PATTERNS OF WINTER SHOREBIRD OCCURRENCE IN A SAN FRANCISCO BAY MARSH

DAVID A. HOLWAY, Department of Biology, University of California, Los Angeles, California 90024

Resource exploitation by shorebirds in marine environments is influenced to a large degree by the tidal cycle. The periodicity of the tides dictates where and when shorebirds will feed (Connors et al. 1981). Some shorebirds that find their prey by touch feed whenever tidal conditions permit, independent of ambient light levels (Goss-Custard 1969).

In this study, I counted shorebirds of nine species in two plots of equal sizes. All censuses were conducted within a fixed interval of tidal height during both the flood and ebb tides. With this important abiotic variable held constant, I addressed three hypotheses: (1) Shorebird numbers in winter are constant in one location at a fixed tidal height. (2) Shorebird numbers in one location do not change in the same tidal height interval on the ebb and flood tides. (3) Shorebird species are distributed in each plot equally (numbers of each species and total biomass of shorebirds within each plot are equal).

STUDY AREA AND METHODS

I conducted this study at Corte Madera Marsh, Marin County, California, inside San Francisco Bay (Figure 1). Once an extensive salt marsh, Corte Madera Marsh is now a complex of diked wetlands with only vestiges of remnant salt marsh. The marsh system is bounded on the north by Corte Madera Creek and on the south by San Clemente Creek. This study focused on shorebirds' use of Muzzi (direct tidal flow) and Marta's (muted tidal flow) marshes. These marshes were diked off from San Francisco Bay in the 1960s.

The mudflats in Muzzi and Marta's marshes are important feeding sites for shorebirds during both ebb and flood tides. I established two plots of approximately 4.5 hectares (150 m × 300 m) in each marsh. I refer to these plots as the plot under direct tidal flow (Muzzi) and the plot under muted tidal flow (Marta's). The mudflats within both plots are several feet above those on the bay side of the dikes. During the flood tide these are the last areas to be inundated; shorebirds concentrate here to feed before the flats get covered when the tide reaches +5 feet. Shorebirds retreat to nearby roost sites when the tide exceeds +5 feet. The first mudflat to be uncovered when the tide begins to ebb is the plot under direct tidal flow, where shorebirds then concentrate. At low tide shorebirds move out onto mudflats in San Francisco Bay to forage.

The plot under direct tidal flow is bordered on two sides by dikes (breached in several places in 1976) and on two sides by salt marsh. The plot encompasses the only extensive mudflat within Muzzi Marsh; the remainder is salt marsh composed of *Salicornia virginica* and *Spartina foliosa*. This mudflat is similar in size to the mudflat in the plot under muted tidal flow and lies about 5 feet above the 0.0 tideline.

The plot under muted tidal flow is a diked tidal pond. The pond has a tidal gate at its western end along San Clemente Creek, which empties the marsh. The drain imparts a lag in the tidal cycle so that the cycle in this pond is several hours later than that of the bay and mutes the tidal flow. The plot is covered when the water level reaches about +4.5 feet during the flood tide but remains a mudflat throughout the flood-tide census interval. The lag time within this pond is a function of the tidal amplitude and the amount of runoff in San Clemente Creek. The mudflat in the plot under muted tidal flow becomes covered slightly later on the flood tide than does the plot under direct tidal flow. In addition, this pond remains full during the ebb census because of the lag and is not used by shorebirds for feeding at this time. The vegetation is the plot under muted tidal flow consists primarily of *Salicornia virginica* distributed along the periphery of the pond.

I conducted censuses from one fixed point for each plot by using a 20× scope, 10× binoculars, and handcounters to count shorebirds. The mudflats were small enough to allow an easy count of all shorebirds present. For each census the time the tide took to rise or fall from one limit of the specified interval to the other, duration of the census, weather, notable shorebird behavior (such as territoriality), raptor presence, and human disturbance were recorded. Censuses were not conducted in the rain or on days when the tidal interval was misjudged.

Both plots were censused on 21 days from 30 September 1988 to 11 March 1989 at roughly 7-day intervals. Censuses were conducted from +3.5 to +4.5 feet on the flood tide and from +4.5 to +3.5 on the ebb tide. During these tidal intervals, chosen early in the fall (July–September 1988), high concentrations of shorebirds fed on the two plots (as shown by observations through the complete tidal cycle). During the flood-tide interval, similar areas of mudflat were exposed within each plot. In addition, there was little change in mudflat area during the flood-tide interval; incoming water during this interval went mostly toward filling tidal channels cut into the mudflat. Because of the complexity of the tidal regime in San Francisco Bay it was necessary to get to the census points well before the tide level predicted from tidal charts. I placed a stake in the plot under direct tidal flow to determine when to begin and end censuses.

Censuses took from 60 to 90 minutes. The height of the tide remained within the specified interval for approximately 60 to 120 minutes, the time varying primarily as a function of tidal amplitude. I remained in the area throughout the tidal interval. For each of the nine study species, I averaged the results of three counts taken in close succession. This method gave a precise count of shorebirds present, as standard deviations of arithmetic means were always fairly small.

Because the two plots were small and juxtaposed, I could conduct censuses simultaneously and note any shorebird movement between the two plots. There was usually little interplot movement during the censuses. When there was movement into or out of the area as a whole during a census, I counted the maximum number of shorebirds present at one time during the interval.

All shorebird species were counted, but only nine occurred regularly (Table 1). Two broad distributional divisions exist among the nine study species: five breed in high latitudes (arctic and subarctic) and four breed in middle latitudes (one of these, the American Avocet, breeds in San Francisco Bay).

I used the coefficient of fluctuation (CF) (Whittaker 1975; see also Holmes et al. 1986) to assess variability in the winter abundance of each species. The CF is an index of population fluctuation based on logarithms and measures fluctuation around the geometric mean. Because

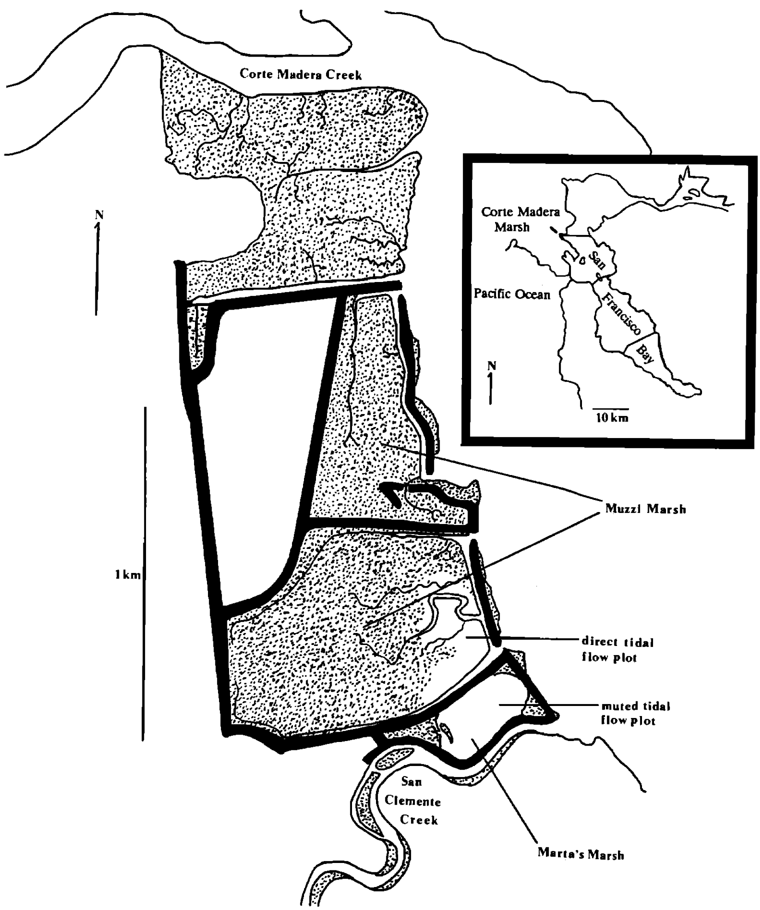

Figure 1. Corte Madera Marsh, Marin County. Stippled area, *Salicornia-Spartina* marsh. Inset, location of study site on San Francisco Bay.

the CF is based on logarithms, it is less affected by absolute differences in population size (as between species) than the coefficient of variation (Whittaker 1975). In other words, populations of different sizes that are fluctuating by the same amount will have comparable CFs. Population sizes used in calculating CFs were the flood-tide totals from both plots combined. Because each species has a unique migration schedule, I used the "winter" periods for each species specified by McCaskie et al. (1979) as the periods of uniform seasonal abundance inclusive of the dates of this study. This simplification is crude, but less so than arbitrarily assigning one wintering period for all nine species. With only two exceptions (see Results), the winter schedule of each species completely overlapped the duration of this study. I used the weights listed by Page et al. (1979) to calculate biomasses and Wilcoxon matched-pair signed-rank tests to test the differences between the plots in shorebird biomass and between the flood- and ebb-tide censuses (Sokal and Rohlf 1981, Mathcad 1988).

RESULTS

Variation in Numbers

By sampling within one tidal height interval, I fixed the principal variable affecting shorebird presence in the two plots. Numbers of Willets (*Catoptrophorus semipalmatus*), Long-billed Curlews (*Numenius americanus*), and Least Sandpipers (*Calidris minutilla*) fluctuated erratically all winter. Although the CFs for these species were not as high as those of others (Table 1), the occurrence of the three in the plots seemed random, showing no obvious patterns (Figures 2–4). The irregularity was

Table 1 Latitudes of Breeding, Mean Weights, and Coefficients of Fluctuation for Shorebirds Studied at Corte Madera Marsh, 1988-1989

Species	Latitude of breeding[a]	Mean weight (grams)[b]	Coefficient of fluctuation[c]
Black-bellied Plover	H	219.0	1.95
American Avocet	M	312.0	1.51
Willet	M	299.3	2.82
Long-billed Curlew	M	691.3	2.09
Marbled Godwit	M,H	371.4	1.17
Western Sandpiper	H	25.0	5.49
Least Sandpiper	H	20.5	3.16
Dunlin	H	50.1	6.76
Dowitcher spp.	H	113.6	1.70

[a]H, high latitudes (arctic and subarctic); M, middle latitudes.

[b]Data from Page et al. (1975).

[c]Antilog $[\Sigma(\log N_x - \log \tilde{N})^2/t-1]^{1/2}$, where N_x is the species' abundance on day x and N is geometric mean density. The coefficient is unitless (Whittaker 1975).

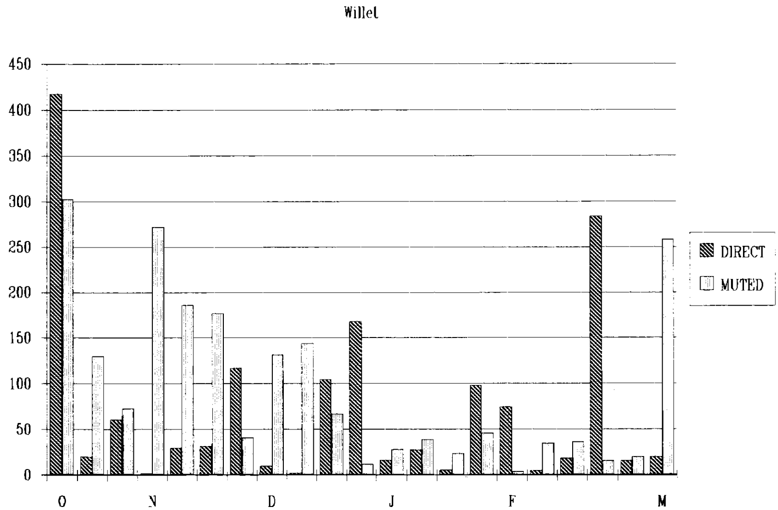

Figure 2. Flood-tide abundance of the Willet in the plots under direct and muted tidal flow at Corta Madera Marsh.

due at least in part to these species' preference for other foraging sites. Willets and Long-billed Curlews commonly fed in salt marsh when the

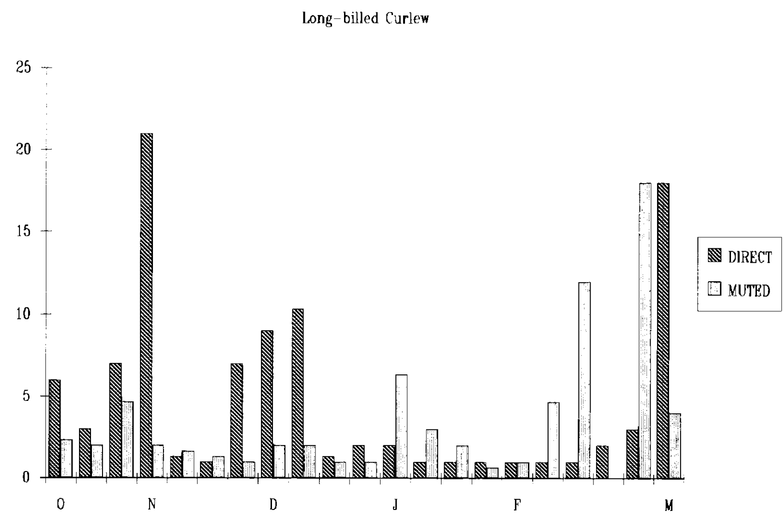

Figure 3. Flood-tide abundance of the Long-billed Curlew in the plots under direct and muted tidal flow at Corte Madera Marsh.

tide was high. Least Sandpipers often fed along tidal channels within the salt marsh or on high exposed mud outside of the plots.

The remaining six species foraged primarily within the two plots during the flood-tide interval. Through the winter, their numbers varied either little or in a nonrandom pattern. In general the mid-latitude breeders have a longer winter residency than do high-latitude breeders, but important differences within each distributional division exist as well.

The Marbled Godwit (*Limosa fedoa*) showed little variation in numbers through the winter (Figure 5). This species had the lowest CF (1.17) of any species (Table 1); Marbled Godwit numbers fluctuated by only about 17% above and below their geometric mean during the winter.

The American Avocet (*Recurvirostra americana*), dowitchers (*Limnodromus* spp.), and Black-bellied Plover (*Pluvialis squatarola*) also showed small fluctuations in abundance during the winter (Figures 6–8). CFs for these species were all less than 2 (Table 1); their fluctuations averaged less than two times the geometric mean. The American Avocet occurred in fairly regular numbers during the winter (early November to early March). Peaks of abundance in October and March probably represented influxes of migrants. It is not known what proportion of the wintering population in San Francisco Bay consists of local breeders or whether these local birds are resident in the bay.

In my analysis, I pooled data for the two species of dowitchers. Dowitchers remaining past mid-October were almost entirely Long-billed (*L. scolopaceus*); the high numbers in late October and November proba-

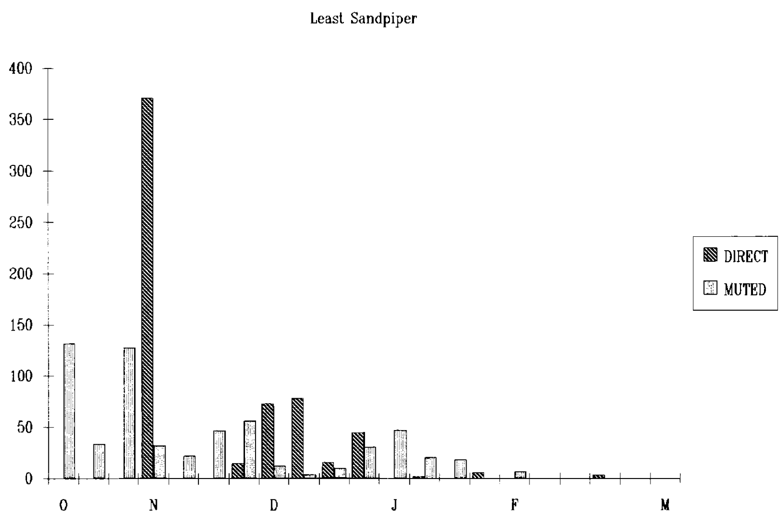

Figure 4. Flood-tide abundance of the Least Sandpiper in the plots under direct and muted tidal flow at Corte Madera Marsh.

bly represented an influx of migrants. The only Short-billed Dowitchers (*L. griseus*) detected (by call) in winter were in the plot under direct tidal flow, which was seldom used by Long-billed Dowitchers on the flood tide (Figure 7). Fewer than five Short-billed Dowitchers wintered in the vicinity, but this species was common in passage from July to September and during that time used primarily the plot under muted tidal flow.

Black-bellied Plovers occurred in fairly stable numbers all winter but demonstrated no clear preference for either of the two plots (Figure 8).

The Western Sandpiper (*Calidris mauri*) and Dunlin (*C. alpina*), which typically fed and flocked together, exhibited similar patterns of fluctuation during the winter (Figures 9 and 10). Both of these species had distinct peaks of abundance in November and January followed by a rapid attenuation in abundance in midwinter. The congruency of these patterns is intriguing because the molt and migratory schedules of the two species are so different. Western Sandpipers molt in migration and on the wintering grounds (Holmes 1972) and pass through this latitude from July through September. This species was common in the plot under muted tidal flow in July and August (mostly adults) and abundant from August to into September (mostly juveniles). Unlike Western Sandpipers, Dunlins migrating down the Pacific coast of North American molt on or near their arctic breeding grounds (Holmes, 1966, 1971) and pass through this latitude in October and early November (the winter period of this species begins in late October). The first Dunlins on the study plots arrived in late September.

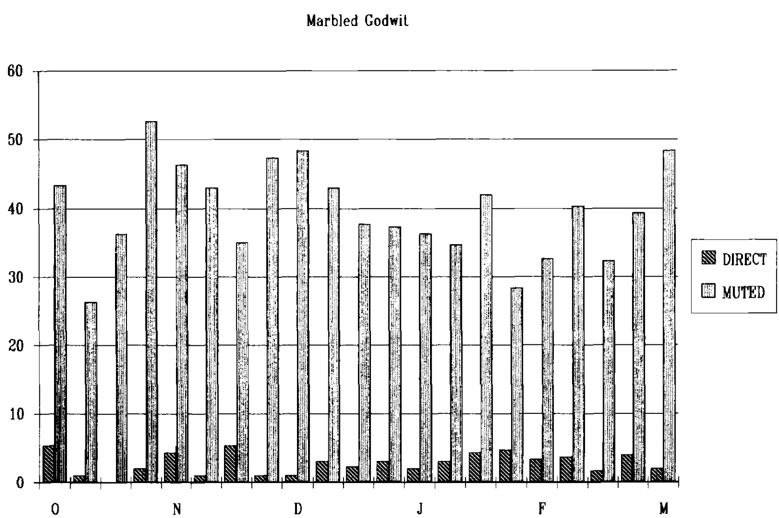

Figure 5. Flood-tide abundance of the Marbled Godwit in the plots under direct and muted tidal flow at Corte Madera Marsh.

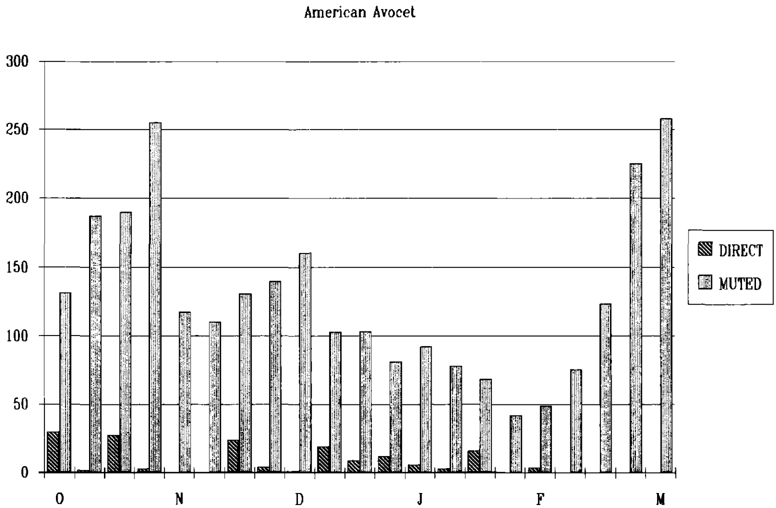

Figure 6. Flood-tide abundance of the American Avocet in the plots under direct and muted tidal flow at Corte Madera Marsh.

Flood–Ebb Comparisons

For all species, numbers counted during the flood-tide interval were higher than numbers counted during the ebb-tide interval (both plots

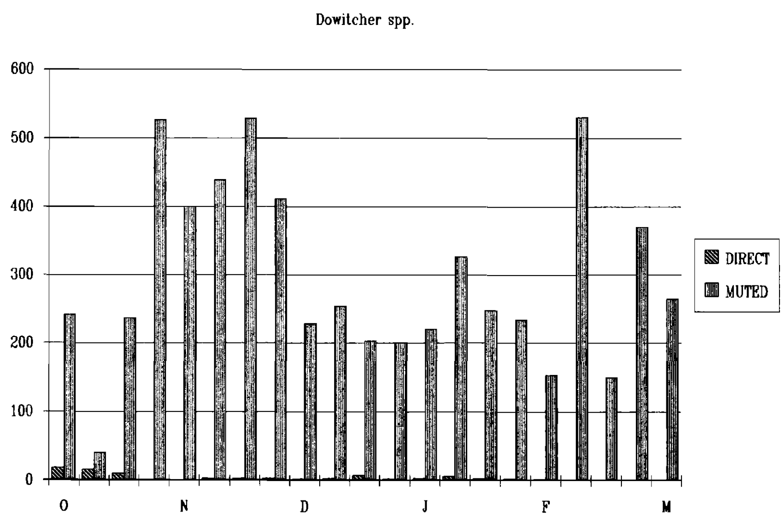

Figure 7. Flood-tide abundance of dowitchers in the plots under direct and muted tidal flow at Corte Madera Marsh.

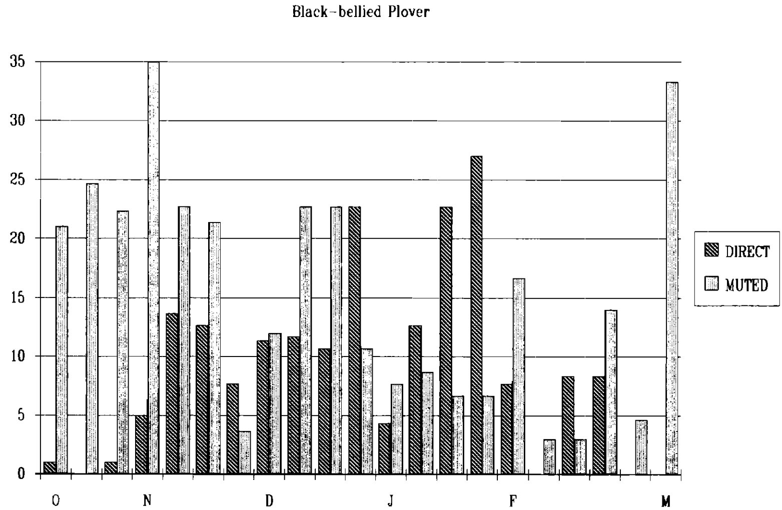

Figure 8. Flood-tide abundance of the Black-bellied Plover in the plots under direct and muted tidal flow at Corte Madera Marsh.

combined). This is most likely an artifact of the smaller (by 50%) mudflat area exposed during the ebb-tide interval. The plot under muted tidal flow remained full during the ebb census, so I could compare (by the

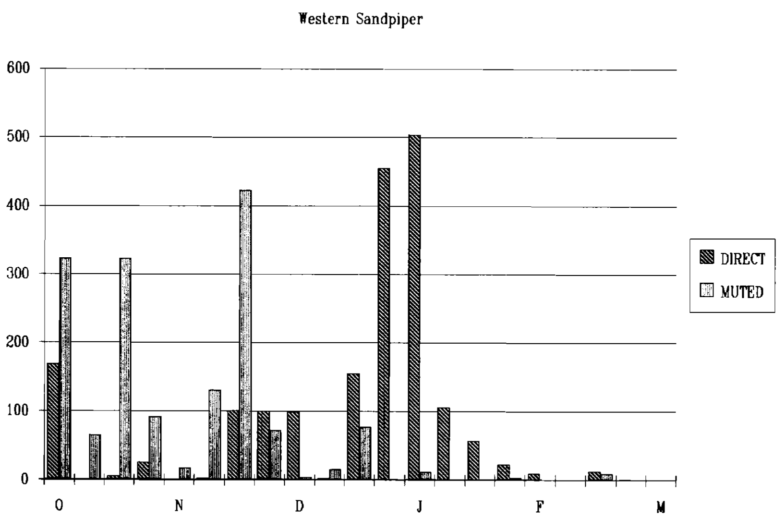

Figure 9. Flood-tide abundance of the Western Sandpiper in the plots under direct and muted tidal flow at Corte Madera Marsh.

Wilcoxon matched-pair signed-rank test) shorebird abundance during the flood and ebb tides only for the plot under direct tidal flow. Numbers counted during the ebb-tide interval were significantly greater ($p < 0.01$) than number counted during the flood-tide interval for all species except the Least Sandpiper and Dunlin, for which the difference was not statistically significant.

Most species remained at roost sites within the marsh throughout the ebb-tide interval. From late December through early February, however, mixed flocks of Western Sandpipers and Dunlins were consistently seen leaving high-tide roosts in Corte Madera Marsh during the ebb-tide interval without feeding. Flocks left Corte Madera Marsh toward either the south or southeast.

Comparison of Plot Use

Three species, the American Avocet, Marbled Godwit, and dowitchers, preferred the plot under muted tidal flow to the near exclusion of the other plot during the flood-tide census (Figures 5–7). Two species, the Western Sandpiper and Dunlin, favored the plot under muted tidal flow during the fall but shifted to the plot under direct tidal flow in early December and January (Figures 9 and 10) before leaving the area entirely in midwinter. Western Sandpipers showed a distinct preference for the plot under muted tidal flow during migration (July–September) as well.

The absolute biomass of shorebirds in each plot was significantly different. The plot under muted tidal flow supported a significantly higher shorebird biomass ($p < 0.005$; Wilcoxon matched-pair signed-rank test)

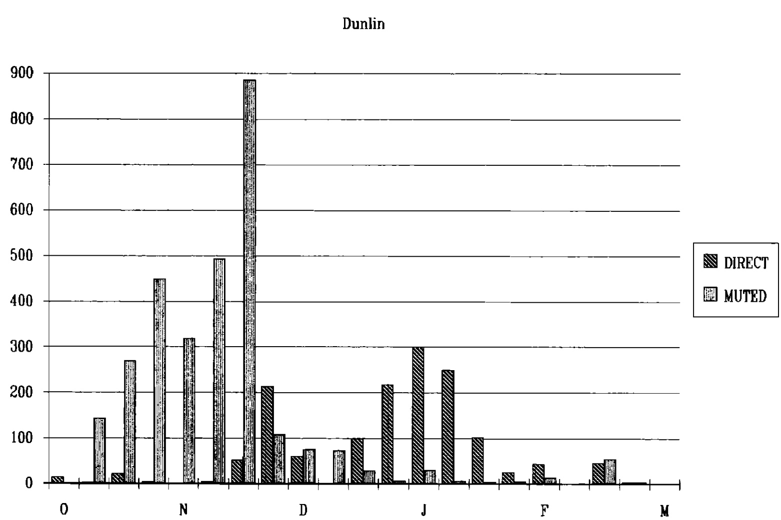

Figure 10. Flood-tide abundance of the Dunlin in the plots under direct and muted tidal flow at Corte Madera Marsh.

than the plot under direct tidal flow all winter (Figure 11). Shorebird biomass was lowest in early February; this depression coincided with a week-long cold snap. A small percentage of shorebirds roosted (rather than fed) in the plots during both tidal intervals, biasing these calculations to some extent, but the overwhelming majority of shorebirds fed in the plots.

DISCUSSION

Despite the unique morphology and foraging behavior of each species, all probably responded to local fluctuations in resource abundance and, as a result, may have shown congruent patterns of winter fluctuation (e. g., the seasonal variation in abundance of Western Sandpipers and Dunlins; Figures 9 and 10).

A late-winter diminution in Dunlin numbers has been described from other parts of San Francisco Bay (Storer 1951, Holmes 1966) and from Bodega Harbor, Sonoma County (P. G. Connors pers. comm.). Where Dunlins go in late winter is unknown; possibilities include a protracted spring migration up the Pacific Coast (Holmes 1966) or a shift from tidal mudflats to nontidal seasonal wetlands as these areas become available and profitable for feeding in midwinter. Ruiz et al. (1989) found that Dunlins wintering in Bodega Harbor constitute two subpopulations, each with distinct foraging patterns. If such subpopulations are a common feature in wintering populations of Dunlins, both of these processes could

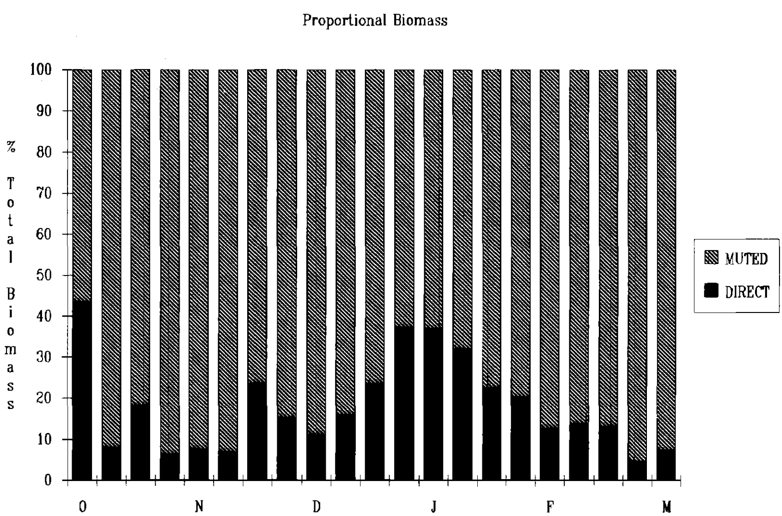

Figure 11. Proportional biomass of shorebirds in the plots under direct and muted tidal flow at Corte Madera Marsh. Calculated with weights from Page et al. (1979).

be important; successive pulses of Dunlins may pass through this latitude during spring migration. Large numbers of Dunlins do occur on San Francisco Bay in mid-April (Stenzel and Page 1988).

Numbers of birds in the plot under direct tidal flow during the ebb tide (when the other plot was unavailable for feeding) were a small fraction of those present in both plots during the flood tide. This suggests two possible ebb-tide feeding strategies: (1) Birds remain at high-tide roosts after feeding areas have been uncovered because they are not energetically constrained to maximize feeding time. (2) Birds move to new feeding areas as these become uncovered by the ebb tide, in order to maximize energy intake. Both tactics may be employed by individuals of some species, but consideration of these alternative strategies may help explain the behavior patterns of certain groups of species. The larger species (American Avocet, Willet, Long-billed Curlew, and Marbled Godwit) often loafed at high-tide roosts in the marsh after mudflats became exposed by the ebb tide, suggesting that these species were not under severe energetic constraints to maximize foraging time.

A different pattern I noted was the exodus of mixed flocks of Western Sandpipers and Dunlins from Corte Madera Marsh during the ebb tide, even though mudflat was exposed in the plot under direct tidal flow. If food was always made available when mud was uncovered, Western Sandpipers and Dunlins were passing up immediate resources in favor of prospective richer resources elsewhere. Perhaps the energy needs of these smaller birds demand that they maximize food intake. I saw none of the other study species leave the area during the ebb tide on a regular basis.

Vagility may vary from species to species owing to energetic demands caused by resource limitation. Smaller species (such as *Calidris* sandpipers) may depend on patchy, concentrated, or ephemeral resources and may be forced to forage widely in search of food. On an estuary as large as San Francisco Bay, roosting sites and feeding sites can be several kilometers apart if the energetic cost incurred by the commute does not exceed the profitability of foraging at a distant location. In contrast, a pattern of local winter residency has been demonstrated for some species of large shorebirds. Kelly and Cogswell (1979) found that a banded population of Willets and Marbled Godwits wintering in south San Francisco Bay showed little local movement. Ruiz et al. (1989) found that different levels of vagility may be important at the intraspecific level as well.

Both of my mudflat plots were used primarily for feeding by all of the study species during the flood-tide interval. It is therefore reasonable to infer that differences in shorebird abundance and biomass were primarily a result of differences between the plots in the resource base.

The midwinter shift between the two plots in abundance of Western Sandpipers and Dunlins (Figure 11) probably paralleled a change in the distribution and abundance of resources. A midwinter decline in prey items in the upper few centimeters of mud could have made the plot under muted tidal flow unsuitable for short-billed species (Western Sandpiper and Dunlin) but not for long-billed species (Marbled Godwit and dowitchers). American Avocets fed primarily by straining the water column (mainly in tidal channels) so are exempt from this hypothesis. Observations of Western Sandpipers and Dunlins regularly leaving the marsh during the ebb tide are consistent with the idea that the area may have been resource-poor for these species and that richer areas existed elsewhere. An increasing depth of prey items has been found to be inversely related to intake rate in some shorebird species (Reading and McGorty 1978, Myers et al. 1980).

The patterns of shorebird occurrence that I found in this study probably result from resource heterogeneity on a spatial scale (between plots) and on a temporal scale (across the winter). A quantification of the resource base is central to any study of community structure, foraging behavior, or habitat selection. With no data on resources such a fit of patterns to processes can be only inferred. Aside from this, the spatial and temporal distributions of shorebirds on a local scale are clearly not uniform.

ACKNOWLEDGMENTS

This study was completed in partial fulfillment of the Senior Honor's Thesis at the University of California at Berkeley. The following people provided helpful suggestions and insightful comments: John Comstock, Peter G. Connors, Richard T. Holmes, Ned K. Johnson, Durrell D. Kapan, Brian J. McCaffery, Tim Manolis, Frank A. Pitelka, Lynne E. Stenzel, and an anonymous reviewer. Barbara Salzman and Roger Harris provided useful information regarding the study site. Finally, I am indebted to the logistical support of John Comstock and Richard and Gail Holway, without whose assistance and patience this study would not have been possible.

LITERATURE CITED

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.

Goss-Custard, J. D. 1969. The winter feeding ecology of the Redshank (*Tringa totanus*). Ibis 111:338-356.

Holmes, R. T. 1966. Breeding ecology and annual cycle adaptations of the Red-backed Sandpiper (*Calidris alpina*) in northern Alaska. Condor 68:3–46.

Holmes, R. T. 1971. Latitudinal differences in the breeding and molt schedules of Alaskan Red-backed Sandpipers (*Calidris alpina*). Condor 73:93–99.

Holmes, R. T. 1972. Ecological factors influencing the breeding season schedule of Western Sandpiper (*Calidris mauri*) in subarctic Alaska. Am. Midland Nat. 87:472–491.

Holmes, R. T., Sherry, T. W., and Sturges, F. W. 1986. Bird community dynamics in a temperate deciduous forest: Long-term trends at Hubbard Brook. Ecol. Monogr. 56:201-220.

Kelly, P. R., and Cogswell, H. L. 1979. Movements and habitat use by wintering populations of Willets and Marbled Godwits, in Shorebirds in Marine Environments (F. A. Pitelka, ed.), Studies Avian Biol. 2:69–82.

Mathcad. 1988. Version 2.09. Mathsoft, Inc., Cambridge, MA.

McCaskie, G., DeBenedictis, P., Erickson, R. A., and Morlan, J. L. 1979. Birds of Northern California: An Annotated Field List. Golden Gate Audubon Soc., Berkeley.

Myers, J. P., Schick, C. T., and Castro, G. 1989. Structure in Sanderling (*Calidris alba*) populations: The magnitude of intra- and inter-year dispersal during the non-breeding season. Proc. XIX Int. Ornithol. Congr., pp. 604–615.

Myers, J. P., Williams, S. L., and Pitelka, F. A. 1980. An experimental analysis of prey availability for Sanderlings (Aves: Scolopacidae) feeding on sandy beach crustaceans. Can. J. Zool. 58:1564–1574.

Page, G., Stenzel, L. E., and Wolfe, C. M. 1979. Aspects of the occurrence of shorebirds on a central California estuary, in Shorebirds in Marine Environments (F. A. Pitelka, ed.), Studies Avian Biol. 2:13–32.

Reading, C. J., and McGorty, S. 1978. Seasonal variations in the burying depth of *Macoma balthica* and its accessibility to wading birds. Estuarine Coastal Mar. Sci. 6:135–144.

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

Sokal, R. R., and Rohlf, R. J. 1981. Biometry, 2nd ed. Freeman, New York.

Stenzel, L. E., and Page, G. W. 1988. Results of the 16–18 April 1988 shorebird census of San Francisco and San Pablo bays. Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, CA 94970.

Storer, R. W. 1951. The seasonal occurrence of shorebirds on Bay Farm Island, Alameda County. Condor 53:186–193.

Whittaker, R. H. 1975. Communities and Ecosystems. Macmillan, New York.

Accepted 7 March 1990