering gulls and shorebirds, ponds with exposed moist soil and shallow water up to about 10 cm deep are recommended. Deeper water ponds are needed for many of the ducks and divers. Salinities of ponds need to be maintained in several ranges, especially the range where fish can live (20-60 ppt), and in the range that promotes a high biomass of invertebrate prey important to a wide range of migrating and wintering shorebirds, waterfowl, gulls, and terns. Our results suggest this latter salinity range centers around 140 ppt. Roosting waterbirds used islands in the middle of salt ponds, and maintenance and creation of island habitat should be incorporated into management plans for salt ponds. An important yet untested component of maintaining salt pond habitat for wintering and migrating waterbirds will be to prevent ponds, especially the lower salinity ponds, from becoming vegetated since many species of waterbirds, especially shorebirds, use vegetated areas, such as tidal marshes, less than open habitat (Warnock and Takekawa 1995; PRBO unpubl. data).

As has already been pointed out for San Francisco Bay (Takekawa *et al.* 2001), in order to maintain current diversity and numbers of waterbird in San Francisco Bay, conversion to tidal marsh habitat will require a greater amount of habitat than the amount of salt ponds being converted. While it is known that the salt ponds of San Francisco Bay support a large number and diversity of birds, it is not known how these birds will react if salt pond habitat is reduced. This should be the focus of major research efforts. Currently, in North America, the majority of shorebird species are thought to be in decline (Morrison 2001; Morrison and Hicklin 2001). Diving duck populations, such as scaup, have also experienced population declines (Afton and Anderson 2001). Until we get a better handle on these important conservation issues, restoring salt ponds to tidal marsh in San Francisco Bay, as is currently being proposed, should proceed with caution.

ACKNOWLEDGMENTS

For financial support we are indebted to the Gabilan Foundation, the Crocker Foundation, the Osher Foundation, and the Rintels Charitable Trust. Logistic support was provided by the Don Edwards San Francisco Bay National Wildlife Refuge, Cargill Salt, East Bay Regional Parks, and Sunnyvale Baylands. We were ably assisted in collection of field data by Chris Rintoul, Sue Abbott, Jim DeStabler, Hildie Spautz, Sue Macias, Cheryl Millett, Yvonne Chan, and Matthew Anderson. Diana Stralberg kindly produced Figure 1. We thank Jaime Collazo for relevant literature and Paul Buchanan for providing salinity conversion protocol. Versions of this manuscript were greatly improved by John Coulson, Chris Elphick, Kathy Parsons, Sarah Warnock, and two unidentified reviewers. This is contribution 894 of Point Reyes Bird Observatory.

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