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DISTRIBUTION AND ABUNDANCE OF WINTER SHOREBIRDS ON TOMALES BAY, CALIFORNIA: IMPLICATIONS FOR CONSERVATION

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ABSTRACT: I analyzed the distribution and abundance of wintering shorebirds (Scolopacidae, Charadriidae, and Recurvirostridae) in Tomales Bay, California, on the basis of 57 baywide counts conducted over 10 years, from 1989–90 to 1998–99. Tomales Bay supports up to 20,689 shorebirds in early winter, thus qualifying as a wetland of "regional" importance in the Western Hemisphere Shorebird Reserve Network. Minimum overall shorebird abundance fell as low as 1291 in late winter. Tomales Bay supported approximately a third of the wintering shorebirds in the Point Reyes/Bodega area in early winter. Observations of tidally structured flock movements of several species suggested that the northern and southern ends of Tomales Bay are occupied by different wintering groups. In association with cumulative seasonal rainfall, most species declined in abundance significantly in midwinter. The Sanderling and Marbled Godwit increased with cumulative rainfall in the north and south bay, respectively, suggesting weather-related influxes from outer coastal beaches. After accounting for the effects of cumulative seasonal rainfall and a 10-year trend in annual rainfall, I detected no trends in species' abundances. Foraging and roosting shorebirds at the northern end of the bay were vulnerable to direct disturbance from concentrated recreational use. Long water-residence times in southern Tomales Bay suggest that shorebirds there may be particularly vulnerable to toxic spills or anthropogenic eutrophication. The closeness of San Francisco Bay implies a high potential for invasion of nonnative organisms established there, which could alter the availability of benthic prey to shorebirds in Tomales Bay. Shorebird feeding habitat at the deltas of Walker and Lagunitas creeks may be adversely affected by heavy rainfall leading to the deposition of sediment. Daily influxes of roosting gulls from a local landfill were associated with reduced shorebird use of tide flats. Shorebirds' use of open tide flats developed for mariculture is reduced, although floating oyster bags provide roosting areas during high tides. Breaching levees that isolate historic wetlands may increase shorebird use in some areas. The likelihood of regular or episodic intraseasonal movements among Point Reyes/Bodega area wetlands suggests Tomales Bay and other nearby wetlands are worthy of broad protection.

Tomales Bay is one of California's largest and least disturbed estuaries. It has been recognized as a wetland of "regional importance" on the basis of its supporting up to 20,000 shorebirds, a criterion for inclusion in the Western Hemisphere Shorebird Reserve Network (WHSRN; Harrington and Perry 1995, Page and Shuford 2000). An analysis of shorebird abundance and distribution on the Pacific coast of the United States identified Tomales Bay as a key wetland for shorebird conservation because it supports in at least one season at least 1% of the total population of 8 of 13 shorebird species that concentrate in estuaries and brackish wetlands (Page et al. 1999). In spite of this recognition, little has been published on the spatial or temporal variations in shorebird abundance on Tomales Bay, or the birds' vulnerability to environmental threats. Kelly and Tappen (1998) reported previously on the value of Tomales Bay to other winter waterbirds.

Shuford et al. (1989) analyzed the results of up to 10 consecutive years of shorebird counts in the adjacent Point Reyes area between 1965 and 1982 but provided little information on shorebird use of Tomales Bay. As part of a statewide survey, Jurek (1974) reported on five years of monthly shorebird counts at the Walker Creek delta, in the northern part of the Tomales Bay, but did not survey abundances baywide. Over recent decades, Tomales Bay has been suggested for protection as habitat for shorebirds (Smail 1972, National Oceanic and Atmospheric Administration 1987, Neubacher et al. 1995, Page and Shuford 2000). However, with one exception dealing with the effects of aquaculture on shorebirds (Kelly et al. 1996), evaluations of conservation issues in Tomales Bay have not directly addressed patterns of shorebird use.

In this paper, I (1) present results from 10 years of baywide winter shorebird censuses on Tomales Bay; (2) compare these results with other studies to provide a historical and geographical perspective on the importance of Tomales Bay to shorebirds; (3) evaluate species' distributions within the bay with regard to the importance of particular areas used by shorebirds; (4) examine processes that influenced abundance trends over the 10 years of study, and (5) identify needs for conservation of wintering shorebirds on Tomales Bay. I address these objectives with regard to all Scolopacidae, Charadriidae, and Recurvirostridae associated with Tomales Bay and immediately adjacent seasonal wetlands (Figure 1).

STUDY AREA

Tomales Bay floods the lower 20 km of the fault-rift Olema Valley on the central California coast, about 45 km northwest of San Francisco (Figure 1; Galloway 1977). Approximately 18% of the bay's 28.5-km^2 area is intertidal, providing primarily sand or mud flats suitable for foraging shorebirds and cobblestone beaches along the east shore. In general, sediments grade from primarily fine to coarse sand in the northern reaches of the bay to muddier substrates in southern portions of the bay (Daetwyler 1966).

Two primary points of freshwater inflow, Lagunitas Creek at the south end of the bay and Walker Creek near the north end of the bay, are associated with large tidal deltas suitable for foraging shorebirds (Figure 1). Numerous smaller delta marshes and tidal flats occur where small perennial

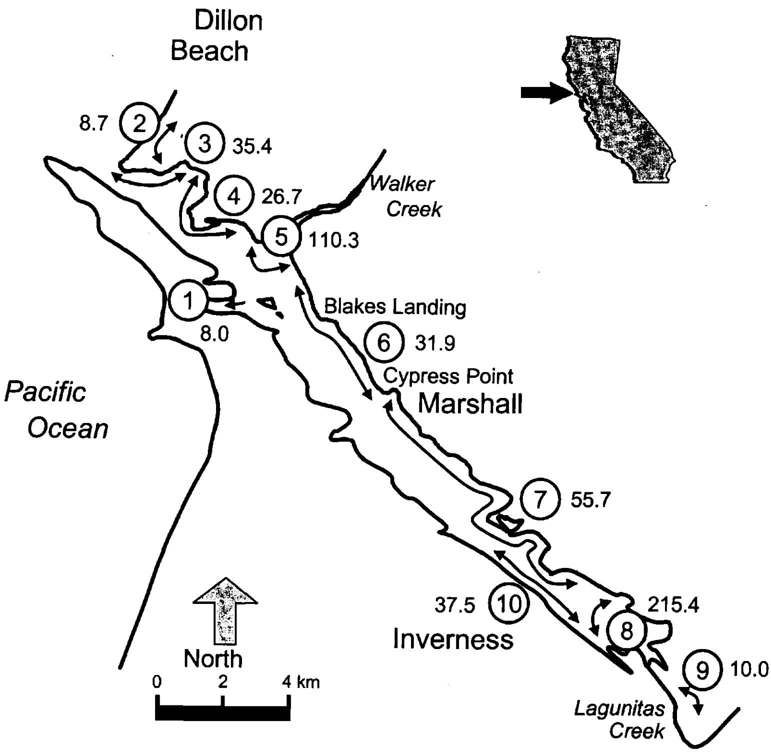

Figure 1. Shorebird count areas on Tomales Bay, California. 1, White Gulch; 2, Lawson's Meadow; 3, Sand Point; 4, Tom's Point; 5, Walker Creek delta; 6, North Marshall; 7, South Marshall; 8, Lagunitas Creek delta; 9, Giacomini Pasture; 10, Inverness shoreline. Arrows indicate length of shoreline in each count area; labels indicate extent (ha) of exposed tidal flat at MLLW.

and ephemeral streams enter the bay. Adjacent seasonal wetlands suitable for shorebirds are normally limited to about 15 ha of a 200-ha diked pasture at the south end of the bay and approximately 20 ha of wet meadow surrounded by sand dunes at the north end of the bay. Additional seasonal wetlands, used by shorebirds during periods of heavy flooding, occur in agricultural areas northeast of the bay.

Most (95%) of the annual rain falls when wintering shorebirds are present, from October through April, with 55% falling from December through February (Audubon Canyon Ranch, unpublished data). Constraints on tidal exchange with the ocean, imposed by the linear shape of the bay, interact with winter runoff to create contrasting habitats at the two ends of the bay. In the southern half of the bay, variably high levels of freshwater inflow during winter, low flows in summer, and long water-residence times result in highly variable salinities (Hollibaugh et al. 1988). Salinities range from nearly fresh after heavy winter runoff to slightly hypersaline in late fall (Smith and Hollibaugh 1997). In northern Tomales Bay, regular tidal mixing maintains salinities that consistently reflect those of nearshore waters along the outer coast. The difference between mean high and mean low tides is about 1.1 m, with an average annual maximum tide swing of about 2.5 m (U. S. National Oceanic and Atmospheric Administration harmonics and correction tables; Tides and Currents, Nautical Software, Inc.).

METHODS

I divided Tomales Bay into 10 subareas within which all shorebirds could be counted in 60 to 90 minutes (Figure 1). These areas include almost all of the intertidal flats in the bay, with the exception of a few small areas at creek mouths along the west shore. Teams of qualified observers counted all shorebirds by species in all subareas simultaneously.

Observers counted during rising tides, at tide levels between 0.76 and 1.22 m above mean lower low water (MLLW) at Blake's Landing (Figure 1). Count-area protocols were coordinated so that adjacent areas were surveyed simultaneously. Abundances generally represented counts of foraging individuals, with estimates of large mobile flocks made only rarely. During three workshops held to examine and reduce observer bias in estimating flock size, biases were inconsistent and without a clear central tendency. Therefore observer bias was assumed not to affect overall estimates of abundance. The time and direction of all flock movements, departures, and arrivals during count periods were recorded and examined later to minimize chances of birds being double counted. Counts were conducted only on days with weather suitable for using telescopes to identify shorebirds.

Each year from 1989–90 to 1998–99, we completed approximately three counts in each of two intraseasonal periods (n = 57): early winter (mean 2.8, range 1–4; 1 November–19 December) and late winter (mean 2.9, range 2–3; 15 January–4 March). I summarized results within intraseasonal groups to compare early- and late-winter population levels. Most individual shorebirds were identified to species. Occasionally, individuals were not identified to species and were recorded in pooled species groups such Least/Western sandpiper. Individuals recorded in pooled species groups were allocated to single species groups in direct proportion to the number of identified birds of each species in each count area on each day (Page et al. 1999). Such adjustments were made, however, only if the number of identified individuals exceeded the number of undifferentiated individuals and was >50 for groups of two species or >100 for groups of three species.

Observations of shorebird flocks revealed restricted movements in the middle section of the bay. Of 19 flocks of several shorebird species observed departing as the tide inundated the feeding area at Walker Creek delta, 100% were oriented to the northwest and only one flock flew by from farther south. In southern Tomales Bay, 56 flocks of several species were observed departing north from feeding areas during rising tides, but only one flock (2%) was seen flying north past Cypress Point in Marshall (Figure 1). These observations suggest that several species winter in discrete groups. In addition, a reciprocal translocation of color-banded Dunlins, the most abundant species in the bay, revealed that wintering populations at the two ends of the bay were separate (Kelly 2000). Therefore, I analyzed the results separately for subregions of Tomales Bay north (areas 1–6) and south (areas 7–10) of Cypress Point, Marshall, in addition to analyzing them for the bay as a whole (Figure 1).

I transformed abundance data into densities, based on the extent of exposed mudflat in each count area, estimated at MLLW with a planimeter on a bathymetric chart (Figure 1; U. S. National Oceanic and Atmospheric Administration Chart 18643, 16th ed., Dec 1995). Estimates of shorebird preferences based on densities among different habitat types may be sensitive to different measures of availability (Warnock and Takekawa 1995), particularly if birds concentrate along the edge of the rising tide (Recher 1966, Burger et al. 1977) and the linear extent of the tide line is not closely correlated with areal extent of the habitat. However, suitable shorebird habitat on Tomales Bay is limited primarily to tidal flats, and each count area represented a similar proportion of the area available for foraging along the tide line at any particular tide level. Consequently, densities based on different widths of tidal exposure did not significantly alter estimates of relative shorebird use by count area.

To examine the effects of count-area location, intraseasonal period, and year on patterns of shorebird use, I used mixed-model analysis of covariance of shorebird densities, controlling for days since the beginning of each intraseasonal (early or late winter) period and treating year as a random effect. Shorebird densities were log-transformed to improve normality and stabilize the variance of residuals. Significant count-area effects were followed by multiple pairwise comparisons within the northern and southern subregions of the bay. I inspected bivariate scatterplots of shorebird abundance on cumulative seasonal rainfall, using Cleveland's robust locally weighted regression algorithm (LOWESS; Cleveland 1979, Chambers et al. 1983), to look for nonlinear thresholds and trends. I selected this method because it uses locally weighted least squares and a robust fitting procedure to define smoothed points that are relatively insensitive to outlying values, and it allows a flexible degree of smoothing by adjusting the proportion of data scanned (f) for each fitted value. To improve the normality of abundances used in the analysis, I based trends for the Semipalmated Plover, Black Turnstone, and Least Sandpiper on the natural logarithms (ln) of the counts; distributions of other species' abundances were approximately normal without this transformation. Annual and cumulative seasonal rainfall were derived from daily rainfall measured at Cypress Point (Figure 1; Audubon Canyon Ranch, unpubl. data). I estimated annual trends in species abundance within subregions as partial regression coefficients on year, independent of the linear effect of cumulative seasonal rainfall. I compared these results with correlated trends in annual rainfall.

RESULTS

Tomales Bay supported as many as 20,689 shorebirds in early winter, with minimum numbers falling as low as 1291 in late winter. The most abundant winter shorebird in Tomales Bay was the Dunlin, accounting for

Table 1 Mean, Minimum, and Maximum Abundances of Wintering Shorebirds on Tomales Bay, 1989–90 to 1998–99[a]

Species	North bay		South bay		Baywide			
	Early winter Mean (SE[b])	Late winter Mean (SE)	Early winter Mean (SE)	Late winter Mean (SE)	Early winter Mean (SE)	Early winter Range	Late winter Mean (SE)	Late winter Range
Black-bellied Plover *Pluvialis squatarola*	139 (11.8)	68 (7.4)***	55 (6.0)	39 (6.1)	194 (13.8)	39–327	107 (11.9)	1–258***
American Golden-Plover *Pluvialis dominica*	+ (0.1)	0 (0.0)	0 (0.0)	0 (0.0)	+ (0.1)	0–2	0 (0.0)	0–0
Pacific Golden-Plover *Pluvialis fulva*	4 (0.7)	3 (0.6)	0 (0.0)	0 (0.0)	4 (0.7)	0–12	3 (0.6)	0–11
Snowy Plover *Charadrius alexandrinus*	13 (2.9)	4 (1.9)*	0 (0.0)	0 (0.0)	13 (2.9)	0–53	4 (1.9)	0–42**
Semipalmated Plover *Charadrius semipalmatus*	14 (3.0)	3 (0.9)**	17 (4.5)	10 (3.4)	31 (5.8)	0–123	13 (3.6)	0–89**
Killdeer *Charadrius vociferus*	14 (2.9)	7 (1.3)*	8 (2.1)	2 (0.5)**	23 (4.6)	2–111	9 (1.7)	0–38**
American Avocet *Recurvirostra americana*	+ (0.1)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0–0	+ (0.03)	0–1
Greater Yellowlegs *Tringa melanoleuca*	2 (0.4)	1 (0.2)*	14 (1.6)	5 (1.1)***	16 (1.8)	3–38	6 (1.2)	0–22***
Willet *Catoptrophorus semipalmatus*	283 (25.4)	235 (18.5)	127 (20.8)	175 (18.0)	410 (26.6)	94–767	410 (24.9)	82–671
Spotted Sandpiper *Actitis macularia*	2 (0.4)	2 (0.3)	+ (0.2)	1 (0.2)	3 (0.4)	0–8	2 (0.3)	0–7*
Whimbrel *Numenius phaeopus*	1 (0.3)	1 (0.2)	+ (0.3)	0 (0.0)	1 (0.5)	0–15	1 (0.2)	0–3
Long-billed Curlew *Numenius americanus*	+ (0.1)	+ (0.1)	+ (0.1)	+ (0.2)	+ (0.1)	0–3	+ (0.1)	0–3

Marbled Godwit								
Limosa fedoa	799 (78.0)	916 (90.2)	85 (14.1)	152 (19.0)***	885 (80.4)	100–1564	1067 (96.8)	73–2233
Ruddy Turnstone								
Arenaria interpres	3 (0.8)	3 (1.2)	2 (1.7)	+ (0.1)	4 (2.0)	0–54	3 (1.2)	0–26
Black Turnstone								
Arenaria melanocephala	39 (5.5)	23 (5.1)	18 (4.9)	12 (3.4)	57 (6.6)	1–124	35 (6.0)	0–126*
Surfbird								
Aphriza virgata	1 (0.1)	+ (0.05)	0 (0.0)	+ (0.03)	+ (0.1)	0–3	+ (0.1)	0–1
Red Knot								
Calidris canutus	2 (1.0)	2 (0.9)	0 (0.0)	0 (0.0)	2 (1.0)	0–19	2 (0.9)	0–18
Sanderling								
Calidris alba	393 (30.1)	559 (56.3)*	69 (12.6)	112 (18.5)	462 (31.3)	170–829	671 (62.2)	116–1479**
Western Sandpiper								
Calidris mauri	1019 (159.4)	811 (105.5)	564 (93.1)	404 (131.5)	1583 (192.1)	198–3962	1216 (170.9)	222–3553
Least Sandpiper								
Calidris minutilla	642 (78.6)	279 (59.0)***	564 (93.1)	199 (58.6)**	1290 (164.3)	181–3811	477 (103.8)	0–1822***
Dunlin								
Calidris alpina	3370 (342.9)	1102 (199.9)***	2930 (411.2)	633 (157.7)***	6200 (684.4)	1013–12,762	1735 (334.3)	5–6951***
Dowitchers								
Limnodromus spp.	29 (6.2)	15 (7.6)	55 (12.0)	17 (6.6)**	84 (13.1)	0–315	32 (10.9)	0–254**
Common Snipe								
Gallinago gallinago	8 (2.2)	4 (2.0)	+ (0.1)	1 (0.6)	8 (2.1)	0–38	5 (2.0)	0–57
Red-necked Phalarope								
Phalaropus lobatus	+ (0.1)	0 (0.0)	0 (0.0)	0 (0.0)	+ (0.1)	0–4	0 (0.0)	0–0
Red Phalarope								
Phalaropus fulicaria	0 (0.0)	+ (0.1)	0 (0.0)	0 (0.0)	0 (0.0)	0–0	+ (0.1)	0–3
Total	6709 (450.8)	4062 (343.2)***	5047 (570.4)	1877 (332.0)***	11,756 (917.0)	4827–20,689	5939 (604.2)	1291–13,787***

[a]Based on 29 counts in early winter and 28 counts in late winter. Asterisks specify significant differences between early and late winter: $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$. +, Mean abundance <0.5. See Figure 1 for count areas included in north and south bay subregions.

[b]SE, standard error.

over half (53%) of all shorebirds in early winter and nearly a third (29%) in late winter. The second most abundant species was the Western Sandpiper, representing 13% in early winter and 20% in late winter (Table 1). The total number of shorebirds declined significantly from early to late winter in northern (t = 4.67, df = 56, $P < 0.001$) and southern (t = 4.80, df = 54, $P < 0.001$) Tomales Bay, as did several individual species (Table 1). In contrast to this pattern, the Marbled Godwit increased significantly during winter in southern Tomales Bay, and the Sanderling increased significantly in the northern bay and baywide (Table 1).

Maximum annual abundance varied by a factor of 8.9 in the Dunlin, 8.0 in the Marbled Godwit, 6.7 in the Killdeer, 6.2 in the Greater Yellowlegs, 4.4 in the Sanderling, 4.2 in the Western Sandpiper, 3.5 in the Spotted Sandpiper, 3.4 in the Willet, 3.2 in the Black Turnstone, 2.3 in the Black-bellied Plover, and 4.1 in all species combined. Maximum annual abundance varied substantially more in some species, by a factor of 17.8 in the dowitchers, 16.7 in the Semipalmated Plover, 15.5 in the Least Sandpiper, and 12.0 in the Pacific Golden-Plover, reflecting proportional changes in smaller populations and/or difficulties in detecting inconspicuous birds. Densities in most species varied significantly from year to year (Table 2).

Winter shorebird densities differed significantly from count area to count area within both subregions of Tomales Bay (Table 2). Most species showed significant annual and intraseasonal shifts in distribution of densities among count areas, indicated by significant interaction terms in analyses of covariance (Table 2). Although average midwinter declines in count-area density, weighted equally for large and small areas, were significant only for the Dunlin and dowitchers (Table 2), several species decreased significantly in overall abundance on the basis of north bay, south bay, and baywide totals (Table 1).

Northern Tomales Bay supported more shorebirds, overall, than southern Tomales Bay in early winter (t=2.92, df=55, P<0.05) and late winter (t = 4.57, df = 55, $P < 0.001$). The Walker Creek (area 5) and Lagunitas Creek (area 8) deltas not only supported the greatest concentrations of shorebirds but also the highest densities for more shorebird species than other areas in Tomales Bay (Table 2, Figure 2). The northeast shoreline from Sand Point (area 3) to Vincent's Landing south of Tom's Point (area 4) also supported relatively high abundances of several species (Table 2, Figure 2). Shorebird use of seasonal wetlands at Lawson's Meadow (area 2) and Giacomini Pasture (area 9) was highly variable; consequently, mean shorebird densities in these areas could not be distinguished clearly from those in other areas (Table 2). Greater Yellowlegs concentrated primarily in the extreme south end of Tomales Bay, while Sanderlings and Marbled Godwits concentrated primarily at the north end of the bay (Figure 2). The Pacific Golden-Plover, Snowy Plover, and Red Knot occurred exclusively in northern Tomales Bay.

Cumulative seasonal rainfall was associated with significant decreases in the use of Tomales Bay by most shorebird species but significant increases by the Marbled Godwit and Sanderling (Figure 3). Bivariate plots suggested that 25–30 cm of rain must fall in a season to trigger the declines of the Western Sandpiper, Least Sandpiper, and dowitchers (Figure 3). Alternatively, rainfall correlations might be the result of intraseasonal changes in abundance

Table 2 Effects of Count Area (A), Intraseasonal Period (S), and Year (Y, Random Effect) on Densities of Wintering Shorebirds in Tomales Bay[a]

	North bay count areas								South bay count areas					
Species	ANCOVA[b] (n = 330)		1	2	3	4	5	6	ANCOVA[b] (n = 202)		7	8	9	10
Black-bellied Plover	A**, Y, AY**, ASY**		D	C	**A**	BC	BD	BCD	A**, Y**, AY**		**A**	**A**	**AB**	B
Semipalmated Plover	A**, Y**, AS*, AY*, ASY**	(E)	B	B	**A**	B	B	B	Y**, AY**, ASY**					
		(L)	**A**	**A**	**A**	**A**	**A**	**A**						
Killdeer	A**, Y**, AY**, SY**, ASY**		B	**A**	B	B	B	B	A*, Y**, AY**, SY**, ASY**		**A**	B	**AB**	B
Willet	A**, Y**, AS*, ASY	(E)	**AB**	**B**	**A**	**A**	**AB**	B	Y**, AS, AY**, ASY**	(E)	**A**	**A**	**A**	**A**
		(L)	**A**	**A**	**A**	**A**	**A**	B		(L)	B	**A**	**AB**	**AB**
Marbled Godwit	A**, Y**, AY**, SY		BC	**ABC**	**A**	**A**	**AB**	C	Y**, AS**, AY*	(E)	**A**	**A**	**A**	**A**
										(L)	B	**A**	B	**AB**
Black Turnstone	A**, AY*, ASY*		B	B	**A**	B	**A**	B	A**		**A**	**AB**	C	B
Sanderling	A**, AS**, AY**	(E)	C	C	**AB**	**A**	BC	C	ASY**					
		(L)	**AB**	C	**A**	**ABC**	**ABC**	C						
Western Sandpiper	A**, AY**, ASY*		B	**AB**	B	**A**	**A**	B	A**, Y, AY*, SY, ASY**		B	**A**	**ABC**	C
Least Sandpiper	A**, Y**, AS**, AY*, SY*	(E)	**A**	**AB**	B	**A**	**A**	B	A**, Y**, AS**	(E)	**A**	**A**	B	B
		(L)	**A**	**AB**	B	B	B	B		(L)	A	**AB**	**AB**	B
Dunlin	A**, S, Y**, AS**, AY**	(E)	C	**ABC**	B	B	**A**	C	A**, Y**, AS*, AY**, SY**, Y**	(E)	B	**A**	**ABC**	C
		(L)	BC	**ABC**	**A**	B	**A**	C		(L)	B	**A**	**AB**	B
Dowitcher species	A**, Y**, S, AY**, SY**, ASY**		BC	**ABC**	**AB**	B	**A**	B	Y*, AY**, SY**, ASY**					
All Shorebirds	A**, Y*, AY**, AS, ASY**		B	**ABC**	**AB**	**AB**	**A**	C	A**, Y**, AY**, ASY*		B	**A**	**ABC**	C

[a]Significant fixed effects of count area are followed by multiple pairwise comparisons, computed separately for early (E) and late winter (L) when AS interaction is significant; areas with the same letter within north bay or south bay subregions are not significantly different (Bonferroni experimentwise error $P > 0.05$) and are ranked: A > B > C > D. Area preferences, suggested by means not significantly different from highest means, are in boldface. See Figure 1 for count area locations.

[b]Mixed-model analysis of covariance; covariate is days since beginning of early winter (November–December) or late winter (January–February) period; each effect listed by letter code has significant F ratio ($P < 0.05$); $^{*}P < 0.01$, $^{**}P < 0.001$.

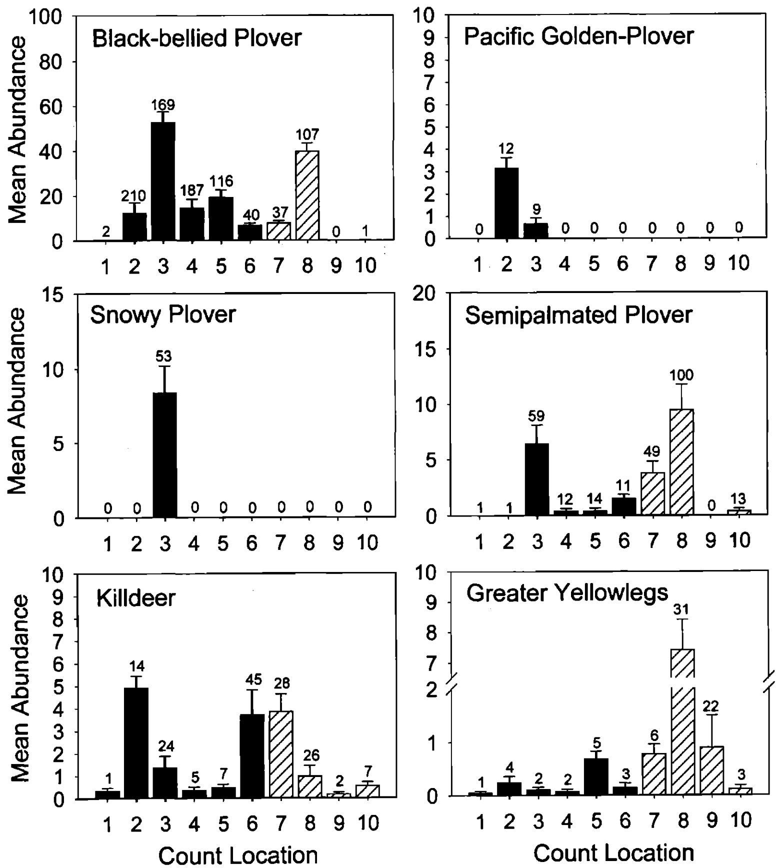

Figure 2. Mean winter abundance of shorebirds, by count area, in northern (solid bars) and southern (striped bars) Tomales Bay, California, 1989–90 to 1998–99. Error bars indicate standard errors; numbers above bars indicate maximum abundance observed during the study period.

unrelated to rainfall. When count date and year were included as covariates, residual (uncorrelated) effects of cumulative seasonal rainfall in the north bay were significant for the Black-bellied Plover ($b = -1.31$, $P < 0.05$), Willet ($b = 2.56$, $P < 0.05$), Dunlin ($b = -27.30$, $P < 0.05$), and (ln) Least Sandpiper ($b = -0.06$, $P < 0.001$); residual effects in the south bay were significant for the (ln) Least Sandpiper ($b = -0.06$, $P < 0.05$). Conversely, intraseasonal trends independent of cumulative seasonal rainfall and year were significant for the Willet (north bay: $b = -1.74$, $P < 0.01$; south bay: $b = 1.01$, $P < 0.05$), Dunlin (north bay: $b = -17.96$, $P < 0.01$; south bay: $b = -22.25$; $P < 0.01$), and (ln) Black Turnstone (south bay: $b = -0.03$; $P = 0.01$).

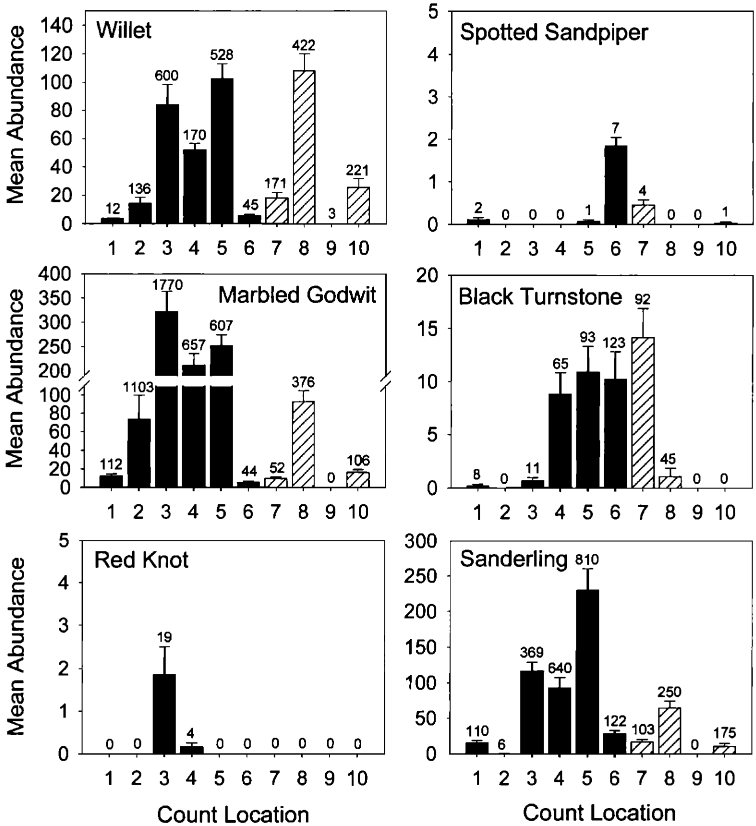

Figure 2 (*continued*).

After the linear effects of cumulative seasonal rainfall and date are accounted for, residual annual trends were not significant ($P > 0.05$), except in five cases. In the south bay, significant linear trends independent of cumulative seasonal rainfall and date suggested 10-year declines in the Black-bellied Plover ($b = -5.62$; $P < 0.001$), (ln) Semipalmated Plover ($b = -0.32$; $P<0.05$), (ln) Least Sandpiper ($b = -0.32$; $P<0.05$), and Dunlin ($b = -223.21$; $P < 0.001$), and increases in the Willet ($b = 14.43$, $P < 0.01$) and Marbled Godwit ($b = 10.68$, $P < 0.05$). In northern Tomales Bay, significant 10-year declines independent of cumulative rainfall and date were evident in the Willet ($b = -13.10$, $P < 0.05$) and Dunlin ($b = -330.26$, $P < 0.01$). Although these changes in shorebird use were independent of cumulative seasonal rainfall, they might have reflected escalating effects of successive increases in annual rainfall ($b = 5.3$ cm/year, $P < 0.05$; Figure 4). The 10-year duration of this study was too short to distinguish between the influence of annual rainfall trend and possible underlying (correlated) population

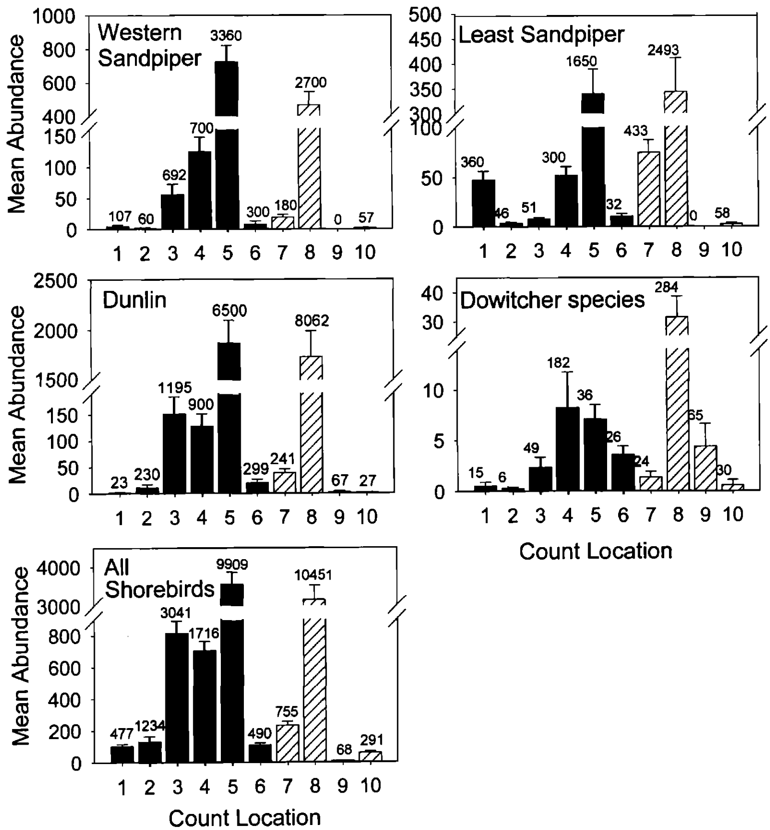

Figure 2 (*continued*).

trends. Annual trends in maximum (fall) abundance were nonsignificant for all species ($n = 10$, $P > 0.05$), after differences associated with cumulative rainfall through November and in the previous year were accounted for.

DISCUSSION

Winter Abundance and Distribution

My results confirm Tomales Bay as a wetland of "regional" importance on the basis of its supporting more than 20,000 shorebirds, a criterion for inclusion in the WHSRN (Harrington and Perry 1995, Page and Shuford 2000). Relative abundances of wintering shorebird species were similar to those reported for other Point Reyes area wetlands (Page et al. 1983, Page et al. 1992). Concurrent counts conducted in 1989–90 in other nearby wetlands indicated that Tomales Bay supported approximately a third of the

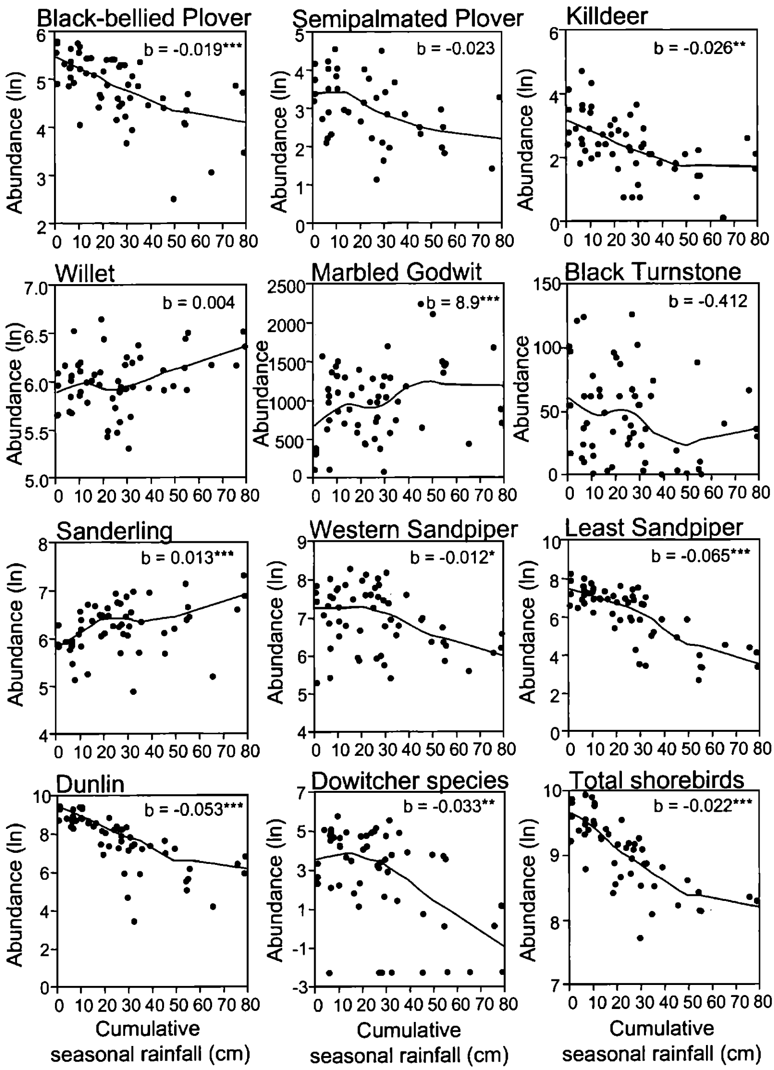

Figure 3. Bivariate plots of baywide shorebird abundance (ln) on cumulative seasonal rainfall in Tomales Bay. Lines represent LOWESS trends, with smoothing parameter $f = 0.6$. Slope of linear regression (b) is indicated in each plot: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. Between northern and southern Tomales Bay linear slopes did not differ significantly ($P < 0.05$). Abundances of the Marbled Godwit and Black Turnstone are not ln-transformed.

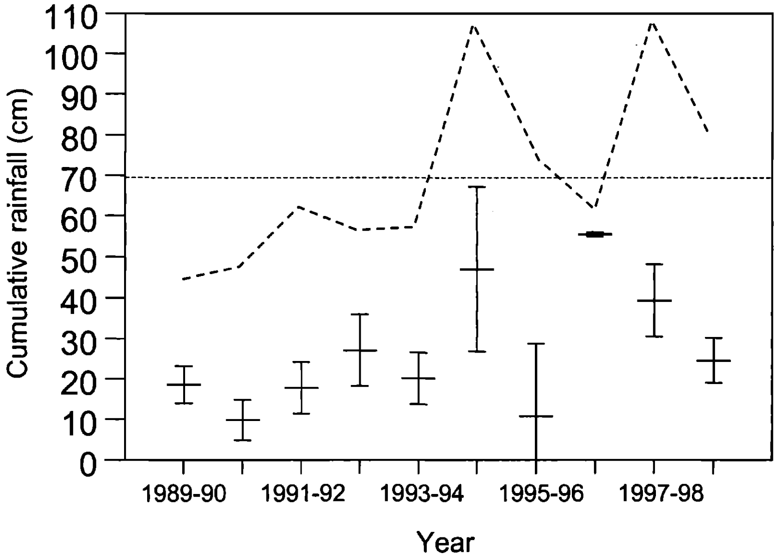

Figure 4. Means and standard errors of cumulative seasonal rainfall measured on shorebird count days on Tomales Bay, from 1989–90 to 1998–99. Dashed line indicates total annual rainfall (July–June) across years. Horizontal dashed line indicates long-term average annual rainfall.

wintering shorebirds in the greater Point Reyes area, which includes Bolinas Lagoon, Drake's and Limantour esteros, Estero Americano, and Bodega Harbor (this study and unpublished data from P. Connors and G. Page).

The only other baywide counts of shorebirds in Tomales Bay are aerial surveys conducted from August 1968 to April 1970 (Smail 1972). Unknown differences in detectability, however, preclude comparisons with these aerial counts, which detected far fewer shorebirds than my study. The aerial counts did indicate that Tomales Bay supported more shorebirds than other Point Reyes area wetlands, including Drake's and Limantour esteros and Bolinas Lagoon (Smail 1972). Jurek (1974) conducted counts at the Walker Creek delta from 1969–70 to 1973–74 (area 5, Figure 1) and reported abundances that do not differ significantly from those I report; however, population trends could be obscured by substantial variability in shorebird use from year to year and count area to count area (Table 2).

Among several species, shorebirds wintering at the northern and southern ends of Tomales Bay appear to represent different groups (this study, Kelly 2000). The apparent separation of shorebirds into local wintering groups in the northern and southern portions of Tomales Bay is consistent with the spatial scale of winter site fidelity demonstrated by other studies along the California coast (Kelly and Cogswell 1979, Warnock and Takekawa 1996).

Although the composition of shorebird species in the northern and southern portions of the bay was similar, habitat conditions differed substantially. Habitat differences resulted from spatial and temporal hydrographic gradients in the estuary that affect salinity (lower and more variable in the south), sediment size (finer in the south), turbidity (greater and more variable in the south), and flood disturbance (more frequent and intense in the south; Daetwyler 1966, Hollibaugh et al. 1988). Such differences are likely to influence the composition, abundance, or availability of invertebrate prey (Johnson 1971, Wolff 1969, 1983) and, consequently, may be associated with spatial or temporal patterns of shorebird use. For example, Marbled Godwits concentrated in northern Tomales Bay, where substrates are composed predominantly of well-sorted medium and fine sand, but not in the southern portion of the bay, where substrates are composed of finer particles (Daetwyler 1966). Within the Point Reyes/Bodega area, godwits also concentrate in nearby Bodega Harbor (Page et al. 1983), where sediments are similar to substrates in northern but not southern Tomales Bay (Standing et al. 1975).

Midwinter influxes of the Sanderling and Marbled Godwit were significantly associated with cumulative seasonal rainfall. These species occur commonly on nearby beaches along the outer coast and are known to switch habitats with the tides (Shuford et al. 1989, Connors et al. 1981, Colwell and Sundeen 2000). My study suggested an intraseasonal influx of these species into estuarine tide flats, correlated with cumulative rainfall and independent of tides. Connors et al. (1981) linked tide-associated movements between habitats with enhanced foraging profitability and found that variation in the timing of these movements varies seasonally to enhance profitability. Thus midwinter influxes of Sanderlings and Marbled Godwits into Tomales Bay might reflect an intraseasonal increase in the profitability of foraging in tide flats over foraging on beaches. Alternatively, movements into Tomales Bay may result from a thermal advantage of refuge from harsher weather along the outer coast.

The significant midwinter declines in several species using Tomales Bay suggest local or regional movements to alternative wintering areas. At Humboldt Bay Colwell (1994) also reported midwinter declines in several shorebirds. Nonmigratory movements of wintering shorebirds, ranging from use of local alternative habitats to interestuarine movements to large-scale flights from the coast inland, have been documented at several California estuaries, but in different areas intraseasonal patterns are not necessarily similar (Page et al. 1979, Ruiz et al 1989, Shuford et al. 1989, Warnock et al. 1995).

Four of six principal wetlands in the Point Reyes/Bodega area are considered, independently, to have potential regional importance by the WHSRN (Harrington and Perry 1995, Page et al. 1999). These are Bolinas Lagoon (Page et al. 1979), Drake's and Limantour esteros (Page et al. 1983, Shuford et al. 1989), Tomales Bay (this study), and Bodega Harbor (Page et al. 1983, Ruiz 1987). The closeness of these areas, along with other locally important wetlands, within approximately 60 km of coast line indicates substantial importance of this area to wintering and migrating shorebirds. Movements of wintering shorebirds among wetlands in the Point Reyes/Bodega area have been suggested by my results and by those of others (Page et al. 1979, Myers et al. 1980, Shuford et al. 1989, Ruiz et al.

1989). Although strong site fidelity often distinguishes wintering groups of coastal shorebirds (Warnock and Takekawa 1996, Kelly 2000), the ability to respond with intraseasonal or episodic movements among wetlands may be crucial to maximizing winter survival in the face of unpredictable changes in foraging conditions (Connors et al. 1981, Myers 1980, Ruiz et al. 1989, Colwell 1993, Warnock et al. 1995). Thus, regional complexes of wetlands such as those in the Point Reyes/Bodega area may need broad protection and cooperation by the numerous agencies responsible for their management (Laubhan and Fredrickson 1993).

Page et al. (1992) reported on the use of Tomales Bay by migrating shorebirds in the context of other sites in the Pacific Flyway. Further information on shorebird use during spring and fall is needed for the importance of Tomales Bay to migrating shorebirds to be understood fully. The spatial scale and flexibility of stopover-site selection by migrating shorebirds within systems of coastal wetlands is poorly understood but might involve short-flight hopping (Iverson et al. 1996) or local movements related to changing habitat conditions, as found at inland wetlands (Skagen and Knopf 1993, 1994). If so, Point Reyes/Bodega area wetlands may provide extended stopover support for migrating shorebirds.

Conservation Implications

Shorebirds tend to concentrate where the density (Goss-Custard et al. 1977, Bryant 1979) or availability (Recher 1966, Goss-Custard 1984) of invertebrate prey is greatest. Midwinter declines in several shorebird species observed in this study may be associated with the adverse effects of heavy freshwater runoff and associated sediment deposition on prey (Wolff 1983, Holland 1985, Anima et al. 1988, Nordby and Zedler 1991). Because of water-residence times as long as four months, prey in southern Tomales Bay may be particularly vulnerable to the effects of toxic spills or anthropogenic eutrophication (Smith and Hollibaugh 1989, 1997). Midwinter changes in shorebird use of key feeding areas at Lagunitas and Walker creeks are consistent with a hypothesis that deposition of sandy sediment during heavy runoff reduces the suitability of some areas to foraging shorebirds. Core samples collected in these areas 4–7 weeks after a major flood in 1982 revealed a surface layer of sandy material that was several centimeters thick and virtually devoid of invertebrates (Anima et al. 1988). Gerstenberg (1979) reported reduced shorebird use in Humboldt Bay after siltation of tide flats during heavy rains. Quammen (1982) found reduced feeding success and abandonment of preferred feeding areas by Dunlins, Western Sandpipers, and dowitchers when tidal feeding areas were treated with a thin layer of sand. Periods of increased sedimentation in Tomales Bay have been associated with logging and intensive farming in the watershed (Rooney and Smith 1999) and could also result from development, overgrazing, or other disturbance of upland soils (Storm 1972).

Daily, tidal, or intraseasonal movements of shorebirds to alternative sites in seasonal wetlands and upland fields have been reported in several areas along the central and northern coast of California (Gerstenberg 1979, Ruiz et al. 1989, Ramer et al. 1991, Colwell 1993). Near Tomales Bay, however, alternative foraging areas are relatively limited, and use of alternative habitats was generally limited to seasonal wetlands at Lawson's Meadow and Giacomini Pasture (Figure 1). Breaching levees that isolate the Giacomini Pasture would restore approximately 150 ha of tidal marsh and at least 36 ha of tidal flats (elevation less than 1.2 m above MLLW) for shorebirds at the southern end of the bay (Philip Williams and Associates et al. 1993). The protection of routinely used seasonal wetlands at Lawson's Meadow adjacent to the north end of the bay may be especially important. During heavy rainfall and flooding, some shorebirds flew to seasonal wetlands 5–15 km northeast of the bay (pers. obs.).

Direct disturbance by people or dogs can have detrimental effects on the continuing use of foraging (Burger 1986, Burger and Gochfield 1991) and roosting (Burger 1981, Kirby et al. 1993) areas by wintering shorebirds. In Tomales Bay, aggregations of roosting and feeding shorebirds along the shoreline below sand dunes at Brazil Beach, and on offshore tide flats north of Tom's Point (areas 3 and 4, Figure 1), were frequently disturbed by people from an adjacent 1000-site campground (Shannon and Associates 1998), who come for clamming or other activities (pers. obs.; Page and Shuford 2000). Dune beaches near the mouth of Tomales Bay may provide critical winter habitat for the threatened Western Snowy Plover (*Charadrius alexandrinus nivosus*; U.S. Fish and Wildlife Service 1995). Direct disturbance of roosting and feeding Snowy Plovers by recreational users in this area was evident during winter; during spring and summer such disturbance may prevent nesting by this species in otherwise suitable habitat (Page and Shuford 2000).

Gulls may interfere with shorebird foraging (Thompson and Lendrem 1985, Warnock 1989, Amat and Aguilera 1990). During winter low tides at the Walker Creek delta (area 5, Figure 1), large concentrations of gulls were inversely correlated with shorebird use of exposed tidal flats, suggesting that gulls displaced shorebirds from otherwise suitable foraging habitat (Kelly et al. 1996). The gulls arrived daily from a garbage dump approximately 20 km to the northeast. Possible indirect adverse effects of local landfills on shorebird use of estuaries should be investigated further, and the use of such landfills by wintering gulls could be reduced.

Currently, leases for commercial oyster culture occupy 208 ha of Tomales Bay, but the limit placed on mariculture leases by the Marin County local coastal plan is 365 ha. (Tom Moore, Calif. Dept. Fish and Game, pers. comm.). Shorebirds' use of open tide flats decreases when these are developed for mariculture (Kelly et al. 1996). The two most abundant shorebirds in Tomales Bay, the Dunlin and Western Sandpiper, avoided areas devoted to mariculture significantly, although Willets were attracted to oyster plots. Expansion of mariculture, or its redistribution to be concentrated more heavily on particular tidal strata, could further reduce foraging opportunities and possibly abundances of wintering shorebirds. The occasional use by roosting Dunlin and Western Sandpipers of floating oyster culture bags in subtidal areas during high tides (pers. obs.) suggests possible benefits to shorebirds.

The invasive nonindigenous European green crab (*Carcinus maenas*) has become established in Tomales Bay and can alter the abundances of benthic invertebrate prey dramatically, although the consequences for shorebirds are unknown (Grosholz and Ruiz 1995, Grosholz et al. 2000). The closeness of San Francisco Bay implies a high potential for invasion by nonindigenous cordgrass (*Spartina alterniflora*), which is established there and known to affect shorebirds adversely (Goss-Custard and Moser 1988, Daehler and Strong 1996). These concerns, along with those related to watershed effects, limited availability of alternative habitats, and human disturbance associated with recreation, mariculture, and garbage dumps, indicate broad management needs for protecting shorebird foraging areas in Tomales Bay.

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LITERATURE CITED

Amat, J. A., and Aguilera, E. 1990. Tactics of Black-headed Gulls robbing egrets and waders. Anim. Behav. 39:70–77.

Anima, R. J., Bick, J. L., and Clifton, H. E. 1988. Sedimentologic consequences of the storm in Tomales Bay, in Landslides, Floods, and Marine Effects of the Storm of January 3–5, 1982, in the San Francisco Bay Region, California (S. D. Ellen and G. F. Waczorek, eds.). U.S. Geol. Surv., Menlo Park, CA.

Bryant, D. M. 1979. Effects of prey density and site character on estuary usage by overwintering waders (Charadrii). Estuarine and Coastal Mar. Sci. 9:369–384.

Burger, J. 1981. The effect of human activity on birds at a coastal bay. Biol. Conserv. 21:231–241.

Burger, J. 1986. The effect of human activity on shorebirds in two coastal bays in northeastern United States. Env. Conserv. 13:123–130.

Burger, J., and Gochfeld, M. 1991. Human activity influence and diurnal and nocturnal foraging of Sanderlings (*Calidris alba*). Condor 93:259–265.

Burger, J., Howe, M., Hahn, A., Caldwell, D., and Chase, J. 1977. Effects of tide cycles on habitat selection and habitat partitioning by migrating shorebirds. Auk 94:743–758.

Chambers, J. M., Cleveland, W. S., Kleiner, B., and Tukey, P. A. 1983. Graphical Methods for Data Analysis. Wadsworth & Brooks/Cole, Pacific Grove, CA.

Cleveland, W. S. 1979. Robust locally weighted regressions and smoothing scatterplots. J. Am. Stat. Assoc. 74:829–836.

Colwell, M. A. 1993. Shorebird community patterns in a seasonally dynamic estuary. Condor 95:104–114.

Colwell, M. A. 1994. Shorebirds of Humboldt Bay, California: Abundance estimates and conservation implications. W. Birds 25:137–145.

Colwell, M. A., and Sundeen, K. D. 2000. Shorebird distribution on ocean beaches of northern California. J. Field Ornithol. 71:1–15.

Connors, P. G., and Maron, J. L. 1989. Estero Americano bird population study. Long-term Detailed Wastewater Reclamation Studies, Santa Rosa Subregional Water Reclamation System. Tech. memorandum to the city of Santa Rosa, 100 Santa Rosa Ave., Santa Rosa, CA 95403.

Connors, P. G., Myers, J. P., Connors, C. S. W., and Pitelka, F. A. 1981. Interhabitat movements by Sanderlings in relation to foraging profitability and the tidal cycle. Auk 98:49–64.

Daehler, C. C., and Strong, D. R. 1996. Status, prediction and prevention of introduced cordgrass *Spartina* spp. invasions in Pacific estuaries, USA. Biol. Cons. 78:51–58.

Daetwyler, C. C. 1966. Marine geology of Tomales Bay, central California. Pac. Mar. Sta. Res. Rep. 6:1–169.

Galloway, A. J. 1977. Geology of the Point Reyes Peninsula, Marin County. Calif. Div. Mines Geol. Bull. 202.

Gerstenberg, R. H. 1979. Habitat utilization by wintering and migrating shorebirds on Humboldt Bay, California. Studies Avian Biol. 2:33–40.

Goss-Custard, J. D. 1977. Optimal foraging and size selection by worms in Redshank, *Tringa totanus*, in the field. Anim. Behav. 25:10–29.

Goss-Custard, J. D. 1984. Intake rates and food supply in migrating and wintering shorebirds, in Behavior of Marine Animals, vol. 6, Shorebirds: Migration and Foraging Behavior (J. Burger and B. L. Olla, eds.), pp. 233–270. Plenum, New York.

Goss-Custard, J. D., and Moser, M. E. 1988. Rates of change in the numbers of Dunlin, *Calidris alpina*, wintering in British estuaries in relation to the spread of *Spartina anglica*. J. Appl. Ecol. 25:95–109.

Grosholz, E. D., and Ruiz, G. M. 1995. Spread and potential impact of the recently introduced European green crab, *Carcinus maenas*, in central California. Mar. Biol. (Berlin) 122:239–247.

Grosholz, E. D., Ruiz, G. M., Dean, C. A., Shirley, K. A., Maron, J. L., and Connors, P. G. 2000. The impacts of a nonindigenous marine predator in a California bay. Ecology 81:1206–1224.

Harrington, B., and Perry, E. 1995. Important shorebird staging sites meeting Western Shorebird Reserve Network criteria in the United States. Report of the Western Hemisphere Shorebird Reserve Network, Manomet Observatory, P. O. Box 1770, Manomet, MA 02345.

Holland, A. F. 1985. Long-term variation of macrobenthos in a mesohaline region of Chesapeake Bay Estuaries 8:93–113.

Hollibaugh, J. T., Cole, B. E., Dollar, S. J., Hager, S. W., Vink, S. M., Kimmerer, W. J., Obrebski, S., Smith, S. V., Valentino, M., and Walsh, W. W. 1988. Tomales Bay, California: A macrocosm for examining biogeochemical coupling at the land–sea interface. Eos 69:843–845.

Holway, D. A. 1990. Patterns of winter shorebird occurrence in a San Francisco Bay marsh. W. Birds 21:51–64.

Iverson, G. C., Warnock, S. E., Butler, R. W., Bishop, M. A., and Warnock, N. 1996. Spring migration of Western Sandpipers along the Pacific coast of North America: A telemetry study. Condor 98:10–21.

Johnson, R. G. 1971. Animal–sediment relations in shallow-water benthic communities. Mar. Geol. 11:93–104.

Jurek, R. M. 1974. California shorebird survey 1969–1974. Spec. Wildlife Invest. Rep. Pro. W-54-R, Job III-1. Calif. Dept. Fish and Game, 1416 Ninth St., Sacramento, CA 95814.

Kelly, J. P. 2000. Foraging distribution and energy balance in wintering Dunlin. Ph. D. dissertation, Univ. of Calif., Davis.

Kelly, J. P., Evens, J. G., Stallcup, R. W., and Wimpfheimer, D. 1996. Effects of aquaculture on habitat use by wintering shorebirds in Tomales Bay, California. Calif. Fish & Game 82:160–174.

Kelly, J. P., and Tappen, S. L. 1998. Distribution, abundance, and implications for conservation of winter waterbirds on Tomales Bay, California. W. Birds 29:103–120.

Kelly, P. R., and Cogswell, H. L. 1979. Movements and habitat use by wintering populations of Willets and Marbled Godwits. Studies Avian Biol. 2:69–82.

Kirby, J. S., Clee, C., and Seager, V. 1993. Impact and extent of recreational disturbance to wader roosts on the Dee estuary: Some preliminary results. Wader Study Group Bull. 68:53–58.

Laubhan, M. K., and Fredrickson, L. H. 1993. Integrated wetland management: Concepts and opportunities, in Trans. N. Am. Wildlife and Natl. Resources Conf. 58 (R. E. McCabe and K. A. Glidden, eds.), pp. 323–334. Wildlife Mgmt. Inst., Washington, D.C. 20005.

Myers, J. P. 1980. Sanderlings *Calidris alba* at Bodega Bay: Facts, inferences and shameless speculations. Wader Study Group Bull. 30:26–32.

National Oceanic and Atmospheric Administration. 1987. Gulf of the Farallones National Marine Sanctuary management plan (J. Dobbin Associates, Inc., eds.). U. S. Dept. Commerce, NOAA, Marine and Estuarine Mgmt. Div., Washington, D. C. 20235.

Neubacher, D., Dell'Osso, J., Livingston, D., and Murray, R. 1995. Tomales Bay/ Bodega Bay watershed boundary study. U.S. Govt. Printing Office 1995-685-430, Point Reyes National Seashore, Point Reyes, CA 94956.

Nordby, C. S., and Zedler, J. B. 1991. Responses of fish and macrobenthic assemblages to hydrologic disturbances in Tijuana estuary and Los Peñasquitos Lagoon, California. Estuaries 14:80–93.

Page, G. W., and Shuford, D. 2000. Southern Pacific Coast Regional Shorebird Plan, version 1.0. U. S. Shorebird Planning Council, U. S. Shorebird Conservation Plan. Point Reyes Bird Observatory, 4990 Shoreline Hwy., Stinson Beach, CA 94970.

Page, G. W., Stenzel, L. E., and Kjelmyr, J. E. 1999. Overview of shorebird abundance and distribution in wetlands of the Pacific coast of the contiguous United States. Condor 101:461–471.

Page, G. W., Shuford, W. D., Evens, J. G., and Stenzel, L. E. 1983. The distribution and abundance of aquatic birds in wetlands of the Point Reyes to Bodega area. Report to the Point Reyes–Farallones National Marine Sanctuary. Point Reyes Bird Observatory, 4990 Shoreline Hwy., Stinson Beach, CA 94970

Page, G. W., Shuford, W. D., Kjelmyr, J. E., and Stenzel, L. E. 1992. Shorebird numbers in wetlands of the Pacific Flyway: A summary of counts from April 1988 to January 1992. Point Reyes Bird Observatory, 4990 Shoreline Hwy., Stinson Beach, CA 94970.

Page, G. W., Stenzel, L. E., and Wolfe, C. M. 1979. Aspects of the occurrence of shorebirds on a central California estuary. Studies Avian Biol. 2:15–32.

Philip Williams & Associates, Ltd., Wetlands Research Associates, Strong Associates, and Butler, L. J. 1993. An evaluation of the feasibility of wetland restoration on the Giacomini Ranch, Marin County. Philip Williams & Associates, Pier 35, The Embarcadero, San Francisco, CA 94113.

Quammen, M. L. 1982. Influence of subtle substrate differences on feeding by shorebirds on intertidal mudflats. Mar. Biol. (Berlin) 71:339–343.

Ramer, B. A., Page, G. W., and Yoklavitch, M. M. 1991. Seasonal abundance, habitat use, and diet of shorebirds in Elkhorn Slough, California. W. Birds 22:157–174.

Recher, H. F. 1966. Some aspects of the ecology of migrant shorebirds. Ecology 47:393–407.

Rooney, J. J., and Smith, S. V. 1999. Watershed land use and bay sedimentation. J. Coastal Res. 15:478–485.

Ruiz, G. M. 1987. Interactions among shorebird, crab, and their invertebrate prey populations. Ph. D. dissertation, Univ. of Calif., Berkeley.

Ruiz, G. M., Connors, P. G., Griffin, S. E., and Pitelka, F. A. 1989. Structure of a wintering Dunlin population. Condor 91:562–570.

Shannon and Associates. 1998. Lawson's Landing Master Plan. Shannon and Associates, P. O. Box 322, Bodega Bay, CA 94923.

Shuford, W. D., Page, G. W., Evens, J. G., and Stenzel, L. E. 1989. Seasonal abundance of waterbirds at Point Reyes: A coastal California perspective. W. Birds 20:137–265.

Skagen, S. K., and Knopf, F. L. 1993. Toward conservation of midcontinental shorebird migrations. Cons. Biol. 7:533–541.

Skagen, S. K., and Knopf, F. L. 1994. Migrating shorebirds and habitat dynamics at a prairie wetland complex. Wilson Bull. 106:91–105.

Smail, J. 1972. The birds of Tomales Bay, in Tomales Bay Environmental Study: Compendium of Reports (R. Corwin, ed.), pp. 124–134. Conservation Foundation, Washington, D. C.

Smith, S. V., and Hollibaugh, J. T. 1989. Carbon-controlled nitrogen cycling in a marine "macrocosm": and ecosystem-scale model for managing cultural eutrophication. Mar. Ecol. Prog. Ser. 52:103–109.

Smith, S. V., and Hollibaugh, J. T. 1997. Annual cycle and interannual variability of ecosystem metabolism in a temperate climate embayment. Ecol. Monogr. 67:509–533.

Standing, J., Browning, B., and Speth, J. W. 1975. The natural resources of Bodega Harbor. Calif. Dept. Fish and Game Coastal Wetland Ser. 11.

Storm, D. R. 1972. Hydrology and water quality aspects of the Tomales Bay Study, in Tomales Bay Environmental Study: Compendium of Reports (R. Corwin, ed.), pp. 84–101. Conservation Foundation, Washington, D.C.

Thompson, D. B. A., and Lendrem, D. W. 1985. Gulls and plovers: Host vigilance. Behaviour 33:1318–1324.

U. S. Fish and Wildlife Service. 1995. Proposed designation of critical habitat for the Pacific coast population of the Western Snowy Plover. Fed. Reg. 60:11767–11809.

Warnock, N. 1989. Piracy by Ring-billed Gulls on Dunlin. Wilson Bull. 101:96–97.

Warnock, N., Page, G. W., and Stenzel, L. E. 1995. Non-migratory movements of Dunlins on their California wintering grounds. Wilson Bull. 107:131–139.

Warnock, S. E., and Takekawa, J. Y. 1995. Habitat preferences of wintering shorebirds in a temporally changing environment: Western Sandpipers in the San Francisco Bay estuary. Auk 112:920–930.

Warnock, S. E., and Takekawa, J. Y. 1996. Wintering site fidelity and movement patterns of Western Sandpipers *Calidris mauri* in the San Francisco Bay estuary. Ibis 138:160–167.

Wolff, W. J. 1969. Distribution of non-breeding waders in an estuarine area in relation to the distribution of their food organisms. Ardea 57:1–27.

Wolff, W. J. 1983. Estuarine benthos, in Ecosystems of the World 26: Estuaries and Enclosed Seas (B. H. Ketchum, ed.), pp. 151–182. Elsevier Scientific, Amsterdam.

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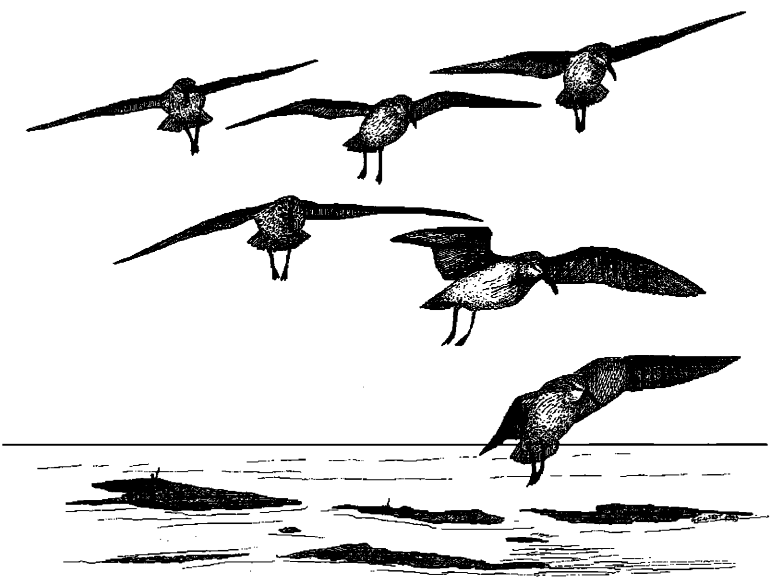

Western Sandpipers

Sketch by George C. West