SHOREBIRD COMMUNITY PATTERNS IN A SEASONALLY DYNAMIC ESTUARY

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Abstract. I examined the influence of environmental factors (exposed intertidal habitat, river volume and invertebrate abundance) on nonbreeding shorebird communities in the Mad River, California, an estuary in which intertidal habitats are affected by seasonal variation in river discharge. The shorebird community exhibited the following temporal (July–April) variation: (1) species composition exhibited a 50% turnover between October and November; (2) species richness peaked in summer, declined in winter and increased in spring; (3) shorebird abundance peaked in summer, when most birds foraged in cobble habitats; and (4) during winter a large percentage of birds roosted, and a small proportion fed in low numbers in aquatic habitats. Exposed intertidal habitat explained significant variation in both community patterns and the abundance of five species; these species were characterized by use of exposed intertidal habitats. Compared with other studies, the relatively weak associations between environmental variables and variation in the shorebird assemblage suggests that shorebirds occupying seasonally dynamic estuaries may exhibit space use and activity patterns different from those reported for birds occupying coastal estuaries where habitat availability and food resources are more predictable.

Key words: Shorebirds; habitat availability; estuary; invertebrates; river discharge; tides; community composition.

INTRODUCTION

The ecology of shorebirds in coastal habitats is strongly influenced by food. Environmental factors, principally tides and weather, constrain food availability on a relatively predictable daily and seasonal basis by limiting access of birds to invertebrate prey (Burger 1984, Evans 1988). Analyses of coastal shorebird assemblages indicate that date, tide and weather explain most variation in species richness and abundance (Burger 1984). Although the impact of abiotic factors varies among habitats, tides influenced communities at both freshwater and estuarine sites (Burger 1984).

Worldwide, many estuaries supporting large numbers of migrating and wintering shorebirds (Senner and Howe 1984, Myers et al. 1987) have tidal regimes that result in relatively predictable temporal patterns of food availability (see Burger 1984). In general, wetlands of the Pacific Coast of North America are either large bays (e.g., San Francisco, Humboldt and Willapa) or river estuaries (e.g., Eel, Klamath and Columbia), which vary in importance to nonbreeding shorebirds (Senner and Howe 1984). The bays, with predictable tidal environments, support large num-

bers of migrating and wintering shorebirds (Senner and Howe 1984). By contrast, river estuaries are more dynamic and less predictable owing to influences of precipitation and river runoff. The importance of river estuaries, however, to nonbreeding shorebirds is poorly understood, as are the ecologies of shorebirds in these dynamic habitats.

In this paper, I examine environmental factors influencing nonbreeding shorebirds. Unlike Burger's (1984) analysis, however, I examine the influence of food and habitat availability on shorebirds in an estuary that is strongly influenced by seasonal variation in precipitation and river runoff. My objectives are to: (1) examine seasonal variation in species richness, relative abundance and community composition; (2) evaluate the relative impact of food abundance, amount of intertidal habitat, and river discharge on shorebird community patterns; and (3) compare results with models (Burger 1984) explaining shorebird distribution and abundance in coastal habitats.

STUDY AREA AND METHODS

I studied shorebirds along a 0.5 km intertidal stretch of the Mad River, approximately 4 km upstream from the confluence of the river and the Pacific Ocean in Humboldt County, Califor-

nia. Within the study area, the Mad River flows north parallel to the ocean and adjacent to cliffs, which mark the eastern boundary of the study area. To the west of the river are gently sloping intertidal flats, which are mostly unvegetated substrates varying in particle size from silt to cobble. Sandy substrates predominate downstream from a riffle that flows through cobble substrates at low tide. During the study, habitat availability varied dramatically in association with temporal variation in tides. Mixed, semidiurnal tides had a maximum amplitude of about 3.3 meters. In addition, river discharge varied substantially during the study (range: 0.7–112.9 cubic meters per second) owing to seasonal variation in precipitation. During periods of low tide and low river discharge, large intertidal flats characterized the area; at high tides, and especially during periods of high runoff, water inundated the site.

Usually I observed shorebirds three times weekly (Wednesday, Friday and Sunday) at 07:30 from 11 July 1990 to 28 April 1991 ($n = 99$). I censused birds from atop a 5 m cliff at the southeast corner of the site using 7 × 50 mm binoculars and a 22× spotting scope. I scan-sampled (Altmann 1974) birds starting at one end of the site and panning to the opposite end until I had counted all shorebirds within the study area. For each individual or flock observed, I recorded species, abundance, behavior (feeding or other) and habitat. I categorized habitats as aquatic or cobble, sand, or mud substrates uncovered by water. I tallied flying birds only if I knew that they had been using the study site prior to their departure. I summarized data as monthly averages (species richness, species abundances and percent use of habitats and behaviors).

In addition to shorebird observations, I obtained data on variation in habitat availability to shorebirds from several sources. First, based on preliminary observations, I established the maximum amount (100%) of exposed intertidal habitat at the lowest tide and upon each visit to the site I estimated the percent (100%; 75%; 50%; 25%; and 0%) of intertidal habitat not covered by water. Second, I indexed the volume of water flowing in the Mad River based on daily logs kept by the Mad River Fish Hatchery, Blue Lake, California. Hatchery personnel recorded river volume at 09:00 from a gauge located approximately 5 km upstream from my study area. No major streams join the Mad River between the gauge and study site; thus, I assumed that runoff was comparable at downstream locations.

Each month at the lowest tide, I sampled potential invertebrate prey organisms from intertidal substrates on the west bank of the river in an area used consistently by foraging birds. I established a 100 m transect immediately adjacent to the tide's edge and extracted core samples from random locations alternating (determined by coin toss) left and right sides of the transect. Although I established transects in the same area each month, the exact location varied owing to fluctuations in water level associated with tides and river discharge (see below). I collected 20 core samples (10 from cobble and 10 from sand substrates) by pushing a 10.5 cm diameter metal cylinder into the substrate to a depth of 10 cm. Within 24 hr I processed invertebrates by washing samples through a 0.43 mm soil sieve and preserving them in formalin. I summarized data as average monthly invertebrate densities for individual taxa and all groups combined.

I analyzed seasonal variation in shorebird community composition using Detrended Correspondence Analysis (DCA; Hill 1979), an ordination technique based on reciprocal averaging. DCA analyzes a community matrix consisting of samples (dates) and species (shorebirds) simultaneously to derive simplified axes that explain variation in the data. Census dates are assigned axis scores based on the presence of bird species. Therefore, dates with similar axis loadings have similar species composition, whereas dates with great differences in species composition are assigned very different axis scores (Gauch 1982). Because of detrending, DCA axes are measured in units of standard deviation of species turnover (Gauch 1982). Full turnover in species composition of samples (dates) occurs over 4 standard deviations; and a 50% change in species composition occurs in approximately 1 standard deviation (Gauch 1982). I used presence/absence data in the ordination in order to minimize the effect of dramatic changes in abundance attributable to tide and weather. In addition, I eliminated from the analysis several species (American Avocet, *Recurvirostra americana*; Willet, *Catoptrophorus semipalmatus*) because I observed them only once during the study. These rare species tend to distort ordination axes and make interpretation difficult (Gauch 1982). See Colwell and Oring (1988) for use of DCA in analysis of shorebird communities.

TABLE 1. Seasonal shorebird abundance ($\bar{x} \pm$ SD) in the Mad River, July 1990 through April 1991.

	Month				
Species	July	August	September	October	November
Black-necked Stilt	—	—	—	—	—
American Avocet	—	0.1 ± 0.3	—	—	—
Black-bellied Plover	—	0.3 ± 0.7	2.1 ± 3.2	3.0 ± 2.2	42.2 ± 103.7
Pacific Golden Plover	—	—	0.1 ± 0.3	—	—
Semipalmated Plover	1.5 ± 2.0	3.2 ± 4.3	3.9 ± 3.5	—	—
Killdeer	5.5 ± 3.6	7.3 ± 5.9	8.0 ± 4.8	9.7 ± 10.6	1.3 ± 2.3
Marbled Godwit	—	0.2 ± 0.4	0.4 ± 0.7	4.2 ± 3.5	0.1 ± 0.3
Whimbrel	0.3 ± 0.5	—	—	—	—
Long-billed Curlew	—	—	—	2.1 ± 6.3	0.2 ± 0.4
Greater Yellowlegs	0.7 ± 1.6	3.1 ± 3.5	1.8 ± 1.7	1.7 ± 0.7	1.5 ± 1.3
Lesser Yellowlegs	0.2 ± 0.4	0.1 ± 0.3	—	—	—
Willet	0.7 ± 1.6	—	—	—	—
Spotted Sandpiper	—	1.2 ± 1.4	0.7 ± 1.1	0.2 ± 0.4	—
Ruddy Turnstone	12.3 ± 12.4	5.4 ± 3.7	0.1 ± 0.3	—	—
Black Turnstone	0.2 ± 0.4	0.9 ± 1.2	0.4 ± 1.0	—	—
Red-necked Phalarope	—	—	0.2 ± 0.6	—	—
Common Snipe	—	—	0.2 ± 0.6	0.3 ± 0.7	—
Dowitcher spp.	7.3 ± 10.3	0.9 ± 1.3	2.4 ± 4.9	4.1 ± 6.1	0.1 ± 0.3
Sanderling	—	—	—	24.8 ± 41.7	2.4 ± 7.5
Western Sandpiper	18.2 ± 15.8	22.7 ± 20.9	18.1 ± 35.6	2.4 ± 4.4	53.4 ± 91.6
Least Sandpiper	65.5 ± 43.0	12.9 ± 10.6	16.7 ± 7.1	66.0 ± 45.0	21.6 ± 59.4
Dunlin	—	—	—	66.9 ± 135.3	527 ± 833
Censuses	6	9	10	9	11
Abund.	110 ± 37	58 ± 20	55 ± 38	185 ± 122	650 ± 1,015
S	6.2 ± 0.8	7.3 ± 1.3	6.8 ± 1.5	7.4 ± 1.1	3.8 ± 1.7

I used one-way ANOVA with months as treatments to evaluate seasonal variation in shorebird and invertebrate communities. I used stepwise multiple regression of transformed ($\log_{10}$) data to assess the contribution of environmental vari-
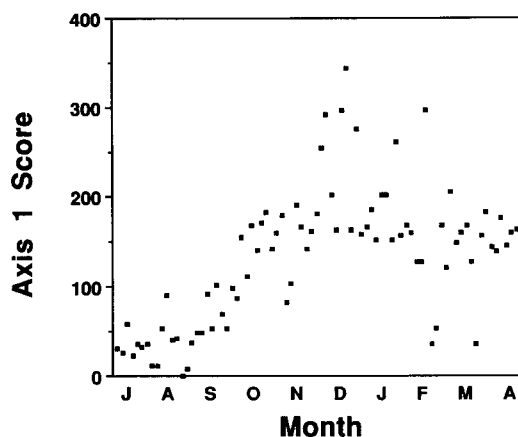

FIGURE 1. Seasonal turnover in shorebird species composition as portrayed by axis I scores of detrended correspondence analysis. Each datum represents the composite of species that were present on that date.

ables to variation in species richness, shorebird abundance, total shorebirds foraging, and species abundances. I excluded uncommon species (present less than 3 months and/or represented by a single individual) from regression analyses.

RESULTS

Shorebird community. I observed 23 shorebird species at Mad River during 10 months (Table 1), which comprise approximately two-thirds of shorebird taxa known to occur in the Humboldt Bay vicinity (Gerstenberg 1979; Colwell, unpubl. data). Species richness (Table 1) varied significantly ($F = 21.2$, df $= 9, 98$, $P < 0.0001$) during the study, ranging from 7.4 ± 1.1 in October to 0.5 ± 0.7 in February. Species richness peaked in summer and early autumn, declined during the winter and increased again in the spring. The average number of shorebirds using the Mad River study site also varied seasonally (Table 1; $F = 3.3$, df $= 9, 98$, $P < 0.002$). From July to October, average shorebird abundance varied between 55–185; monthly averages varied more thereafter (3–650).

The eigenvalue of the first ordination axis ac-

TABLE 1. Continued.

	Month			
December	January	February	March	April
0.1 ± 0.3	—	—	—	—
—	—	—	—	—
7.0 ± 14.3	1.5 ± 3.7	—	0.4 ± 1.2	7.6 ± 15.6
—	0.1 ± 0.3	—	—	—
—	—	—	—	—
2.4 ± 2.3	5.3 ± 12.2	0.5 ± 1.8	3.2 ± 6.9	0.8 ± 1.6
—	—	—	—	3.8 ± 5.5
—	—	—	—	2.1 ± 4.3
1.0 ± 3.2	—	—	—	0.1 ± 0.3
0.1 ± 0.3	1.3 ± 1.3	—	2.8 ± 3.7	2.2 ± 1.8
—	—	—	—	—
—	—	—	—	—
—	—	—	—	—
—	—	—	—	—
—	—	—	—	—
—	—	—	—	—
—	—	—	—	10.5 ± 15.7
2.2 ± 6.7	2.0 ± 5.3	0.6 ± 2.1	—	—
0.6 ± 1.7	0.3 ± 0.6	—	0.5 ± 1.2	7.7 ± 11.6
6.3 ± 13.8	28.7 ± 38.8	1.2 ± 2.3	15.1 ± 28.4	35.2 ± 31.2
43.0 ± 78.5	9.7 ± 14.5	0.1 ± 0.3	0.5 ± 0.8	4.0 ± 6.3
9	13	11	11	10
63 ± 110	49 ± 57	3 ± 4	23 ± 37	74 ± 51
1.6 ± 1.9	2.9 ± 2.5	0.5 ± 0.7	1.7 ± 1.9	5.0 ± 2.7

counted for 38% of the variation in the data set and spanned 3.4 standard deviations; the second axis explained 19% of variation and measured 2.9 standard deviations. Axis 1 scores plotted against date (Fig. 1) portrayed a 50% turnover in species composition between September and October (Table 1). At this time, several species (Whimbrel, *Numenius phaeopus*; Lesser Yellowlegs, *Tringa flavipes*; Ruddy Turnstone, *Arenaria interpres*; Black Turnstone, *A. melanocephala*) departed and several winter residents (Dunlin, *Calidris alpina*; Sanderling, *C. alba*; Long-billed Curlew, *Numenius americanus*) either arrived or first used the estuary. Killdeer (*Charadrius vociferus*), year-round residents in the Humboldt Bay area, used the estuary most during summer.

The manner in which shorebirds used the estuary also varied. Overall, shorebird use of aquatic habitats increased from July through March, whereas the percent of birds using cobble habitats decreased (Fig. 2). Species differed, however, in their use of terrestrial and aquatic habitats (Table 2). Plovers and turnstones used terrestrial habitats more than other shorebirds. The proportion of birds foraging in the estuary averaged

63–78% from July through October, whereas monthly averages were much more variable (range: 9–89%) thereafter (Fig. 3). During November large numbers of Dunlins, Least Sandpipers, and Western Sandpipers roosted in aquatic habitats.

Invertebrates. I identified five invertebrate taxa from core samples: two amphipods (*Corophium* spp.; *Eogammarus* spp.), an isopod (*Gnorimosphaeroma* spp.), polychaetes, and unidentified invertebrates. All invertebrate groups exhibited significant seasonal variation in abundance in both cobble and sand substrates (Table 3). For all groups except unidentified invertebrates, densities peaked in summer and early autumn, decreased between October and December, and either remained low (polychaetes; *Gnorimosphaeroma*) or increased (*Eogammarus*; *Corophium*) from January through April. Unidentified invertebrates were never abundant, nor did they exhibit very dramatic seasonal variation, but they increased in abundance in spring.

Invertebrate densities often differed between substrates (Table 3; *t*-test; df = 18; *P* < 0.05). During July and August *Corophium* and poly-
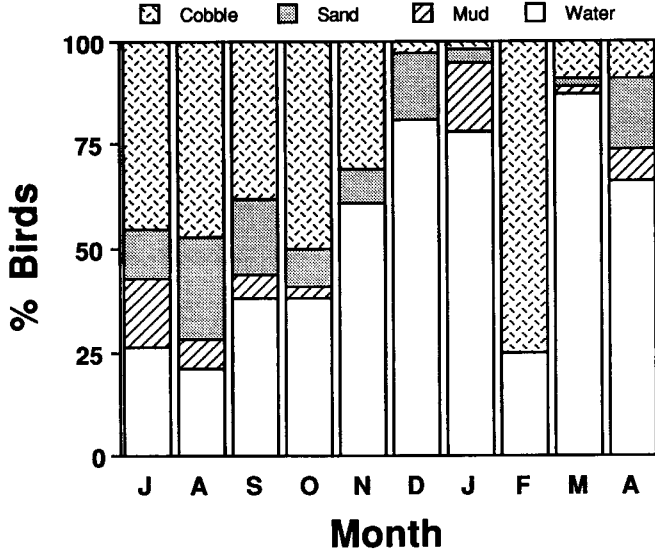
FIGURE 2.   Seasonal variation in shorebird habitat use ($\bar{x} \pm$ SD percent). Sample sizes given in Table 1.

chaete densities in sand exceeded those in cobble; densities of *Gnorimosphaeroma* in cobble exceeded those of sand from January through April.

Habitat availability. River discharge varied significantly ($F = 9.9$, df = 9, 98, $P < 0.0001$) among months (Fig. 4a). River volume remained low between July and November, but increased thereafter owing to increased precipitation. As a result average percent of exposed intertidal habitat (Fig. 4b) varied greatly ($F = 11.4$, df = 9, 98,

$P < 0.0001$), and was inversely associated with river volume ($r_s = -0.60$, df = 9, $P = 0.02$). From July through October, average exposed intertidal area ranged from 69–92%, whereas values ranged between 30–40% from November to April.

Environmental factors influencing shorebirds. I used stepwise regression to analyze the effects of environmental variables on shorebirds in two ways. First, I examined the impact of total in-
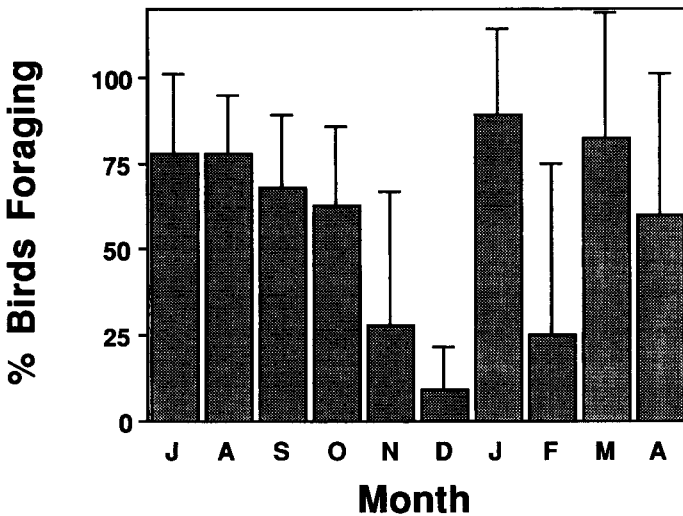

FIGURE 3.   Seasonal variation in percent shorebirds foraging ($\bar{x} \pm$ SD). Sample sizes given in Table 1.

TABLE 2. Interspecific differences in habitat use by shorebirds expressed as percent use of terrestrial and aquatic habitats.

Species	Habitat				
	Cobble	Sand	Mud	Water	n
Black-necked Stilt	0.0	0.0	0.0	100.0	2
American Avocet	0.0	0.0	0.0	100.0	1
Black-bellied Plover	7.3	24.4	0.2	68.2	606
Pacific Golden Plover	0.0	0.0	0.0	100.0	1
Semipalmated Plover	43.2	44.6	1.4	10.8	74
Killdeer	49.8	14.6	11.4	24.3	412
Marbled Godwit	0.0	2.7	0.0	97.3	73
Whimbrel	0.0	0.0	0.0	100.0	23
Long-billed Curlew	3.1	0.0	0.0	96.9	32
Greater Yellowlegs	1.4	1.4	0.7	96.5	141
Lesser Yellowlegs	0.0	0.0	0.0	100.0	2
Willet	0.0	0.0	0.0	100.0	1
Spotted Sandpiper	66.7	16.7	5.6	11.1	18
Ruddy Turnstone	94.4	3.7	0.0	1.9	107
Black Turnstone	69.2	23.1	0.0	7.7	13
Red-necked Phalarope	0.0	0.0	0.0	100.0	2
Common Snipe	0.0	0.0	60.0	40.0	5
Dowitcher spp.	0.9	0.5	2.4	96.2	213
Sanderling	47.0	12.9	0.0	40.1	202
Western Sandpiper	17.0	32.3	0.5	50.2	971
Least Sandpiper	33.1	17.5	10.1	39.2	2,412
Dunlin	0.4	14.3	0.1	85.2	5,954

vertebrate abundance, river discharge and exposed intertidal habitat on variation in the shorebird community using data from monthly averages ($n = 10$). Second, based on seasonal dynamics of the estuary (Fig. 4) and changes in the shorebird community (Fig. 1), I divided the study period into two intervals, July–October ($n = 33$) and November–April ($n = 64$). I then examined the impact of exposed habitat and river discharge on short-term temporal (date) variation in species richness and shorebird abundance, excluding food because it was only measured monthly.

Analysis of monthly data (Table 4) indicated that exposed habitat explained significant variation (48–75%) in the abundance of five species (Semipalmated Plover, Killdeer, Spotted Sandpiper, Ruddy Turnstone, and Black Turnstone). In all cases, these species were more abundant during summer months when more exposed habitat existed. Exposed habitat also explained significant variation in species richness ($P = 0.03$); highest species richness coincided with periods of greatest exposed intertidal substrate. None of the independent variables explained monthly variation in shorebird abundance. Percent of shorebirds foraging correlated positively with to-

tal invertebrate abundance ($r_s = 0.75$, $n = 10$, $P = 0.012$).

Food explained 46% and 48% of variation in Black-bellied Plover and Dunlin abundances, respectively. Unexpectedly, however, the abundance of both species was highest when food availability was lowest. Finally, river volume contributed significantly to the model explaining variation in Western Sandpiper abundance ($P = 0.05$); abundance was greater with lower river volume.

Exposed habitat and river discharge explained little of the daily variation in species richness and shorebird abundance (Table 5). During the November–April period, exposed habitat explained significant, but only a small proportion (10%) of variation in species richness. Between July and October, exposed habitat explained 15% of variation in shorebird abundance.

DISCUSSION

Nonbreeding shorebird communities are highly dynamic assemblages influenced by numerous environmental factors (e.g., temporal, weather and tidal variables; Burger 1984), which interact to constrain the availability of food resources. These environmental factors influence species by

TABLE 3. Seasonal variation in invertebrate abundance ($\bar{x}$ ± SD) associated with cobble and sand substrates.

Species	Substrate	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr
Corophium	Cobble	47 ± 48	46 ± 47	149 ± 80	173 ± 35	0 ± 0	1 ± 1	363 ± 197	140 ± 90	125 ± 65	162 ± 24
	Sand	203 ± 42	352 ± 132	171 ± 58	10 ± 10	1 ± 2	1 ± 1	193 ± 42	107 ± 26	151 ± 67	189 ± 25
Eogammarus	Cobble	0 ± 0	0 ± 0	20 ± 19	7 ± 11	0 ± 0	0 ± 0	14 ± 18	36 ± 37	2 ± 3	1 ± 1
	Sand	12 ± 30	6 ± 16	41 ± 40	2 ± 4	0 ± 0	0 ± 0	2 ± 2	3 ± 4	1 ± 1	0 ± 0
Gnorimosphaeroma	Cobble	35 ± 13	28 ± 27	74 ± 32	144 ± 59	4 ± 4	1 ± 0	7 ± 7	22 ± 16	14 ± 9	14 ± 9
	Sand	25 ± 54	22 ± 20	58 ± 43	1 ± 1	1 ± 1	0 ± 0	0 ± 0	1 ± 1	1 ± 1	1 ± 1
Polychaetes	Cobble	30 ± 18	4 ± 7	18 ± 6	4 ± 3	0 ± 0	0 ± 0	1 ± 0	1 ± 1	1 ± 1	1 ± 1
	Sand	26 ± 9	35 ± 15	20 ± 7	1 ± 1	0 ± 0	0 ± 0	0 ± 0	1 ± 1	1 ± 1	1 ± 1
Other	Cobble	1 ± 3	4 ± 3	0 ± 0	0 ± 0	1 ± 1	0 ± 0	2 ± 3	2 ± 2	17 ± 9	5 ± 3
	Sand	5 ± 4	0 ± 0	1 ± 1	1 ± 1	2 ± 1	1 ± 1	0 ± 0	1 ± 1	6 ± 6	1 ± 1
Total		196 ± 109	248 ± 202	275 ± 101	170 ± 170	4 ± 3	1 ± 1	290 ± 162	156 ± 103	158 ± 68	185 ± 28

shaping space use and activity patterns of coastal shorebirds, which influence the distribution and abundance of species.

Temporal variation. Temporal factors influence shorebirds in two general ways. First, it has been argued (Evans 1988) that seasonal variation in food availability has influenced the timing of energetically demanding segments of a species' annual cycle. This argument relies on food as an ultimate factor explaining the evolution of molt and migration patterns. Second, temporal variation in food availability operates as a proximate ecological factor influencing space use and daily activity patterns (Evans 1979, Puttick 1984).

The dynamic nature of the shorebird community of the Mad River estuary results from an interaction between seasonal and daily changes in species richness and relative abundances. Species composition exhibited a 50% turnover between October and November (Fig. 1) and the abundance of most species changed abruptly at this time (Table 1). Some of the variation in species abundances is associated with the phenology of migration (e.g., Dunlin arrive in October after completing prebasic molt). However, the winter absence of some species from the estuary (e.g., Semipalmated Plover, Black Turnstone) requires other explanations because these species occurred in other habitats (mudflats of Humboldt Bay, sand beaches and agricultural lands) within 1–10 km of the Mad River estuary throughout the winter (Colwell, unpubl. data).

Activity patterns of shorebirds vary diurnally, but mostly in association with tides (Evans 1979, Puttick 1984). Thus, time of day may influence shorebird community patterns (Burger 1984). In Burger's (1984) analysis, the effect of time of day on shorebird abundance varied between tidal and non-tidal habitats. In freshwater ponds adjacent to Jamaica Bay, New York shorebird numbers peaked at mid-day when birds roosted. On tidal flats, however, time of day did not significantly affect variability in shorebird abundance. I did not evaluate the influence of time of day. Instead, I attempted to minimize this effect by standardizing observation time.

Abiotic factors. Tidal variation constitutes the most important and predictable environmental factor influencing nonbreeding shorebirds in coastal environments. Tides influence the behavior and activity patterns of many coastal species (e.g., Sanderling; Connors et al. 1981) by altering the amount of available foraging habitat.
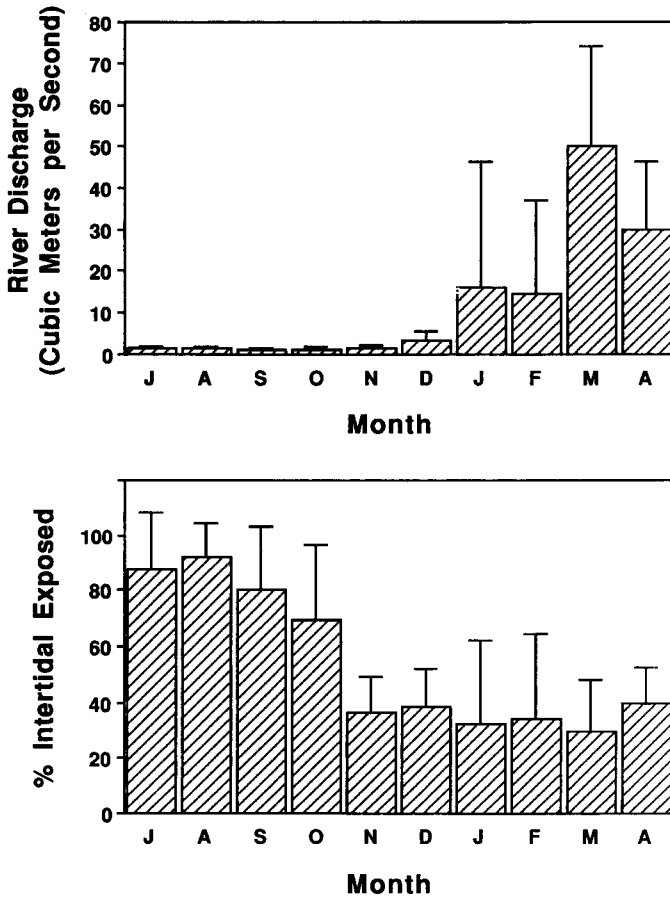
FIGURE 4.   Seasonal variation ($\bar{x} \pm$ SD) in river discharge and exposed intertidal habitat of the Mad River estuary, July 1990 through April 1991. Sample sizes given in Table 1.

Shorebirds typically move between habitats in response to changes in the amount of available habitat. Tidal variables strongly influenced patterns of shorebird assemblages in both tidal and adjacent, non-tidal habitats (Burger 1984).

Within the Mad River estuary, exposed intertidal habitat, which was inversely correlated with river discharge, explained significant variation in shorebird community patterns and the abundance of individual species (Table 4). In analyses of monthly data, exposed habitat explained 48% of variation in species richness, which was highest during periods of greatest exposed intertidal habitat. However, exposed habitat contributed little to understanding variation in total shorebird abundance. For individual species, exposed habitat explained 48–75% of variation in abundance of five species (Semipalmated Plover, Killdeer, Spotted Sandpiper, Ruddy Turnstone and

Black Turnstone). These species are characterized by extensive use of exposed substrates and minimal use of flooded habitats (Table 2). At least two of these species (Semipalmated Plover and Ruddy Turnstone) have been characterized as being strongly influenced by tides (Burger 1984). The lack of relationship between environmental variables and the abundance of most other species occupying the Mad River estuary is noteworthy given the observations of others (see review in Burger 1984) associating shorebird abundance with tidal factors.

In analyses of daily data, exposed habitat explained less variation in community patterns, despite the fact that I divided analyses into low- and high-flow conditions in the river associated with different shorebird assemblages (Fig. 1). Overall, I suspect that community patterns are poorly explained by abiotic variables because

TABLE 4. Results of stepwise multiple regression analyses examining the contribution (partial R^2) of invertebrate abundance, river volume and exposed intertidal habitat to species abundances, species richness and total shorebird abundance.

Species	Partial R^2			F	P
	Food	River volume	Exposed habitat		
Black-bellied Plover	0.46	—[a]	—	6.90	0.03
Semipalmated Plover	—	—	0.75	24.13	0.001
Killdeer	—	—	0.48	7.46	0.03
Long-billed Curlew	0.15	0.08	—	1.38	0.27
Greater Yellowlegs	0.19	—	—	1.91	0.20
Spotted Sandpiper	—	—	0.55	9.84	0.01
Ruddy Turnstone	0.08	0.04	0.62	12.96	0.007
Black Turnstone	—	—	0.69	17.96	0.003
Dowitcher spp.	0.06	—	0.25	2.67	0.14
Sanderling	0.11	0.09	0.28	0.83	0.40
Western Sandpiper	—	0.40	—	5.40	0.05
Least Sandpiper	—	—	0.12	1.14	0.32
Dunlin	0.48	—	—	7.41	0.03
Species richness	—	—	0.48	7.46	0.03
Shorebird abundance	0.09	—	—	0.83	0.39
Average birds foraging	—	—	0.21	2.13	0.18

[a] Indicates contribution of variable exceeded 0.50 significance criterion for entry into regression model.

species or groups of ecologically similar taxa used the estuary differently (Table 2) and many taxa probably respond independently to habitat and food availability within the estuary.

In addition to tides, other abiotic factors are known to influence the ecology of nonbreeding shorebirds. Weather acts as a proximate factor influencing habitat and food availability of some species (Evans 1976). Low temperatures and high wind velocity reduce prey availability, which influences the distribution and abundance of shorebirds (Evans 1976, Burger 1984). I did not assess the impact of weather directly on shorebirds by measuring wind velocity, precipitation, etc. River volume, however, represents an indirect effect of weather because it varies seasonally with precipitation.

Prey abundance and availability. Spatial and temporal variation in the abundance of non-breeding shorebirds is strongly associated with variation in their food resources (Colwell and Landrum 1993). During the annual cycle, Mad River shorebirds experienced fluctuations in prey populations similar to shorebirds wintering at northern latitudes (Evans 1988). Prey abundance peaked during summer, declined in late fall and increased during late winter and spring (Table 3). *Corophium,* a burrowing amphipod known to be an important prey species of many shorebirds (see Colwell and Landrum 1993), exhibited the most dramatic seasonal fluctuations in abundance. Although *Corophium* increased and remained abundant between January and April, their availability as prey to shorebirds was probably reduced owing to rising river levels.

Abiotic factors act to constrain the availability

TABLE 5. Results of stepwise regression analysis examining the contribution (partial R^2) of river discharge and exposed intertidal habitat to seasonal variation in shorebird species richness and abundance.

	July–October			November–April		
	R^2	F	P	R^2	F	P
Species richness						
Exposed habitat	0.04	1.1	0.31	0.10	7.0	0.01
River discharge	0.03			—[a]		
Shorebird abundance						
Exposed habitat	0.15	5.6	0.02	0.04	2.5	0.12
River discharge	0.02			0.02		

[a] Indicates contribution of variable exceeded 0.50 significance criterion for entry into regression model.

of these resources by reducing access to prey by birds. In the Mad River, seasonal invertebrate abundance (a measure of food resources) varied substantially, with lowest densities occurring during winter months of low habitat availability. Shorebirds foraged extensively in the Mad River estuary during low-flow periods, but the percent of shorebirds foraging declined and varied greatly during high-flow periods. A positive correlation between food and percent birds foraging suggests that shorebird use of the estuary was linked to food resources. In general, months with lower invertebrate abundance, less exposed habitat, and higher river volume coincided with a lower proportion of birds foraging. However, food abundance either explained little variation in community patterns or it was inversely associated with shorebird abundance (Dunlin and Black-bellied Plover). The results of this study support the contention (Recher 1966) that the amount of intertidal habitat (which is related to food availability) is the most important variable influencing nonbreeding shorebird abundance.

Unlike large coastal bays, where predictable tidal regimes exert strong abiotic impacts on the availability of habitat and food resources, the Mad River estuary is influenced by tides and marked seasonal variation in precipitation and river runoff. Even during drought conditions of recent times, winter rains are sufficient to cause dramatic changes in estuary habitats. During extreme weather, however, river discharges may exceed 2,000 m³/sec. Consequently, an abrupt change in the estuary occurs with the onset of winter rains which increases river discharge (Fig. 4). As a result, the availability of intertidal habitats for foraging shorebirds varies inversely with river volume.

Shorebird communities varied in the Mad River in association with seasonal dynamics of the estuary. Data suggest that shorebirds relied less on the estuary as a feeding site as the study progressed and the site became less predictable. In the Humboldt Bay area shorebird use of agricultural lands increases during winter when rains develop (Hoff 1979). At this time access to foraging sites within the estuary is constrained, but adjacent agricultural lands also become more profitable for foraging (Colwell, unpubl. data).

Unlike shorebirds occupying other coastal areas, Mad River shorebirds must contend with lower food availability owing to seasonal changes in river volume in combination with tidal fluc-

tuations. Compared with large bays, habitats within estuaries such as the Mad River offer less predictable resources to nonbreeding shorebirds owing to marked seasonal variation in river discharge associated with precipitation. I suspect that shorebirds using these dynamic estuaries exhibit different patterns of space use compared with birds occupying more stable estuaries.

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