PART 1:

DISTRIBUTION, MIGRATION, AND CONSERVATION

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ASPECTS OF THE OCCURRENCE OF SHOREBIRDS ON A CENTRAL CALIFORNIA ESTUARY

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ABSTRACT.—All shorebirds on Bolinas Lagoon in central California were censused every other five-day period from June 1971 to May 1976. These censuses, together with observations of molting birds, revealed that shorebird occurrence on Bolinas Lagoon fits four general patterns: (1) occurring only during fall migration, departing prior to the prebasic molt, and usually occurring again during spring migration; (2) arriving early in fall, undergoing prebasic molt, and wintering; (3) arriving late in the fall after the prebasic molt is mostly completed and overwintering; and (4) breeding, overwintering, and probably molting on Bolinas Lagoon. In densities, smaller species outnumbered larger species but contributed less to total shorebird biomass on the estuary. Considerable annual variation in numbers was observed in some species but not in others.

Censuses of salt marsh and tidal flat habitats revealed considerable variation among species in use of different areas within Bolinas Lagoon. The salt marsh was most important as a roosting area although a few species also fed there. Most species used the tidal flat as their main feeding area. Different species segregated onto tidal flats of different substrate types, and tidal flats of intermediate substrate texture supported the highest densities and widest variety of birds. Extralimital habitats, such as open coast adjacent to Bolinas Lagoon and pastureland on the Bolinas mesa, were also used by certain shorebirds indicating the importance of habitats outside the estuary in support of local shorebird populations. Comparisons of shorebird densities between Bolinas Lagoon and Limantour Estero revealed that densities for given species often varied considerably between estuaries only a few kilometers apart. Some of this variation appeared to be due to obvious habitat differences, but often the variation could not be explained.

Some problems of interpreting shorebird census data are discussed, and factors affecting numbers and kinds of shorebirds occurring in coastal wetlands are mentioned. It is suggested that, due to variability in densities of shorebirds supported by different wetland habitats, destruction of an entire system or even a part of one may result in habitat loss for some species that may not be compensated for by remaining habitat. An example is presented illustrating that some wetland areas do not support wintering shorebirds independently but, instead, as parts of larger integrated wetland systems.

Conservation and management of California's remaining coastal wetlands requires an understanding of the variation in the numbers and kinds of wildlife supported by different wetland areas. This understanding should begin with a knowledge of the relative abundance throughout the year of each species using each area, the amount of natural variation that can be expected between different years in numbers, and the ways areas differ in meeting the needs of each species. Several studies based on censuses of birds in coastal wetland habitat have generated a good deal of information on the number of birds using specific areas during different times of the year, and when looked at together provide valuable information on the importance of different coastal areas to many species (Storer 1951, Smail and Lenna 1969, Bollman et al. 1970, Gerdes 1970, Gerstenberg 1972, Gill 1972, Jurek 1973). The interpretations that can be made from these studies are limited, however, because in most cases censuses were only conducted for one year and because most study sites were part of larger wetland areas, making it difficult to distinguish between fluctuations in the numbers of birds at the study sites caused by local movements of the birds and fluctuations caused by changes in seasonal abundance.

Between 1971 and 1976 we regularly censused shorebirds on Bolinas Lagoon, an estuary at the south end of Point Reyes National Seashore in California.

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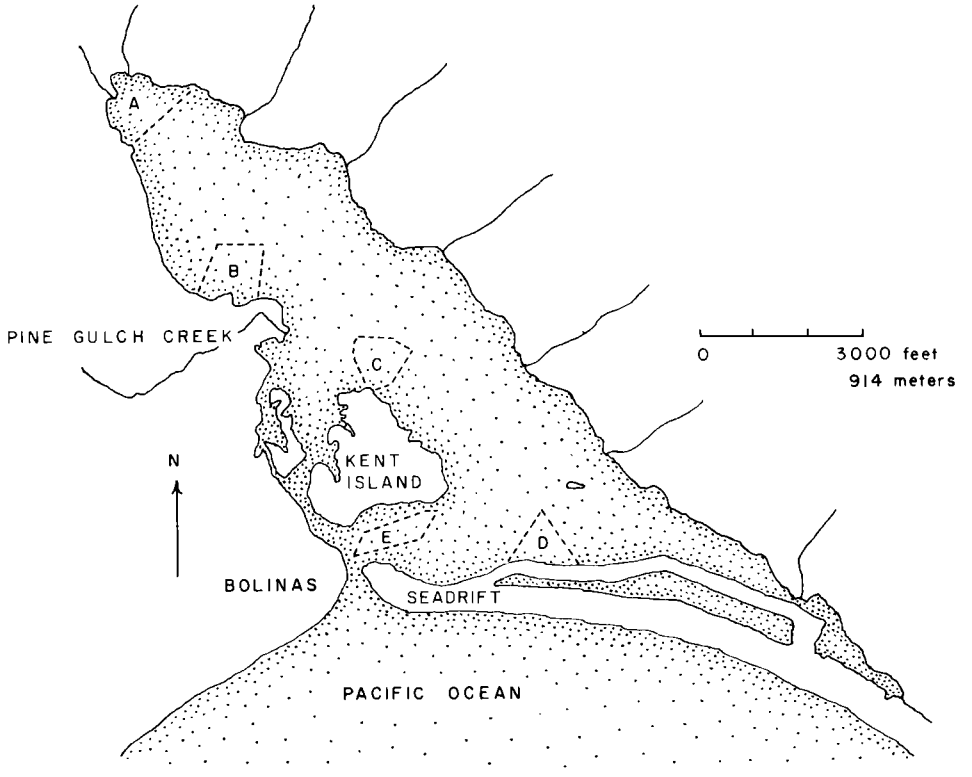

FIGURE 1. Sketch of Bolinas Lagoon. Areas A (12.6 ha), B (9.8 ha), C (8.0 ha), D (7.0 ha), and E (8.4 ha) are the five areas of tidal flat censused.

Several features of Bolinas Lagoon allowed us to obtain more precise census data than has been possible in most other shorebird census studies and, therefore, to make some interpretations different from those made in other studies. Bolinas Lagoon is small enough to be censused by three parties in three hours yet large enough to regularly hold from 3000 to 7000 shorebirds of at least 18 species. It is relatively isolated from other wetlands so that, for most species, census results do not reflect large fluctuations due to local movements of the birds. Finally, Bolinas Lagoon was quarantined against human use throughout the study and, consequently, received minimal human disturbance. We were able to graph the seasonal abundance patterns for most species, to compare the annual abundance over five years for each species, to examine variation in shorebird densities and biomass between different sub-areas of Bolinas Lagoon, and to compare bird densities between Bolinas Lagoon and Limantour Estero, a nearby estuary.

STUDY AREA AND METHODS

Bolinas Lagoon is a small shallow estuary 24 km northwest of San Francisco, California. High hills, marshy pastures and the Seadrift sand spit surround this wedge-shaped estuary except for a narrow opening to the ocean on the southwest side (Fig. 1). Pine Gulch Creek drains into it year round and is the main source of the estuary's fresh water. Kent Island is a 40-ha island within the estuary. A large part of Kent Island and the Pine Gulch Creek delta are salt marsh where the chief plant species

are *Salicornia virginica* and *Spartina foliosa*. At mean low water about 70% of Bolinas Lagoon comprises tidal flats which are divided by several channels (Ritter 1969).

We censused all shorebirds on Bolinas Lagoon during alternate five-day periods, except in June some years, from June 1971 to May 1976. Censuses were taken on rising tides, or falling tides if rising tides were not available, at 1.1–1.7 m above mean low water. During a census the estuary was divided into three areas and a team of observers in each area counted or estimated all shorebirds in that area. The counts in the areas were made simultaneously. Dowitchers were not identified to species on censuses but were sometimes identified between censuses. Some censuses included numbers of small sandpipers that could not be separately identified as Dunlin (*Calidris alpina*), Least Sandpiper (*Calidris minutilla*), or Western Sandpiper (*Calidris mauri*) but on no census did such observations exceed 20% of the identified small sandpipers. The unidentified sandpipers were incorporated into a census total as Dunlins, Least Sandpipers, and Western Sandpipers according to the relative abundance of firm identifications of these species on the census. Sometimes we counted rare or uncommon species prior or subsequent to a census, but within the five-day census period, because these birds were easily overlooked on the regular census. Because Snowy Plovers (*Charadrius alexandrinus*) are present year round but are difficult to find when their roosting area has been disturbed, we ignored zero values for this species in all calculations.

Additional censuses of specific areas on or near Bolinas Lagoon were also made to find out which were most used by the birds. During 1973 and 1974 we censused shorebirds in the salt marsh on Kent Island at low and moderate tides several times a month and on 8.5 km of open coast (comprising sand to pebble beaches and soft shale reef) adjacent to and north of Bolinas Lagoon three times a month. During the winters of 1972–73 and 1973–74 at high tide we frequently censused shorebirds on closely-cropped pastures about 2 km west of Bolinas Lagoon.

We selected five areas within the tidal flat of the estuary (Fig. 1) for intensive censusing in 1973 and 1974. The substrate of area A was very poorly sorted, very fine sand (Ritter 1969) containing considerable organic debris such as twigs and leaves. Much of the high-water zone of this area was covered by a layer of sediment which dried and cracked into leathery plates when exposed to air for long periods. The high-water zone abutted a small salt marsh through which a freshwater stream ran year round; the low-water zone bordered a basin. Area B was similar to area A except that a freshwater stream ran into it only during periods of heavy rain and the substrate ranged from fine to medium sand (Ritter 1969). The substrate of area C was a well to moderately sorted fine sand (Ritter 1969) and lacked the terrestrially derived organic debris of areas A and B. Unlike areas A and B the high-water zone of area C was pock-marked with the burrow openings of the ghost shrimp (*Callianassa californiensis*) and was not covered by hard dried plates of sediment. The high-water zone of area C abutted the Kent Island salt marsh on one side and a channel on the other; the low-water zone bordered a small basin. Area D had a substrate of moderately sorted fine sand (Ritter 1969) and was bordered on two sides by channels and on a third by a basin. The high-water zone in the center was less burrowed than area C. Area E differed markedly from the other areas. It comprised sediment ranging from medium sand through pebble. The pebble fraction contained numerous shell fragments and was largely in the low-water zone. The high-water zone was separated from the Kent Island sand beach by a shallow channel; the low-water zone bordered a main channel.

In each of the five areas 10 censuses in which feeding and non-feeding birds were counted were made each month during the 1973–74 season. Each month we tried to census on all combinations of high, moderate, and low water with ebb tides, flood tides and slack water. We tried to take censuses for a particular tidal condition in all areas on the same day.

To fit our census data with the shorebird's annual cycles we defined one "season" as lasting from June to the end of May the following year. A fall period is defined as July through October; a winter period as November through February; a spring period as March through May; and a summer period as the month of June. The fall period, characterized by relatively warm dry weather at Bolinas, is when most of the autumn shorebird migration occurs. The winter period normally corresponds with most of the rainy weather and a minimal amount of shorebird migration compared to fall and spring. The spring period heralds the return of warmer, drier weather to Bolinas and encompasses most of spring migration. During June most shorebirds have left the area for breeding grounds elsewhere and the number of birds in the area is at the seasonal low.

Mean weights were calculated from at least 30 weights for each species from birds trapped on Bolinas Lagoon or elsewhere in North America, from museum specimens, and from Johnston and McFarlane (1967), Easterla (1969), and Hamilton (1975). The mean number of birds of each species

TABLE 1
SEASONAL USE PATTERNS OF SHOREBIRDS ON BOLINAS LAGOON

1 Early arriving migrants	2 Early arriving, wintering	3 Late arriving, wintering	4 Breeding and wintering
Semipalmated Plover	Blacked-bellied Plover[a]	American Avocet	Killdeer
		Common Snipe	Snowy Plover
Ruddy Turnstone	Black Turnstone	Long-billed Dowitcher	
Whimbrel[a]	Marbled Godwit[a]	Dunlin	
Short-billed Dowitcher	Long-billed Curlew		
Red Knot	Greater Yellowlegs		
Western Sandpiper	Willet		
Baird's Sandpiper	Long-billed Dowitcher		
Pectoral Sandpiper	Sanderling		
Northern Phalarope	Least Sandpiper		

[a] Species for which evidence that adults migrate before juveniles in the fall comes from Bent (1927 or 1929).

on all censuses was calculated for each period. These means were multiplied by the mean weights to give the mean biomass of each species on Bolinas Lagoon in each period.

During fall periods we trapped small sandpipers (Page 1974a, b; Page et al. 1972) and made field observations of other species to determine when adults and juveniles first arrived and which species molted remiges at Bolinas Lagoon. We were able to separate the age classes of most species when they arrived in fall.

Between 1965 and 1976 personnel of Point Reyes Bird Observatory censused shorebirds at Limantour Estero, a small shallow estuary on Point Reyes, 21 km northwest of Bolinas Lagoon. Censuses at Limantour were less regular in relation to timing and tidal conditions than at Bolinas Lagoon. Limantour censuses included the major part but not the total amount of available shorebird habitat; a long arm of the estero near the mouth was omitted.

SEASONAL ABUNDANCE

Seasonal abundance patterns for regularly occurring shorebirds are illustrated for Bolinas Lagoon in Figures 2–4. From the abundance patterns and observations on the molt of birds four general strategies of shorebird use of the estuary were detected.

Strategy 1 used by nine species (Table 1) was to arrive early in fall and pass through Bolinas Lagoon before most of the adult and usually juvenile prebasic molt had been completed. Adult birds arrived prior to juveniles (Table 2). Wintering individuals occurred in small numbers or were absent but migrants of most species were relatively abundant in spring. A portion of the prealternate molt in some individuals of some species took place during spring migration at Bolinas Lagoon but this was not closely examined by us. The importance of Bolinas Lagoon to birds using this strategy was the support it provided to migratory staging birds; support during molt and during winter came largely from other areas.

Some variation within pattern 1 was exhibited by the Baird's Sandpiper (*Calidris bairdii*), the Pectoral Sandpiper (*Calidris melanotos*), and the Northern Phalarope (*Lobipes lobatus*) (Fig. 2). Adult Baird's and Pectoral sandpipers occurred rarely on fall migration so that juveniles made up almost all the birds observed

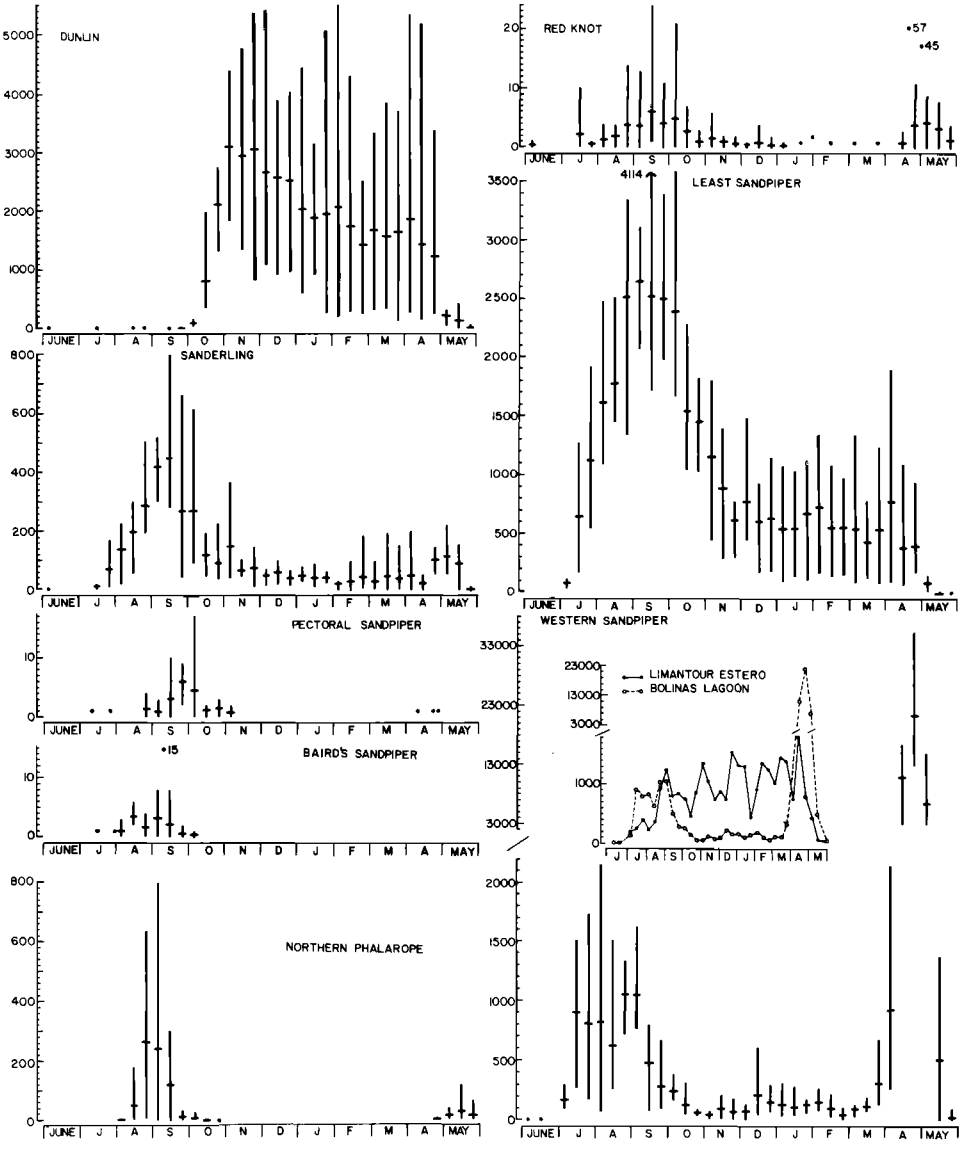

FIGURE 2. Seasonal abundance patterns of calidridine sandpipers and the Northern Phalarope on Bolinas Lagoon. Lines define extremes of high and low numbers observed in 10-day intervals over five years; horizontal lines indicate means. A dot indicates a single observation within a 5-day period, or an unusually high number of birds between census periods.

on Bolinas Lagoon; Baird's and Pectoral Sandpipers were very rare or absent in spring. The Northern Phalarope was the only species for which adult-before-juvenile migration in fall has not been reported in the North American literature or observed in our study, although such differential timing very likely occurs in California (D. W. Winkler pers. comm.). Juveniles greatly outnumbered adults in fall at Bolinas Lagoon and made up 93% of the 111 Northern Phalaropes banded there between 14 August and 19 September 1971. Most adults staged

TABLE 2
ARRIVAL DATES FOR ADULT AND JUVENILE SHOREBIRDS AT BOLINAS LAGOON

Species	Adult		Juvenile	
	First 1972	Usual	First 1972	First 1973
Semipalmated Plover	3 July	30 June–19 July	15 Aug	1 Aug
Ruddy Turnstone	17 July	5 July–19 July	17 Aug	15 Aug
Black Turnstone	5 July	30 June–9 July	20 Aug	no data
Greater Yellowlegs	17 July	5 July–9 July	18 Aug	12 Aug
Willet	no data	15 June–24 June	15 July	17 July
Short-billed Dowitcher	3 July	30 June–14 July	10 Aug	6 Aug
Red Knot	15 July	15 July–29 July	26 Aug	no data
Sanderling	17 July	10 July–19 July	31 Aug	21 Aug
Western Sandpiper	3 July	30 June–4 July	7 Aug	2 Aug
Least Sandpiper	3 July	30 June–4 July	10 Aug	30 July
Baird's Sandpiper	1 probable 15 July		9 Aug	30 July
Pectoral Sandpiper	1 on 13 July 1971, 21 and 25 July 1972		11 Sep	13 Sep

elsewhere making it difficult to detect temporal differences in migration between the two age groups. During spring migration Northern Phalaropes made sporadic appearances at Bolinas Lagoon, occurring in some years but not in others.

A second use pattern exhibited by nine species (Table 1), was characterized by the early fall arrival of migrating or wintering birds, adult-before-juvenile fall arrival, and a prebasic molt largely completed on Bolinas Lagoon. Some prealternate molt also took place on the estuary. Considerable variation occurred among these species in the size of the spring and fall migratory peaks. For most species of this group the estuary supported migratory staging individuals but, unlike the first group, it also supported numbers of molting and overwintering birds. Although relatively few Sanderlings (*Calidris alba*) occurred in winter compared to fall, this species is included with this group because many adults underwent much of their prebasic molt on the estuary. Many Sanderlings and Least Sandpipers (Page 1974b) probably left the area near or after completion of their prebasic molt (Fig. 2).

Short-billed Dowitcher (*Limnodromus griseus*) and Long-billed Dowitcher (*Limnodromus scolopaceus*) abundance patterns (Fig. 3) merit some discussion because of the difficulty of identifying the two species during censuses. Many observations between censuses using call notes and morphological characters to

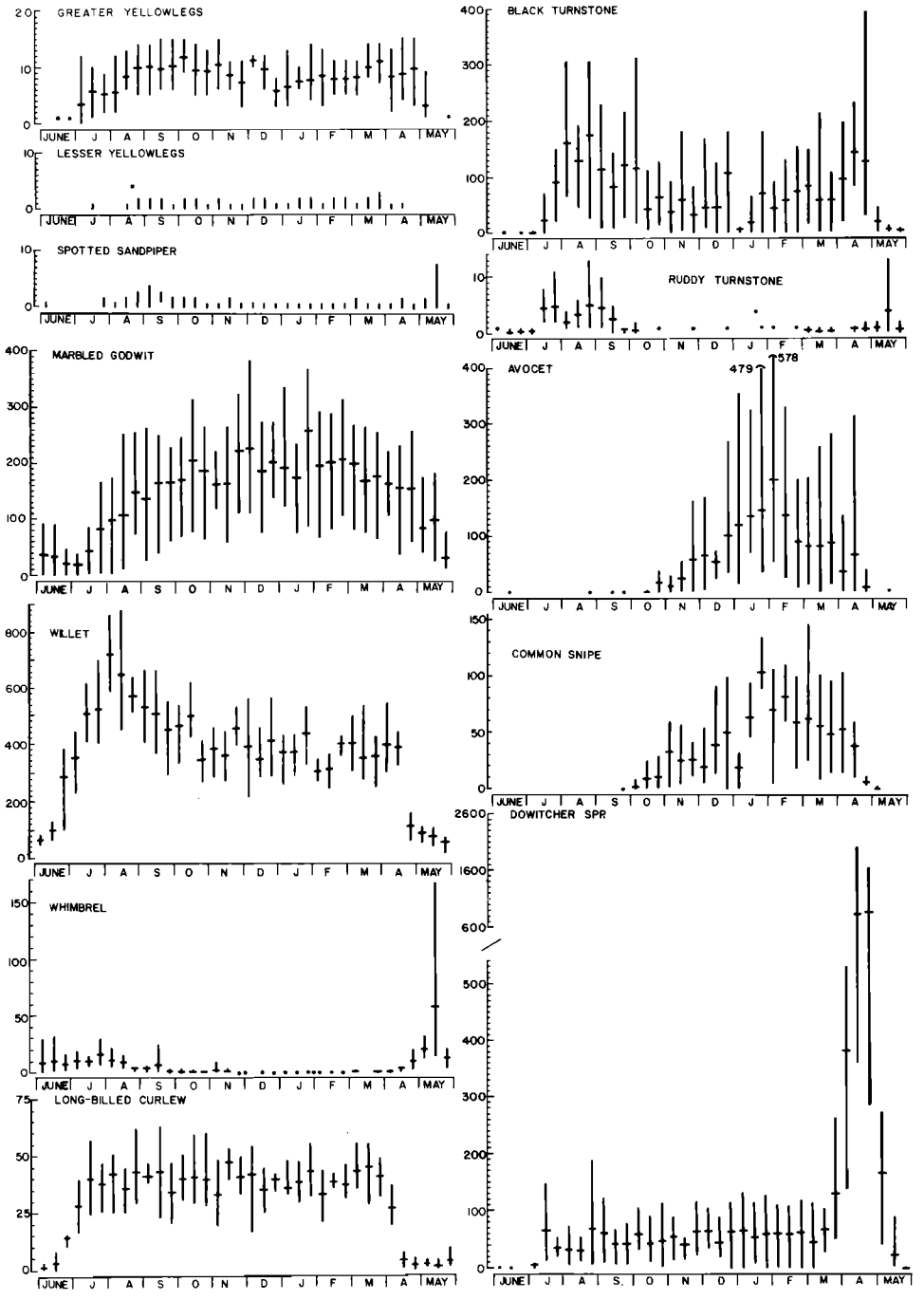

FIGURE 3. Seasonal abundance patterns of tringine sandpipers, curlews, turnstones, dowitchers, Common Snipe and Avocet. See Figure 2 for explanation.

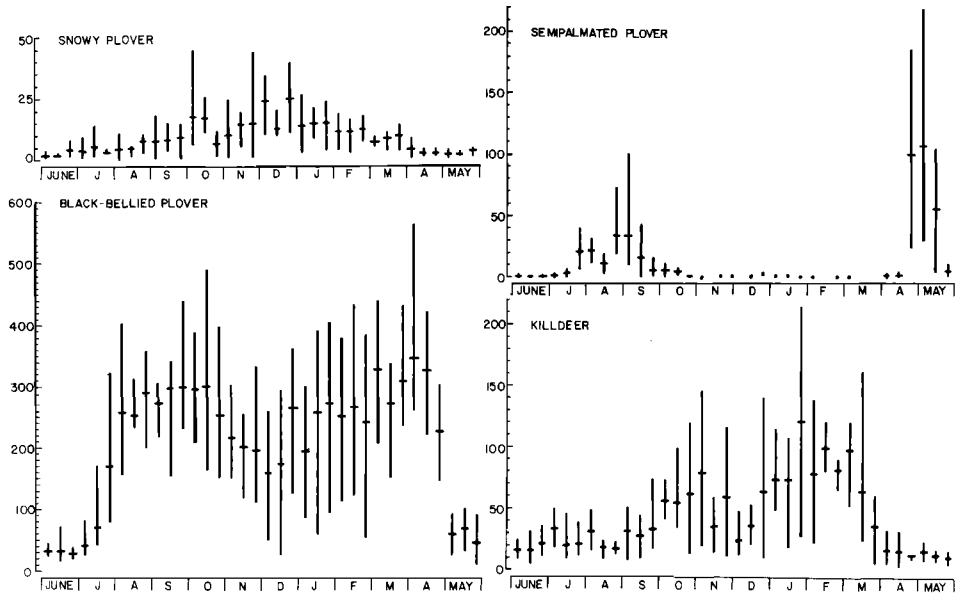

FIGURE 4. Seasonal abundance patterns of common plovers. See Figure 2 for explanation.

identify birds indicated that most dowitchers on Bolinas Lagoon from July through mid-September were short-bills and almost all birds between November and February were long-bills; the majority of dowitchers in April were short-bills. These plus other observations on molt confirmed that the Short-billed Dowitcher fits well into the first use pattern. During the 1975–76 season we found the first Long-billed Dowitchers on 31 July. These two individuals, and subsequent ones that appeared until the number had increased to nine birds, were adults that were all molting primaries on 26 August. The first immatures were identified in late September although they may have arrived earlier that month. That year about 75 Long-billed Dowitchers occurred during winter (November through February). Pitelka (1950) and Lenna (1969) reported that immature long-bills are more likely to be found than adults in coastal habitats, and Lenna (1969) observed that in the Point Reyes area, of which Bolinas Lagoon is a part, the species usually does not appear in fall until late September or early October. Probably in all years immatures form the bulk of long-bills wintering at Bolinas Lagoon; in some years the early arriving adults may not be present. More remains to be learned about Long-billed Dowitcher migration patterns at Bolinas Lagoon. We have tentatively placed it in two groups in Table 1 until further information becomes available.

Four species are listed under the third occurrence pattern (Table 1), including the Long-billed Dowitcher already discussed. The remaining three species arrive late in the fall (Figs. 2–3). Adult and juvenile Dunlins arrived simultaneously although at first juveniles heavily outnumbered adults in trapped samples (Page 1974a). Information on arrival times of adult and juvenile Common Snipes (*Capella gallinago*) and American Avocets (*Recurvirostra americana*) was not obtained in our study or in the literature. Adult prebasic molt was largely completed by the time the Dunlin (Holmes 1966, Page 1974a) and probably the other two

TABLE 3
RECORDS OF IRREGULARLY OCCURRING SHOREBIRDS AT BOLINAS LAGOON

Species	Numbers and dates
Himantopus mexicanus	1 on 21 Jan 1976
Pluvialis dominica	1 between 27 Aug 1974 and 11 Apr 1975 1 on 28 Aug and 2 Sep 1975[a] 1 adult on 9 occasions 8 Sep–17 Nov 1975[a] 2 on 9 Sep 1975[a] 1 on 12 and 22 Apr 1974
Limosa lapponica	1 between 26 Oct and 2 Dec 1973
Heteroscelus incanus	2 adults on 25 July 1973 1 adult on 29 July 1973 1 on 22 Aug 1974 1 on 30 Aug 1973
Aphriza virgata	1 on 7 Sep 1972 1 on 9 Oct 1971
Calidris acuminata	1 juvenile banded on 5 Oct 1972
Calidris ferruginea	1 juvenile 7–14 Sep 1974
Micropalama himantopus	1 adult on 7 and 13 July 1971
Steganopus tricolor	1 from 14 to 21 July 1972 (at least 2 different birds including an adult on 17 and 21 July) 7 on 26 July 1973 4 on 1 Aug, 1 on 4 Aug 1975 3 on 7 Aug 1972, 2 adults and 1 unknown age
Phalaropus fulicarius	1 on 23 Oct and 15 Nov 1972 3–75 from 2 Nov to 1 Dec 1973 1 on 16 Nov 1971 3 on 17 Apr and 3–44 from 11 to 21 May 1976 2 on 11 May 1974 1 on 2 June 1971

[a] These were singletons or at most two individuals.

species (Palmer 1967, Gibson 1971, Tuck 1972) arrived at Bolinas Lagoon. Fall and to a much lesser extent spring passages of migrants were apparent in the Dunlin but not in the snipe or the avocet.

The Killdeer (*Charadrius vociferus*) and Snowy Plover (*Charadrius alexandrinus*) make up a fourth group which includes only species that breed on Bolinas Lagoon (Fig. 4). Resident numbers were augmented and perhaps even replaced beginning in late August for the Snowy Plover and in September for the Killdeer; the duration of immigration into the area was not clearly defined because of difficulties in censusing these species. Some adults underwent prebasic molt and undoubtedly also prealternate molt in the area. Convincing evidence of fall or spring migratory passages was not found for either species. Fluctuations of Killdeer numbers in November and December were most likely related to local movements of birds between pastures and the estuary rather than to true migratory movements.

A fifth group consists of uncommon or irregularly occurring species. These include the regularly occurring but uncommon Spotted Sandpiper (*Actitis macularia*), and the Lesser Yellowlegs (*Tringa flavipes*). Their seasonal abundance

patterns are illustrated in Figure 3. An additional ten irregularly occurring species are listed with dates of occurrence in Table 3.

Seasonal occurrence patterns sometimes varied somewhat among species within the groups listed in Table 1. Thus Willet (*Catoptrophorus semipalmatus*) and Least Sandpiper patterns while conforming to the generalities previously described for birds in the second group differed in that non-breeding Willets regularly oversummered at Bolinas Lagoon whereas Least Sandpipers did not (Figs. 2–3). In fact, large non-breeding shorebirds such as the Willet, Marbled Godwit (*Limosa fedoa*), Black-bellied Plover (*Pluvialis squatarola*), and Whimbrel (*Numenius phaeopus*) occurred regularly on Bolinas Lagoon in June unlike members of most smaller species (Figs. 3–4).

Abundance patterns sometimes probably reflected local rather than widespread population shifts. This has already been mentioned for the Killdeer and is probably reflected in the Black-bellied Plover by the dip in November and December, and in the Black Turnstone (*Arenaria melanoleuca*) by the dip in January (Figs. 3–4). Both of these species used areas away from the estuary, and in winter, departure near or at high tide sometimes occurred prior to the completion of a census, resulting in undercounts of these species. These winter undercounts occurred mostly when high winds and rainfall increased the rate at which the tide flooded the tidal flats.

The seasonal abundance graphs formulated for Bolinas Lagoon (Figs. 2–4) do not necessarily represent species abundance patterns in other California estuaries. This was particularly apparent when Western Sandpiper numbers at Bolinas Lagoon and Limantour Estero were compared (Fig. 2). At Bolinas Lagoon the abundance pattern was characterized by a large fall and a massive spring migratory peak but a relatively low winter population. At Limantour Estero winter numbers were generally similar to fall numbers and there was only a slight indication of a spring migratory peak, mostly as a result of unusually high spring numbers in 1976. Bolinas Lagoon was important to Western Sandpipers as a fall and spring migratory staging area; Limantour Estero was important as an overwintering area. At Bay Farm Island, Storer (1951) found yet another abundance pattern for the Western Sandpiper. Other variability in abundance patterns at different California estuaries can be expected as more areas are examined.

SPECIES COMPOSITION BY NUMBERS AND BIOMASS

The percent composition of species by number and biomass during three periods are given for Bolinas Lagoon's shorebird fauna in Table 4. Individuals of small species, with mean weights of less than 150 g (Table 4), collectively outnumbered larger species, with mean weights exceeding 150 g, by ratios of 3:1 in fall and winter and 9:1 in spring. But larger species dominated in biomass. Larger species made up 75, 65 and 48% of the total biomass in fall, winter and spring respectively. The morphologically similar Least Sandpiper, Western Sandpiper and Dunlin varied considerably in relative abundance during the three periods; Least Sandpipers were most numerous in fall, Dunlins in winter and Western Sandpipers in spring. These relative abundance changes support Recher's (1966) hypothesis that small morphologically similar shorebirds may reduce competition by staggering their peak periods of abundance in a particular area. Since a similar staggering of abundance does not appear to occur, at least between the

TABLE 4
THE SHOREBIRD FAUNA OF BOLINAS LAGOON; PER CENT COMPOSITION BY NUMBER (N) AND BIOMASS (B)[a]

Species	Per cent composition						Mean weight (g)
	Fall		Winter		Spring		
	N	B	N	B	N	B	
Least Sandpiper	44.2	9.4	15.8	3.1	4.8	1.6	20.5
Western Sandpiper	14.1	3.6	2.5	0.6	63.5	26.4	25.0
Northern Phalarope	1.4	0.4	0	0	0.1	*	30.1
Snowy Plover	0.2	0.1	0.3	0.1	0.1	*	40.3
Semipalmated Plover	0.3	0.2	*	*	0.4	0.3	45.6
Dunlin	6.4	3.3	53.3	25.6	15.1	12.6	50.1
Sanderling	4.8	2.9	1.2	0.7	0.8	0.7	58.0
Killdeer	0.9	0.8	1.6	1.3	0.4	0.7	89.2
Ruddy Turnstone	0.1	0.1	*	*	*	*	101.7
Common Snipe	0.1	0.1	1.1	1.1	0.4	0.7	104.0
dowitcher spp.	1.1	1.4	1.3	1.4	3.9	7.5	113.6
Black Turnstone	2.4	2.9	1.1	1.3	0.9	1.8	116.8
Red Knot	0.1	0.1	*	*	*	0.1	150.9
Greater Yellowlegs	0.2	0.4	0.2	0.3	0.1	0.3	182.4
Black-bellied Plover	6.0	13.6	5.2	10.9	3.1	11.3	219.1
Willet	13.1	40.5	8.6	24.8	3.4	17.1	299.3
American Avocet	*	0.1	2.2	6.5	0.6	2.9	312.0
Marbled Godwit	3.2	12.4	4.5	16.2	1.9	11.8	371.4
Whimbrel	0.2	0.6	*	*	0.2	1.1	378.9
Long-billed Curlew	1.0	7.1	0.9	5.9	0.3	3.0	691.3

[a] Percentages by number and biomass were calculated from mean census numbers over the five-year study period. An asterisk indicates a percentage >0 and <0.05%. Species not included contributed less than 0.05% of numbers and biomass during all periods.

Western Sandpiper and Dunlin during winter at Limantour Estero, other behavioral differences must also serve to reduce competition between these species.

ANNUAL VARIATIONS IN NUMBERS

Some species such as the Northern Phalarope varied considerably while others such as the Willet remained remarkably constant in number from season to season at Bolinas Lagoon (Table 5). American Avocets and Marbled Godwits increased in numbers over the five-season study period; mean winter numbers of godwits rose from 96 to 298 and avocet winter numbers from 37 to 252 over the study period. In contrast mean fall numbers of Northern Phalaropes declined from 161 to 1 over the five seasons. Whether this decline of Northern Phalaropes represented a significant change in the species' occurrence on the estuary or was just an artifact of a generally erratic migration pattern was not clear. The high magnitude of variation for Sanderlings in the spring period (Table 5) resulted from the unexplained absence of Sanderlings from the estuary in March and early April of some years but not others.

Variability in Dunlin and Least Sandpiper mean winter and spring numbers (Table 5) was correlated with rainfall (Table 6). Heavy rainfall caused flooding of the estuary and resulted in decreased tidal flat availability. The winters of heaviest rainfall corresponded with the lowest winter numbers of Dunlins and Least Sandpipers (Table 6). Rain probably created fresh water habitats and may affect the

TABLE 5
ANNUAL VARIATION IN SHOREBIRD NUMBERS AT BOLINAS LAGOON, 1971–72 THROUGH 1975–76 SEASONS

Species	Range in mean number			Mean over 5 years			Magnitude of variation[b]		
	F[a]	W	S	F	W	S	F	W	S
American Avocet		35–252	7–137	2	95	40		7.2	19.6
Black-bellied Plover	182–268	110–304	174–271	236	228	223	1.5	2.8	1.6
Semipalmated Plover	8–17		15–53	13		30	2.1		3.5
Killdeer	25–43	48–93	14–50	34	69	32	1.7	1.9	3.6
Snowy Plover	6–13	8–19	3–7	9	15	5	2.2	2.4	2.3
Marbled Godwit	38–189	96–298	60–181	127	199	137	5.0	3.1	3.0
Whimbrel	3–9		5–24	6		12	3.0		4.8
Long-billed Curlew	28–46	35–44	15–21	39	39	19	1.6	1.3	1.4
Greater Yellowlegs	7–10	6–11	6–8	8	8	7	1.4	1.8	1.3
Willet	445–575	335–425	219–288	515	379	246	1.3	1.3	1.3
Black Turnstone	33–159	17–86	32–117	94	49	65	4.8	5.1	3.7
Northern Phalarope	1–161		0.1–23	56		6	201.3		230.0
Common Snipe		44–61	18–52	2	50	30		1.4	2.9
dowitchers	24–73	20–94	124–447	45	59	284	3.0	4.7	3.6
Sanderling	147–285	41–88	17–123	189	54	54	1.9	2.1	7.2
Western Sandpiper	391–747	67–138	2264–5834	552	108	4565	1.9	2.1	2.6
Least Sandpiper	1430–2154	295–1071	109–824	1736	693	343	1.5	3.6	7.6
Dunlin	236–282	1040–4304	284–2790	253	2341	1089	1.2	4.1	9.8
Total shorebirds	3664–4482	2746–7076	4091–10,887	3923	4380	7184	1.2	2.6	2.7

[a] F, fall; W, winter; S, spring.
[b] Magnitude of variation is the highest divided by the lowest yearly mean.

salt water–fresh water distribution of these two small shorebirds. Since substantial variation in shorebird numbers on an estuary may occur from year to year, one season's censuses do not completely measure the capacity of an area to hold shorebirds; only several years of censuses will do that.

USE OF INTRAESTUARINE HABITATS

Shorebirds used the salt marsh on Bolinas Lagoon as a feeding and roosting area. Willets, Least Sandpipers and Pectoral Sandpipers often fed in the salt marsh; Black-bellied Plovers, Long-billed Curlews (*Numenius americanus*) and Common Snipes occasionally fed there. The salt marsh was most important to shorebirds as a high-tide and night-time roost. At high tides most species roosted

TABLE 6
RAINFALL AND WINTER NUMBERS OF SANDPIPERS AT BOLINAS LAGOON

Season	1971–72	1972–73	1973–74	1974–75	1975–76
Inches of rain[a]					
1 Oct–28 Feb	19.0	50.2	34.5	22.1	13.6
Mean winter number[b]:					
Dunlin	2268	1187	1040	2906	4304
Least Sandpiper	773	295	344	981	1071
Total shorebirds	4093	2786	2746	5197	7076

[a] Rainfall was recorded at a station about 6 km from Bolinas Lagoon.
[b] Numbers of birds are means from November through February censuses.

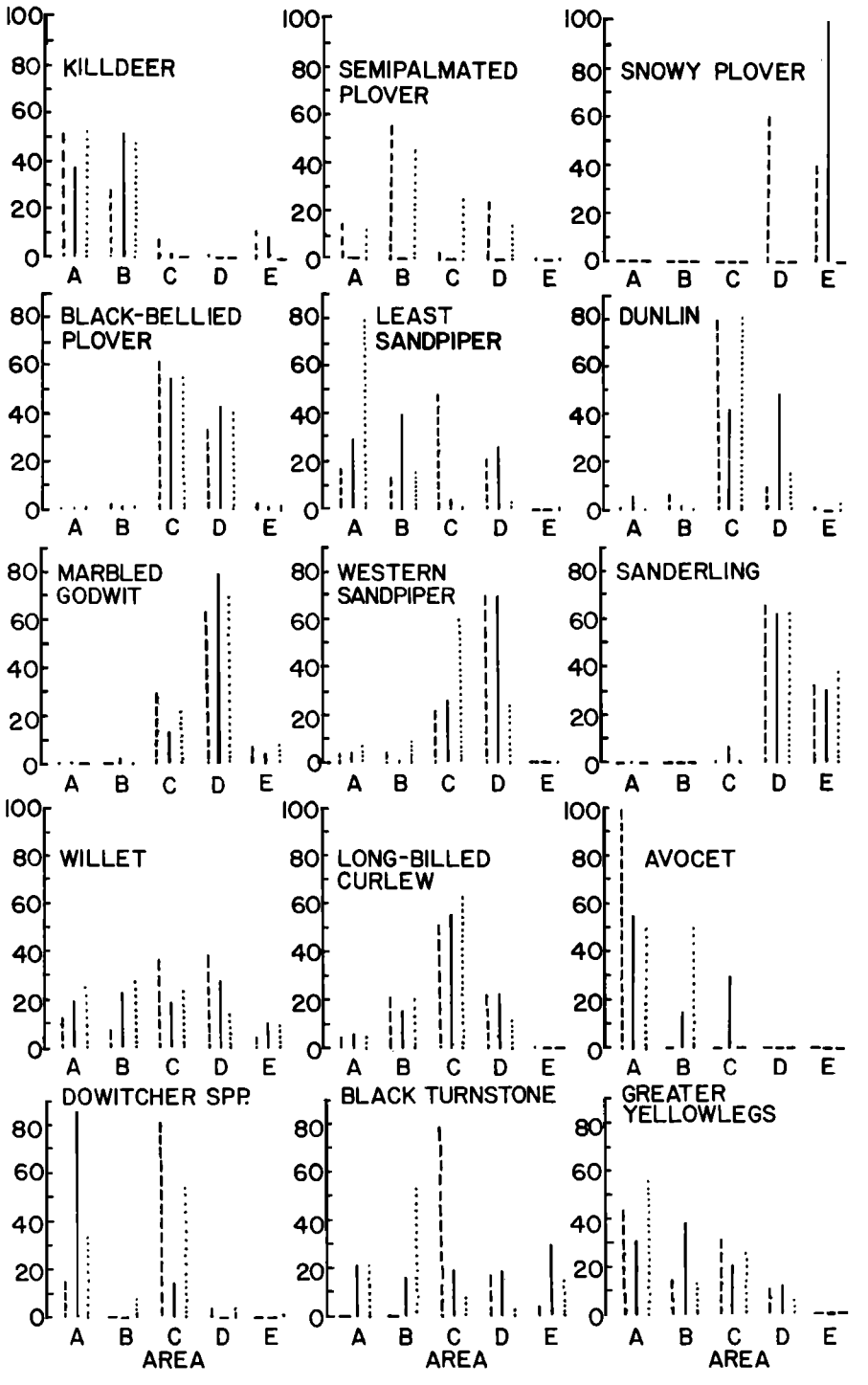

FIGURE 5. Per cent occurrence of shorebirds on five areas of tidal flats on Bolinas Lagoon during fall (dashed line), winter (solid line) and spring (dotted line). Data are corrected to eliminate bias resulting from differences in area sizes.

TABLE 7
VARIATION IN SHOREBIRDS USE OF DIFFERENT TIDAL FLAT AREAS ON BOLINAS LAGOON

	Mean number of species per census			Mean number of birds/10 ha per census			Mean biomass of birds per census (kg/10 ha)			Mean area exposed per census		
Area	F[a]	W	S	F	W	S	F	W	S	F	W	S
A	5.0	5.8	4.7	99	94	294	7.2	9.3	12.3	51	50	50
B	4.2	4.7	3.6	90	93	287	5.5	9.5	12.5	50	51	48
C	7.6	6.1	6.2	387	171	717	36.6	23.5	33.6	69	68	71
D	7.2	5.8	5.6	382	271	328	36.4	37.9	27.6	61	62	58
E	3.2	2.6	2.5	41	21	45	5.5	4.5	4.4	39	43	37

[a] F, fall; W, winter; S, spring.

in the high-tide zone of the tidal flat. If high tides forced the birds from these areas they usually moved into the salt marsh or the sand beach on Kent Island. Most Long-billed Curlews, Willets, Marbled Godwits and some Least Sandpipers usually moved into the salt marsh; many other species moved to the sand beach. Least Sandpipers, Dunlins, Western Sandpipers and dowitchers regularly used the salt marsh as a nighttime roost.

The tidal flat was by far the most important feeding habitat. On the tidal flat shorebirds segregated into areas with different types of substrate (Fig. 5). The Killdeer, Greater Yellowlegs (*Tringa melanoleuca*), American Avocet and Least Sandpiper fed on the muddiest substrates and were prominent shorebirds in areas A and B. The Snowy Plover and Sanderling occurred most frequently in areas D and E where the sediment was coarser. The Black-bellied Plover, Dunlin, Western Sandpiper and Marbled Godwit were most abundant in areas C and D (Fig. 5). Lenna (1969) reports that the two species of dowitchers feed in different habitats in the Point Reyes area. According to him, the Short-billed Dowitcher occurs primarily during fall and prefers sandier tidal flats than the Long-billed Dowitcher which occurs primarily during winter. During spring both species occur simultaneously at Bolinas Lagoon. Our census data generally agree with Lenna's (1969) observations; dowitchers were most abundant in area C in fall, in area A in winter and in areas A and C in spring (Fig. 5).

The distribution of some shorebirds could not easily be related to substrate differences. The Willet was more scattered over the different areas than any other shorebird (Fig. 5). The distribution of Long-billed Curlews was probably related to the distribution of its major prey rather than to substrate type (Stenzel et al. 1976). The Black Turnstone's distribution was undoubtedly influenced by the location of algae on the tidal flat, but we did not measure algal abundance in the five areas and were not able accurately to demonstrate this point.

Among the five tidal flat areas the number and biomass of birds censused per unit area varied substantially (Table 7). In area E, the sandiest area, shorebird density and biomass were lowest; in areas C and D, tidal flats of intermediate substrate texture, density and biomass were highest. A similar trend was also apparent for the mean number of species observed per census (Table 7). Therefore, not only did areas C and D support more birds and a greater biomass but they also supported a wider variety of species than the other areas.

TABLE 8
PER CENT OF SHOREBIRDS USING OUTER COAST HABITATS[a]

Species	Per Cent				
	Fall		Winter		Spring
Black-bellied Plover	4.5		8.0		4.4
Black Turnstone	13.4	*	43.0		39.8
Willet	9.2	*	16.4		14.4
Marbled Godwit	2.6	*	7.4		7.3
Sanderling	5.6	*	51.0	*	11.7

[a] Based on census data from Bolinas Lagoon and 8.5 km of adjacent open coast taken from July 1973 through May 1974. An asterisk indicates a significant difference ($P < 0.05$) between adjacent percentages.

USE OF EXTRALIMITAL HABITAT

The 8.5 km of open coast adjacent to and north of Bolinas Lagoon was used by several species that also occurred on the estuary. Birds were often seen flying between the estuary and coast indicating that both areas were used by some individuals. Except for summer on the open coast we consistently found Willets, Black Turnstones, Sanderlings, Least Sandpipers, Black-bellied Plovers, Marbled Godwits, Killdeers, and a Spotted Sandpiper; in addition during migration periods we regularly found Whimbrels. Semipalmated Plovers (*Charadrius semipalmatus*), Ruddy Turnstones (*Arenaria interpres*), Baird's Sandpipers, Dunlins, dowitchers, Red Phalaropes (*Phalaropus fulicarius*), and Northern Phalaropes occurred sporadically along the coast. A greater proportion of the estuary-open coast population of some species occurred along the coast in the winter than in the fall period. Black Turnstones and Sanderlings substantially increased their relative use of the open coast from fall to winter and smaller but significant increases were noted for the Willet and Marbled Godwit (Table 8). The relative increase in the use of the coast from fall to winter may have been due to increased pressure on birds to use more of the available feeding habitat in the Bolinas area in winter (Stenzel et al. 1976).

After the winter rains began in October or November each year, some shorebirds used the pastures on Bolinas mesa. Most of the Black-bellied Plovers and Dunlins and some Least Sandpipers from the estuary moved there and fed or roosted during high tides and rain. During the winter a few Killdeers and snipes feed in the pastures regardless of the tides. Greater Yellowlegs, Western Sandpipers, and dowitchers also used the mesa pastures occasionally. On the Ythan Estuary in Scotland, Goss-Custard (1969) found that pastures can be important alternate feeding habitat for Redshanks (*Tringa totanus*) during winter. These observations suggest that habitats outside the commonly observed boundaries of an estuary may directly contribute to the support of the birds using the estuary.

INTERESTUARINE VARIATIONS IN SHOREBIRD DENSITIES

Shorebird densities varied markedly between Bolinas Lagoon and Limantour Estero (Table 9), two relatively similar estuaries located 21 km apart. Greater densities of Killdeers and Common Snipes at Bolinas Lagoon were undoubtedly related to the greater amount of marshy pastureland bordering Bolinas Lagoon

TABLE 9
SEASONAL VARIATION IN MEAN DENSITIES (NO./100 HA) OF SHOREBIRDS IN BOLINAS LAGOON (B) AND LIMANTOUR ESTERO (L)[a]

Species	Fall		Winter		Spring		Magnitude of variation[b]		
	B	L	B	L	B	L	Fall	Winter	Spring
American Avocet	0.3	0.1	21.3	0.1	9.0	0	3.0	213.0	?
Black-bellied Plover	52.8	13.3	51.0	18.4	49.9	3.8	4.0	2.8	13.1
Semipalmated Plover	2.9	7.7	0.1	4.8	6.7	7.1	2.7	48.0	1.1
Killdeer	7.6	2.2	15.4	1.8	7.2	1.3	3.5	8.6	5.5
Snowy Plover	1.9	6.2	3.4	19.2	1.1	6.6	3.3	5.6	6.0
Marbled Godwit	28.4	12.4	44.5	19.6	30.7	3.6	2.3	2.3	8.5
Whimbrel	1.4	1.3	0.1	0.1	2.7	1.1	1.1	1.0	2.5
Long-billed Curlew	8.7	0.3	8.7	0.3	4.3	0.2	29.0	29.0	21.5
Greater Yellowlegs	1.8	0.4	1.8	0.6	1.5	0.9	4.5	3.0	1.7
Willet	115.2	61.6	84.8	73.9	55.0	33.7	1.9	1.1	1.6
Black Turnstone	21.0	10.0	11.0	6.5	14.5	6.2	2.1	1.7	2.3
Northern Phalarope	12.5	2.7	0	0.1	1.4	<0.05	4.6	?	?
Common Snipe	0.5	0.1	11.2	0.2	6.7	0	5.0	56.0	?
dowitchers	10.1	9.2	13.2	1.5	63.5	5.8	1.1	8.8	10.9
Sanderling	42.3	85.9	12.1	70.5	12.1	51.4	2.0	5.8	4.2
Western Sandpiper	123.5	313.7	24.2	548.5	1021.5	432.1	2.5	22.7	2.4
Least Sandpiper	388.5	99.4	155.1	100.5	76.8	47.5	3.9	1.5	1.6
Dunlin	56.6	101.6	523.8	843.4	243.7	222.0	1.8	1.6	1.1

[a] Data derived from five seasons of censusing at Bolinas Lagoon and ten seasons at Limantour Estero.
[b] Magnitude of Variation is the higher mean density divided by the lower for each period. Species whose densities did not reach 1.0 birds/100 ha in any period were excluded. Queries (?) indicate unreasonable quotients because of zero or minor fractional values for either location.

compared to Limantour Estero, whereas greater densities of Snowy Plovers and Sanderlings at Limantour Estero were likely related to the greater extent of sandy habitat at Limantour Estero compared to Bolinas Lagoon. Marked differences in avocet densities between the two estuaries may also have been due to differences in habitat type since Bolinas Lagoon has larger low intertidal areas of muddy substrate than Limantour Estero. Other observed differences in shorebird densities such as occurred for the Semipalmated Plover in winter, Black-bellied Plover in spring, Long-billed Curlew at all periods and Western Sandpiper as previously mentioned are difficult to account for on the basis of obvious habitat differences between the two estuaries. Only careful study will clarify these differences.

DISCUSSION

Our shorebird censusing studies provide insights into avian numerical variation in wetland habitats that should be considered for the interpretation of water bird census data. Obviously censuses from only part of a season (bird year) give a distorted view of a wetland's use by birds. Censuses conducted regularly over an entire season reveal the abundance patterns for most species for that area but not necessarily the total number of birds the area can support; this varies from year to year. Censuses from part of a wetland form an unreliable index of what is present in the whole; only thorough knowledge of the habitat distribution within the whole system would make extrapolation from the part to the whole possible and to date a comprehensive description of wetland habitat as it relates to birds

has not been developed. Censuses from discrete wetlands can not even be relied upon to provide general species abundance patterns for other wetlands as was illustrated by the discrepancies observed in the Western Sandpiper abundance patterns between Limantour Estero and Bolinas Lagoon.

The many factors that determine the number and kinds of birds that are found in a wetland are difficult to separate. Certainly the wetland must provide an acceptable physical environment and food resource for the birds. The surrounding environment plays an important role when it contributes to the overall needs of birds using the wetland. Annual variations in productivity on the breeding grounds may also be reflected in the overall numbers and the adult to juvenile ratios of shorebirds in a wetland. Tradition may partially determine where birds occur locally; it has often been demonstrated that individual shorebirds return to the same wetland to overwinter year after year (Page 1974a, Kelly 1976, P. G. Connors pers. comm.). The presence of Long-billed Curlews and American Avocets at Bolinas Lagoon and their absence in other wetlands in the Point Reyes area in winter may be related more to traditional patterns than other differences between the areas.

Our observations reveal that an estuarine habitat–complex, rather than being uniform in the densities of birds supported, is really quite variable. These observations imply that destruction of part of a wetland may result in habitat loss for some species that is not easily substituted for by remaining habitat nearby. Even species with a high tolerance for a broad range of different habitats may, in the event of being displaced from traditional wintering areas, find alternative sites filled to capacity. Even if a group of adjacent wetlands does not support the full complement of birds it is capable of holding, reduction of the wetland's area may still have detrimental long-term effects for birds because the flexibility for choice between areas is reduced; this could have important consequences during years of some restriction such as drought.

Over relatively small geographical distances there must definitely be an additive effect within a wetland system such that the whole system is able to support more than the sum of its parts if each part were totally independent. The basis for this concept can be observed on Point Reyes when small shorebirds from Drake's Estero fly 2.5 km to Abbott's Lagoon at high tide in winter to roost and feed and then return to Drake's Estero at a lower tide. These birds would not likely appear at Abbott's Lagoon if Drake's Estero were not nearby. Whether as many small shorebirds would overwinter at Drake's Estero if Abbott's Lagoon did not exist can not definitely be stated although it is evident that Abbott's Lagoon contributes positively to the support of small sandpipers wintering in Drake's Estero. Obviously considerable study remains before a thorough appreciation of the factors promoting the uneven spatial and temporal distribution of water birds in California's coastal wetlands will emerge.

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