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ABUNDANCE AND DISTRIBUTION OF SHOREBIRDS IN THE SAN FRANCISCO BAY AREA

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ABSTRACT: On 13 comprehensive censuses of the San Francisco–San Pablo Bay estuary and associated wetlands we counted 325,000–396,000 shorebirds (Charadrii) from mid-August to mid-September (fall) and in November (early winter), 225,000 from late January to February (late winter); and 589,000–932,000 in late April (spring). Twenty-three of the 38 species occurred on all fall, early winter, and spring counts. Median counts in one or more seasons exceeded 10,000 for 10 of the 23 species, were 1,000–10,000 for 4 of the species, and were less than 1,000 for 9 of the species. On rising tides, while tidal flats were exposed, those flats held the majority of individuals of 12 species groups (encompassing 19 species); salt ponds usually held the majority of 5 species groups (encompassing 7 species); 1 species was primarily on tidal flats and in other wetland types. Most species groups tended to concentrate in greater proportion, relative to the extent of tidal flat, either in the geographic center of the estuary or in the southern regions of the bay. Shorebirds' densities varied among 14 divisions of the unvegetated tidal flats. Most species groups occurred consistently in higher densities in some areas than in others; however, most tidal flats held relatively high densities for at least one species group in at least one season. Areas supporting the highest total shorebird densities were also the ones supporting highest total shorebird biomass, another measure of overall shorebird use. Tidal flats distinguished most frequently by high densities or biomass were on the east side of central San Francisco Bay and adjacent to the active salt ponds on the east and south shores of south San Francisco Bay and along the Napa River, which flows into San Pablo Bay. The bay is critical to large numbers of wintering, migrating, and breeding shorebirds, despite extensive loss of natural wetlands. Geographic limitations of species' distributions in the bay should be considered when wetland restoration is planned.

The San Francisco–San Pablo Bay estuary and associated wetlands (hereafter, the bay) are of hemispheric importance (Harrington and Perry 1995) to wintering and migrating shorebirds. On the conterminous U. S. Pacific coast, the bay holds more total shorebirds than any other wetland in all seasons, and it holds the majority of individuals of the 13 most abundant shorebirds in one or more seasons (Page et al. 1999). While a variety of natural and artificial habitats support shorebirds in the bay, more detailed patterns of habitat use are known only generally for all shorebirds and locally for a few species.

In 1964 and 1965, Bollman et al. (1970) conducted a large-scale but not comprehensive census of water birds in the bay, documenting sizable populations and general distribution patterns. Otherwise, past studies of shorebirds using the bay have focused primarily on seasonal abundance patterns, species composition at individual sites (Storer 1951, Recher 1966, Holway 1990), or occurrence in specific nontidal habitats (Anderson 1970, Swarth et al. 1982, R. Pratt unpubl. data). While studies of shorebirds' habitat use in the bay have addressed the Marbled Godwit, Willet, and Western Sandpiper (Luther 1968, Kelly and Cogswell 1979, Warnock and Takekawa 1995), there has been no overall assessment of the relative role of different habitat types or areas in supporting shorebirds. Detailed knowledge of habitat use is critical for recognizing the importance of different parts of the bay to shorebirds, for maintaining the integrity of habitat systems used by individual birds, and for maximizing the quality of wetlands created, restored, or managed in the bay. It is also important to understanding the sources and significance of environmental contaminants found in shorebirds, especially in urbanized environments such as San Francisco Bay (Ohlendorf and Fleming 1988).

In this paper we report the abundance and spatial distribution of the bay's most common shorebirds and compare their densities by 14 divisions of the tidal flat.

STUDY AREA

Our study area was the intertidal portion of the San Francisco–San Pablo Bay estuary and associated nontidal wetlands (Figure 1). Habitats covered during surveys included intertidal (flats, sloughs, and marshes), actively managed salt ponds, and "other" wetlands (sewage and other water-treatment ponds, salt ponds in disuse, and a wide variety of diked wetlands). Prior to the first census, we reconnoitered the bay's shore, salt ponds, and other wetlands extensively. From these visits we outlined and described census areas and devised protocols for coverage intended to minimize undetected flock movements that would introduce count errors (Stenzel and Page 1988). Prior to subsequent censuses we made a reconnaissance for the availability of salt ponds and other wetlands to keep our census-site descriptions current with changes in habitat conditions and accessibility.

We divided the bay into four major regions: San Pablo Bay (SPB) between the Carquinez Bridge and points San Pedro and San Pablo, North San Francisco Bay (SFN) between points San Pedro and San Pablo and the San Francisco–Oakland Bay Bridge, Central San Francisco Bay (SFC) between the San Francisco–Oakland Bay and San Mateo bridges, and South San Francisco Bay (SFS) south of the San Mateo Bridge (Figure 1). SFN and SFC combined were called Central San Francisco Bay by Stenzel and Page (1988) and the Goals Project (1999). We further subdivided the intertidal flats of the four regions into 14 tracts (Figure 1).

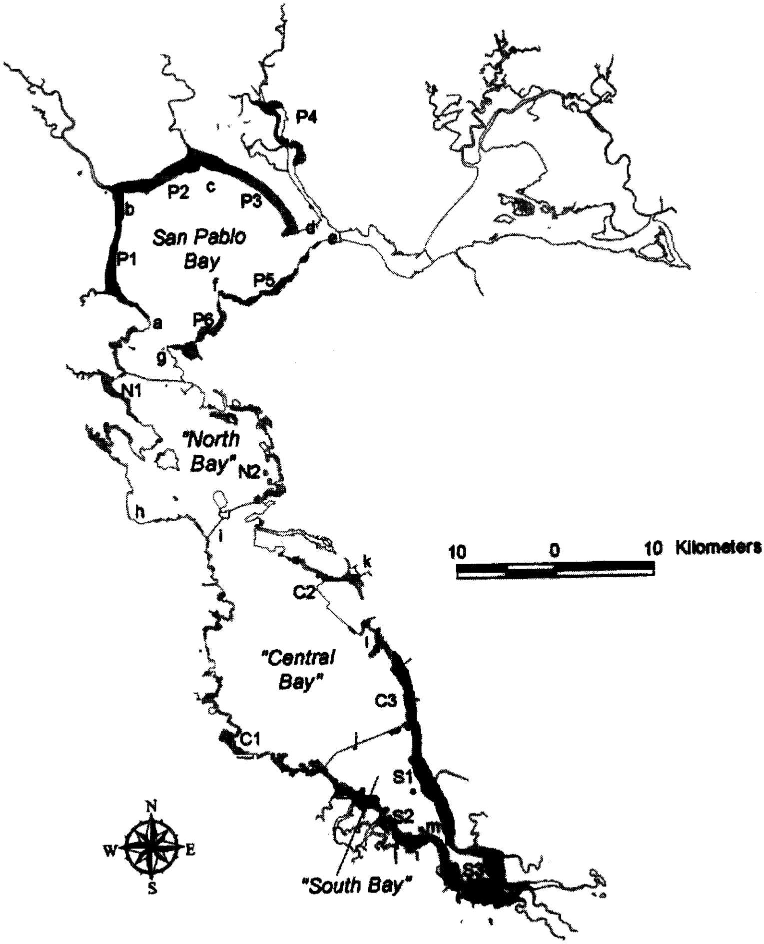


Figure 1. San Francisco–San Pablo Bay estuary, showing San Pablo Bay and three regions of San Francisco Bay. Tidal tracts in San Pablo Bay Region comprise P1, the west shore between Point San Pedro (reference point a) and the Petaluma River mouth (b); P2, the northwest shore between point b and Sonoma Creek (c); P3, the northeast shore between point c and the Napa River mouth (d); P4, Napa River flats north of point d; P5, the east shore between the Carquinez Bridge (e) and Point Pinole (f); and the southeast shore between point f and Point San Pablo (g). Tidal tracts in north San Francisco Bay comprise N1, the west shore between point a and the Golden Gate (h); and N2, the east shore between point g and the Bay Bridge (i). Tidal tracts in central San Francisco Bay comprise C1, the west shore between i and the Hayward–San Mateo Bridge (j); C2, San Leandro Bay (k) and the south shore of Alameda; C3, Hayward shoreline between Bay Farm Island (l) and j. Tidal tracts in south San Francisco Bay include S1, the west shore between j and the Dumbarton Bridge (m); S2, the east shore between j and m; and S3, the shore south of m. Base map from the EcoAtlas, version 1.5003, July 1998, San Francisco Estuary Institute.

The western and northern shores of San Pablo Bay are surrounded by extensive agricultural and undeveloped diked baylands, the largest expanses of tidal marsh in the bay, and actively managed salt-evaporation ponds. The eastern shore of SPB is partially developed for residences and industry. San Pablo Bay itself is relatively shallow; a broad swath of tidal flat rims the west and north shores, and about half the bay is under less than 2 m of water at low tide. SPB comprises six tidal tracts (Figure 1), which together were 34–36% of the total tidal flat surveyed on our three fall and five spring counts.

North San Francisco Bay is distinguished by a heavily urbanized shoreline, with most of the rocky intertidal and bluff-backed shore in the bay, and a small amount of supralittoral wetland habitat. SFN is mostly deep water with relatively little tidal flat, which we allocated into two tidal tracts (Figure 1). Only 8–9% of the total tidal flat surveyed on our three fall and five spring counts was in SFN.

The western shoreline of central San Francisco Bay is developed mostly for industry but the eastern side is a mixture of developed and undeveloped uplands and restored wetlands. A wide swath of tidal and shallow subtidal flat dominates the southeast shore, but tidal flat is patchy elsewhere in this region (Figure 1). SFC comprises three tidal tracts (Figure 1), which combined were 14–16% of the tidal flat surveyed on our three fall and five spring counts.

South San Francisco Bay is rimmed by a large system of managed and disused salt ponds, with residentially developed shoreline limited to the northwest portion of the region. Tidal and shallow subtidal flats lie outside the outer levees of the salt ponds. SFS comprises three tidal tracts (Figure 1), together making up 41–44% of the tidal flat surveyed on our three fall and five spring counts.

There were approximately 11,400 ha of tidal flats above 0.0 mean lower low water (MLLW) and 14,000 ha of actively managed salt ponds in the bay during our study. We covered 83–91% of the tidal flat on the surveys. North of San Pablo Bay were 2890 ha of salt ponds; reconnaissance trips revealed few shorebirds and little shallow habitat, so we covered only 7.2–13% of the salt ponds in this area. At the south end of the bay there were 11,100 ha of salt ponds, of which we covered 26–87% on the surveys.

METHODS

We conducted 13 censuses between April 1988 and April 1993 to estimate total numbers of shorebirds in the bay. We made three fall counts between mid-August and mid-September, 1988–1990, three "early winter" counts in early November 1990–1992, a late winter count in late January to early February 1991, and six spring counts in late April 1988–1993. Censusers included Point Reyes Bird Observatory (PRBO) staff biologists, other trained biologists, and volunteers recruited from local Audubon societies. We offered training sessions, attended by over 100 participants, on methods of identifying and counting shorebirds.

We counted birds on moderately high rising tides (starting censuses at approximately +0.3 m MLLW at the Golden Gate Bridge), covering SPB and SFN on one day of a weekend, SFC and SFS on the other. We divided the shoreline into segments that could be surveyed in 1 to 2 hrs by a single census team (there were usually three to six census segments per tidal tract). All habitat within the shoreline segments was surveyed, including flat, slough, riprap, and marsh. To avoid counting the same flocks twice, we surveyed wetlands and salt ponds before birds counted on the tidal flats moved into the ponds at high tide. Census teams comprised one to six people with binoculars and, at minimum, a 20× spotting telescope; each team included one or more observers experienced at identifying and counting shorebirds. When necessary, census team leaders met after the counts and discussed bird movement to reduce the likelihood that individual flocks of birds were counted by more than one census team. Approximately 100 counters took part in the censuses each day. In April 1993, extensive dredging along outer levees in parts of SFS prevented us from reaching some large shoreline census segments; where possible we made our best estimates of the birds in these areas from nearby segments. Also on that census, because of a shortage of experienced observers for San Pablo Bay, we conducted an aerial survey of the western and northern shores and used ground censuses from the same day in those areas to refine our estimates of species composition. We use the 1993 spring count only in our presentation of shorebird totals for the entire bay, acknowledging that the poorer coverage in SFS and the use of aerial censuses in San Pablo Bay may have biased the totals from this census (probably downward).

We conducted winter censuses at high-tide roosting areas (primarily salt ponds) under high spring tides. This was necessary because, after significant rain, we could not reach most of the shoreline of SFS. Counts within general regions of the bay were conducted simultaneously. We used fewer observers than on spring and fall counts and took 4–9 days to complete each winter count.

We instructed counters to identify to species all shorebirds except the Short and Long-billed dowitchers. When identification to species of most individuals in a flock was not feasible, observers estimated flock size, noted which species were included in those flocks, and estimated proportions of the different species. Methods of data collation for unidentified shorebirds are in Page et al. (1999). The percentage of total small *Calidris* sandpipers unidentified was 27% in fall, 24% in winter, and 11% in spring; of total yellowlegs 8% in fall, 4% in winter, and 11% in spring; of total phalaropes 8% in fall and 9% in spring. For intra-estuarine analyses, we combined into species groups (1) small *Calidris* sandpipers, including, the Western, Least, and Dunlin; (2) the Greater and Lesser Yellowlegs; (3) the Wilson's and Red-necked Phalaropes; and (4) rocky-coast species, including the Black Oystercatcher, Wandering Tattler, Ruddy Turnstone, Black Turnstone, and Surfbird.

We intended the study primarily to estimate the total number of shorebirds in the bay; examining the species' spatial distribution was a secondary objective. High annual return rates of individual shorebirds to their wintering grounds (Kelly and Cogswell 1979, Warnock et al. 1997) and the persistence of some individuals in the bay over a winter season (Kelly and Cogswell

1979, Evans and Pienkowski 1984, Warnock and Takekawa 1996) result in potentially high correlations between censuses. This inherent nonindependence of the data and the small sample sizes for each season limit the legitimacy and usefulness of significance tests and determined the exploratory approach to the data we use here.

We use medians to estimate abundance because the median is less sensitive than the mean to outlying values, but we also present means and coefficients of variation (corrected for small sample sizes) for comparisons of variability within fall and spring counts. We categorize each species' overall abundance by the season of the species' highest median abundance: abundant, >10,000; moderately abundant, 1000–10,000; common, <1000 and occurring on all fall, early winter, and spring counts; uncommon to rare, not occurring on all fall, early winter, and spring counts. Species' abundances from the single late winter census (February 1991) are reported as ratios of abundance from the previous early winter census (November 1990), giving an indication of whether that species' abundance increased or decreased between one early and late winter count.

We estimated densities (number per hectare) for total shorebirds and for species groups counted on the tidal flats on both fall and spring censuses. Fixed tidal areas for density calculations were derived from the EcoAtlas (beta version 1.5003, July 1998), a digital map of the bay generated by the San Francisco Estuary Institute. The lower extent of tidal flat in the EcoAtlas represents the mean lower low-water datum (0.0 MLLW). We calculated the intertidal area above 0.0 MLLW for each shoreline census segment. Although counters surveyed all tidal habitat within their shoreline segments, they rarely reported birds to be in tidal marshes, so we used only the area of tidal flats to generate densities. For each census, we summed the area and the shorebird totals for the segments that were covered (for each of the 14 tidal tracts and for the total tidal flat of the bay) to obtain estimates of density and biomass.

We used the maximum overall (total tidal flat) densities for each species group per season as benchmarks with which we compared densities by individual tidal tract. We identified two categories of important tidal tracts for each species group: frequent high use—densities exceeding the seasonal benchmark on more than one half of the censuses, and consistent high use—densities exceeding the seasonal benchmark on all censuses.

As an alternative perspective on densities of total shorebirds, we also estimated total shorebird biomass (kilograms per hectare) for each tidal tract covered on each census and for all tidal flats combined. Because the two to four most abundant species in an estuary on average may account for over 90% of the total (Page et al. 1999), these totals are often dominated by a few species. We used the masses from Dunning (1992) and Page et al. (1979) to calculate the biomass in each tidal tract for each census. Warnock and Bishop (1998) reported mean body masses for Western Sandpipers 23–29% higher after mid-April than in winter on San Francisco Bay. Because data reflecting the potentially greater body masses of shorebirds during migration periods were not available for all species, we limited our comparisons to among tidal tracts within the same season and not between seasons.

RESULTS

Overall Abundance

Shorebirds of 38 species totaled 340,000 to 396,000 individuals on fall surveys, 325,000 to 358,000 on early winter surveys, 225,000 on the late winter survey, and 589,000 to 932,000 on spring surveys. Although more species were at maximum abundances in fall and winter, two of the most abundant taxa (Western Sandpiper and dowitchers) reached peak numbers in spring, making spring the period of highest overall shorebird abundance. Twenty-three species, including the Short- and Long-billed dowitchers combined, occurred on all fall, early winter, and spring censuses (Table 1). All of the above species except the Red-necked Phalarope also occurred on the late winter census. The Western Sandpiper was the most abundant species on each census, exceeding 100,000 individuals on all but one census. Median numbers for this species exceeded 100,000 individuals in fall and winter and 500,000 in spring (Table 1). The Dunlin was the next most abundant species, with median numbers of over 100,000 individuals in winter and 75,000 in spring. Abundant species with median numbers of 10,000 to 100,000 individuals were the Marbled Godwit, Least Sandpiper, and dowitchers (every season), Black-bellied Plover, American Avocet, and Willet (fall and winter), and Red-necked Phalarope (fall). Moderately abundant species included the Semipalmated Plover, Black-necked Stilt, Long-billed Curlew, and Red Knot. Common species included the Snowy Plover, Killdeer, Greater Yellowlegs, Lesser Yellowlegs, Spotted Sandpiper, Whimbrel, Ruddy Turnstone, Black Turnstone, and Sanderling (Table 1).

Most occurrences of rare to uncommon species were during migration periods (Table 2), with the exception of the golden-plovers, Black Oystercatcher, Pectoral Sandpiper, and Common Snipe, recorded on the November "early winter" survey as well (still within the fall migration period for the Pectoral Sandpiper and snipe). The Semipalmated Sandpiper and Buff-breasted Sandpiper occurred only in fall, the Solitary Sandpiper occurred only in spring, and the Wandering Tattler, Surfbird, Baird's Sandpiper, and Ruff occurred on both fall and spring censuses. The Red Phalarope migrates, primarily over ocean waters, through November and occurred on one fall count and one early winter count. The single record for the Stilt Sandpiper was in early winter.

Some species were consistently more abundant in one or two seasons than the others (Table 1). The Black-necked Stilt, American Avocet, Willet, and Long-billed Curlew were more abundant in fall and winter than in spring. The Whimbrel, Western Sandpiper, and Least Sandpiper were more abundant in fall and spring than in winter; the Western Sandpiper was most abundant in spring, and the Least Sandpiper was most abundant in fall. The Spotted Sandpiper and Red-necked Phalarope were most abundant in fall; the Red-necked Phalarope was least abundant in winter. Dunlins do not normally arrive in central California in large numbers until after September and thus were more abundant on winter and spring counts than on fall counts. Dowitchers were most abundant in spring every year.

Table 1 Censuses of Common Shorebirds by Season in the San Francisco Bay Area

	Fall[a]			Early Winter[b]				Spring[c]		
Species	Median	Mean	CV[d]	Median	Mean	CV	Ratio[e]	Median	Mean	CV
Black-bellied Plover *Pluvialis squatarola*	12,165	12,619	10	13,246	12,596	14	1.00	4451	5706	62
Snowy Plover *Charadrius alexandrinus*	122	128	25	153	130	37	0.22	75	73	52
Semipalmated Plover *Charadrius semipalmatus*	2369	2106	25	924	981	65	0.87	1579	1745	57
Killdeer *Charadrius vociferus*	477	448	27	214	222	9	1.36	206	197	48
Black-necked Stilt *Himantopus mexicanus*	5589	6239	20	4975	5104	46	0.53	880	1088	78
American Avocet *Recurvirostra americana*	17,429	17,671	43	23,125	23,164	10	0.90	3879	4253	40
Greater Yellowlegs *Tringa melanoleuca*	439	465	35	323	320	6	0.23	327	407	54
Lesser Yellowlegs *Tringa flavipes*	68	58	50	26	37	71	0.14	56	51	76
Willet *Catoptrophorus semipalmatus*	24,056	23,045	9	16,971	17,864	21	0.96	3353	3121	55
Spotted Sandpiper *Actitis macularia*	43	45	32	8	11	64	1.43	17	17	39
Whimbrel *Numenius phaeopus*	133	188	69	71	70	10	0.92	124	123	25
Long-billed Curlew *Numenius americanus*	1956	1780	38	1474	1592	52	0.25	283	342	50
Marbled Godwit *Limosa fedoa*	24,673	24,216	22	16,812	16,430	5	0.79	20,312	19,984	45

Ruddy Turnstone										
Arenaria interpres	59	73	64	47	50	41	1.85	72	78	54
Black Turnstone										
Arenaria melanocephala	53	77	74	103	105	39	2.07	86	88	89
Red Knot										
Calidris canutus	1827	1698	29	507	790	130	2.50	761	854	72
Sanderling										
Calidris alba	825	1292	68	539	563	23	1.28	414	475	64
Western Sandpiper										
Calidris mauri	181,607	189,359	17	122,968	120,449	24	1.00	516,670	536,423	19
Least Sandpiper										
Calidris minutilla	48,294	49,465	18	14,475	12,099	47	0.30	23,812	24,314	34
Dunlin										
Calidris alpina	16	14	71	121,329	110,147	22	0.60	62,382	76,406	53
Dowitchers										
Limnodromus spp.[f]	23,805	22,666	10	18,130	19,160	16	0.65	43,638	45,040	24
Red-necked Phalarope										
Phalaropus lobatus	18,969	16,588	42	3	3	108	0.00	1785	2961	100

[a]Three censuses, mid-August–mid-September 1988–1990.
[b]Three censuses, early November 1990–1992.
[c]Six censuses, late April 1988–1993.
[d]CV, coefficient of variation.
[e]Ratio of results of a census in February 1991 to those in November 1990.
[f]*L. scolopaceus* and *L. griseus*.

Table 2 Frequency of Occurrence and Maximum Number of Rare and Uncommon Species on Shorebird Censuses of the San Francisco Bay Area

	Fall[a]		Early Winter[b]		Spring[c]	
Species	Freq.	Max.	Freq.	Max.	Freq.	Max.
Golden-plovers *Pluvialis dominica/fulva*	3	11	2	3	2	2
Black Oystercatcher *Haematopus bachmani*	2	4	1	2	4	4
Solitary Sandpiper *Tringa solitaria*	0	0	0	0	1	4
Wandering Tattler *Heteroscelus incanus*	3	16	0	0	5	7
Surfbird *Aphriza virgata*	3	17	0	0	4	77
Semipalmated Sandpiper *Calidris pusilla*	2	1	0	0	0	0
Baird's Sandpiper *Calidris bairdii*	3	20	0	0	2	2
Pectoral Sandpiper *Calidris melanotos*	2	12	1	1	2	3
Stilt Sandpiper *Calidris himantopus*	0	0	1	1	0	0
Buff-breasted Sandpiper *Tryngites subruficollis*	1	2	0	0	0	0
Ruff *Philomachus pugnax*	1	2	0	0	1	2
Common Snipe *Gallinago gallinago*	3	2	3	15	4	5
Wilson's Phalarope *Phalaropus tricolor*	3	1642	0	0	2	213
Red Phalarope *Phalaropus fulicaria*	1	15	1	22	0	0

[a]Three censuses, mid-August–mid-September 1988–1990.
[b]Three censuses, early November 1990–1992.
[c]Six censuses, late April 1988–1993.

Annual variability in abundance was lower in fall and winter, when the median coefficient of variation (CV) for species' totals was 30.5 each season, than in spring, when the median CV was 53.0 (Table 1). Variability among counts was low relative to other species in fall for the Black-bellied Plover and Willet, in winter for the Killdeer, American Avocet, Greater Yellowlegs, and Marbled Godwit, in spring for the Spotted Sandpiper, and in fall and spring for the Western Sandpiper, Least Sandpiper, and dowitchers (Table 1). Although variability in numbers was also relatively low in winter and spring for the Whimbrel, it was relatively high in fall for this species. The variability of abundant species was sometimes high at that species' season of minimal occurrence (e.g., Dunlin in fall, Red-necked Phalarope in winter). It was high for species associated with rocky coasts, which we did not cover completely (e.g., Ruddy Turnstone in fall, Black Turnstone in fall and spring), for less abundant species (e.g., Lesser Yellowlegs and Spotted Sandpiper in winter), and for the Red Knot (Table 1).

Distribution by Habitat

Twelve of 18 species groups (see Methods) occurred mostly in tidal habitats, when these were exposed (surveyed only in fall and spring). For all 12 species groups, at least 60% of the individuals were in tidal habitat on all surveys (Figure 2).

Of other species, only phalaropes occurred predominantly in salt ponds on all surveys, but 50% or more of the Black-necked Stilts were in salt ponds on four of five spring censuses. Also, at least 35% of Snowy Plovers and American Avocets during fall and at least 40% of Snowy Plovers and yellowlegs during spring surveys were in salt ponds (Figure 2). We found a higher proportion of both stilts and avocets in salt ponds in fall than in spring (with one exception). In contrast to this pattern for stilts and avocets, we found a higher proportion of yellowlegs in salt ponds in spring than in fall.

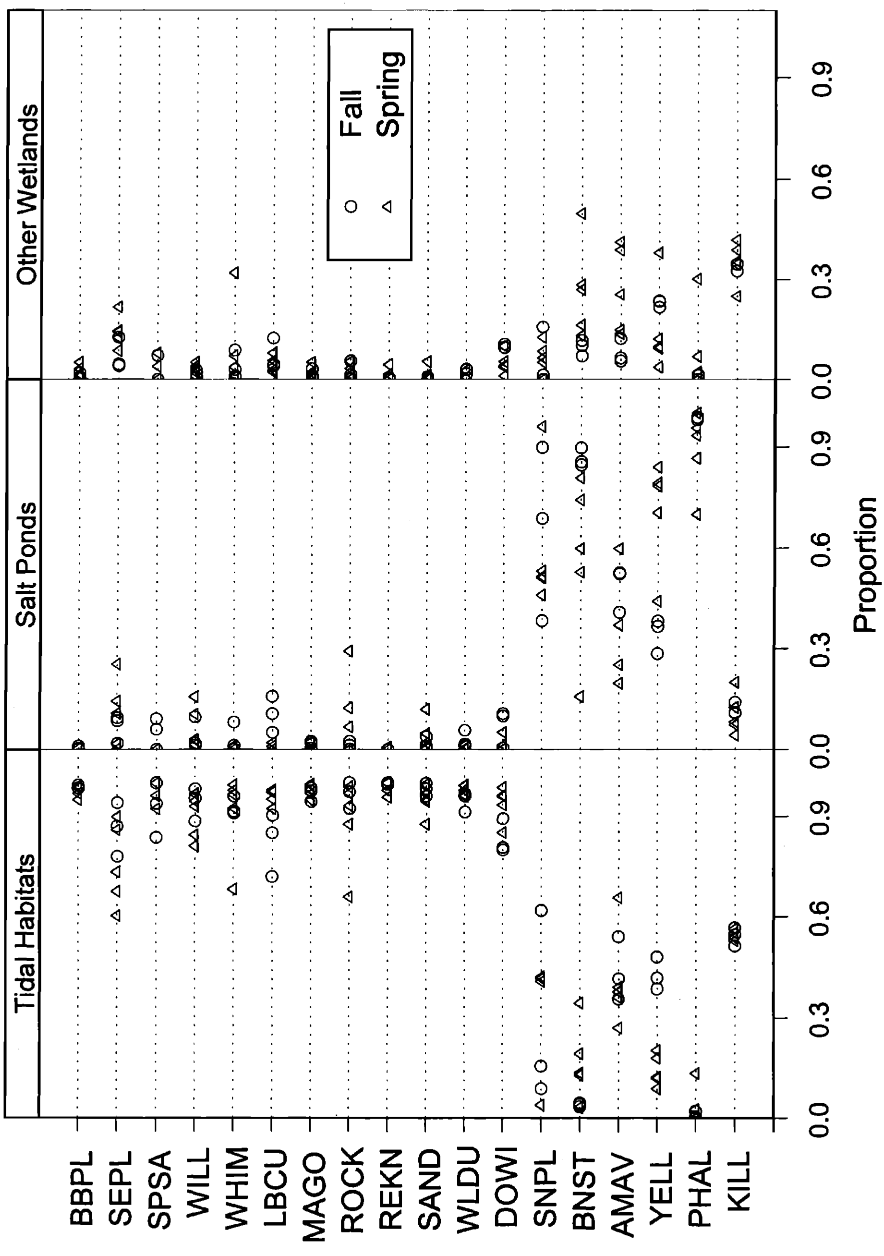
The Killdeer was the only shorebird for which at least 20% of the individuals were consistently in wetland habitats other than tidal flats or salt ponds.

Distribution by Region of the Bay

There were major differences in distribution among species groups over the four regions of the bay. The proportional distributions of the species-group totals relative to the proportional distribution of tidal flats fell mostly into one of two patterns: (1) occurring mostly in the north and central San Francisco Bay regions (SFN and SFC), or (2) occurring mostly in the central and south San Francisco Bay regions (SFC and SFS). Nevertheless, all regions of the bay supported high proportions of some species groups on some censuses.

Although the majority of tidal flat in the bay lies in San Pablo Bay (SPB) and SFS, high proportions of some species were found in SFN and SFC. This tendency was most pronounced for the Spotted Sandpiper in SFN, for the Semipalmated Plover, Red Knot, and dowitchers in SFC, and for the Killdeer, rocky-coast species, Whimbrel, and Sanderling in both regions (Figure 3). These species groups all have habitat distributions biased toward tidal flats, or tidal flats and other wetlands, when the tidal flat was exposed (Figure 2).

The tendency for a higher proportion of some species to occur in SFS, relative to the proportion of tidal flat, was very prominent for salt-pond specialists (Figure 2) but was also evident for some of the 12 tidal flat species. The proportions of the Snowy Plover, stilt, avocet, yellowlegs, and phalaropes in SFS almost always exceeded the proportion of tidal flat in the region, a result largely due to the numbers of these species groups counted in the salt ponds of SFS. Additionally, the proportion of the Black-bellied Plover and dowitchers always exceeded, and the proportion of the Willet and Marbled Godwit usually exceeded, the proportion of tidal flat habitat in SFS (Figure 3).


Tidal Habitats
Salt Ponds
Other Wetlands
Fall
Spring
BBPL
SEPL
SPSA
WILL
WHIM
LBCU
MAGO
ROCK
REKN
SAND
WLDU
DOWI
SNPL
BNST
AMAV
YELL
PHAL
KILL
0.0
0.3
0.6
0.9
Proportion

The proportion of most species in SPB tended to be smaller than the relative proportion of the tidal flat. The one exception, the Long-billed Curlew, occurred in this region in a proportion higher than that of tidal flat on all fall and most winter and spring counts (Figure 3).

In most regions of the bay, occurrence of the Red Knot was highly variable. On all but one fall and one winter census, knots concentrated in SFC. Proportions in SFS in fall and winter were also higher than expected. Although the proportion in SPB usually was less than that predicted by the extent of tidal flat, on one spring census over 80% of the knots were found in that region (Figure 3).

Shorebird Densities on Tidal Flats

Total shorebird biomass was 2.8–3.2 (median 2.9) kg/ha in fall and 2.5–4.3 (median 3.5) kg/ha in spring (with body masses not seasonally adjusted). Tidal tracts that supported the greatest biomass in fall were the Napa River flats (P4), San Leandro Bay (C2), and the east and south shores of central and south San Francisco Bay (C3, S2, S3; Figure 4). In spring the areas of highest biomass were noncontiguous segments of SFC and SFS: San Leandro Bay and the east shore of SFS (S2; Figure 5). The difference between the tidal tracts with the highest and lowest biomasses was largest in fall (Figure 6). In spring the biomass within tidal tracts was highly variable, and the estimates for tracts of high and low median biomass often overlapped broadly (Figure 6).

Densities of total shorebirds were greater in spring than in fall and were dominated by the abundance of small *Calidris* sandpipers at both seasons. In fall, total shorebird densities on all tidal flats combined, 29–34 (median 33) shorebirds/ha, were never as high as in spring, when they were 58–90 (median 72) shorebirds/ha. On individual tidal tracts, densities ranged from 2.5 to 89 (median 22) shorebirds/ha in fall and 4.1–270 (median 54) shorebirds/ha in spring.

Areas of consistent high use (with densities higher than benchmark on all censuses, see Methods) for *Calidris* sandpipers were the Napa River flats (P4), Hayward Shoreline (C3), and the south end of SFS (S3) in fall and the east shore of SFS (S2) in fall and spring (Figure 7). Tidal tracts getting frequent high use in spring, where small sandpipers exceeded season benchmark densities on at least half the spring censuses, were the west shore of SPB (P1) and the south end of SFS. We recorded densities of less

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Figure 2. The proportion of bay totals for 18 shorebird species or species groups found in three wetland habitat types on three fall and five spring censuses. A proportion for each habitat type is displayed for each taxon for each census. BBPL, Black-bellied Plover; SEPL, Semipalmated Plover; SPSA, Spotted Sandpiper; WILL, Willet; WHIM, Whimbrel; LBCU, Long-billed Curlew; MAGO, Marbled Godwit; ROCK, Ruddy and Black turnstones, Black Oystercatcher, Wandering Tattler, and Surfbird; REKN, Red Knot; SAND, Sanderling; WLDU, Western and Least sandpipers and Dunlin (combined); DOWI, dowitcher spp.; SNPL, Snowy Plover; BNST, Black-necked Stilt; AMAV, American Avocet; YELL, yellowlegs; PHAL, phalaropes; KILL, Killdeer.

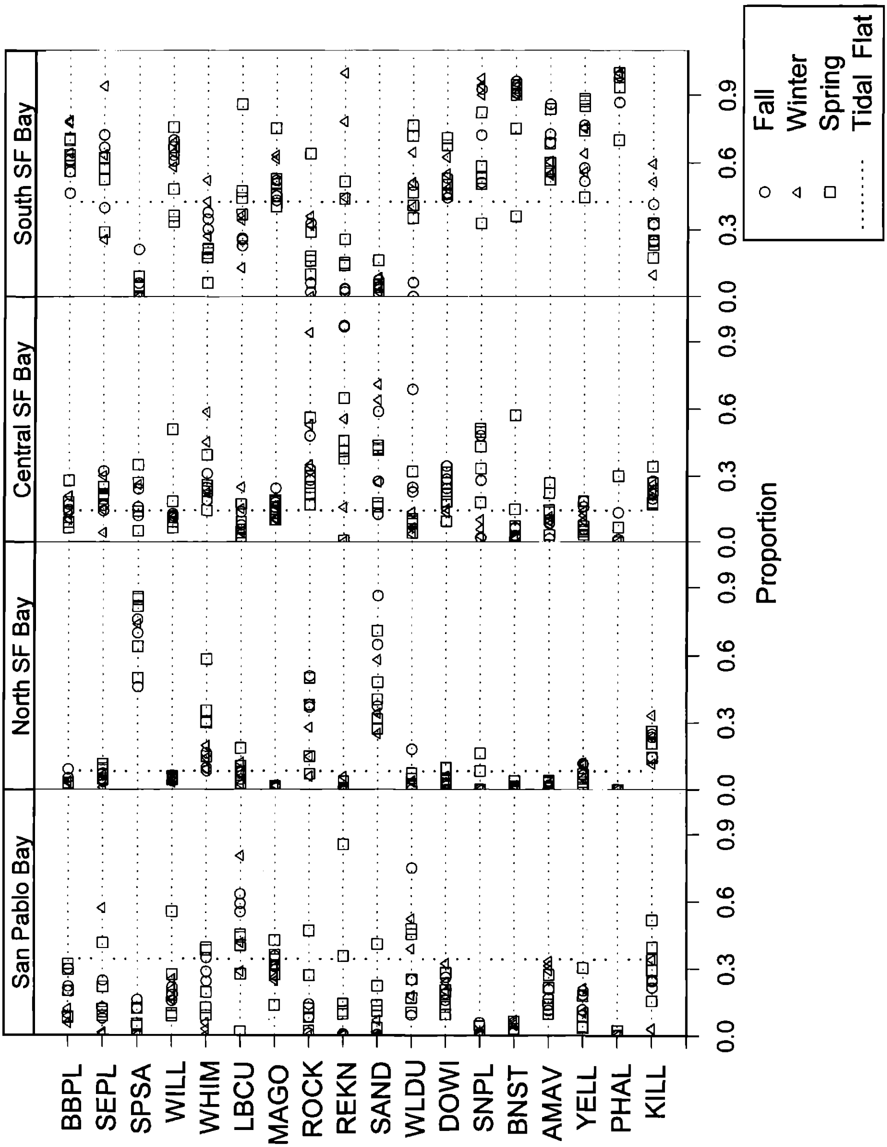


Figure 3. The proportion of the totals for 18 shorebird species or species groups that were found in four regions of the bay. Dotted vertical reference lines in each panel indicate the proportion of the total estuary tidal flat that was located in each of the four regions. Data from three fall, three early winter, and five spring censuses except when fewer than 10 individuals of that species were counted in the bay. For abbreviations, see Figure 2.

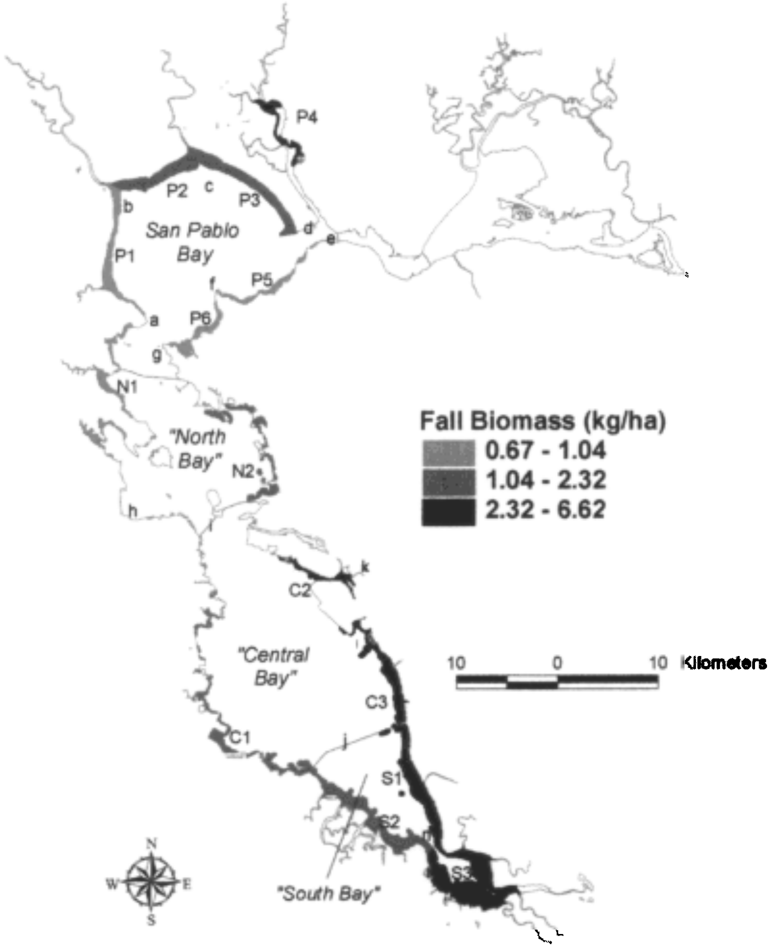


Figure 4. Median fall shorebird biomass on 14 tidal tracts (see Figure 1 for description of tracts). Base map from the EcoAtlas, version 1.5003, July 1998, San Francisco Estuary Institute.

than 50 sandpipers/ha in fall (except on the Napa River flats), and usually less than 150 sandpipers/ha in spring (Figure 7).

Among the species groups, dowitchers had the second highest densities. Among the tidal tracts, densities were consistently high on the Napa River (P4), the Hayward Shoreline (C3), and at the south end of SFS in fall and in San Leandro Bay (C2) in fall and spring (Figure 8). Tracts getting frequent high use by dowitchers were the southeast shore of SPB (P6), the west shore of SFC (C1), and the east shore of SFS (S2) in spring. Densities were usually

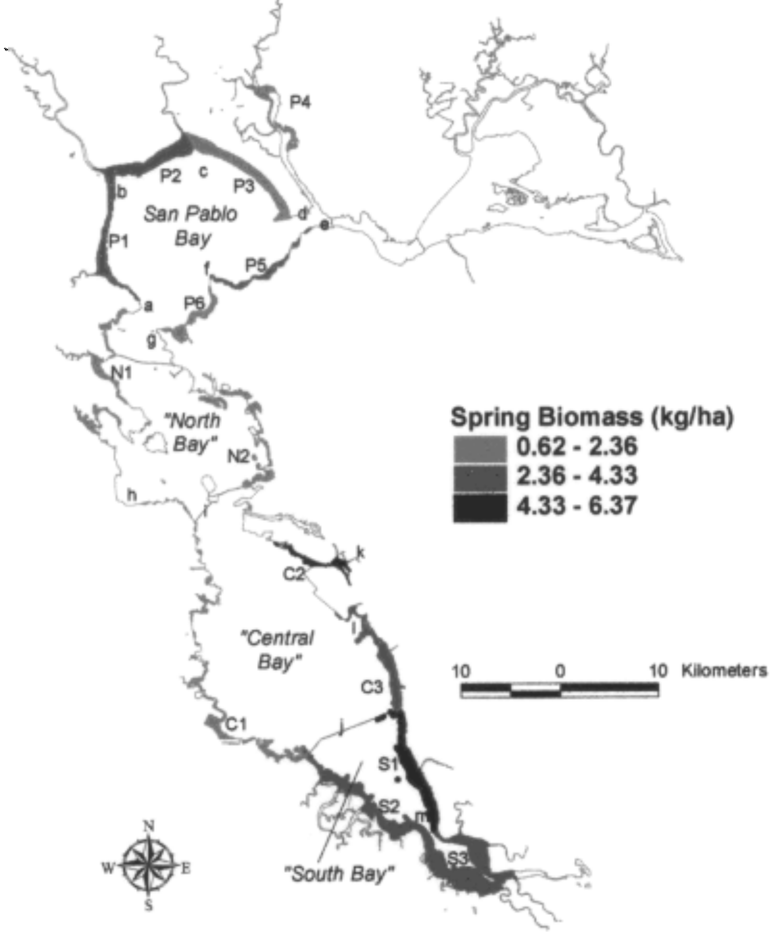
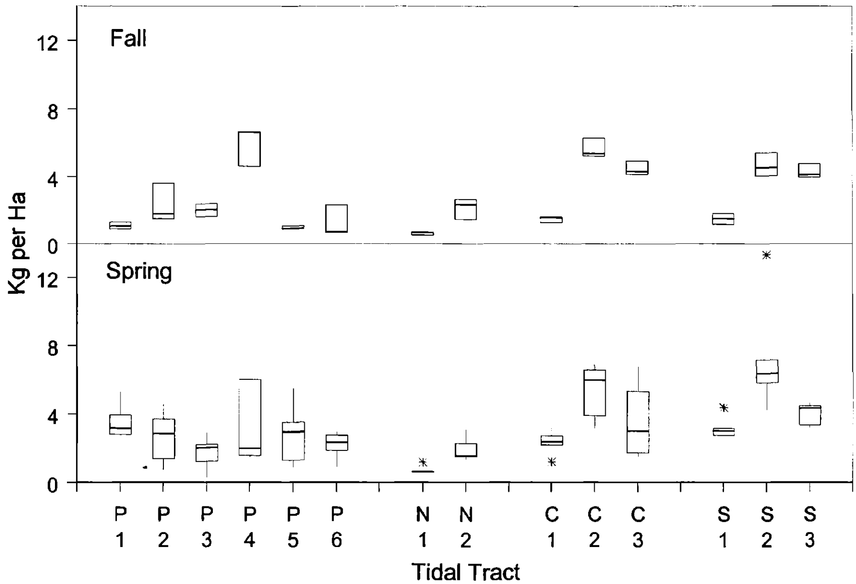


Figure 5. Median spring shorebird biomass on 14 tidal tracts (see Figure 1 for description of tracts). Base map from the EcoAtlas, version 1.5003, July 1998, San Francisco Estuary Institute.

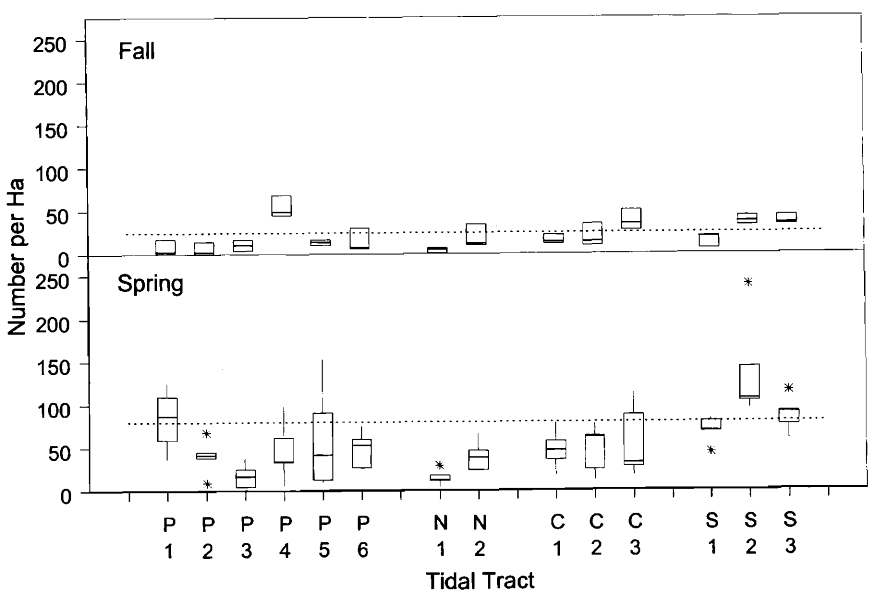
Figure 6. Biomass comparison of all shorebirds combined on 14 tidal tracts on three fall and five spring comprehensive censuses (see Figure 1 for description of tracts). Central 50% of data (interquartile range) for each tidal tract indicated by boxes, medians by thicker lines in boxes, data within 1.5 times interquartile range of boxes by vertical whiskers on boxes, and outlying values (beyond limit of whiskers) by asterisks.

Figure 7. Density comparison of *Calidris* sandpipers on 14 tidal tracts of the bay on three fall and five spring comprehensive censuses. See Figure 1 for description of tracts and Figure 6 for description of boxplots. Dashed horizontal reference lines indicate the maximum overall density for this species group in the bay; all plotted data lie above the reference line for consistent high use of tidal tracts, and median lies above reference line for frequent high use of tidal tracts.

Shorebird Biomass



Western Sandpiper, Least Sandpiper, & Dunlin



less than 10 dowitchers/ha but were consistently higher in San Leandro Bay (Figure 8).

The Napa River flats (P4), San Leandro Bay (C2), and Hayward Shoreline (C3) were tidal tracts of consistent high use for the Marbled Godwit in fall (Figure 9). Tracts of frequent high use were the northwest shore of SPB (P2) and south end of SFS (S3) in fall and San Leandro Bay, Hayward Shoreline, and the east shore of SFS (S2) in spring (Figure 9). Densities were usually less than 6 godwits/ha but were occasionally higher in spring (Figure 9).

American Avocet and Willet densities were higher on most tidal tracts in fall than in spring. Densities of 0.5–1.5 avocets and 1–3 Willets per hectare were common in fall, while spring densities were usually less than 0.5 avocets and 0.5 Willets/ha (Figures 10 and 11). Tracts with fall densities consistently exceeding the fall benchmark for the Willet were the Napa River (P4), San Leandro Bay (C2), and the east shore of SFS (S2). Tracts with densities frequently exceeding the benchmark were the Napa River flats and Hayward Shoreline (C3) for the avocet in fall, the south end of SFS (S3) for the Willet and avocet in fall, and San Leandro Bay and the east shore of SFS for the Willet in spring (Figures 10 and 11). Median avocet densities did not exceed benchmarks on any single tidal tract in spring.

Black-bellied Plover densities also were higher in fall than in spring on most tidal tracts (Figure 12). In fall, most densities did not exceed 3 plovers/ha, but like the Willet's, were consistently highest on the Napa River flats (P4), San Leandro Bay (C2), and the east shore and south end of SFS (S2 and S3), and frequently high on the east shore of SFN (N2) (Figure 12). Spring densities rarely exceeded 1 plover/ha, except in SFS, and did not exceed the spring maximum overall density on more than half of the censuses in any tidal tract (Figure 12).

Densities of two highly localized species, the Red Knot and Sanderling, seldom exceeded 2 Sanderlings/ha and 3 knots/ha in fall and 0.5 individuals/ha of either species in spring, but each reached about 5 individuals/ha on one survey. Hayward Shoreline (C3) got consistent high use by Red Knots in fall, and east SPB (P5) and Hayward Shoreline got frequent high use in spring (Figure 13). Consistent high-use areas for the Sanderling were the east shore of SFN (N2) and San Leandro Bay (C2) in both fall and spring; the east shore of SPB was a frequent high-use tract in spring (Figure 14).

Semipalmated Plovers usually occurred at densities of less than 0.5 plovers/ha. In fall, their densities on the west shore of SFC (C1) and at the south end of SFS (S3) were consistently higher than the species' maximum overall density (Figure 15). Frequent high-use tidal tracts for this species

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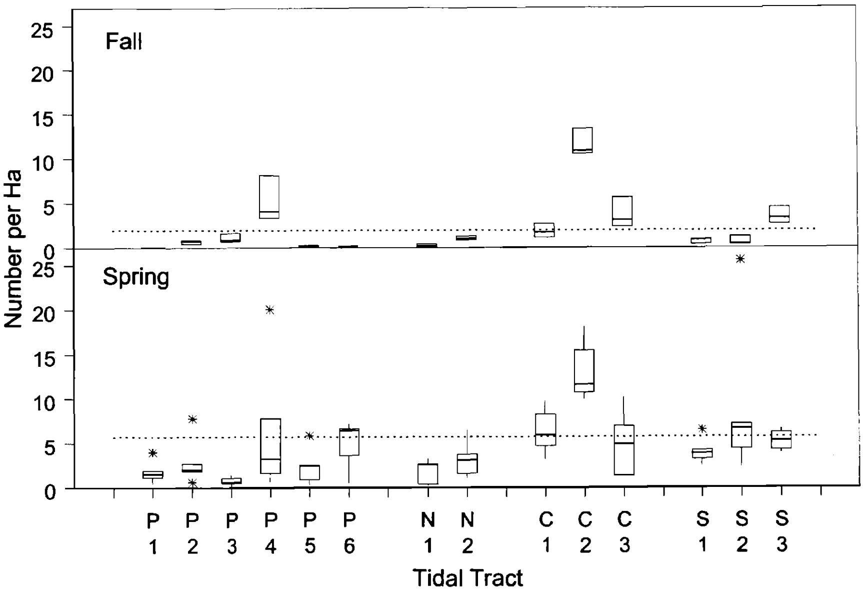
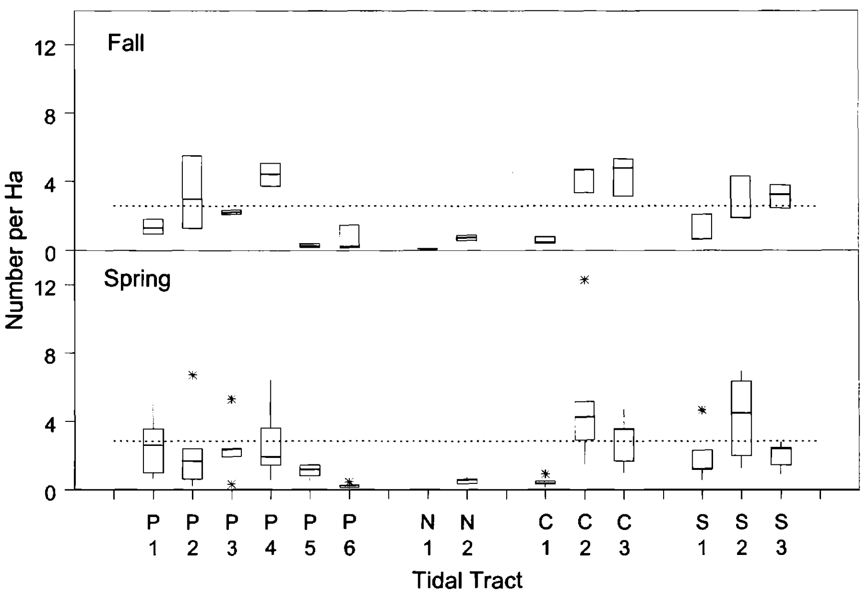
Figure 8. Density comparison of dowitchers on 14 tidal tracts of the bay on three fall and five spring comprehensive censuses. See Figure 1 for description of tracts and Figures 6 and 7 for boxplot specifications.

Figure 9. Density comparison of Marbled Godwits on 14 tidal tracts of the bay on three fall and five spring comprehensive censuses. See Figure 1 for description of tracts and Figures 6 and 7 for boxplot specifications.

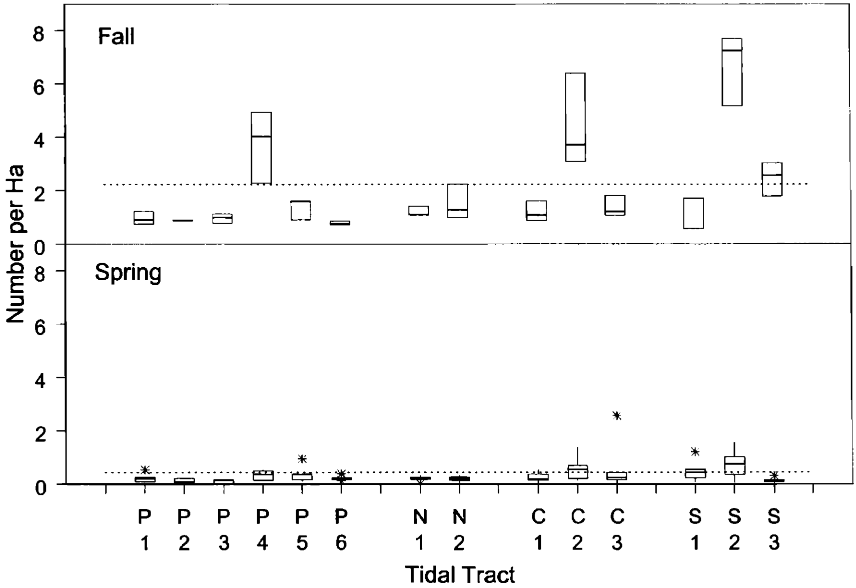
dowitcher spp.



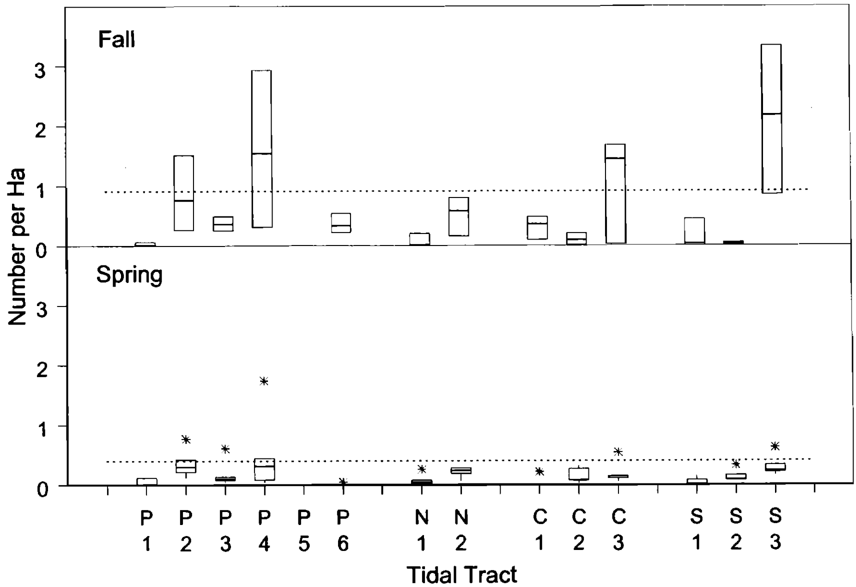
Marbled Godwit



Willet



American Avocet



included San Leandro Bay (C2) and the west and east shores of SFS (S1 and S2) in fall, and five geographically scattered tracts in spring (Figure 15).

Long-billed Curlew densities in fall were consistently high on the Napa River flats (P4) and the northeast shore of SPB (P3) and also were frequently high on the northwest shore of SPB (P2). Densities usually did not exceed 0.5 curlews/ha (Figure 16). Spring densities were much lower, only once exceeding 0.2 curlews/ha, and the median did not exceed the maximum overall density in any tidal tract.

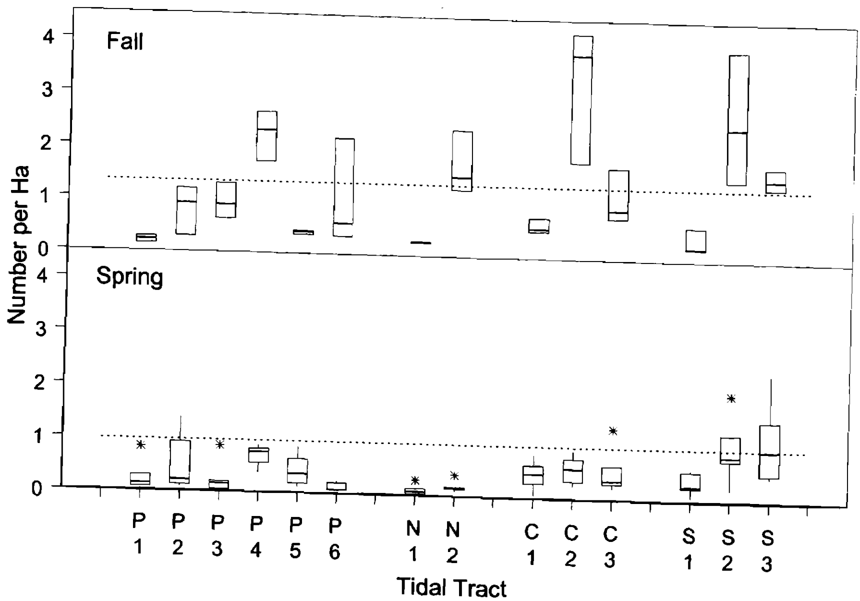
Less common species groups also consistently or frequently occurred in some tidal tracts at densities greater than their maximum overall density for the season. The Hayward Shoreline (C3) was the only tidal tract that stood out as a high-use area for the Snowy Plover; this area frequently held high densities in both fall and spring. The Hayward Shoreline is close to one of the Snowy Plover's major salt-pond breeding areas. The Killdeer was consistently at highest densities in both tidal tracts of SFN and in San Leandro Bay (C2) in both fall and spring, and on the east shore of SPB (P5) and on Hayward Shoreline in fall. Frequent high-use areas for the Killdeer were the northwest shore of SPB (P2) and the Napa River flats (P4) in spring. Yellowlegs consistently concentrated in high densities along Hayward Shoreline in fall and in San Leandro Bay in spring; the west shore of SFN (N1) was also a frequent high-use area in spring. The Whimbrel was the only species to concentrate consistently at both seasons on the west shore of SFC (C1); it also consistently occurred at high densities on the east shore of SFN (N2) in spring. Frequent high-use areas for the Whimbrel included the northeast shore of SPB (P3) and east shore of SFN in fall, the Napa River flats, southeast shore of SPB (P6), west shore of SFN (N1), and San Leandro Bay in spring. Rocky-coast species concentrated consistently on the east shore of SFN (N2) and along Hayward Shoreline (C3) in fall. Frequent high-use areas for this species group were the east shores of SPB and SFN, and the west shore of SFC during spring.

In the southern two regions of San Francisco Bay, we found that densities of many species groups tended to be higher on the eastern than the western side of the bay (Figures 6–14, 16). The only cases in which densities were higher on the west than on the east shore were in SFC for the Semipalmated Plover in fall (Figure 15) and for the Whimbrel at both seasons.

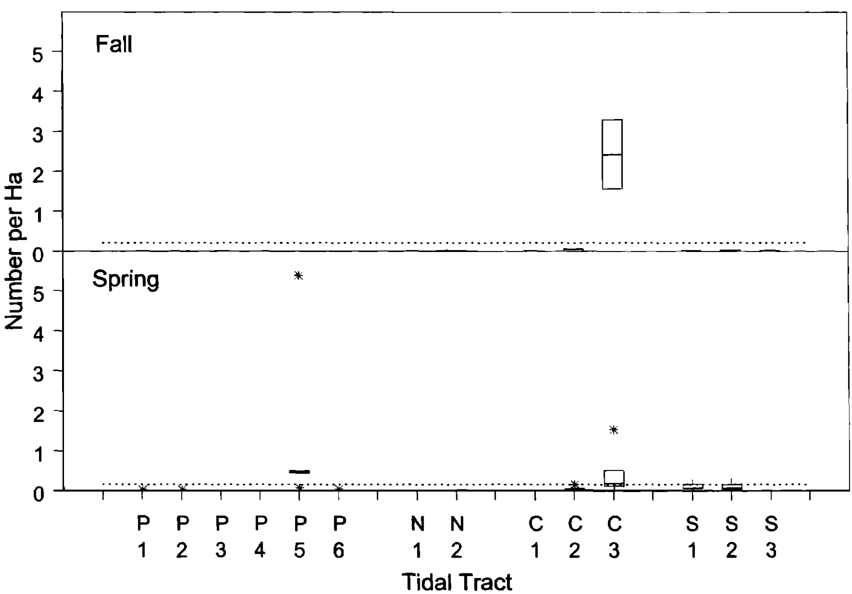
Figure 10. Density comparison of Willets on 14 tidal tracts of the bay on three fall and five spring coFigure 10. Density comparison of Willets on 14 tidal tracts of the bay on three fall and five spring comprehensive censuses. See Figure 1 for description of tracts and Figures 6 and 7 for boxplot specifications.

Figure 11. Density comparison of American Avocets on 14 tidal tracts of the bay on three fall and five spring comprehensive censuses. See Figure 1 for description of tracts and Figures 6 and 7 for boxplot specifications.

Black-bellied Plover



Red Knot



DISCUSSION

Total Numbers and Distribution Patterns of Shorebirds within the Bay

The primary purpose of these censuses was to provide an estimate of shorebird abundance in the bay against which future estimates could be compared. The shorebird numbers we recorded were the largest yet documented for the bay, owing largely to the completeness of our coverage relative to previous studies. Unfortunately, no details from regions or smaller areas of the bay are available from the Fish and Game study (Bollman et al. 1970, Gill 1972) that might allow comparisons between those 1964–65 censuses and our numbers. The distributions by region, habitat, and tidal tract we describe can provide baselines for subareas of the bay should coverage of the entire bay not be feasible in the future.

The concentrations of some species we observed within the bay were related to the distribution of important intertidal and supralittoral habitats, particularly rocky intertidal shoreline and salt ponds. Most natural and artificial rocky shoreline occurs on mainland and island shorelines of SFN. Gravelly beaches are present in portions of SFN and the eastern shoreline of SPB and in SFC. Species typical of rocky coasts concentrated in these areas on our censuses. We covered only the accessible rocky shoreline near tidal flats. Had our censuses covered all rocky shoreline in the bay the high concentration of rocky-coast species in SFN undoubtedly would have been even greater than it was.

Clearly, the location (in SFS) of most of the salt ponds influenced the distribution of salt-pond specialists. For the Snowy Plover, Black-necked Stilt, and American Avocet, this pattern arises partly because they use salt ponds for breeding. For other species (phalaropes and yellowlegs), the pattern suggests that they must be finding adequate prey within the ponds at all tides.

The distribution of species that feed primarily on the tidal flats at low tide ("tidal-flat specialists") also may be influenced by salt ponds. Salt ponds and levees are important as high-tide roosting areas for tidal-flat specialists, but the ponds may provide these birds still other values. Since the ponds' water levels do not change with the tides, shorebirds can feed in shallow salt ponds throughout the tidal cycle. Salt ponds, therefore, may also provide high-tide feeding areas for tidal-flat specialists, particularly when the birds' energy demands are increased. This effect could increase the number of shorebirds that a nearby tidal flat would otherwise support. On our censuses, a high proportion of Black-bellied Plovers, Willets, Marbled Godwits, small sandpipers, and dowitchers were concentrated in SFS. We also consistently found high fall densities for at least six species groups on the Napa River

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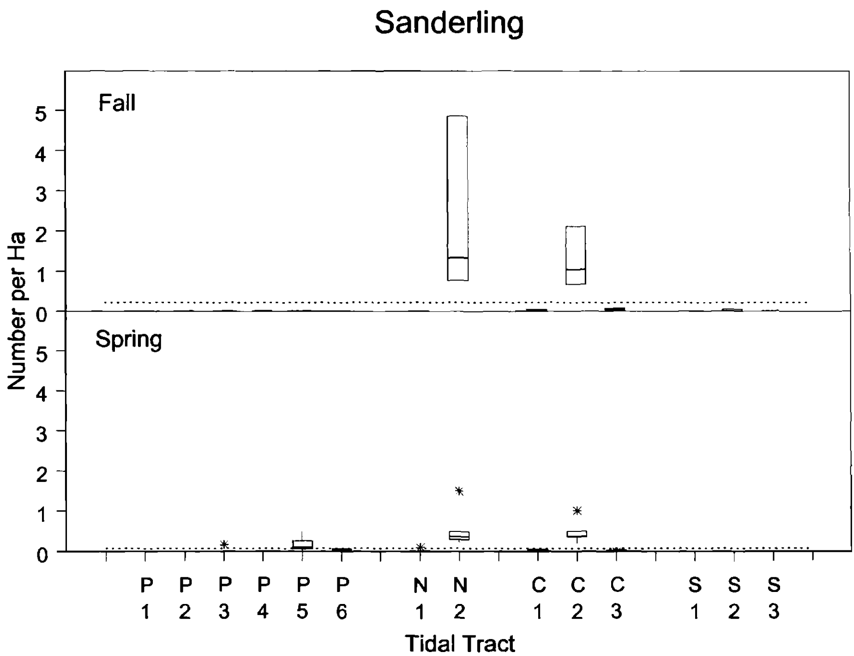
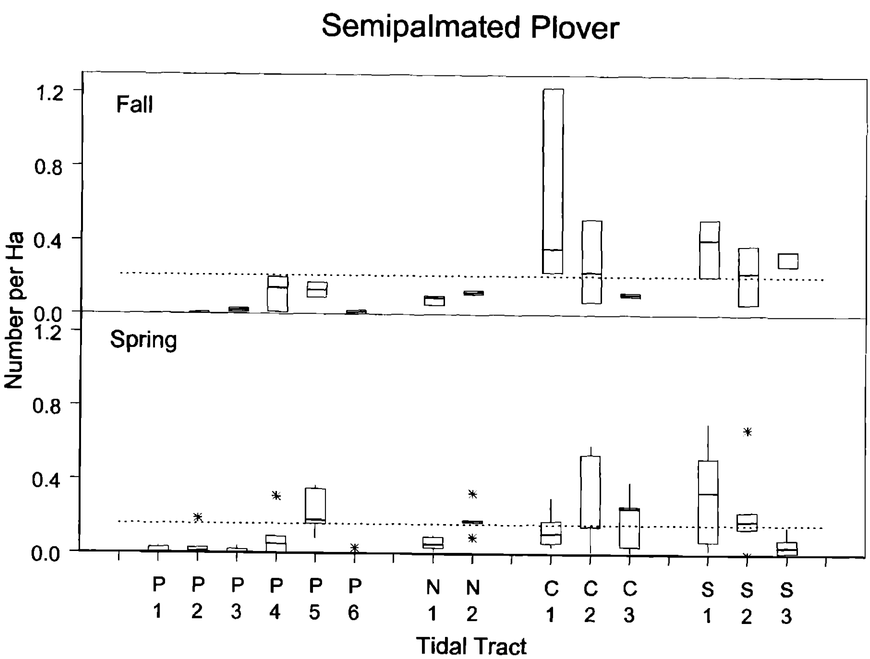
Figure 12. Density comparison of Black-bellied Plovers on 14 tidal tracts of the bay on three fall and five spring comprehensive censuses. See Figure 1 for description of tracts and Figures 6 and 7 for boxplot specifications.

Figure 13. Density comparison of Red Knots on 14 tidal tracts of the bay on three fall and five spring comprehensive censuses. See Figure 1 for description of tracts and Figures 6 and 7 for boxplot specifications.


Sanderling
Fall
Spring
Number per Ha
0
1
2
3
4
5
P 1
P 2
P 3
P 4
P 5
P 6
N 1
N 2
C 1
C 2
C 3
S 1
S 2
S 3
Tidal Tract


Semipalmated Plover
Fall
Spring
Number per Ha
0.0
0.4
0.8
1.2
P 1
P 2
P 3
P 4
P 5
P 6
N 1
N 2
C 1
C 2
C 3
S 1
S 2
S 3
Tidal Tract

flats, the only tidal tract immediately adjacent to salt ponds in SPB. In ongoing studies of avian use of the salt ponds throughout the tidal cycle we have found all these species except the Black-bellied Plover feeding at least irregularly in salt ponds (PRBO unpubl. data).

Studies in other estuarine systems comprising tidal flats, tidal marshes, and salt ponds (or other diked wetlands) reveal that shorebirds use salt ponds and, sometimes, salt marshes as foraging areas. In a South African estuary, Velasquez and Hockey (1992) found several species feeding in both salt ponds and salt marshes at both high and low tides, although other species, notably the Black-bellied Plover, rarely foraged in these areas. In diked managed wetlands in South Carolina, Weber and Haig (1996) observed densities in diked wetlands managed for waterfowl higher than observed even in nearby tidal areas. On Cadiz Bay, Spain, Masero et al. (2000) found some species feeding primarily in the salt ponds, some primarily on the tidal flats, and others in both habitats. All three studies found that use of salt ponds for foraging increased in the premigratory and migratory periods. Both Velasquez and Hockey (1992) and Masero et al. (2000) suggested that the availability of supratidal habitat contributes significantly to the maintenance of relatively high densities of wintering shorebirds in nearby tidal areas. There is much evidence suggesting that shorebirds use diked managed wetlands, including salt ponds, in preference to natural tidal marsh in San Francisco Bay (Bollman et al. 1970, Warnock and Takekawa 1996, PRBO unpubl. data) and elsewhere (Burger et al. 1982, Burger 1984, Davidson and Evans 1986, Burton et al. 1996, Erwin 1996, Weber and Haig 1997). For example, Burger et al. (1982) compared birds' use of varying wetland habitats and found that diked managed wetlands held significantly more species and individuals of shorebirds than did natural salt marshes. Bollman et al. (1970) censused all waterbirds on ebbing tides at many of the areas we covered in the bay and also found very low use of salt marsh by all waterbirds (excluding the Rallidae). There were only occasional reports of shorebirds using salt marsh on any of our surveys of the bay. Because of the deliberately limited set of conditions under which we conducted our censuses, though, we cannot infer a lack of use of a habitat or an area at other periods of the tidal cycle. A full assessment of the values of different areas and habitats of the bay to shorebirds will require knowledge of habitat use throughout the daily tidal cycle at all seasons.

Conservation of Shorebirds in the Bay

San Francisco Bay is one of the largest and most modified estuaries in the United States. Major historic physical changes include greatly accelerated sediment accretion as a result of the Gold Rush and diking of tidal marshes

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Figure 14. Density comparison of Sanderlings on 14 tidal tracts of the bay on three fall and five spring comprehensive censuses. See Figure 1 for description of tracts and Figures 6 and 7 for boxplot specifications.

Figure 15. Density comparison of Semipalmated Plovers on 14 tidal tracts of the bay on three fall and five spring comprehensive censuses. See Figure 1 for description of tracts and Figures 6 and 7 for boxplot specifications.

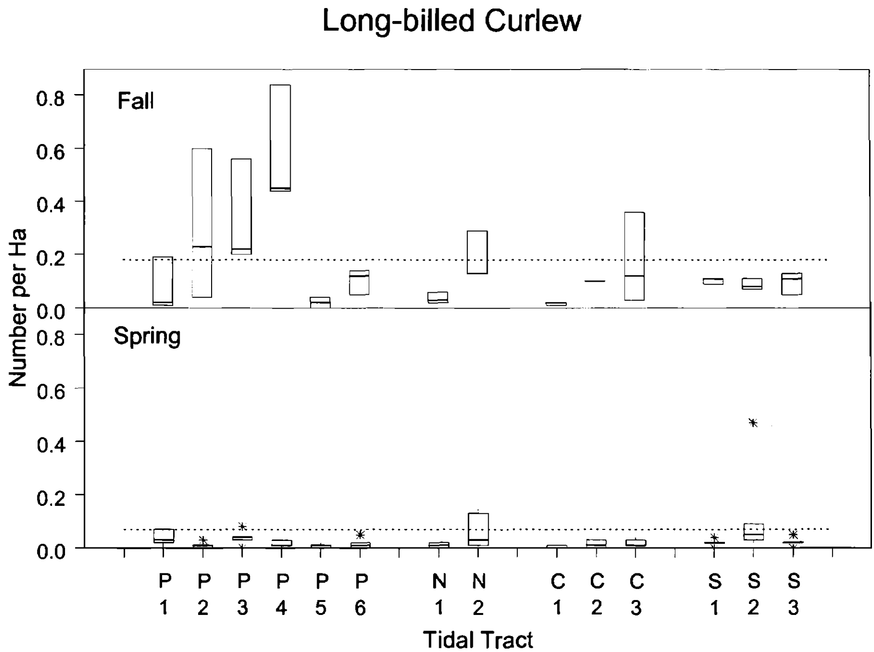

Figure 16. Density comparison of Long-billed Curlews on 14 tidal tracts of the bay on three fall and five spring comprehensive censuses. See Figure 1 for description of tracts and Figures 6 and 7 for boxplot specifications.

and flats to create farmland and salt-evaporation ponds and to allow residential and industrial development. Within our study area, tidal flats have decreased 43% from 19,440 ha in 1850 to the present 11,340 ha. Tidal marsh has decreased 79% from 50,220 to 10,530 ha (Steere and Schaefer 2000). It is unlikely that the number of shorebirds the bay supports has been immune to these habitat losses; however, without historical population estimates for the bay and the west coast, it is difficult to deduce which species, other than salt-pond specialists, have increased or decreased in abundance.

Debate over the ecological costs and benefits of the impoundment of marshes continues. Many species dependent on tidal marshes have suffered significant population declines, and conservation plans for the bay region call for restoration of much of the bay's diked wetlands, including active and inactive salt ponds, to tidally influenced marsh (Goals Project 1999, Steere and Schaefer 2000). To preserve biological resources and diversity in the bay, the needs of the many species (e.g., colonial waterbirds, waterfowl, and shorebirds) that may have benefited from the creation of other types of wetland cannot be neglected; these wetlands currently may provide compensatory habitat for species that have suffered loss of unvegetated tidal habitat in the bay or loss of wetlands in other portions of their range (Harvey et al. 1992). Currently, the bay is one of only a few sites in North America that regularly holds shorebirds in the hundreds of thousands, sometimes up to a million.

With its current configuration and quality of wetlands, the bay is clearly critical to shorebirds, but as human and conflicting natural-resource demands increase, the fate of shorebirds here is uncertain. The demands of the expanding human population include new commercial and residential development and expansions of existing facilities such as airports and harbors, which exert both direct and indirect impacts on wetland quality, extent, configuration, and location. Tidal flats have been lost because of a number of human influences on the bay, including the spread of introduced smooth cordgrass, *Spartina alterniflora* (Callaway and Josselyn 1992). The spread of invasive *Spartina* spp. has been suggested to affect bird numbers in other estuaries by removing feeding area and by reducing feeding time (Goss-Custard and Moser 1988), thus we consider it a threat to shorebird habitat within the bay. Other anthropogenic effects include the demand for the fresh water flowing into the bay (Nichols 1979) and exotic benthic invertebrates introduced repeatedly from other estuaries through mariculture and shipping (Carlton 1979). A global rise in sea level, which has accelerated in the past 30 years over the more gradual rate of the prior 5000 years, is expected to accelerate further (SFBCDC 1988). In the bay, sea-level change combined with local subsidence may cause wetland loss where the shoreline has been developed by preventing wetlands from shifting inland (SFBCDC 1988).

Our results suggest that opportunities to reestablish habitat for shorebirds within the bay may be constrained by factors that cannot be overcome by restoration feasible in a local project. For example, considerable development pressure continues to threaten intertidal areas of SFN and SFC, where most supralittoral habitat has already been converted to residential, commercial, and transportation uses. SPB encompasses extensive diked land that could be restored to tidal habitat and is often suggested as the region where habitat loss elsewhere in the bay can be mitigated. However, shorebirds supported mainly by habitats found in SFN and SFC might not be easily accommodated in SPB. Furthermore, the comparatively low shorebird densities we found on SPB tidal flats imply that this region may require more habitat than other regions to support a given number of shorebirds. Similar constraints for these or other regions of the bay may apply to organisms other than shorebirds.

Because of the importance of the bay to shorebirds on the Pacific coast (Page et al. 1999), and because of the importance of shorebirds in the San Francisco Bay avian community (Bollman et al. 1970), wetland restoration should address shorebird habitat. Encroaching development, the limited amount of land available for wetland restoration, and the limited funds for acquisition, restoration, and management make management for multiple species and purposes daunting. Obtaining maximum habitat value from restoration and management will require identification of habitat characteristics most important to each species. Conservation planners and managers need to be efficient and creative in devising ways to accommodate species with conflicting habitat requirements.

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The field effort would not have been possible without the organizing efforts and participation of the following very helpful and committed individuals: Steve Cochran, Doug Ellis, Leora Feeney, Geoff Geupel, Kathy Hobson, Bob Hogan, Robin Leong, Bob Richmond, Mike Rippey, Dave Shuford, Larry Spear, Rich Stallcup, Nils Warnock, Sarah Griffin Warnock, and Peg Woodin. Over 100 people contributed their time and expertise as censusers; we sincerely thank everyone who participated in the project for their time, talent, and enthusiasm.

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