SHOREBIRD DISTRIBUTION IN A CHANGING ENVIRONMENT: PATTERNS AT ELKHORN SLOUGH

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ABSTRACT

SHOREBIRD DISTRIBUTION IN A CHANGING ENVIRONMENT: PATTERNS AT ELKHORN SLOUGH

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From spring 1999 through spring 2000, shorebird use of mudflat regions in Elkhorn Slough's wetlands was evaluated, including seasonal and spatial abundance patterns, high vs. low tide use of muted tidal regions, influence of physical parameters, and changes in distribution on Elkhorn Slough's main channel since the 1970s. In general, at low tide, sandpipers were most abundant in the upper slough; sediment grain size was finer there than any other region. Most larger shorebird species were distributed throughout fully tidal regions. Sandpiper abundance was greater in muted tidal regions at high tide than low tide. In the 1990s, density of large shorebird species was greater in the lower section of Elkhorn Slough, relative to other slough sections, where erosion of the upper intertidal was greatest. This may be a result of reduced mudflat area since the 1970s. Persistence of this important migratory stopover is important to maintain sustainable population levels.

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CHAPTER 1.

IMPORTANCE OF MUDFLAT HETEROGENEITY FOR MIGRATING AND WINTERING SHOREBIRDS

The intertidal mudflat zone is the primary coastal feeding habitat for most shorebird species (Charadriiformes) during migration and winter (Recher 1966, Gerstenberg 1979, Long and Ralph 2001, Stenzel et al. 2002). The dynamic nature of this habitat, however, precludes a continuous food supply in any one region. Inter- and intraspecific variation in migration patterns, feeding strategies, diet, and habitat use reduce competition and promote more efficient use of intermittent food resources (Baker and Baker 1973). These strategies enhance shorebird survival, particularly during periods of resource limitation (Evans 1979, Connors et al. 1981, Schneider and Harrington 1981).

Shorebird species composition varies temporally and spatially on mudflats, primarily because of physical factors that limit the accessibility of food (Evans 1976, Burger 1984). Tidal fluctuations and weather (primarily temperature and wind) have the greatest influence on distribution patterns of nonbreeding shorebirds (Evans 1976, Burger et al. 1977), although the presence of avian predators influences distribution of shorebird flocks at the local level (Page and Whitacre 1975). The mixed semi-diurnal tidal regime of the Pacific coast limits the accessibility of invertebrate prey to shorebirds because of daily and seasonal variability in extent of mudflat exposure. Other physical factors, including salinity (Wolff 1969) and sediment grain size (Quammen 1982), also influence the invertebrate assemblage and its availability to shorebirds (Goss-Custard 1970, Myers et al. 1979, Hicklin and Smith 1984). The positive correlation between density of foraging shorebirds and density of invertebrates indicates that shorebirds select sites that have a greater abundance of prey (Goss-Custard 1970, Bryant 1979, Evans 1979, Colwell 1993, Weber and Haig 1997).

During fall, declining temperatures, shorter days, and increased height of water at low tide contribute to reduced accessibility of shorebird prey (Goss-Custard 1969). This is coincident with greater shorebird density during migration, and may result in a food- or space-limited feeding environment (Recher 1966). Morphologically similar species, such as the Western Sandpiper (*Calidris mauri*) and the Least Sandpiper (*Calidris minutilla*), may use different feeding areas or have staggered peaks in migration, reducing competition for food (Recher 1966). As space becomes increasingly limited, subdominant individuals may be forced onto suboptimal feeding sites (Goss-Custard 1979). Although such sites may support few shorebirds during periods of relatively low abundance, they may become critically important for shorebird survival during migration.

Along the central coast of California, coastal wetlands support large concentrations of migrating shorebirds. The wetland ecosystem at Elkhorn Slough, located on Monterey Bay, provides essential habitat for migrating, wintering, and resident shorebirds, and serves as one of the most important migratory staging areas in California (Senner and Howe 1984, Page et al. 1992). Elkhorn Slough's wetlands comprise a diverse network of ecologically distinct mudflat regions, including areas exposed to full tidal influence, such as the main channel of Elkhorn Slough, Parsons Slough, and Moss Landing's North Harbor, and areas with restricted tidal flow, including Moro Cojo Slough, North Marsh, and salt ponds (Fig. 1). Although mudflats in these wetlands appear homogeneous, each is a distinct habitat, unique in physical and biological characteristics (Harvey et al. 1986). The heterogeneity among these mudflat units creates a mosaic of diverse habitats that are alternately available for feeding or roosting.

I evaluated shorebird use of tidally restricted and unrestricted mudflat regions in Elkhorn Slough's wetlands and identified the physical variables that characterized mudflat regions used by each shorebird species, seasonal changes in shorebird distribution, and relative use of different mudflat regions. My hypotheses were as follows.

1) Physical factors influence shorebird use of mudflats. I predicted that differences in shorebird assemblages among mudflat regions would reflect corresponding differences in physical factors.

2) Shorebird distribution within the study area differs among seasons because of variation in abundance. During periods of greater abundance, shorebirds may be found in more regions than during periods of lesser abundance,

potentially because of increased competition in available habitat for space and/or food.

METHODS

Study Area.—My study area comprised thirteen mudflat regions within the Elkhorn Slough wetlands (Fig. 1). Each of these fit into one of three categories: 1) the main channel of Elkhorn Slough; 2) mudflats peripheral to the main channel that are exposed to full tidal exchange; and 3) mudflats peripheral to the main channel that are exposed to muted tidal exchange because of tide gates restricting tidal flow. Regions are described below.

MAIN CHANNEL OF ELKHORN SLOUGH

Elkhorn Slough is a tidal seasonal estuary at the head of the Monterey Submarine Canyon. It extends inland approximately 10 km, with depths of 9 m near the mouth and <1 m at the head of the slough (Brantner 2001); width is approximately 150 m near the mouth and 25 m at the head of the slough (Malzone 1999). Salt marsh, mudflats, salt ponds, and tributaries border the main channel. Sediment grain size becomes finer with increasing distance from the mouth (Nybakken et al. 1977). Freshwater input varies seasonally; the predominate source is direct precipitation.

The slough was divided into five segments of unequal length (Fig. 1). Section distances from the Highway 1 bridge (entrance to the slough) and mudflat area were: Section A: Hwy 1 bridge to 2.4 km (2.47 ha of mudflats at 0.75 m tide, 12.17 ha at -0.15 m tide); Section B: 2.4 to 3.8 km (8.18 ha of mudflats at 0.75 m tide, 20.65 ha at –0.15 m tide); Section C: 3.8 to 5.4 km (4.59 ha of mudflats at 0.75 m tide, 24.6 ha at –0.15 m tide); Section D: 5.4 to 6.6 km (5.9 ha of mudflats at 0.75 m tide, 16.36 ha at –0.15 m tide); Section E: 6.6 to 9.8 km (5.9 ha of mudflats at 0.75 m tide, 16.36 ha at –0.15 m tide).

PERIPHERAL MUDFLATS EXPOSED TO FULL TIDAL EXCHANGE

South Marsh became open to full tidal exchange in the early 1980s when dikes were breached. At that time, parallel rows of islands were constructed in an effort to enhance habitat for wildlife; these islands became predominantly covered with pickleweed (*Salicornia virginica*). Broad mudflats were located in the northern and western parts of the region. Area of exposed mudflats was 0.27 ha at 0.45 m tide and 25.72 ha at –0.15 m tide.

Parsons Slough branched off the main channel of Elkhorn Slough approximately 4 km from the mouth. This region was composed of five prominent fingers with extensive mudflats and minimal salt marsh habitat. Dike breakage in the early 1980s opened this region to full tidal exchange. Combined with South Marsh, this area accounted for 30% of the total tidal volume in the Elkhorn Slough system (Malzone 1999). Area of exposed mudflats was 27.03 ha at 0.45 m tide and 66.83 ha at –0.15 m tide.

Fully tidal salt ponds were used for commercial salt production until 1973; this region became exposed to full tidal exchange after levees broke down in the 1980s. Mudflats were interspersed with salt marsh habitat. Elevation of this area was higher than mudflats along the main channel and was exposed for foraging and roosting when other mudflats are flooded. Mudflats were fully exposed at a 0.75 m tide with area of 10 ha.

Gibsons Landing has been exposed to full tidal exchange since 1989, when tide gates became ineffective following the Loma Prieta earthquake; consequently, it has become a predominantly salt water marsh system, bordered primarily by salt marsh vegetation. Tidal water flowed from the North Harbor through unrestricted culverts into Gibsons Landing. Area of exposed mudflats was approximately 1 ha at 0.75 m tide and 4.75 ha at –0.15 m tide.

Northern portion of North Harbor was a broad mudflat that received full tidal influence and was bordered by Gibsons Landing, Highway 1, and Moss Landing Harbor. Area of exposed mudflats was 1.44 ha at 0.75 m tide and 5.61 ha at –0.15 m tide.

Old Salinas River channel was exposed to full tidal exchange from the South Harbor and usually open to freshwater flow from the Salinas River; the mudflats were bordered by salt marsh vegetation. Salinity readings ranged from 2 – 32 psu (practical salinity units), depending on tidal phase and distance from the harbor and river. Area of exposed mudflats was 2.54 ha at 0.75 m tide and 6.26 ha at –0.15 m tide.

MUDFLATS EXPOSED TO MUTED TIDAL EXCHANGE

Porter Marsh, located at the head of the slough, was separated from the main channel by culverts equipped with tide gates under Elkhorn Road that allowed fresh water to drain out into the main channel of Elkhorn Slough but prevented most salt water from flowing into Porter Marsh. Salinity readings ranged from 2 – 45 psu. Freshwater input was received from creeks to the north and to the east and from direct precipitation. The marsh was predominantly covered with salt grass (*Distichlis picata*) and pickleweed; small mudflat areas provided nesting, roosting, and feeding habitat for shorebirds. Area of mud habitat was 5.58 ha.

Estrada Marsh bordered the main channel of Elkhorn Slough approximately 6.5 km from the mouth, and was covered with pickleweed interspersed with regions of bare substrate. It was separated from North Marsh on its southern border by a dike and had no connection with Elkhorn Slough. The marsh flooded seasonally but was dry for most of the year; salinity readings ranged from 18 – 70 psu, largely influenced by evaporation and rainfall. Area of Estrada Marsh was 15 ha; approximately half of this area was mud.

North Marsh (approximately 42 ha) bordered the main channel of Elkhorn Slough on its western edge and Estrada Marsh on its northern edge and had some higher areas of pickleweed marsh, interspersed with bare mudflat. This region was subject to tidal inundation through four culverts under the railroad tracks; tidal flow could be manipulated by adjusting tide gate openings on each of the culverts. Full tidal flow was restricted to prevent flooding of Elkhorn Road. Salinity readings ranged from 18 – 56 psu. The region was part of the Elkhorn Slough National Estuarine Research Reserve and was closed to the public. Area of North Marsh was 42.21 ha; area of mud was approximately 14 ha.

Strawberry Marsh comprised two ponds separated by a small road that meets North Marsh at Elkhorn Road. The northern pond, primarily bordered by pickleweed, was exposed to salt water intrusion and tidal influence from North Marsh; salinity readings in this lagoon ranged from 10 – 55 psu. The southern pond was more characteristic of a freshwater system, with rushes, sedges, and cattails bordering the open water. Surveys were conducted in the northern marsh only. Surveyed area was 2.63 ha; area of mud was approximately 0.9 ha.

Salt ponds were used as evaporation ponds for salt mining from 1916 until 1973 (Gordon 1996). The salt ponds consisted of four principal ponds, each with rudimentary tide gates to control water flow. Water entered the salt ponds from Elkhorn Slough through a primary channel. The elevation of the ponds was higher than the mudflats along the main channel; thus, the region was available for foraging and roosting when other mudflats were inundated (Strong 1990). Manipulation of water levels during the breeding season provided mudflat habitat for foraging, roosting, and nesting shorebirds. The area was closed to the public year-round to reduce disturbance to the threatened Western Snowy Plover (*Charadrius alexandrinus nivosus*). To enhance the region for nesting Snowy Plovers, water level in the salt ponds was managed by Point Reyes Bird Observatory (PRBO) from March through September; the ponds were largely unmanaged the remainder of the year. Area of salt ponds, including ponds along Hwy. 1, was approximately 49 ha.

<u>Moro Cojo Slough</u> was exposed to minimal tidal influence, connected to Moss Landing Harbor where tidal action was restricted. Salinity readings ranged from 2 – 100+ psu, depending on distance from the harbor, rainfall, and evaporation. The channel was bordered by salt marsh, agricultural land, and rangeland presently grazed by cattle. I surveyed shorebirds in this region from Moss Landing Road, where the slough meets the harbor, to the railroad tracks approximately 3.5 km east; this area comprised approximately 5.4 ha of mudflat on the channel borders.

Data Collection.—From 1 March 1999 to 1 July 2000, I surveyed the entire study area two to three times each month for shorebirds on mudflat habitat (Fig. 1); it generally took five to six days to survey all regions in the study area once. Regions were surveyed within a six-hour period around low tide. I used a motorboat to survey the main channel of Elkhorn Slough, either alone or with one assistant. Moro Cojo Slough was surveyed from a kayak or on foot, depending on water depth; I surveyed all other regions on foot. All shorebirds on mudflats were identified to species and counted; birds in flight were not counted. Birds were not counted in other habitats.

Seasonal and spatial patterns were evaluated for 11 species, including Willet (*Catoptrophorus semipalmatus*), Marbled Godwit (*Limosa fedoa*), Long-billed Curlew (*Numenius americanus*), Black-necked Stilt (*Himantopus mexicanus*), American Avocet (*Recurvirostra americana*), Black-bellied Plover (*Pluvialis squatarola*), Dunlin (*Calidris alpina*), Sanderling (*Calidris alba*), Western Sandpiper, and Least Sandpiper; Long-billed Dowitcher (*Limnodromus scolopaceus*) and Short-billed Dowitcher (*L. griseus*) were not differentiated and were identified as "dowitchers".

The following variables were recorded during each survey: tide height (meters; derived from local tide table), tide phase (number of minutes before or after low tide), air temperature (°C), wind speed (km/hr), wind direction, salinity (psu), time of day, and day length. Approximate water depth during time of survey was recorded in regions with muted tides; water depth gauges were placed in these marshes to track relative differences in water level among surveys. Presence of avian predators or other disturbances were recorded. Substrate composition and grain size were determined in each region from sediment samples collected in the summer of 2000 (five random samples for each region), using sieve analysis for the coarse fraction and hydrometer analysis for the fine fraction (Nybakken et al. 1977).

Data Analysis.—Seasons were defined as: spring migration (1 March to 30 May), fall migration (1 July to 30 November) and winter (1 December to 28 February). Data collected in June were excluded from statistical analyses because most birds had vacated the area at this time. Within a season, all surveys containing at least 10% of the greatest survey count for a given species were included in data analysis. I defined a survey as single coverage of the entire study area. Abundance less than 10% of greatest count within a season was considered insufficient for evaluation of distributional patterns. Data from spring 1999 and spring 2000 were statistically evaluated before pooling (2-factor ANOVA, factors: location and year).

To calculate density, extent of exposed mudflat at different tides was determined. In March 2000, the study area was photographed on a series of flights, occurring between -0.15 m and +0.75 m (the range of tide levels during which my surveys were conducted). Photographs were taken every hour and approximated 0.3 m changes in tide height (i.e. –0.15, +0.15, +0.45, and +0.75 m), for a total of four passes. Photos were georectified to existing corrected photos of Elkhorn Slough's wetlands using ImageWarp 2.0 extension (author: K. R. McVay) with ArcView 3.2 Geographical Information System Software (Environmental Science Research Institute, Redlands, CA). Area of exposed mudflat was determined for each set of photos using ArcView 3.2., then groundtruthed; only viewable areas from survey vantage points on land or by boat were included in area determination. This area calculation was then used to approximate mudflat area during each shorebird survey.

Canonical correlation analysis was used to test the relationship between shorebird density and environmental variables (Tabachnick and Fidell 1996; SPSS 10.0). Data from two seasons, winter and fall, were used for this analysis and tested separately. Data for winter were analyzed because shorebird abundance was the most consistent during that season. Salinity could not be used as a variable in winter, however, because of several cases with missing salinity measurements. Data from mid to late fall, September through November (when abundance was relatively stable), were tested with salinity and salinity range included as additional variables. Physical variables in the winter data set included tidal amplitude, tidal phase (ebbing, low, or flooding; measured as minutes before or after low tide at time of survey), time of day, and mean sediment grain size. Physical variables in the fall data set included tidal amplitude, tidal phase, mean sediment grain size, salinity, and range of salinity. Weather variables (temperature, wind speed, and wind direction) were not included in the analysis because the range of values was fairly narrow.

Shorebird species included in the winter data set were Willet, Marbled Godwit, Long-billed Curlew, dowitchers, Western Sandpiper, Black-bellied Plover, and American Avocet; species included in the fall analysis were Willet, Marbled Godwit, dowitchers, Western Sandpiper, Least Sandpiper, and Black-necked Stilt. Increasingly large canonical loadings of shorebird density reflected greater densities.

If variables were skewed (absolute value ≥ 2.0), data were square root transformed. Those variables that were still skewed after transformation were not included in analyses. Transformations were applied to all shorebird species except American Avocet. Variables within a set (environmental variables set and shorebird species set) were tested for correlation using Pearson correlation; if variables were strongly correlated ($r \geq 0.9$), one of the pair was not included in the test. Canonical loadings with an absolute value ≥ 0.3 were interpreted as ecologically significant (Tabachnick and Fidell 1996). Increasingly large canonical loadings reflected greater tidal amplitude, flooding tidal phase, later time of day, small sediment grain size, hypersaline water, and a broad range of salinity within a region.

A two-factor Analysis of Variance (factors: season and location) was used to detect differences in relative habitat use for each species among regions within the study area (SYSTAT 9). Both density and abundance were evaluated as dependent variables. Individual regions within the study area varied in size, therefore, an evaluation using density (birds/ha) standardized use within each region. An evaluation of relative abundance (number of birds in each region/total number of birds) provided information on proportional distribution of birds within the study area. A region was included in the statistical analysis if it met one or both of the following criteria for spring, fall, or winter: 1) contained a mean proportion of at least 5% of a species (relative abundance); or 2) ranked as supporting one of the five greatest densities (mean) of all regions for a given species. An equal number of surveys was used for each season; surveys were randomly eliminated from seasons that had more surveys to get equal replication. I was only interested in the interaction term in this analysis; a significant interaction term identified differences in habitat use among seasons. When variances were heterogeneous, data were square root transformed. If variances were still unequal after two transformations, data were not statistically analyzed. Alpha level for all statistical tests was 0.05.

RESULTS

Relationship between physical variables and shorebird density.—In the winter data set, the first canonical root pair was significant ($\chi^2 = 58.69$, df = 28, $P = 0.001$; Fig. 2). The physical variables correlated with this axis (i.e. having canonical loadings with an absolute value ≥ 0.3) were tidal amplitude (0.408), tidal phase (-0.426), and sediment grain size (0.704); the corresponding shorebird species were Willet (-0.638), Marbled Godwit (-0.870), Black-bellied Plover (-0.386), and Long-billed Curlew (-0.486). This axis indicated that greater densities of larger shorebird species were associated with larger grain size, flooding tides, and neap tides.

In the fall data set, the first canonical root pair was significant ($\chi^2 =$ 124.95,df = 30, $P < 0.001$; Fig. 3). The physical variables that were correlated with this axis were sediment grain size (-0.568) and range of salinity (0.794); the shorebird species correlated with this axis were Western Sandpiper (-0.665) and Black-necked Stilt (0.762). This axis indicated that greater Western Sandpiper density was associated with regions characterized by small sediment grain size and minimal range of salinity; greater Black-necked Stilt density, in contrast, was associated with regions that had larger grain size and broader range of salinity.

The second canonical root pair in the fall data set was also significant, representing a significant pattern between the sets of variables, although weaker than the first root pair ($\chi^2 = 61.50$, df = 20, $P < 0.001$). The physical variables correlated with this axis were sediment grain size (0.675), tidal phase (-0.451), and salinity range (0.564). Among the shorebird species, Willet (0.527), Marbled Godwit (0.595), Least Sandpiper (0.366), and Black-necked Stilt (-0.564) correlated with the second axis. This axis indicated that greater densities of Willet, Marbled Godwit, and Least Sandpiper were associated with regions characterized by smaller sediment grain size, and broader salinity range during ebbing tides, whereas greater Black-necked Stilt density was associated with larger sediment grain size and narrower salinity range during flooding tides.

Seasonal abundance.—Seasonal abundance patterns varied considerably among shorebird species (Fig. 4). Among the large shorebirds, abundance patterns of Willet, Marbled Godwit, and Long-billed Curlew were similar, with the population decreasing substantially in early spring (March), increasing again by early fall (July), and maintaining relatively constant levels through the winter season.

Black-necked Stilt and American Avocet, both local breeders in the Elkhorn Slough watershed, exhibited contrasting patterns in seasonal abundance. Whereas Black-necked Stilt abundance was greatest from mid-fall to early winter (September through December), decreasing in late winter, American Avocet numbers were greatest in early spring, then decreased substantially until late fall, when abundance increased again and remained fairly constant until spring.

Seasonal differences in maximum numbers among the most morphologically similar species, the sandpipers, were pronounced. Western Sandpiper abundance was greatest in spring, Least Sandpiper numbers were greatest in fall, and Dunlin, a slightly larger sandpiper, was most abundant in winter. During spring migration, Least Sandpiper abundance decreased substantially by March, whereas Western Sandpiper numbers were greatest in April and decreased to few by mid-May. Few Dunlins were observed during spring (no survey total exceeded 150 individuals); however, survey totals exceeded 3,500 in fall and 5,000 in winter. Sandpiper abundance decreased dramatically in February 2000; this pattern may be explained by the resulting scarcity of available muted tidal regions after substantial rain in January 2000.

Relative abundance.—The sandpipers were the most abundant shorebirds in the region in winter, spring, and fall (Fig. 5). During spring 1999, Western Sandpiper was the most abundant species, accounting for 47% (SE = 8.8) of all shorebirds in the region, followed by Least Sandpiper (12%, SE = 1.8). During fall migration, Least and Western Sandpipers accounted for 74% of all shorebirds in the region (Least Sandpiper: 38%, SE: 3.4; Western Sandpiper: 36%, SE = 2.2). In the winter, three sandpiper species accounted for over two-thirds of all shorebirds observed (Least Sandpiper: 31%, SE = 4.1; Western Sandpiper: 26%, SE: 4.8; Dunlin: 11%, SE = 3.5).

Distribution patterns.—Willet density was greatest at Gibsons Landing and the old Salinas River in all seasons (Fig. 6). Abundance was greatest at Parsons Slough in all seasons and at the lower slough (Sec. A) in winter, the upper slough in spring, and mid to upper slough in fall. No statistically significant differences, however, were found in distribution among seasons for density or abundance.

Seasonal differences in density and abundance of Marbled Godwits among regions were statistically significant (Fig. 7; density: $F = 2.41$, df = 16, $P = 0.004$; abundance: $F = 2.13$, df = 16, $P = 0.014$). In fall and winter, godwit density was greatest at the mouth of the slough and at North Harbor; however, in spring, density at North Harbor was much less relative to the lower slough.

The main channel of the slough, Parsons Slough, and North Harbor had the greatest abundance of godwits in fall and winter; during spring, godwit abundance in Section B and North Harbor decreased, relative to other regions used in fall and winter.

During winter and spring, the mid-slough had the greatest density and abundance of Long-billed Curlews within the watershed (Fig. 8). Distribution shifted in the fall; density was greatest in the lower slough and abundance was greatest in Parsons Slough. Statistical analyses were not performed for density because variances were unequal after transformation; there were no significant differences in abundance among seasons.

American Avocet density was significantly different among seasons (Fig. 9; $F = 3.55$, df = 18, $P < 0.001$). During fall and winter, density was greatest in the middle slough (Sections C and D), North Marsh, and old Salinas River; in spring, with the onset of the breeding season, density was greatest in Moro Cojo Slough. Avocet abundance was greater at North Marsh in winter and spring than in any other region. However, relative abundance shifted in fall, with the middle slough, the salt ponds and North Marsh with the greatest abundance of avocets. Seasonal differences in relative abundance could not be tested statistically because of unequal variances.

Density and abundance of Black-necked Stilt differed significantly among regions seasonally (Fig. 10; density: $F = 3.51$, df = 12, $P = 0.001$; abundance: $F = 3.96$, df = 12, $P < 0.001$). In all seasons, density was greatest at Moro Cojo

Slough. In fall, the old Salinas River also had greater densities, relative to the rest of the study area. Abundance of stilts was relatively greater at North Marsh and Moro Cojo Slough than other regions in all seasons; abundance was also greater in the salt ponds during winter.

Seasonal differences in density of Black-bellied Plover among regions were significant (Fig. 11; $F = 3.47$, df = 12, $P < 0.001$). In winter and spring, density was greatest in Sections A, B, and E of the slough, Gibsons Landing, and Parsons Slough. In fall, density was greater at Gibsons Landing than at any other region. In contrast, abundance of Black-bellied Plover was greatest in all seasons at Parsons Slough, but these abundances could not be tested statistically due to unequal variances.

Density and abundance of dowitchers were significantly different seasonally among regions in the study area (Fig. 12; density: $F = 1.95$, df = 20, $P = 0.004$; abundance: $F = 2.11$, df = 20, $P = 0.008$). During fall and winter, density was greatest at the upper slough and old Salinas River; during spring, density was more consistent throughout most of the study area. In fall and winter, dowitchers were most abundant at the upper slough and Parsons Slough. In spring, however, dowitchers were distributed more evenly among several fully tidal and muted tidal regions.

Density and abundance of Dunlin differed significantly among regions seasonally (Fig. 13; density: $F = 2.49$, df = 18, $P = 0.004$; abundance: $F = 2.60$, df = 18, $P = 0.003$). During winter and fall, when Dunlin were most abundant, density was greatest at North Harbor; however, the greatest abundance was found in the upper slough and Parsons Slough.

Seasonal differences in Western Sandpiper density among regions were not significant; however, there were significant differences in seasonal patterns of relative abundance (Fig. 14; $F = 2.34$, df = 14, $P = 0.01$). Western Sandpiper density was greatest at the upper portion of Elkhorn Slough (Section E) and North Harbor in the winter and spring; in the fall, additional areas with high density included the mid-slough (Sections C and D). Western Sandpipers were most abundant in Section E in all seasons, as well as at Parsons Slough in fall and winter.

Density and abundance of Least Sandpiper differed significantly among regions seasonally (Fig. 15; density: $F = 4.90$, df = 24, $P < 0.001$; abundance: $F = 4.14$, df = 24, $P < 0.001$). During fall and winter, when Least Sandpipers were most abundant, density was greatest in the mid to upper slough (Sections D and E) and North Harbor. In spring, Gibsons Landing also supported a high density of Least Sandpipers. During fall and winter, the upper slough (Section E) had the greatest number of Least Sandpipers; however, in the spring, they were more evenly distributed throughout the study area.

Sanderling density was greatest during winter at North Harbor, whereas in spring and fall, the greatest concentration of Sanderling was at the old Salinas River (Fig. 16). Density was not tested statistically because of unequal variances. Seasonal patterns of relative abundance differed significantly among the regions ($F = 3.02$, df = 10, $P = 0.004$). In winter, the greatest abundance of Sanderling was found at the lower slough (Sections A and B), North Harbor, and old Salinas River. During spring and fall, most Sanderling in the region used old Salinas River.

DISCUSSION

Physical factors associated with shorebird distribution

TIDAL INFLUENCE

Tides dictate availability of intertidal feeding areas for shorebirds. The effect of tidal phase around low tide on shorebird foraging efficiency is not clearly understood and may vary among species, seasonally and geographically. The strong association in the multivariate analysis between flooding tides and greater densities of large shorebirds may be shorebirds' response to prey availability. Burger et al. (1977) and Burger et al. (1996) observed a similar pattern of shorebird use of available feeding areas, with the greatest numbers of feeding shorebirds occurring during flooding tides. Some prey species retreat to greater depths with the receding tide and return to the surface to feed soon before they are covered by the incoming tide (McClusky 1989). Daborn et al. (1993) observed that, with the arrival of a large number of shorebirds, the grazing amphipod, *Corophium volutator*, stopped coming to the sediment surface during the ebbing tide. On the flooding tide, many intertidal polychaetes become more active and thus, more accessible to predators (Evans 1979). Shorebird density may increase with a flooding tide simply because of the diminishing feeding opportunities as mudflats become unavailable until the next low tide.

With increasing duration of mudflat exposure, the substrate becomes drier and many invertebrate species burrow to greater depths to avoid desiccation, becoming less accessible to tactile, probing feeders (Evans 1976). In colder climates, the exposed substrate is more vulnerable to environmental elements such as wind and ambient temperature, potentially enhancing the downward migration of invertebrates (Evans 1976, Burger et al. 1977). Weather may not restrict accessibility of prey in relation to tidal phase in the moderate climate of coastal California as it does in more northerly latitudes during winter.

Interestingly, I found no pattern between tidal phase around low tide and sandpiper density. In general, energy requirements per unit mass increase with decreasing body size because of the increasing surface area to volume ratio and decreasing thickness of plumage (Lasiewski and Dawson 1967, Kendeigh 1970). Furthermore, prey items of small shorebirds are usually smaller than prey of larger shorebirds, increasing the amount of foraging time required to meet energy demands (Goss-Custard et al. 1977a). Some prey species may be accessible throughout the period of mudflat exposure, thus making it profitable for shorebirds to continue foraging until mudflats become unavailable. Goss-Custard et al. (1977b) and Baker and Baker (1973) observed shorebirds feeding during the entire tide cycle when intertidal mudflats were available in winter. Regardless of potential differences in food availability at varying tides, shorebird energy demands during migration and winter may require opportunistic feeding whenever intertidal mudflats are exposed (Baker and Baker 1973).

The negative correlation between tidal amplitude and density of several large shorebird species identified in the multivariate analysis may simply be a result of the increasing available area at low tide with an advancing spring tide. During spring tides (coinciding with full and new moons), tidal amplitude is greater than during neap tides (coinciding with quarter moons), resulting in increased mudflat area exposed at low tide. Lower densities of shorebirds during periods of greater tidal amplitude were most likely because of increased available area.

SEDIMENT GRAIN SIZE

Substrate texture (i.e. grain size and composition) significantly influences benthic infaunal assemblages (Goss-Custard and Yates 1992). I found a strong association between sediment grain size and the density of several shorebird species at Elkhorn Slough. The larger species, Willet, Marbled Godwit, Long-billed Curlew, Black-necked Stilt, and Black-bellied Plover, were associated with coarser-grained sediments, whereas the Western Sandpiper was associated with finer substrates. These patterns suggest that the principal prey items for larger shorebirds are associated with coarser sediment grain size, and for small sandpipers, are associated with finer grain size. Goss-Custard et al. (1991) observed that densities of several shorebird species coincided with the densities of their main prey species. Yates et al. (1993) took this one step further; they found that densities of several shorebird species were correlated with their primary prey species that were, in turn, correlated with particular particle size classes.

Finer substrates, having a greater water retentive capacity than coarser substrates, exhibit a comparably slower rate of desiccation as the tide recedes (Stopford 1951). Consequently, invertebrates may be available to shorebirds for a greater length of time in finer sediments than in a region composed of coarser material (Green and Hobson 1970). Birds with shorter bills, morphologically restricted to foraging in the upper few centimeters of the substrate, may have greater feeding efficiency in finer substrate, particularly with increasing duration of mudflat exposure. Food acquisition also may be directly affected by particle size. Quammen (1982) suggested that coarse particles may hinder shorebird feeding success when prey items similar in size to sand grains were sought. Additionally, more probing attempts, and thus more time, are required to penetrate coarser substrates, further increasing energy cost of feeding efforts, which may be significant for smaller shorebirds (Myers et al. 1980).

Three species of small sandpipers, Western Sandpiper, Least Sandpiper, and Dunlin, were more abundant at the upper reaches of Elkhorn Slough than any other region in the study area during seasons when each of these species was most numerous. Sediment grain size was finer there than in any other region in the study area (Table 1). Ramer (1985) also found that Western Sandpiper density increased with increasing distance from the mouth of Elkhorn Slough.

In contrast to the large proportion of small sandpipers at the head of the slough, large shorebirds were more evenly distributed throughout the main channel and other fully tidal regions in the watershed. Large shorebirds are not as restricted in foraging opportunities or technique in the intertidal environment as are sandpipers, having morphological characteristics that allow access to a greater range of the infaunal assemblage.

SALINITY

The Western Sandpiper was associated with intertidal regions having a small range of salinity that, for this species, represented regions exposed to full tidal exchange. This pattern is most likely a reflection of the salinity tolerances of this species' preferred prey. Black-necked Stilt density, in contrast, was positively correlated with salinity range, suggesting that the stilt's diet encompasses benthic fauna with a broader salinity tolerance. The regions where stilt density was greatest, Moro Cojo Slough and old Salinas River, have both freshwater and tidal influence, resulting in an environment with a broad range of salinity. Salinity at a given location in these regions is influenced by tidal phase and distance from tidal and freshwater sources.

Infaunal species composition is constrained by the local salinity regime (Stopford 1951, Wolff 1969). Salinity in an estuarine environment such as Elkhorn Slough may vary from 33 psu at the mouth to 5 psu at the upper reaches, depending on extent of evaporation, precipitation, and runoff and direction of the tide. Muted tidal regions often become hypersaline in spring and summer, with salinity exceeding 50 psu (pers. obs.). Variation in salinity among available mudflat regions in and surrounding Elkhorn Slough may largely contribute to different invertebrate assemblages, and consequently, variation in shorebird species composition among sites.

Seasonal patterns in migration.—Differences in timing of migration between the most morphologically similar species in this region were distinct during spring migration, when Least Sandpiper abundance decreased substantially in early spring (March) and Western Sandpiper numbers peaked in April. Recher (1966) also observed a staggering of migration peaks in spring between Western and Least Sandpipers on the central California coast, with the majority of Least Sandpipers migrating six to eight weeks before Western Sandpipers. Temporal or spatial segregation among morphologically similar species effectively reduces competition that may occur during periods of high population density, limited food availability, or high physiological demands (e.g. molt).

Seasonal distribution patterns.—Seasonal changes in distribution of some shorebirds suggest that during periods of greater abundance, some species' densities reached carrying capacity in principal regions. When Marbled Godwit abundance was relatively low in spring, high densities of godwits were only found in the lower slough (Fig. 7). When godwit abundance was greatest, during fall and winter, an additional region, North Harbor, also had a high density of godwits, in addition to the lower slough. These two regions had the largest sediment grain size in the study area. It is possible that the lower slough is the preferred feeding area for godwits. When abundance increases, density may reach a maximum in this region, forcing birds to use an area where feeding efficiency may be reduced (Recher 1963, Goss-Custard 1977). Increased bird density may result in greater competition for food resources (Goss-Custard 1979) and consequently, a reduction in feeding efficiency because of time spent in aggressive encounters with other birds (Recher 1963, Burger et al. 1977, Goss-Custard 1977). Barbosa (1997) observed a decrease in intake rate when shorebird density was greater. Erosion of the upper intertidal habitat is most pronounced in the lower slough (see Chapter 3). Continued loss of this habitat may result in displacement of birds to less optimal regions in the watershed or reduction in overall carrying capacity of Elkhorn Slough for shorebirds during periods of greater abundance.

In a similar way, changes in Black-necked Stilt distribution corresponded with changes in annual abundance patterns. When abundance of stilts was relatively low, in spring and winter, only one region, Moro Cojo Slough, supported a high density of stilts. However, when abundance was greatest (during fall) relatively high densities of stilts were found at Moro Cojo Slough and the old Salinas River (Fig. 10). Stilt density may have reached carrying capacity at Moro Cojo Slough during fall, pushing a portion of the population out to another region. I observed juvenile stilts during fall at old Salinas River that may have been forced out of Moro Cojo Slough by adults because of overcrowding. Adult stilts with young are often aggressive toward young that are not their own, which may have accelerated the dispersal of juvenile stilts from Moro Cojo Slough (Robinson et al. 1999).

To identify the existence of inter- or intraspecific competition in a system, one must be able to identify a limiting factor essential to the fitness or survival of the organisms in question. Recher (1966) suggested that available space, rather than available food, was the factor that most limited shorebird abundance and density during migration. Whether shorebirds are space-limited or food-limited during periods of high population density is difficult to quantify. Foraging shorebirds are often patchily distributed on intertidal mudflats, possibly in response to clumped distribution of their prey or as a response to the presence of avian predators (Page and Whitacre 1975). Available foraging space over these energy-rich patches may limit the number of shorebirds that can feed in a region where energy intake is maximized. Food limitation and space limitation may actually be interrelated processes during migration. Resource partitioning through morphological and behavioral differences of shorebirds allows different species to coexist in a food-limited environment. Habitat partitioning serves as a mechanism of coexistence in a space-limited environment.

To better understand shorebird distribution patterns, it is important to understand the distribution of their prey. Little information is available regarding key prey species of shorebirds in Elkhorn Slough and even less is known about the invertebrate assemblages inhabiting peripheral mudflats surrounding the slough. Furthermore, the impact of introduced invertebrates on native infauna has not been examined. In the mid-1970s, the first quantitative study of invertebrate abundance and species distribution in Elkhorn Slough was conducted (Nybakken et al. 1977); this study was duplicated in the early 1990s to assess potential changes in abundance, distribution, and seasonality (Kvitek et al., unpubl. data; see Chapter 3). Species diversity decreased from the mouth to the head of the slough; the greatest density of invertebrates, however, was near the head of the slough (Nybakken et al. 1977). Polychaeta was the most dominant taxonomic group throughout most of the slough; the upper slough was an exception, where Crustacea (*Corophium* sp.) was the most abundant group of infauna. Mollusc abundance and diversity were minimal throughout the slough (Kvitek et al. unpubl. data). Seasonal patterns for taxonomic groups and species richness were weak; both studies indicated that longer-term studies were necessary to identify seasonal patterns that may exist.

Information on shorebird diet in Elkhorn Slough is available for only three species. Ramer (1985) examined stomach contents of Marbled Godwit, Willet, and Western Sandpiper in Elkhorn Slough. Marbled Godwit diet generally consisted of polychaetes (*Capitella capitata*, *Boccardia hamata*, Spionidae) and bivalves (*Gemma gemma*, *Macoma* sp., and *Hemigrapsus oregonensis.* Willet diet largely consisted of crustaceans (*Hemigrapsus oregonensis, Pachygrapsus crassipes*). Western Sandpiper diet included polychaetes (*Capitella capitata*), crustaceans (*Corophium* sp., Harpacticoida), and bivalves (*Gemma gemma*). Additional studies of shorebird diet and feeding strategies are necessary to increase our understanding of seasonal energy demands and use patterns in the region.

Species differences in patterns of distribution in the wetlands of Elkhorn Slough illustrate the importance of heterogeneous mudflat habitat to meet the demands of multiple species. The lack of information of benthic infaunal assemblages and seasonal patterns of availability in mudflats adjacent to the slough, however, limits the ability to assess the relative energetic value of these regions for shorebirds. Future studies evaluating the relationship between physical properties of mudflats and invertebrate assemblages throughout the study area may further explain factors influencing shorebird distribution patterns.

CHAPTER 2.

SHOREBIRD USE OF MUTED TIDAL MUDFLATS

Energy demands of shorebirds generally increase during migration, and are particularly pronounced during spring migration when birds must arrive at their breeding grounds in optimal condition for successful egg production and chick rearing (Davidson and Evans 1988). The intertidal mudflat zone is the primary feeding area for shorebirds during migration and winter (Recher 1966, Ramer 1985). The mixed semi-diurnal tidal regime along the Pacific coast, however, limits the accessibility of invertebrate prey to shorebirds because of daily and seasonal variability in extent of mudflat exposure. Shorebirds exhibit adaptive strategies that enhance their foraging opportunities, particularly during periods of higher energy demands (Evans 1979, Connors et al. 1981, Schneider and Harrington 1981*)*. One important strategy is the use of alternative foraging areas when intertidal regions are inundated at high tide. Alternative foraging habitats include coastal beaches (Burger et al. 1977, Connors et al. 1981), agricultural fields and pastures (Colwell and Dodd 1995, Rottenborn 1996, Long and Ralph 2001), and salt evaporation ponds (Strong 1990).

Mudflats with muted tidal flow, also referred to as peripheral or managed wetlands, can provide foraging areas at high tide when most other mudflat regions are flooded (Furness 1973, Davidson and Evans 1986, Strong 1990, Velasquez 1992, Warnock and Takekawa 1995). Such areas can be critical during periods of food limitation when birds are continually seeking available foraging habitat to maximize food intake (Connors et al. 1981, Skagen and Knopf 1994). Many coastal wetlands have some regions that are tidally restricted, either naturally or more often because of diking and restoration. Few data have been gathered examining the benefit of these regions to shorebirds during migration and winter. To successfully manage coastal wetlands and maximize habitat quality for birds, baseline information of seasonal and daily use patterns of various habitats within the wetland is necessary.

Elkhorn Slough supports one of the largest concentrations of shorebirds in California's coastal wetlands, with as many as 30,000 shorebirds using the region in fall and winter (Page et al. 1992). Elkhorn Slough's wetland complex includes mudflat regions exposed to full tidal influence and mudflats with restricted tidal flow (Fig. 1). The heterogeneity among these mudflat units creates a mosaic of habitats that may provide diverse, alternately available feeding grounds for migrating and wintering shorebirds. I evaluated seasonal shorebird use of mudflats with muted tidal flow in Elkhorn Slough's wetlands and tested the hypothesis that mudflat regions with muted tidal regimes support a greater number of shorebirds during high tide, when other mudflats are flooded, than during low tide.

METHODS

Data Collection.—Muted tidal mudflats evaluated in this chapter included North Marsh, the salt ponds, and Moro Cojo Slough (Fig. 1; see Chapter 1 for description). From 1 March 1999 to 1 July 2000, I surveyed these regions for shorebirds two to three times each month within a six-hour period around low tide and a six-hour period around high tide on the same day. All shorebirds on mudflats were identified to species and counted; birds in flight were not counted unless seen on the mudflat. Behavior was recorded as feeding, roosting, or "other". The number of surveys varied for each region based on availability of the habitat to shorebirds. The greatest number of surveys for a single location was 6 in winter, 8 in spring, and 10 in fall.

Data Analysis.—Data were evaluated for winter, spring, and fall seasons (see Chapter 1). A paired *t*-test was used to compare abundances of each species during high tide and low tide in each region. When variances were heterogeneous, data were square root transformed. A Mann-Whitney *U*-test was used on data that did not meet assumptions after transformations. Alpha level was set at 0.05. Abundances were evaluated rather than density because change in mudflat area between low tide and high tide was minimal. Species that were most abundant, relative to all species using a region, were referred to as "common" for a particular region and evaluated statistically. The salt ponds were surveyed from the outer boundaries in spring to reduce disturbance of the Snowy Plover during the breeding season; therefore, data collected in spring were not included in statistical analyses because visibility was less than optimal.

RESULTS

Shorebirds using peripheral mudflats.—Among the small shorebirds, Dunlin, Western Sandpiper, and Least Sandpiper were common in at least one season in all three regions. Snowy Plover and Semipalmated Plover (*Charadrius semipalmatus*) were common at the salt ponds. Of the larger shorebirds, Black-necked Stilt (*Himantopus mexicanus*) and American Avocet were common in at least one season in all regions. During at least one season, Marbled Godwit was relatively abundant at North Marsh, dowitchers (Long-billed and Short-billed Dowitchers were not differentiated) were common at North Marsh and Moro Cojo Slough, and Black-bellied Plover was common at the salt ponds.

In all seasons, the most abundant shorebirds using peripheral mudflats were small sandpipers. This may be a reflection of overall species composition in the area; small sandpipers constituted more than two-thirds of all shorebirds in Elkhorn Slough wetlands during fall (77%) and winter (68%), and nearly two-thirds (65%) of all shorebirds in spring of 1999 (Chapter 1, Fig. 5). A few shorebird species common in Elkhorn Slough's wetlands did not use peripheral mudflats, including Willet, Long-billed Curlew, and Sanderling.

High tide vs. low tide use.—At North Marsh, all sandpiper species combined ("peeps") were significantly more abundant at high tide than low tide in all seasons, with greatest numbers in the fall exceeding 8,000 birds during high tide (Fig. 17; fall: $t = 14.97$, df = 6, $P < 0.001$, winter: $U = 16.0$, df = 3, $P = 0.02$, spring: $t = 3.69$, df = 5, $P = 0.014$). Sandpipers in North Marsh often were not identified to species because of insufficient visibility. Among the larger shorebirds, Marbled Godwit was significantly more abundant at high tide during fall and winter (fall: $t = 2.78$, df = 10, $P = 0.02$, winter: $U = 16.0$, df = 3, $P = 0.014$) and dowitchers were more abundant during high tide in winter ($t = 4.34$, df = 3, $P = 0.023$). Counts of Black-necked Stilt and American Avocet were not significantly different between high and low tide.

At Moro Cojo Slough, shorebird abundance was greatest during winter (Fig. 18). Small sandpipers were most abundant during high tide in fall and winter (fall: $U = 78.5$, df = 9, $P = 0.021$, winter: $U = 16.0$, df = 3, $P = 0.018$), with Least Sandpiper the most common sandpiper during those seasons. In spring, however, the Western Sandpiper was the most abundant sandpiper, with fairly consistent numbers at high and low tide. For the most part, the larger shorebird species that commonly used this region were consistently present throughout high and low tide, with a few exceptions during winter. There were fewer avocets and dowitchers at low tide in the winter (avocet: $t = 3.65$, df = 3, $P = 0.035$; dowitcher: $U = 16.0$, df = 3, $P = 0.02$). Stilts and avocets nest along the banks of Moro Cojo Slough; thus, similar numbers at high and low tide were not surprising during the spring.

At the salt ponds, abundance of Dunlin, Western Sandpiper, and Least Sandpiper was significantly greater at high tide in fall and winter (Fig. 19; fall: Dunlin: $U = 25.0$, df = 4, $P = 0.005$, Western Sandpiper: $U = 25.0$, df = 4, $P = 0.005$, Least Sandpiper: $t = -11.1$, df = 4, $P < 0.001$; winter: Dunlin: $U = 9.0$, df = 2, $P = 0.037$, Western Sandpiper: $U = 9.0$, df = 2, $P = 0.037$, Least Sandpiper: $t = -7.24$, df = 2, $P = 0.019$; spring not analyzed). The greatest count of sandpipers during high tide was more than 12,000 individuals near the end of January. The Semipalmated Plover was more abundant at high tide in winter and fall (winter: $U = 9.0$, df = 2, $P = 0.037$; fall: $U = 22.5$, df = 4, $P = 0.019$); Black-bellied Plover was more abundant at high tide during fall ($U = 25.0$, df = 4, $P = 0.008$). Black-necked Stilt and American Avocet were the most common larger shorebird species in the salt ponds. I did not find a significant difference in their abundance between high and low tide in winter or fall.

Behavior.—Among the larger shorebird species that commonly used muted tidal regions (Marbled Godwit, American Avocet, and Black-necked Stilt), more than 50% of each species were observed feeding at high tide in all three regions (Fig. 20); the others were roosting. More than 50% of dowitchers were observed feeding in North Marsh and 45% in Moro Cojo Slough.

Among the sandpipers, more than 70% of each species (Dunlin, Western Sandpiper, Least Sandpiper) were roosting in the salt ponds at high tide (Fig. 20; spring surveys not included). At North Marsh, of more than 64,000 “peeps” counted (all sandpipers combined), 65% were observed roosting at high tide. At Moro Cojo Slough, of more than 15,000 peeps, 51% were roosting and 49% were feeding at high tide. More than 90% of Western Sandpipers using the Moro Cojo Slough at high tide, however, were feeding.

Among the plovers, all three species (Black-bellied Plover, Semipalmated Plover, and Snowy Plover) were only common at the salt ponds of the three muted tidal areas evaluated. The majority of Black-bellied Plovers (94%) and Snowy Plovers (81%) were observed roosting at the salt ponds at high tide, whereas 27% of Semipalmated Plovers were roosting and 73% were feeding.

DISCUSSION

Importance of muted tidal regions for shorebirds.—Muted tidal mudflats provide foraging opportunities for shorebirds during periods of high energy demand (Furness 1973, Davidson and Evans 1986, Weber and Haig 1996). During migration and winter, mudflat habitat with restricted tidal flow was clearly an important component of Elkhorn Slough’s wetlands for several shorebird species. Use of Elkhorn Slough’s peripheral mudflats at high tide emphasizes their valuable role for shorebirds in a coastal wetland system when intertidal mudflats are unavailable.

The value of peripheral mudflats for shorebirds is largely dependent upon their proximity to intertidal feeding grounds. The less time spent in transit between foraging areas and roosting sites at high tide, the less energy is expended in transportation costs and time that could be spent feeding or resting. High tide roosts also provide a place for preening. Feather maintenance is critical, particularly during migration, to ensure efficient flight and insulation. Brennan et al. (1985) observed Dunlins in constant flight for up to two hours during high tide in coastal Washington and suggested this behavior may have been a response to lack of suitable high tide habitat. Farmer and Parent (1998) found that the more disconnected the wetland complex was, the less likely Pectoral Sandpipers were to move among the various foraging regions, probably because of the energetic costs of transportation. They suggested that the more disconnected the wetland complex, the less energetically beneficial is the area for shorebirds, and the shorter the period that migrating birds will reside in the area.

Muted tidal mudflats can provide an additional source of food that may be essential for birds to meet their daily energy demands. Intertidal mudflat exposure varies seasonally on the Pacific coast. During fall, the average height of low tide is greater than in spring, resulting in reduced mudflat exposure. Additionally, the lowest low tide of the two low tides within a day occurs at night.

Consequently, substantially less mudflat area is available to shorebirds for foraging during daylight hours in fall than in spring. The additional foraging opportunity that muted tidal regions provide may reduce mortality rate during energetically demanding periods. Peripheral wetlands also may provide valuable foraging habitat at low tide for some shorebird species. Black-necked Stilts and American Avocets used peripheral mudflats surrounding Elkhorn Slough at all tides in all seasons, indicating that these areas provided a source of food and a resting place. Weber and Haig (1996) found a greater concentration of shorebirds using managed wetlands than natural coastal mudflats, coinciding with greater invertebrate density.

Muted tidal regions also can provide greater protection from human disturbance than other high tide roosts, such as coastal beaches. The muted tidal regions in this study were closed to human access, allowing birds to feed and rest with minimal disturbance. Birds on beaches expend additional energy when flushed by humans and dogs, and lose much of the benefits that a high tide roost can provide as a place for rest between foraging bouts in the intertidal (Brown 1996). Peripheral mudflats also may provide more protection from wind than coastal beaches, which usually offer little refuge from environmental elements.

Regional characteristics and value for shorebirds.—Elkhorn Slough wetlands provide several foraging alternatives during high tide that help shorebirds meet their energy demands and serve as roosting areas when intertidal feeding areas are flooded. In all of the muted tidal regions, salinity varied from brackish to hypersaline, depending on amount of rainfall and evaporation and amount of tidal flow allowed into the region (based on the tide gate adjustment).

North Marsh was an important feeding and roosting area, particularly for sandpipers during fall and winter. The reduced tidal amplitude provided shorebird foraging and roosting habitat at high tide. Management of water levels in this region varied seasonally depending on the number of shorebirds in the area, amount of rainfall expected, and amount of algae on the water surface. During late spring, summer, and early fall, a thick layer of algae (*Ulva* sp. and *Enteromorpha* sp.) formed on the water surface, providing an alternative feeding and roosting "substrate" for small shorebirds. Water level could be maintained at a greater depth when algae was present, providing deeper water for other birds such as ducks and herons, and still supporting short-legged species such as Western and Least Sandpipers. The presence of algal mats on the substrate may have increased foraging success for some shorebird species. Allen (1992) found a greater number of amphipod crustaceans within algal mats overlying mudflats than on mudflats without algae.

Moro Cojo Slough provided nesting habitat for three of the four shorebird species that breed in this region (Black-necked Stilt, American Avocet, and Killdeer), and during high tide was an important roosting and feeding area for sandpipers during winter and migration. Moro Cojo Slough provided a variety of foraging habitats. Stilts and avocets foraged in the channel; Least Sandpipers used the channel edge and trampled pickleweed habitat lining the slough border; and Killdeer fed on mudflats, in pickleweed, and in the adjacent rangeland. Water level in Moro Cojo Slough was not managed during any season; the region became unavailable for foraging and roosting during periods of heavy rainfall in the winter. Salinity at the lower end of the slough was generally that of seawater. Salinity further up the channel ranged from hypersaline to nearly freshwater, creating a variety of aquatic environments that likely supported different assemblages of invertebrates.

The salt ponds were important to sandpipers during winter and migration. Slightly higher in elevation than Elkhorn Slough's mudflats, the salt ponds served as an important refuge at high tide. Strong (1990) observed similar use of the region in the late 1980s. In San Francisco Bay, salt pond levees were important roosting grounds at high tide for Western Sandpipers (Warnock and Takekawa 1995). During fall and winter, deeper water levels in the salt ponds provided a safe roost from predators for various avian species, including the endangered California Brown Pelican (*Pelecanus occidentalis*). Managing water level year-round in this region would likely improve habitat for a variety of avian species.

Shorebird species that did not use muted tidal mudflats, or that used them inconsistently, included Willet, Marbled Godwit, Long-billed Curlew, and

Sanderling. These species tend to use coastal beaches at high tide and at low tide, which may partly explain their restricted use of muted tidal regions.

Management considerations.—Water depth in muted tidal regions is influenced by rainfall, evaporation, and tide gate adjustment, and can be manipulated to provide habitat for different avian species. Knowledge of seasonal occurrence patterns of migrating birds is necessary in planning water level management. Minor adjustments in water depth can make a tremendous difference in habitat availability to small shorebirds such as sandpipers (Safran et al. 1997, pers. obs.). During this study, I began adjusting the tide gates in North Marsh, in coordination with the Elkhorn Slough Reserve, to create more suitable habitat for a variety of avian species. My goal was to provide habitat for the most abundant species in the watershed during migration, the sandpipers, while also providing habitat for other avian species, including longer-legged shorebirds, herons, pelicans, and ducks. Because of the variation in marsh topography, any given water level provided a variety of water depths to suit a broad assemblage of species. Similarly, Boettcher et al. (1994) found that variation in bottom topography and gradual flow of water into an impoundment created a variety of microhabitats.

In addition to depth considerations, the degree of tidal exchange in a muted tidal region also influences other important factors that delimit invertebrate species composition, including amount of dissolved oxygen and salinity. Salinity is additionally influenced by rainfall and ambient temperature. Salinity strongly dictates the diversity and abundance of invertebrate species (Wolff 1969), and may largely determine whether a region is important for feeding or roosting. Velasquez (1992) studied waterbird use of artificial saltpans and found that large shorebirds predominantly fed in saltpans with lesser salinity where the benthic infauna was similar to the intertidal assemblage. Small shorebirds, in contrast, primarily fed in saltpans with greater salinity, where amphipods and chironomid fly larvae were most abundant. Reduced water level fluctuation, generally associated with muted tidal regions, also may be a desirable habitat trait for stilts and avocets. Boettcher et al. (1995) found that as water level fluctuations increased in brackish water impoundments, avocet numbers decreased. Maintaining a relatively stable water level in muted tidal regions also may serve other purposes, including reduction of the mosquito population (P. Ghormley, pers. comm.) and reduced risk of flooding nests during spring and summer.

Species diversity is generally a reflection of habitat diversity (MacArthur and MacArthur 1961, Ricklefs 1979). Mudflats with muted tidal flow provide an additional habitat dimension within a wetland ecosystem. An understanding of the essential habitat components that constitute a species' seasonal requirements is necessary to explain its presence or absence in a region. With knowledge of shorebird habitat use patterns, seasonal requirements, and regional habitat limitations, peripheral mudflats can be effectively managed to optimize habitat quality for shorebirds and a variety of other waterbirds including pelicans, waterfowl, herons, and egrets. Mudflats with muted tidal influence provide excellent opportunities for habitat enhancement for shorebirds, particularly during periods of greater energy needs.

CHAPTER 3.

PATTERNS OF SHOREBIRD DISTRIBUTION IN A CHANGING ENVIRONMENT: EFFECTS AFTER 20 YEARS OF EROSION AT ELKHORN SLOUGH

Coastal wetlands along the Pacific Flyway are critical for shorebird survival during migration and winter (Senner and Howe 1984, Page et al. 1992). As shorebirds migrate to and from breeding and wintering grounds, staging areas (or stopovers) provide a place for feeding and resting, enabling shorebirds to complete their journey. Birds need an abundant caloric supply to meet the demands of homeothermy, but food is usually seasonally abundant at any one location. Natural selection favors arrival at staging areas when prey is most abundant, thereby increasing survivorship and reproductive success. Shorebird migration in coastal regions relies upon the persistence of staging areas with adequate food resources (Myers et al. 1987).

Since the turn of the century, more than two-thirds of coastal wetlands in California have been developed (Speth 1979). Of California's remaining coastal wetlands, 11 sites support concentrations of shorebirds exceeding 1,000 individuals during migration and winter (Page et al. 1999). These sites, and numerous other smaller wetlands in the state, form a chain of stopovers along the migratory corridor of the Pacific coast. Elkhorn Slough supports one of the largest concentrations of shorebirds in California's coastal wetlands, with as many as 30,000 shorebirds using the region in fall and winter (Page et al. 1992). In 2000, Elkhorn Slough received international recognition as a site of regional importance for shorebirds by the Western Hemisphere Shorebird Reserve Network (WHSRN).

Substantial alterations in habitat composition along the main channel of Elkhorn Slough are largely attributed to human-induced changes during the last half century (Oliver et al. 1990, Malzone 1999, Brantner 2001). The construction of Moss Landing Harbor in 1947 immediately increased tidal volume and current velocity in the slough (Malzone 1999, Brantner 2001). Most coastal wetland systems are low-energy depositional systems (Dyer 1979), as Elkhorn Slough was before channel excavation in 1947 increased the cross-sectional opening of the slough mouth 5-fold (Crampton 1994, Philip Williams and Assoc. 1992). The increase in volume of seawater entering the slough following excavation initiated erosion, which has consequently transformed the slough from a quiet, shallow estuarine embayment with little tidal influence to a tidally flushed, well-mixed estuary (Nybakken et al 1977, Schwartz et al. 1986). Erosion has been further accelerated because of intentional and unintentional destruction of dikes around historic salt marshes throughout the slough between 1980 and 1987, resulting in the return of approximately 840 acres to tidal flow. Consequently, the volume of water moving in and out of the system (tidal prism) increased by 33% (Malzone 1999).

The effects of these changes in habitat structure on shorebirds are unknown. A comparison of present shorebird distribution with past distribution (Ramer 1985, Ramer et al. 1991) in Elkhorn Slough may indicate effects of erosion on shorebird use of the slough. I compared shorebird abundance and distribution along the main channel of Elkhorn Slough in the late 1970s (Ramer 1985) with the late 1990s (my data). I hypothesized that density of shorebirds along the main channel of Elkhorn Slough changed since the late 1970s due to alterations in habitat structure (e.g. changes in channel bathymetry, mudflat to salt marsh ratio, and sediment grain size). I expected increased density of shorebirds in regions where salt marsh had substantially deteriorated, increased density in regions where intertidal erosion was greatest, and decreased density of sandpipers in regions where sediment grain size had increased (Chapter 1).

METHODS

Data Collection.—From 1 March 1999 to 1 July 2000, shorebird surveys were conducted two to three times each month in the main channel of Elkhorn Slough. Shorebird surveys occurred within a six-hour period around low tide. I surveyed the slough alone or with one assistant. The slough was divided into five segments of unequal area, duplicating Ramer (1985) and allowing for comparison with her data (Fig. 1).

Substrate grain size was determined in each region from mud samples collected in the summer of 2000 (Chapter 1). Sediment samples from three locations between the mouth and Kirby Park were evaluated and compared with samples from 1974 to 1976 (see Nybakken et al. 1977).

Data analysis.—Area of exposed mudflats at different tide heights was determined for calculations of density (Chapter 1). To estimate area for the 1970s data set, mudflat area was calculated from a georectified 1980 photo in which time and predicted tide height were known; then, mudflat area for the remaining three tide height increments was calculated based on proportional differences among tide heights in the photos of year 2000. Data from different years were statistically evaluated before pooling (2-factor ANOVA, factors: location and year).

The most common shorebird species that use Elkhorn Slough were evaluated for changes in distribution along the main channel: Willet, Marbled Godwit, Long-billed Curlew, American Avocet, Black-bellied Plover, dowitchers (Long-billed and Short-billed combined), Dunlin, Western Sandpiper, Least Sandpiper, and Sanderling. Data were evaluated for winter, spring, and fall seasons (Chapter 1).

A two-factor ANOVA was used to identify changes in distribution within each season between the 1970s and the 1990s. The factors were location (4 sections of the slough, between the mouth and Kirby Park) and time (1978-79, 1999-2000). Sufficient data for Section E (Kirby Park to Hudsons Landing) was not available from the 1970s; thus, this section was not included in this evaluation. Density (number of birds/ha) and abundance (total numbers) were the dependent variables. If variances were unequal, data were square root transformed. If variances were still unequal after two transformations, data were not statistically analyzed. I was only interested in the interaction between the factors to identify changes in density among slough sections between time periods; thus, main effects were not evaluated. Ryan's Q test was used to perform unplanned multiple comparisons when significant interactions were identified (Day and Quinn 1989). When sample sizes between the 1970s and 1990s were unequal, a number of samples equivalent to the smaller data set were randomly selected from the larger sample set three times; each set was then tested against the smaller data set.

A one-factor ANOVA was used to evaluate shorebird densities among slough sections within each time period; the entire slough channel (slough mouth to Hudsons Landing) was surveyed in the 1990s data set; Sections A through D were evaluated for the 1970s. Ryan's Q test was used to perform unplanned multiple comparisons when significant differences were found (Day and Quinn 1989). Kruskal-Wallis one-way ANOVA was used when variances were not equal after square root transformation. Games and Howell test (Day and Quinn 1989) was used to perform unplanned multiple comparisons on non-parametric tests when significant differences were found.

A one-sample *t*-test was used to identify significant changes in sediment grain size along the main channel between the late 1970s and the late 1990s. Sediment data from Lindquist (1998; collected in 1998) were included in the 1990s data set. Alpha level for all statistical tests was 0.05.

RESULTS

Distribution of large shorebird species changed between the 1970s and 1990s in at least one season, with significantly greater densities in the 1990s in the lower slough than in the 1970s, relative to other regions along the main channel (Fig. 21). During winter and spring of 1970s, Willets were evenly distributed among the sections, whereas in 1990s, Willet density in these seasons was greatest in the lower slough (winter: $F = 4.79$, df = 3, $P = 0.007$; spring: $F = 2.87$, df = 3, $P = 0.048$; Fig. 21). I found no change in proportional distribution of Willets between the 1970s and 1990s in spring; however, winter analysis of proportional abundance showed a relative increase in Willets in Section A (lower slough; $F = 3.46$, df = 3, $P = 0.032$). During fall of 1970s, Marbled Godwits were evenly distributed throughout the lower and middle slough, with a significantly lesser density near Kirby Park, and Long-billed Curlew density was greatest in the mid-slough. In contrast, densities of godwit and curlew were greatest in the lower slough in fall of 1990s (godwit: $F = 3.67$, df = 3, $P = 0.02$; curlew: $F = 3.80$, df = 3, $P = 0.023$; Fig. 21). No increase in abundance in the lower slough relative to the other slough sections was found between time periods for godwits or curlews.

Among sandpipers and dowitchers, I found significant changes in distribution between time periods for the smallest sandpipers, Western Sandpiper and Least Sandpiper (Fig. 21). In winters of 1970s, Western Sandpiper density was greatest in the mid slough (Section C), compared with an even distribution in Sections A through C and greater density in Section D in winter of 1990s ($F = 10.18$, df = 3, $P < 0.001$). Least Sandpiper density was consistent among sections during winter and fall of 1970s, whereas in the 1990s, the upper slough (Section D) had greater density than all other regions of the slough (winter: $F = 4.52$, df = 3, $P = 0.009$; fall: $F = 6.30$, df = 3, $P = 0.005$). Evaluation of proportional abundance of Western and Least Sandpipers revealed greatest abundance in Section D in the 1990s, relative to other sections, compared to the 1970s, when the greatest abundance was in Section C (Western Sandpiper: $F = 6.78$, df = 3, $P = 0.002$; Least Sandpiper: $F = 4.83$, df = 3, $P = 0.009$). No significant changes in relative density between time periods were found for dowitchers and Sanderling in any season (Fig. 21).

In the analysis of 1990s distribution of the entire length of the slough (Sections A through E), densities of dowitchers, Western Sandpiper, and Least Sandpiper were significantly greater in Section E (head of the slough) than in all other sections in at least one season (dowitchers – winter: $F = 10.60$, df = 4, $P < 0.001$; Western Sandpiper – winter: $F = 17.04$, df = 4, $P < 0.001$, fall: $F = 15.17$, df = 4, $P < 0.001$; Least Sandpiper – fall: $F = 7.90$, df = 4, $P < 0.001$; Fig. 21). Marbled Godwit density was greater in Section A (mouth of the slough) than in all other sections during fall ($F = 14.84$, df = 4, $P < 0.001$; Fig. 21).

Sediment grain size increased significantly in all 3 locations between 1970s and 1990s (Table 2; lower slough (Section A): $t = 2.8$, df = 9, $P = 0.021$; Dairies (Section B): $t = 23.03$, df = 3, $P < 0.001$; Kirby Park (boundary between Section D and Section E): $t = 4.60$, df = 8, $P = 0.002$).

DISCUSSION

As Elkhorn Slough continues to erode, habitat availability for migrating and wintering shorebirds is changing. In the 1980s, dike and levee breaches caused an increase in tidal volume (43%) and tidal habitat surface area (48%) in the slough, thus enhancing current velocity and tidal scour (Malzone 1999). In the mid-1990s, Malzone (1999) determined that the entire length of the slough channel was widening; the lower intertidal habitat was eroding at a greater rate than the upper intertidal and subtidal habitats, with the greatest erosion rate in the mid-slough (Sections B and C; $8.4 \times 10^4 m^3/yr$). Upper intertidal erosion was greatest in the lower slough (Section A; $1.8 \times 10^3 m^3/yr$) and subtidal habitat loss was greatest in the upper slough (Section E; $1.2 \times 10^3 m^3/yr$). The greatest structural changes occurred in the lower to middle slough (Sections A through D), with loss of lower intertidal habitat and temporary infilling of subtidal habitat with sediment from the upper slough. Because sediments in the upper slough are porous and less dense than sediments in the lower reaches of the slough, they are more easily eroded (Malzone 1999). In 2001, Brantner (2001) determined that cross-sectional area of the channel in the lower slough had increased by an average of 20% since 1993; in contrast, cross-sectional area in the mid-slough had increased by an average of only 4%. Brantner (2001) suggested that the substantial disparity in erosion rates was attributed to the tremendous volume of water flowing in and out of Parsons Slough (30% of Elkhorn Slough's total volume), located downstream of the middle slough.

In the 1990s, there were significantly greater densities of large shorebird species (Willet, Marbled Godwit, and Long-billed Curlew) in the lower slough (Section A) relative to the middle sections (Sections B, C, and D). This pattern did not exist in the 1970s, and may be the result of a reduction in intertidal habitat in the lower slough since that time. No significant increases in abundance were found in the lower slough relative to the other sections in the 1990s, indicating that the observed increases in density were due to loss of mudflat habitat rather than a shift in proportional distribution since the 1970s. When Marbled Godwit abundance was relatively low in spring, high densities of godwits were only found in the lower slough (Fig. 7). When godwit abundance was greatest, during fall and winter, an additional region, North Harbor, also had a high density of godwits, in addition to the lower slough. It is possible that the lower slough is the preferred feeding area for godwits. When abundance increases, density may reach a maximum in this region, forcing birds to use an area where feeding efficiency may be reduced (Recher 1963, Goss-Custard 1977). Erosion of the upper intertidal habitat is most pronounced in the lower slough. Continued loss of this habitat may result in greater shorebird densities and consequently, displacement of birds to less optimal regions in the area or reduction in overall carrying capacity of Elkhorn Slough for shorebirds during periods of greater abundance.

Increasing bird density may result in greater competition for food resources (Goss-Custard 1979) and consequently, reduced feeding time because of aggressive encounters with other birds (Recher 1963, Burger et al. 1977, Goss-Custard 1977). Recher (1963) found that shorebird aggression was most pronounced during migration when population densities were greatest. He observed increased aggressive interactions among Western Sandpipers when limited space precluded the maintenance of *individual distance,* defined by Recher (1963) as "the area around each individual shorebird within which other individuals are not tolerated". Consequently, some birds may move to less suitable areas where feeding efficiency may be reduced, risk of predation greater, or distance to roost site greater, and ultimately result in greater shorebird mortality (Goss-Custard 1979). An additional outcome of greater bird density is its potential effect on prey availability. Goss-Custard (1970) found that greater shorebird density caused invertebrates to become less active or burrow deeper into the substrate as a response to increased shorebird activity on the substrate surface.

Visual feeders, such as Black-bellied Plovers, may be particularly sensitive to greater shorebird densities because of the large search area required by each individual for locating their prey (Pienkowski 1983). Black-bellied Plovers generally feed on the upper reaches of mudflats, whereas most tactile feeders are usually closer to the water line (Recher 1966, Gerstenberg 1979); thus, competition for space between plovers and probers would most likely not be significant.

Continued loss of intertidal habitat will reduce the overall carrying capacity of the region as a migration stopover and wintering grounds for shorebirds. Malzone (1999) surmised that the progression of tidal scour has lead to a much reduced upper intertidal, a much broader, deeper lower intertidal, and a wider subtidal zone (Fig. 22). Brantner (2001) determined that maximum channel depth throughout the slough had increased by an average of 12% in eight years. As erosion continues, progressively less mudflat habitat will be exposed at a given tide height as mudflat elevation decreases, reducing shorebird foraging habitat and the period of time that mudflats are available for feeding (Fig. 22). Lindquist (1998) found that erosion in Elkhorn Slough had directly impacted invertebrates; density and diversity of invertebrates had decreased since the 1970s, and was attributed to loss or alteration of habitat.

In addition to changes in slough channel bathymetry, salt marsh habitat also has been altered, largely due to anthropogenic influences, most notably, the excavation of the channel mouth in the 1940s (Lowe 1999). Since the 1970s, the most significant change in salt marsh cover occurred between 1989 and 1993, following the Loma Prieta earthquake. During that period, salt marsh cover in the middle and upper slough (Sections C through E) significantly declined, resulting in a substantial increase in bare mud (Lowe 1999). In the 1990s, densities of Western and Least Sandpipers were significantly greater in the upper slough (Section E) relative to all other sections. In contrast, Western Sandpiper density in the 1970s was greatest in the mid-slough (Section C) and Least Sandpiper density was evenly distributed from the mouth to Kirby Park (sufficient data were not available to evaluate shorebird use of the upper slough (Section E) in the 1970s). The increase in mudflat habitat in the upper slough region, derived from degraded salt marsh, combined with a graded increase in sediment grain size along the entire length of the slough (Table 1), may explain this shift of sandpipers to the head of the slough.

Salt marsh provides valuable roosting and foraging habitat for shorebirds as the mudflats become inaccessible on a flooding tide (Stenzel et al. 1976, Ramer 1985, Lowe 1999). Ramer (1985) observed Willet, Marbled Godwit, and Long-billed Curlew in the salt marsh during high tide; some Willets and curlews continued feeding in this habitat during low tide. Salt marsh habitat is an important roost site at night for several shorebird species, including dowitchers, Dunlin, Western and Least Sandpipers (Page et al. 1979). It also provides shelter from inclement weather and predators. The potential effects of loss of salt marsh habitat in Elkhorn Slough are unclear. Is there an optimal salt marsh/mudflat ratio for shorebirds? The formation of mudflat habitat from lost salt marsh may temporarily benefit shorebirds by providing additional foraging areas, but in time, if the substrate continues to erode and subside (Crampton 1994), these regions will only be available at very low tides.

Sediment grain size influences benthic infaunal assemblages and their availability to shorebirds in various ways (Goss-Custard and Yates 1992). Finer substrates, having a greater water retentive capacity than coarser substrates, exhibit a comparably slower rate of desiccation as the tide recedes (Stopford 1951). Consequently, invertebrates may be available to shorebirds for a greater length of time in finer sediments than in substrate composed of coarser material. Furthermore, food acquisition may be directly affected by particle size; Quammen (1982) found that shorebirds spent less time feeding in substrate containing sand, and suggested that coarse particles hindered shorebird feeding success when prey items were similar in size to sand grains; this hypothesis probably only applies to small shorebirds that generally prey on smaller invertebrates than larger shorebirds (Goss Custard 1977b). Substrate penetrability is more difficult in coarser substrates, further increasing energy expenditure and cost of feeding efforts (Myers et al. 1980).

Sediment grain size increased significantly throughout the main channel of Elkhorn Slough since the 1970s (Table 2). Increasing grain size along the main channel may alter invertebrate species composition. As sediments along the entire main channel of the slough coarsen with continued erosion, the mudflats may support fewer suitable prey species for small sandpipers. Greater sandpiper density in the upper slough in the 1990s may be explained, in part, by the increase in grain size throughout the slough since the 1970s, with finest particles at the head of the slough. In the 1970s, mean particle size at Kirby Park was 9.51ø; by the 1990s, mean particle size had increased significantly to 7.87ø (Table 2; note: the smaller the phi value, the larger the particle size). Ferns (1983) documented an immediate decline in shorebird abundance after prolonged high winds and wave action removed fine sediments along with the invertebrate fauna from the Severn Estuary in the British Isles. Goss-Custard and Yates (1992) attributed changes in shorebird distribution over a 13-year span between surveys to changes in sediment composition; he found that shorebird abundance (Dunlin, Black-bellied Plover, and Eurasian Curlew (*Numenius arquata*)) was negatively correlated with amount of sand. If finer sediments in the slough continue to be lost, how will this influence the suitability of Elkhorn Slough for sandpipers, the slough's most numerous shorebirds?

Many shorebirds return faithfully to very specific locations along their migration route. The return rate for Semipalmated Plovers in Massachusetts during fall migration was 72% for 31 banded individuals during a 4-year period

(Smith and Houghton 1984). The return rates (i.e. minimum annual survival rate) for shorebirds at the Tees Estuary in England during fall and winter included 80% Grey Plovers (71 banded), 82% Eurasian Curlews (119 banded), and 91% Sanderling (93 banded; Evans 1981). Such evidence of site fidelity among shorebirds underscores the need to protect traditional stopovers.

Elkhorn Slough is a vital link among several stopover sites along the Pacific flyway. Continued loss of intertidal habitat in Elkhorn Slough may result in redistribution of shorebirds to other regions in the area, and ultimately, reduced carrying capacity overall for shorebirds, particularly during periods of greater abundance. Findings from recent erosion studies in the slough emphasize the need to pursue strategies to reduce the rate of erosion. Persistence of traditional migratory stopovers and wintering grounds such as Elkhorn Slough is essential for shorebirds to maintain sustainable population levels.

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Table 1. Mean sediment grain size in each region of the study area in the Elkhorn Slough wetlands. Grain size is inversely related to phi value, i.e. the larger the grain size, the smaller the phi value (*n*=5).

	mean phi (ø)	SD
North Harbor	3.58	2.17
old Salinas River	4.15	2.07
Elkhorn Slough - A	5.04	1.60
Gibsons Landing	5.62	2.29
North Marsh	6.08	0.56
South Marsh	6.20	0.94
fully tidal salt ponds	6.31	0.80
Strawberry Marsh	6.55	0.39
Estrada Marsh	6.74	0.25
Elkhorn Slough - B	6.80	0.54
Moro Cojo Slough	6.83	1.00
Parsons Slough	6.87	1.03
Elkhorn Slough - D	6.88	0.56
Elkhorn Slough - C	7.21	0.34
Porter Marsh	7.25	0.50
Elkhorn Slough - E	7.45	0.33

Table 2. Comparison of mean particle size (phi) between 1970s and 1990s in Elkhorn Slough. The smaller the phi value, the larger the particle size.

	1970s	1990s
Lower slough	5.27	4.94
Mid-slough	9.11	7.26*
Upper slough	9.51	7.87*

* data from Lindquist (1998)

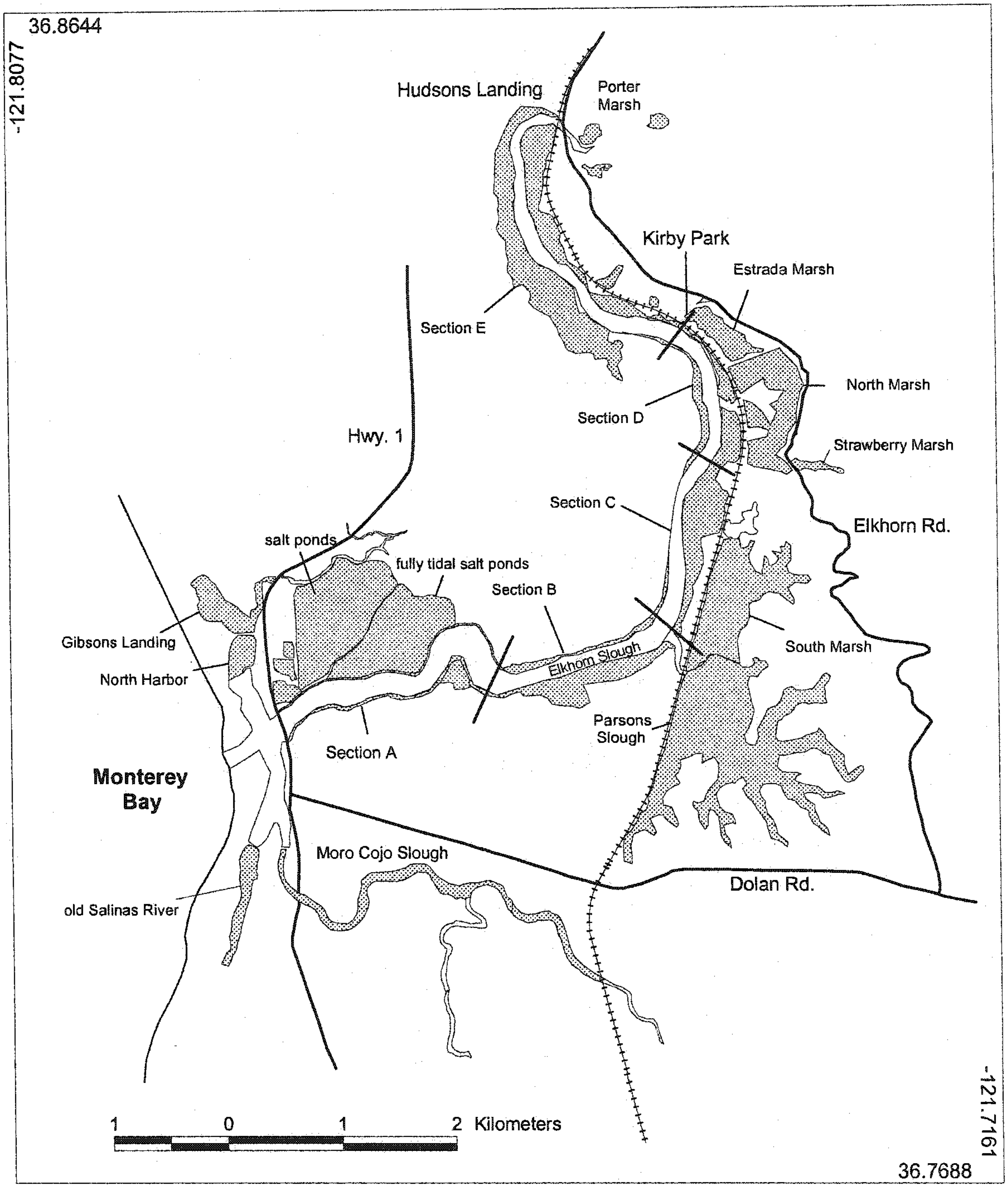


Figure 1. Regions surveyed for shorebirds within Elkhorn Slough's wetlands on Monterey Bay, California from spring 1999 through spring 2000. The main channel was divided into five sections according to Ramer (1985).

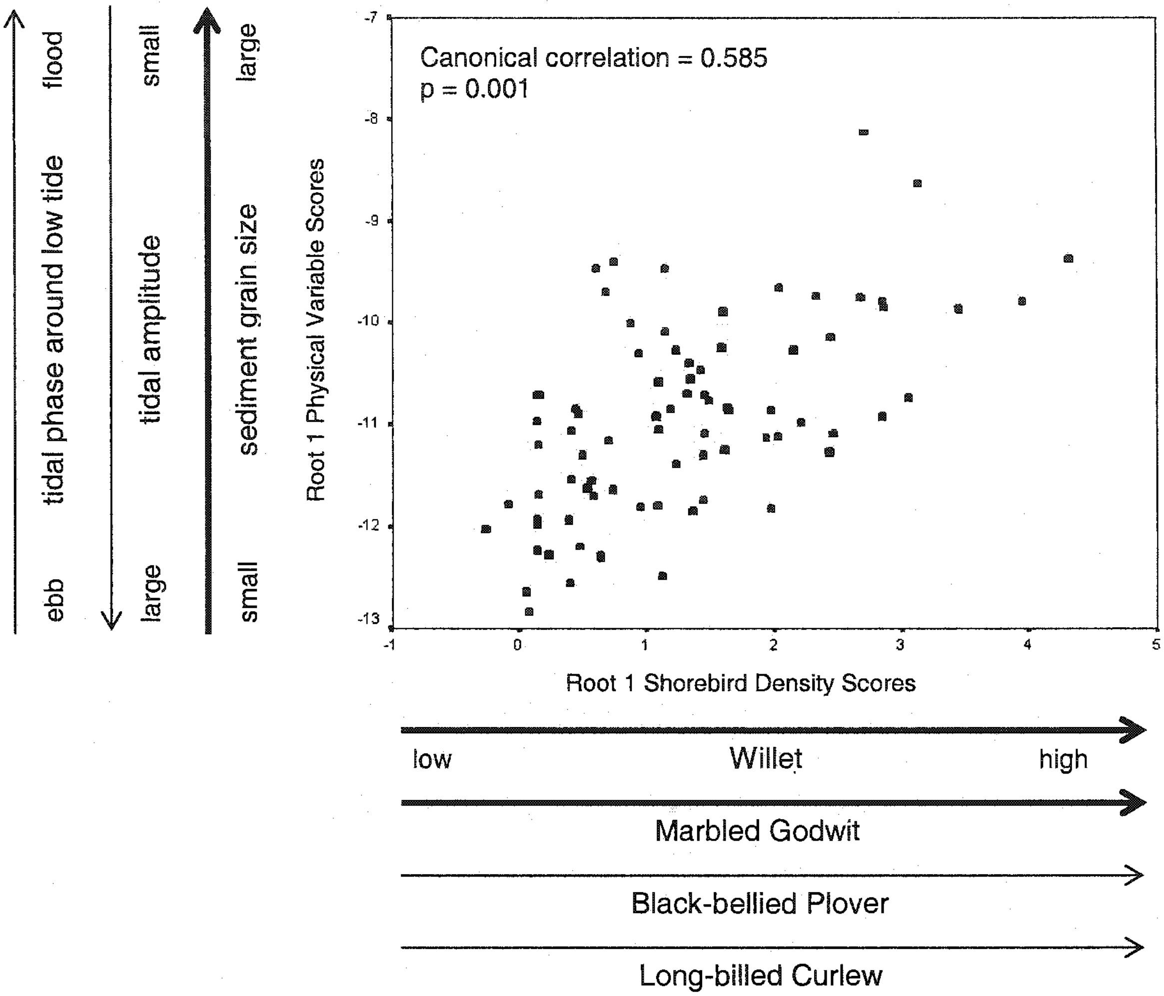


Figure 2. Results of first canonical root pair in winter data set. Variables included in figure were significant (canonical loading ≥ 0.3). Direction of arrow indicates increasingly larger value of variable. Width of line represents strength of significance.

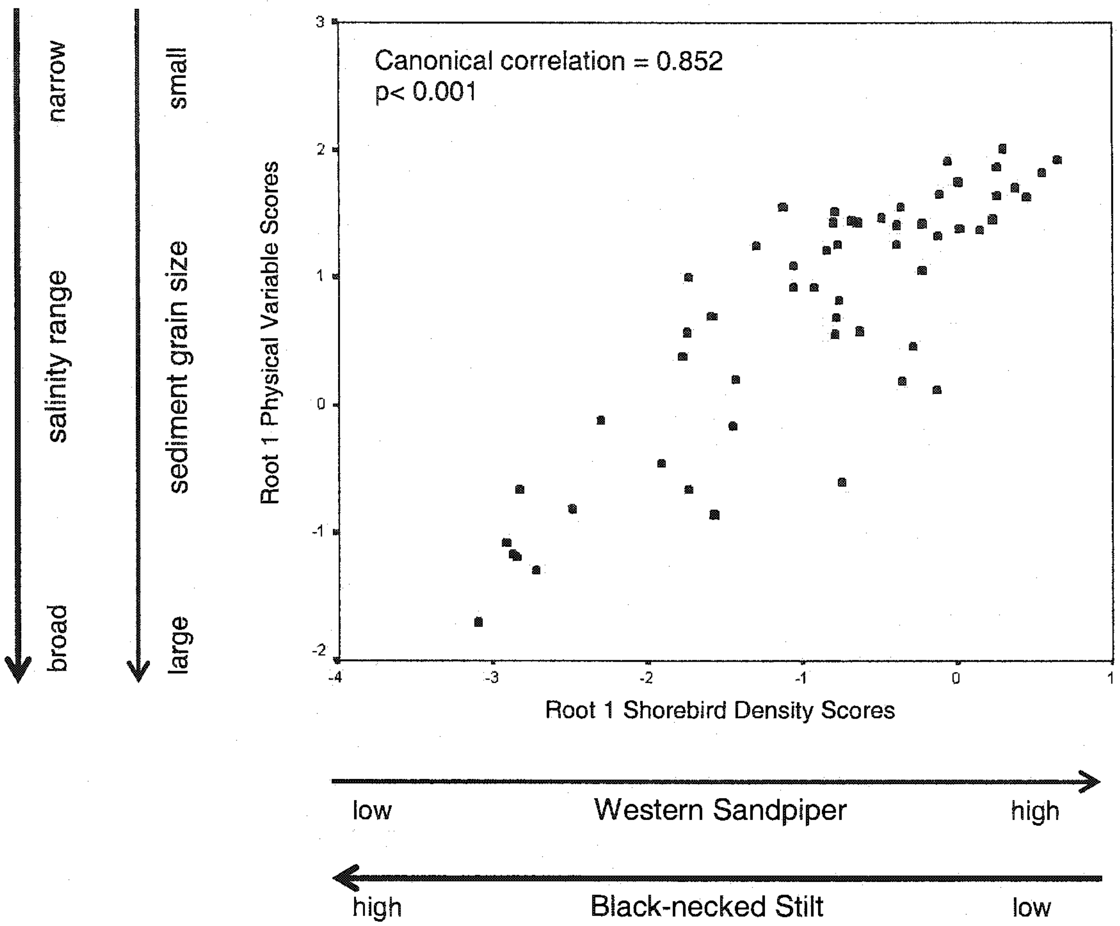


Figure 3. Results of first canonical root pair in fall data set. Variables included in figure were significant (canonical loading ≥ 0.3). Direction of arrow indicates increasingly larger value of variable. Width of line represents relative strength of significance.

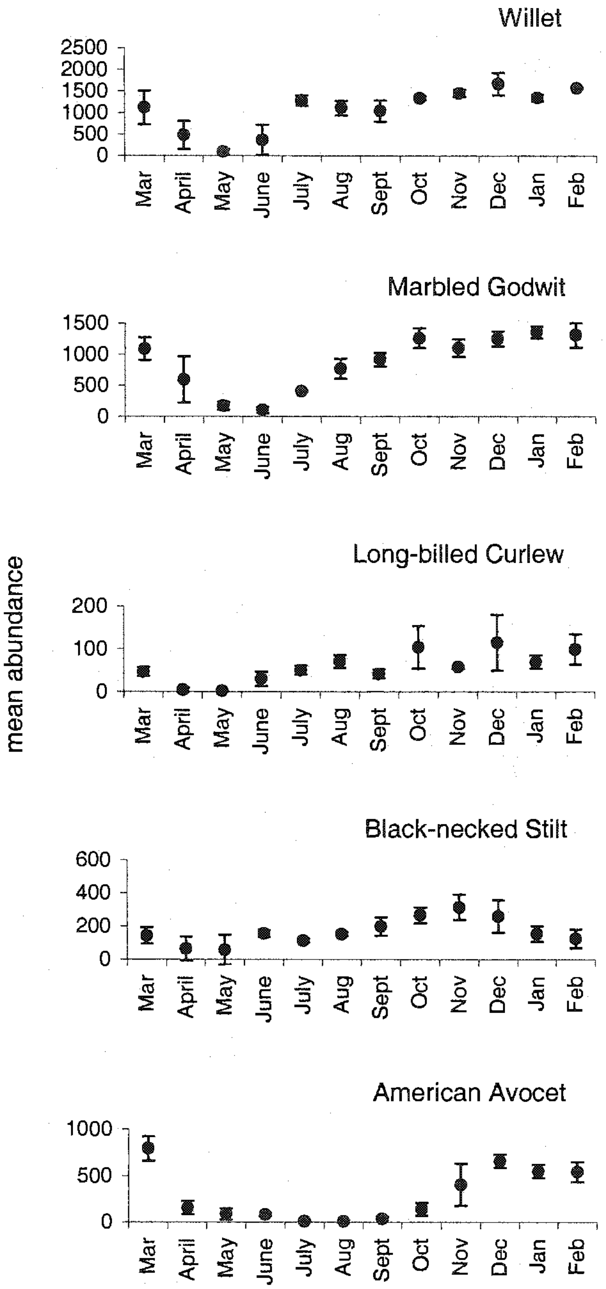


Figure 4. Mean abundance of common shorebird species in Elkhorn Slough's wetlands from March 1999 through February 2000; error bars represent ± one standard deviation. Note differences in y-axis values.

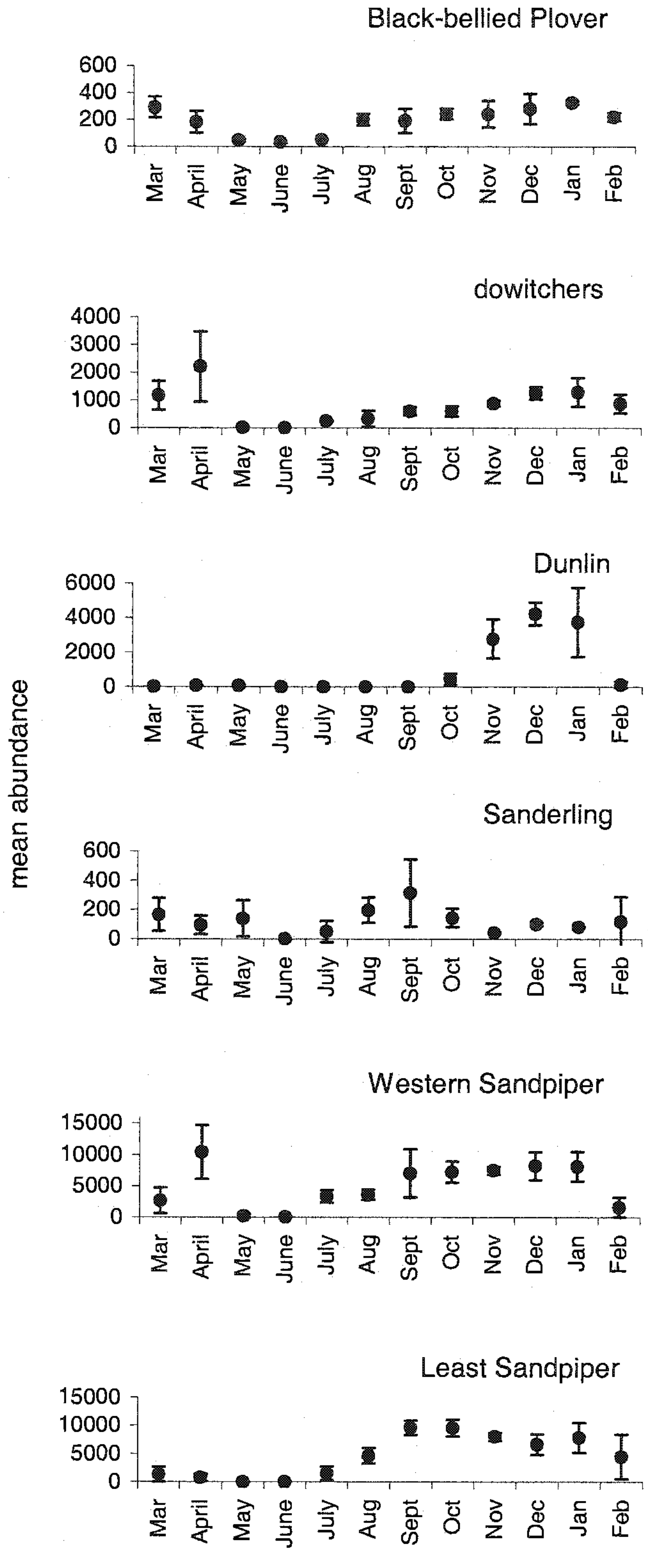


Figure 4 (cont.).

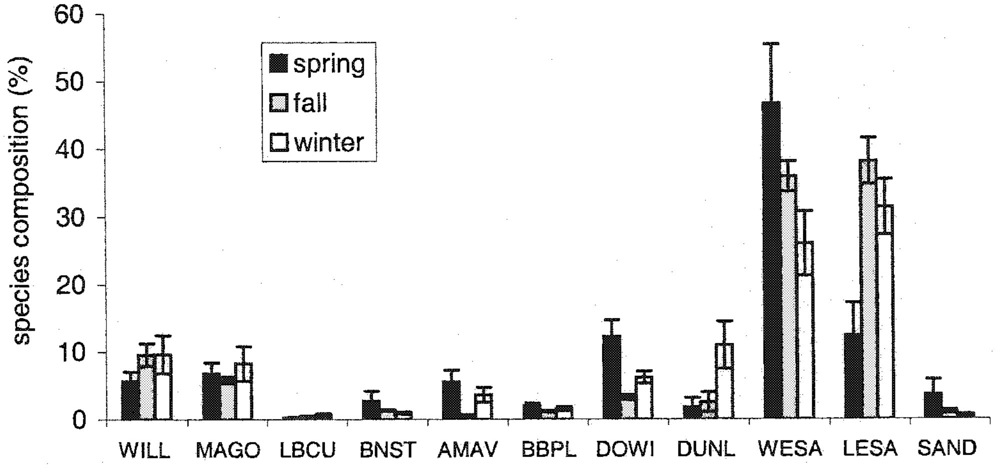


Figure 5. Relative abundance of shorebirds (±SE) in the Elkhorn Slough study area from spring 1999 through winter 2000. See Appendix 1 for species abbreviations.

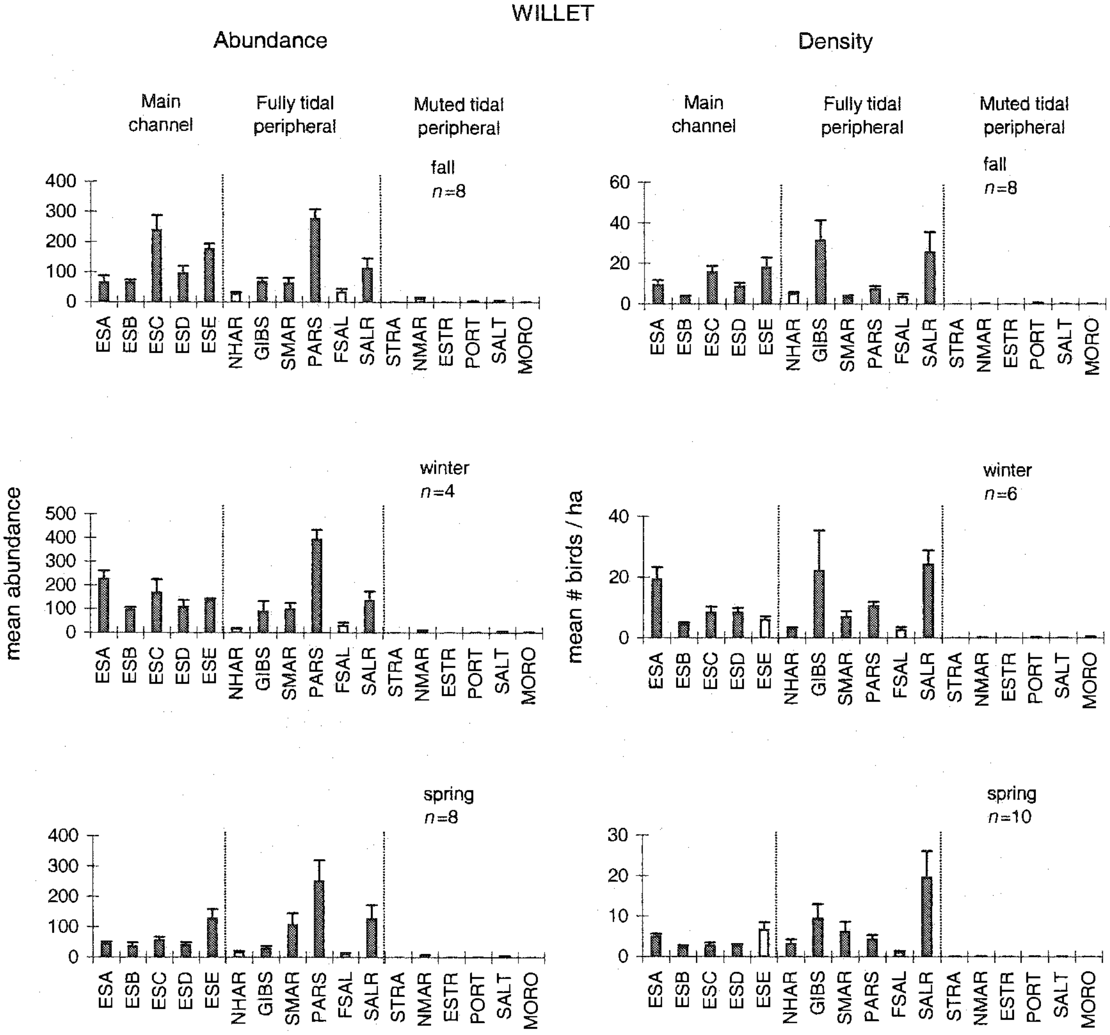


Figure 6. Mean abundance and density (± SE) of Willets in the Elkhorn Slough study area based on spring 1999 through spring 2000 surveys. Shaded bars met criteria for statistical analysis (see Methods). ESA = Elkhorn Slough Sec. A (mouth) through ESE = Elkhorn Slough Sec. E (head); NHAR = North Harbor; GIBS = Gibsons Landing; SMAR = South Marsh; PARS = Parsons Slough; FSAL = fully tidal salt ponds; SALR = Old Salinas River; STRA = Strawberry Marsh; NMAR = North Marsh; ESTR = Estrada Marsh; PORT = Porter Marsh; SALT = salt ponds; MORO = Moro Cojo Slough. Regions to the right of SALR are muted tidal regions; regions to the left of SALR, including SALR, are fully tidal. See Figure 1 for location of regions. Note differences in y-axis values.

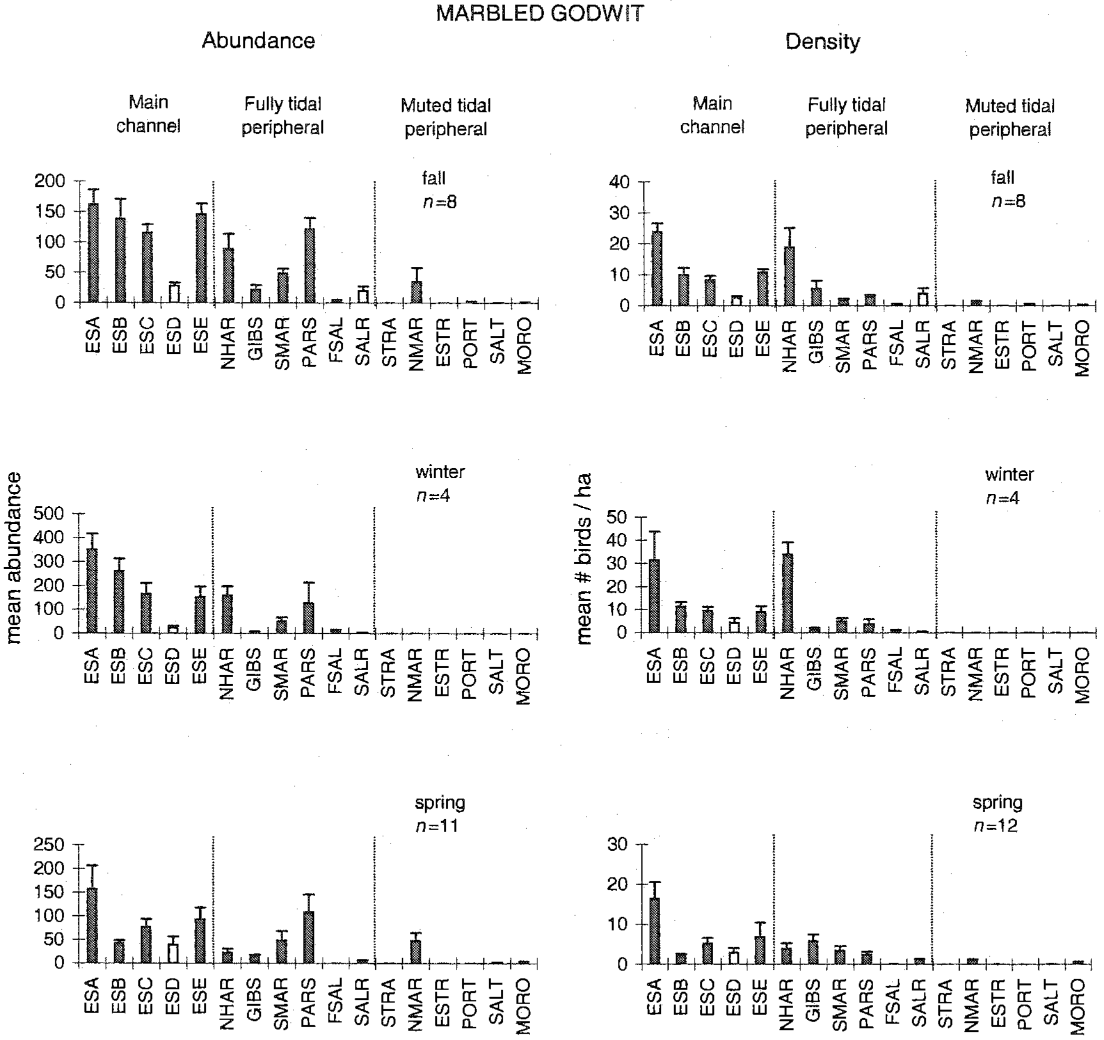


Figure 7. Mean abundance and density (± SE) of Marbled Godwits in the Elkhorn Slough study area based on spring 1999 through spring 2000 surveys. Shaded bars met criteria for statistical analysis (see Methods). See Figure 6 for locations represented by abbreviations. Note differences in y-axis values.

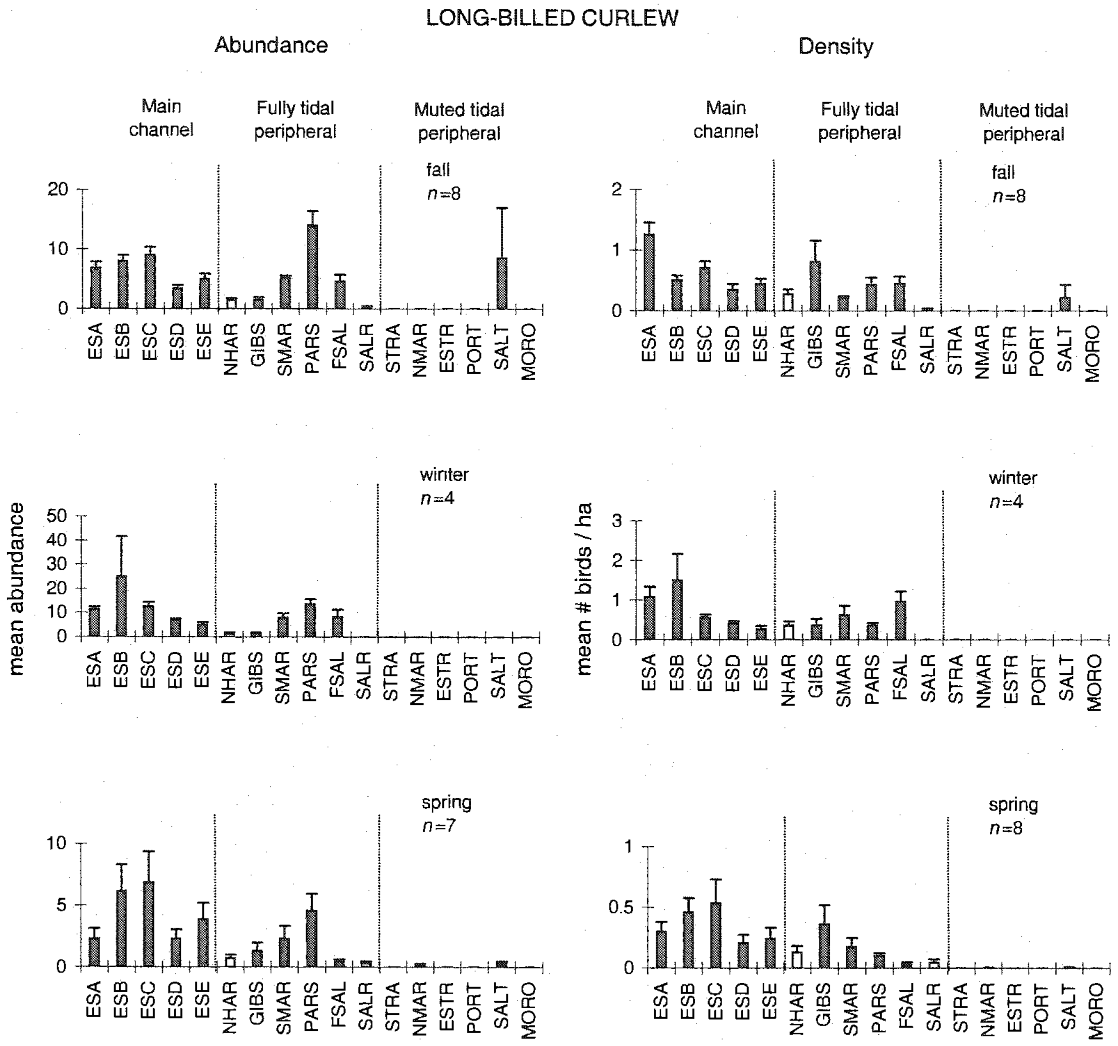


Figure 8. Mean abundance and density (± SE) of Long-billed Curlews in the Elkhorn Slough study area based on spring 1999 through spring 2000 surveys. Shaded bars met criteria for statistical analysis (see Methods). See Figure 6 for locations represented by abbreviations. Note differences in y-axis values.

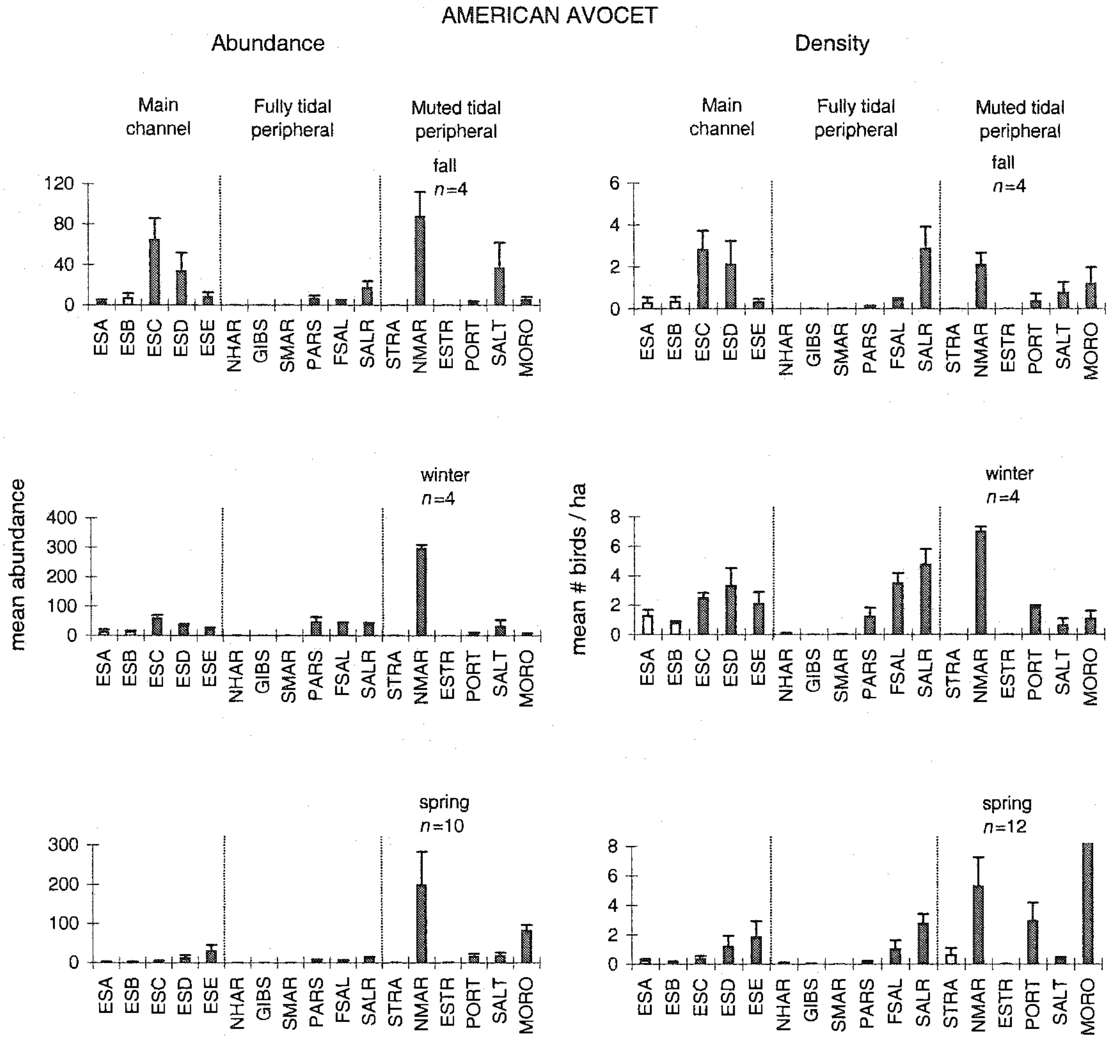


Figure 9. Mean abundance and density (± SE) of American Avocets in the Elkhorn Slough study area based on spring 1999 through spring 2000 surveys. Shaded bars met criteria for statistical analysis (see Methods). See Figure 6 for locations represented by abbreviations. Note differences in y-axis values.

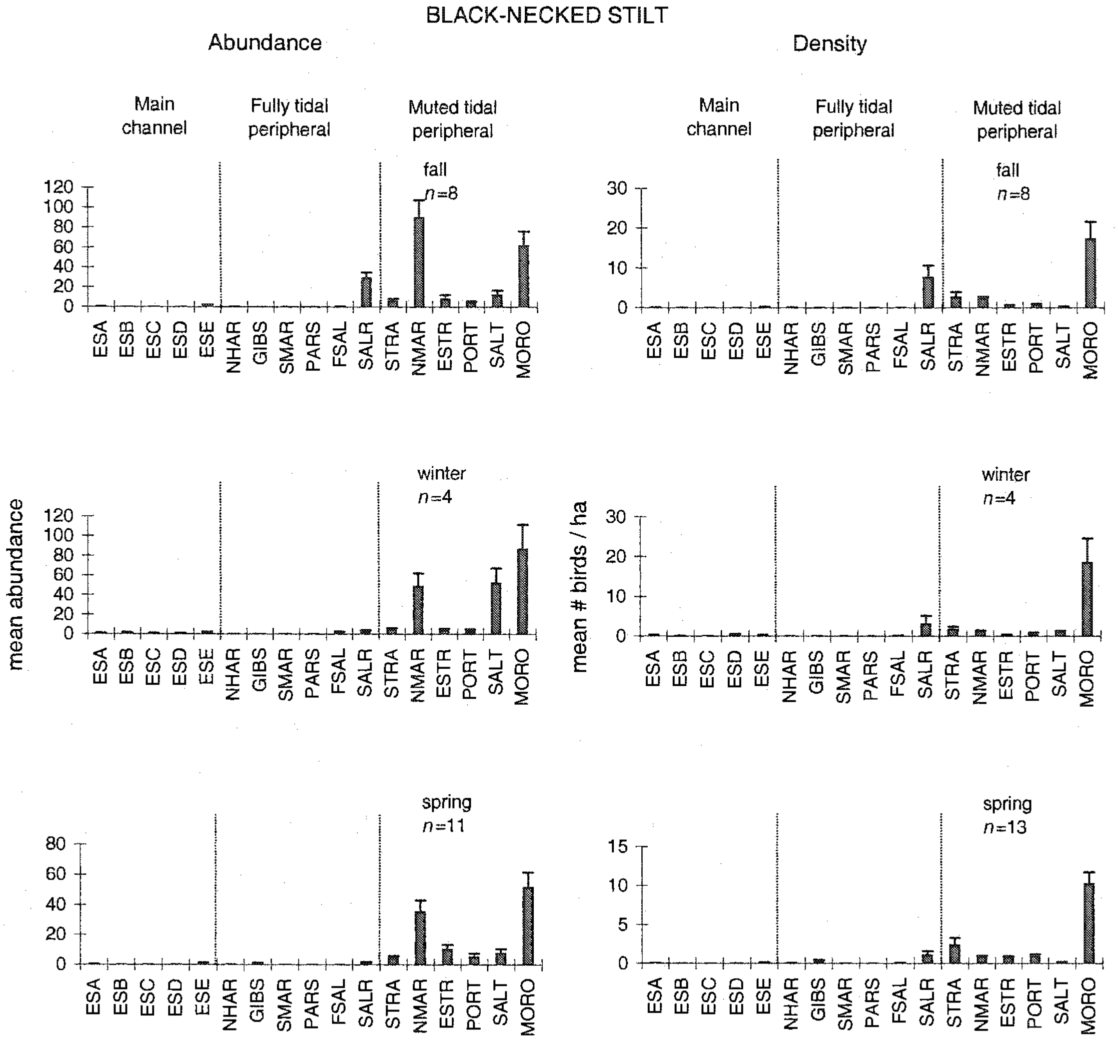


Figure 10. Mean abundance and density (± SE) of Black-necked Stilts in the Elkhorn Slough study area based on spring 1999 through spring 2000 surveys. Shaded bars met criteria for statistical analysis (see Methods). See Figure 6 for locations represented by abbreviations. Note differences in y-axis values.

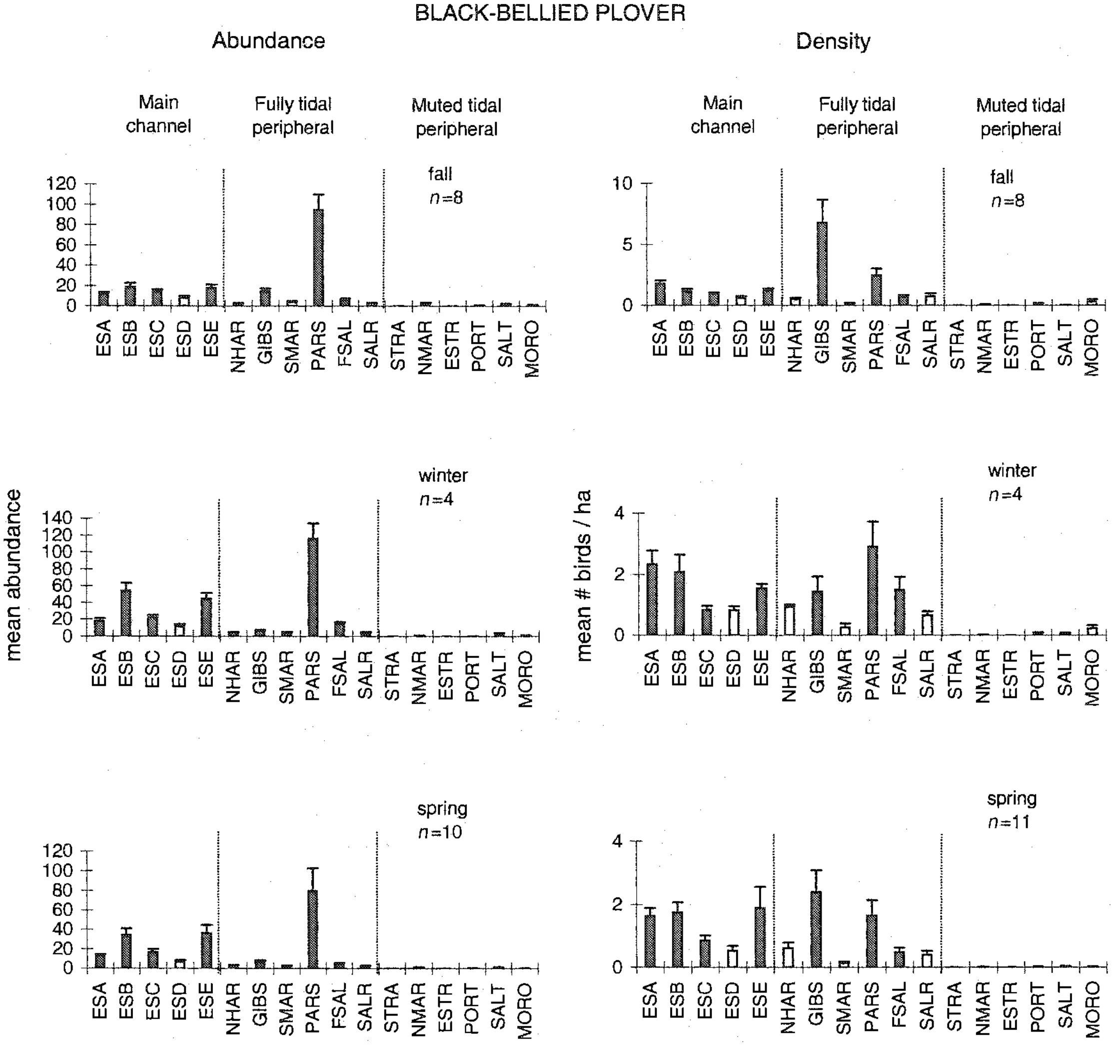


Figure 11. Mean abundance and density (± SE) of Black-bellied Plovers in the Elkhorn Slough study area based on spring 1999 through spring 2000 surveys. Shaded bars met criteria for statistical analysis (see Methods). See Figure 6 for locations represented by abbreviations. Note differences in y-axis values.

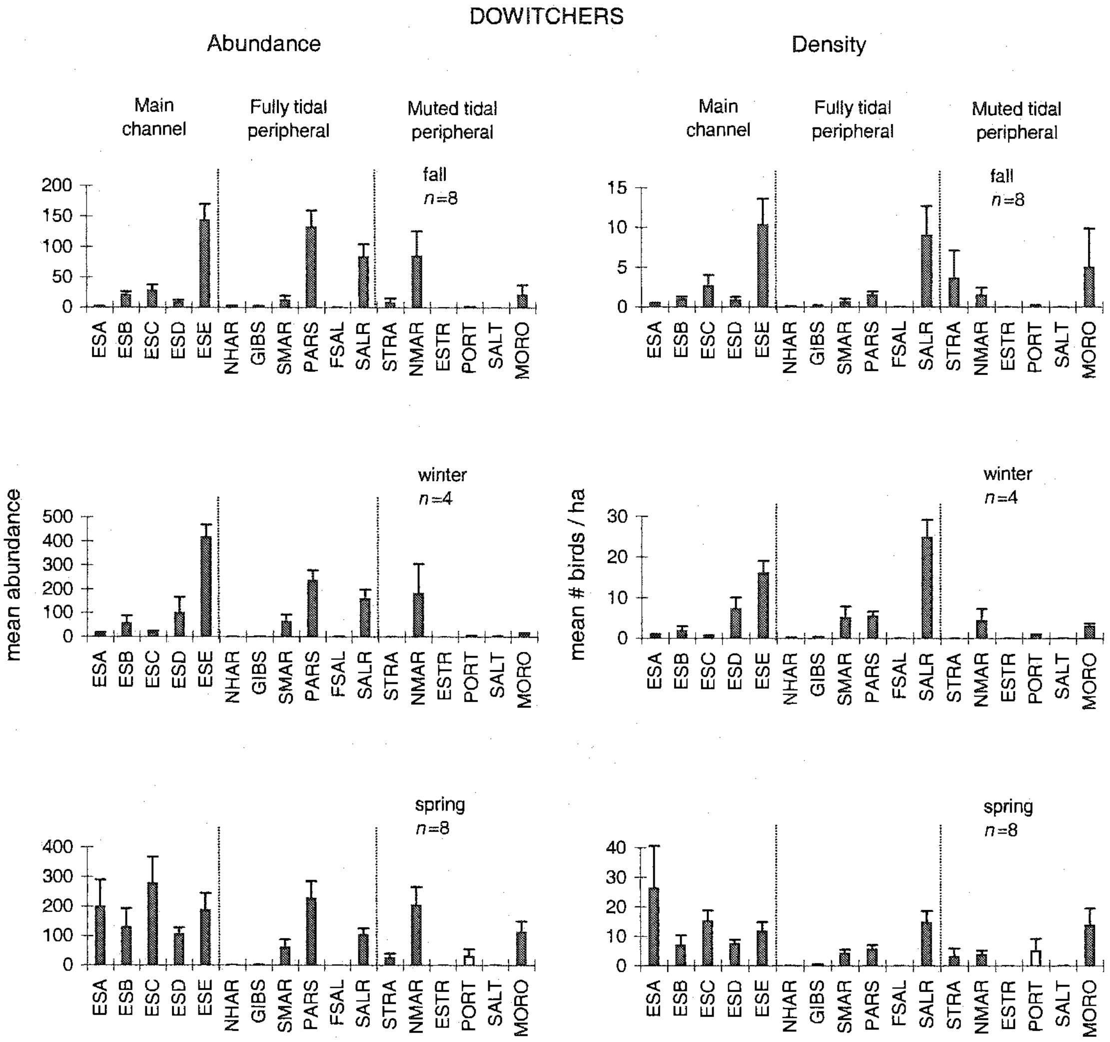


Figure 12. Mean abundance and density (± SE) of dowitchers in the Elkhorn Slough study area based on spring 1999 through spring 2000 surveys. Shaded bars met criteria for statistical analysis (see Methods). See Figure 6 for locations represented by abbreviations. Note differences in y-axis values.

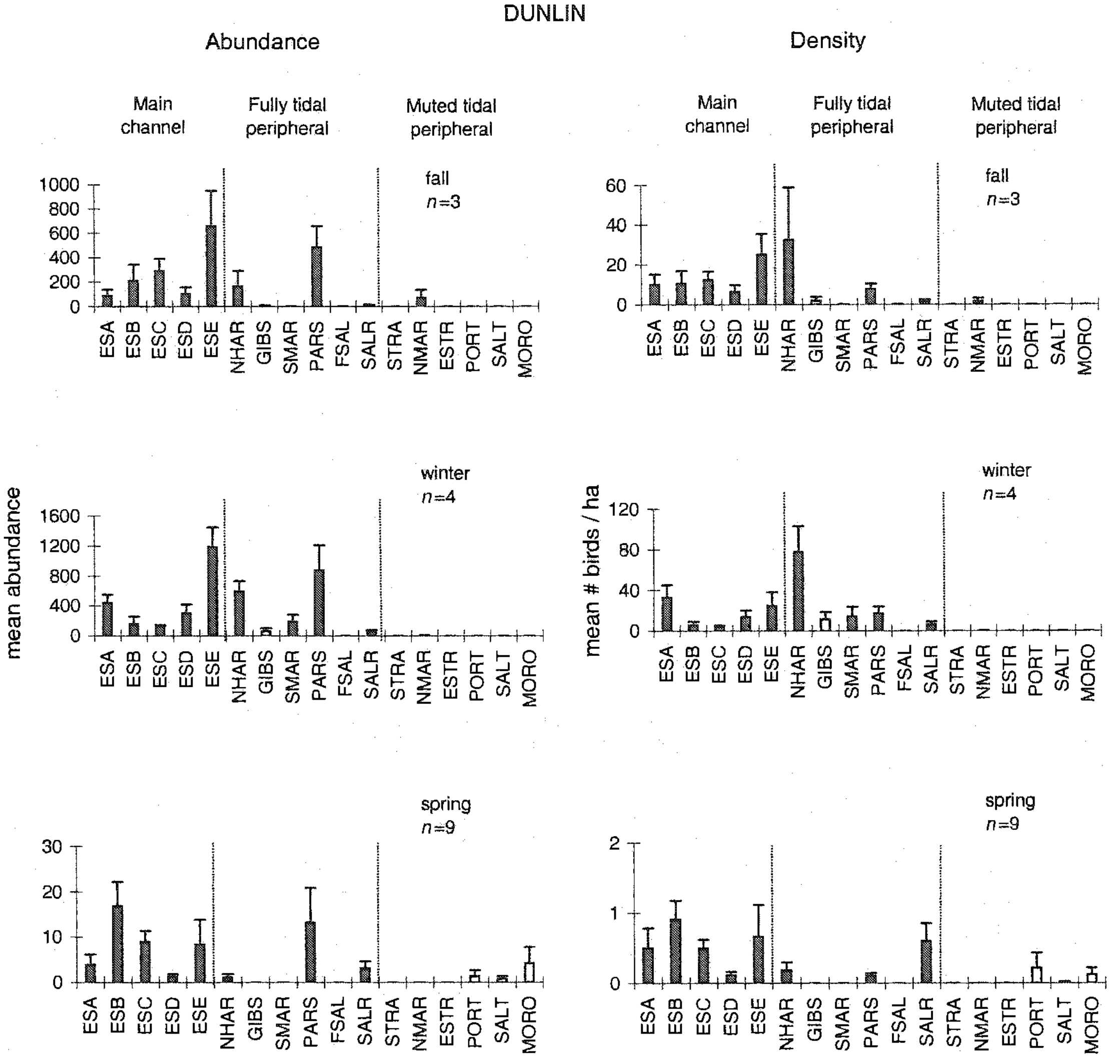


Figure 13. Mean abundance and density (± SE) of Dunlins in the Elkhorn Slough study area based on spring 1999 through spring 2000 surveys. Shaded bars met criteria for statistical analysis (see Methods). See Figure 6 for locations represented by abbreviations. Note differences in y-axis values.

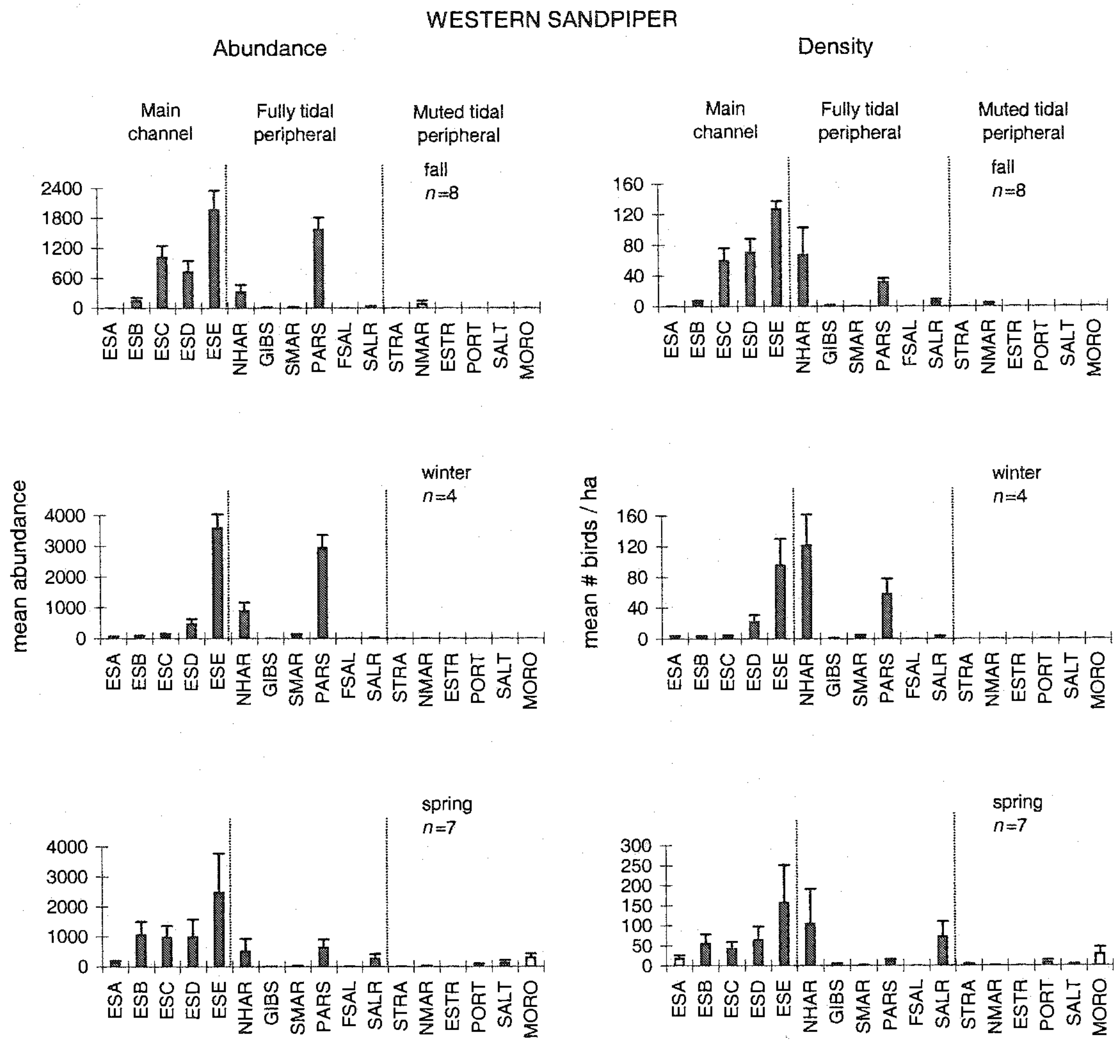


Figure 14. Mean abundance and density (± SE) of Western Sandpipers in the Elkhorn Slough study area based on spring 1999 through spring 2000 surveys. Shaded bars met criteria for statistical analysis (see Methods). See Figure 6 for locations represented by abbreviations. Note differences in y-axis values.

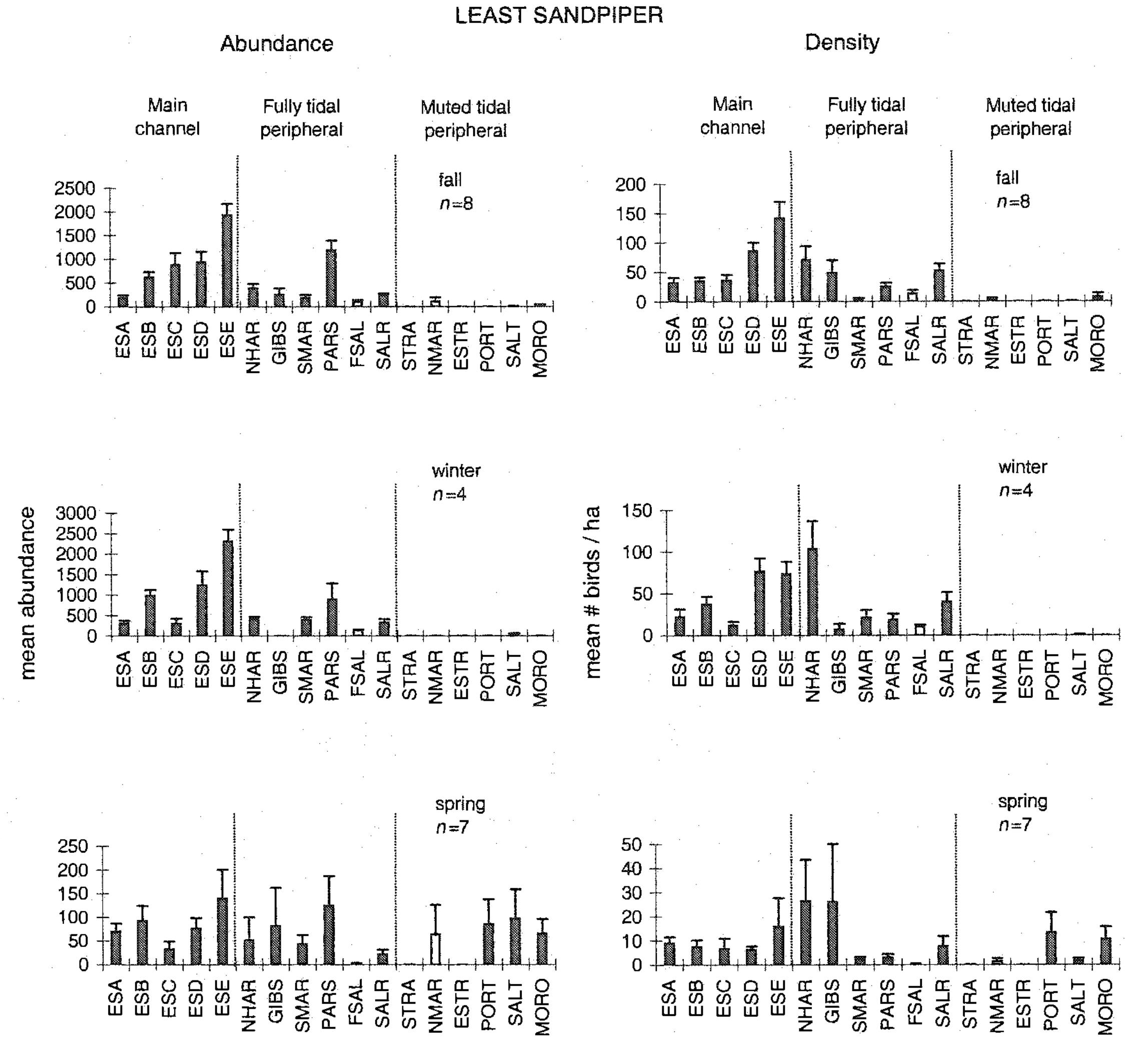


Figure 15. Mean abundance and density (± SE) of Least Sandpipers in the Elkhorn Slough study area based on spring 1999 through spring 2000 surveys. Shaded bars met criteria for statistical analysis (see Methods). See Figure 6 for locations represented by abbreviations. Note differences in y-axis values.

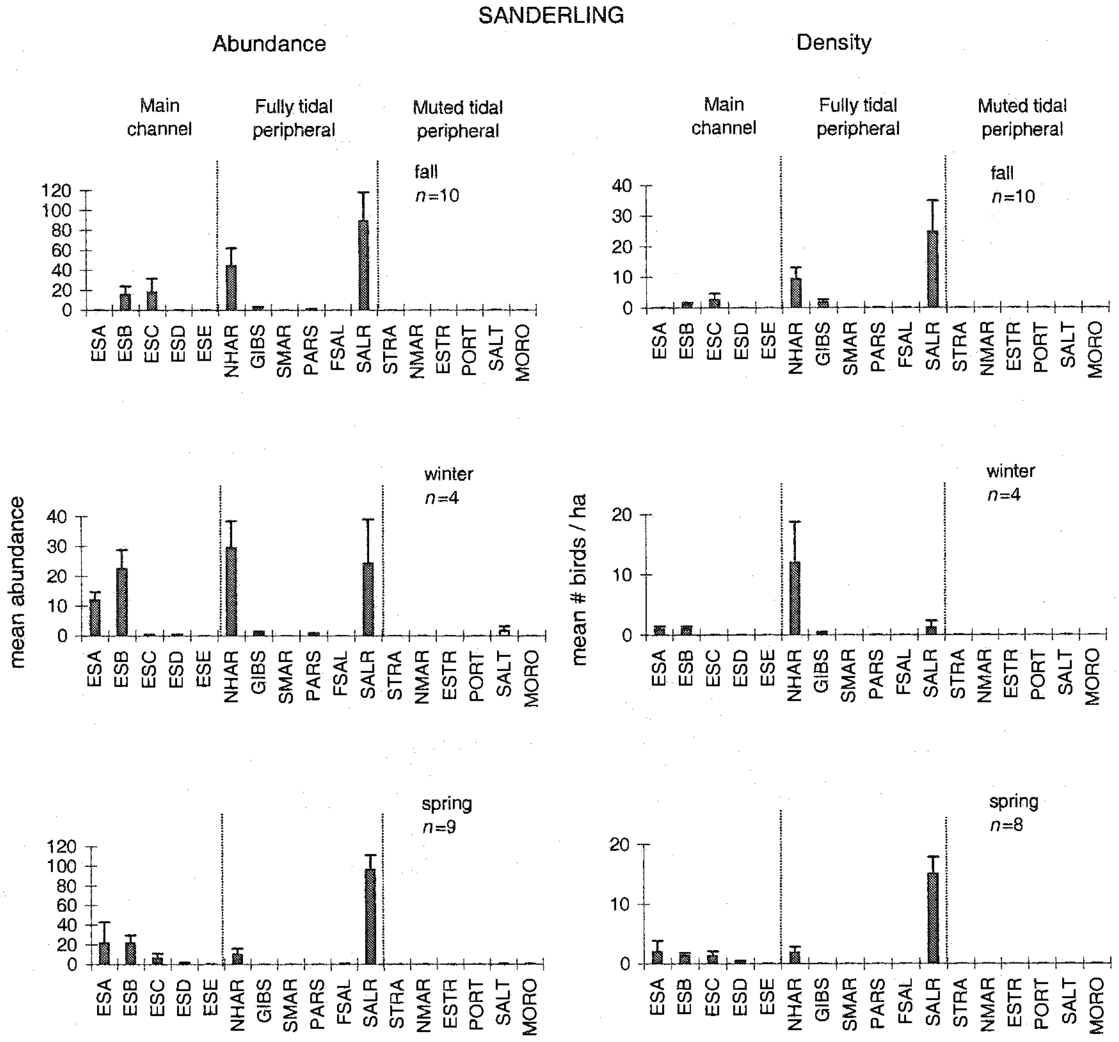


Figure 16. Mean abundance and density (± SE) of Sanderlings in the Elkhorn Slough study area based on spring 1999 through spring 2000 surveys. Shaded bars met criteria for statistical analysis (see Methods). See Figure 6 for locations represented by abbreviations. Note differences in y-axis values.

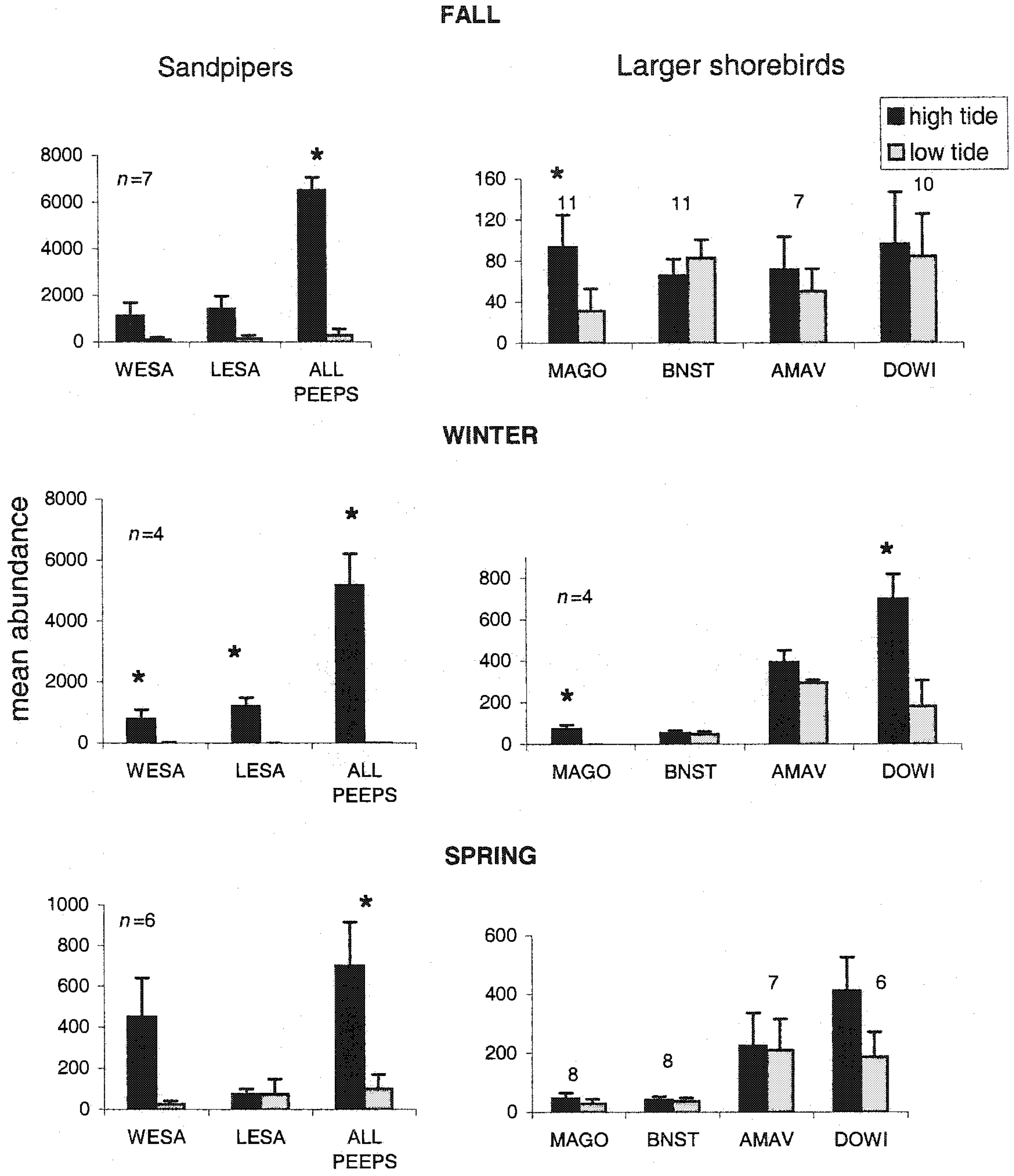


Figure 17. Comparison of shorebird abundance at high and low tide (± SE) within a tide cycle at North Marsh, spring 1999 through spring 2000. Bars with asterisk (*) were significant (*P*<0.05); sample size is noted above bars. Note differences in y-axis values. See Appendix 1 for species abbreviations.

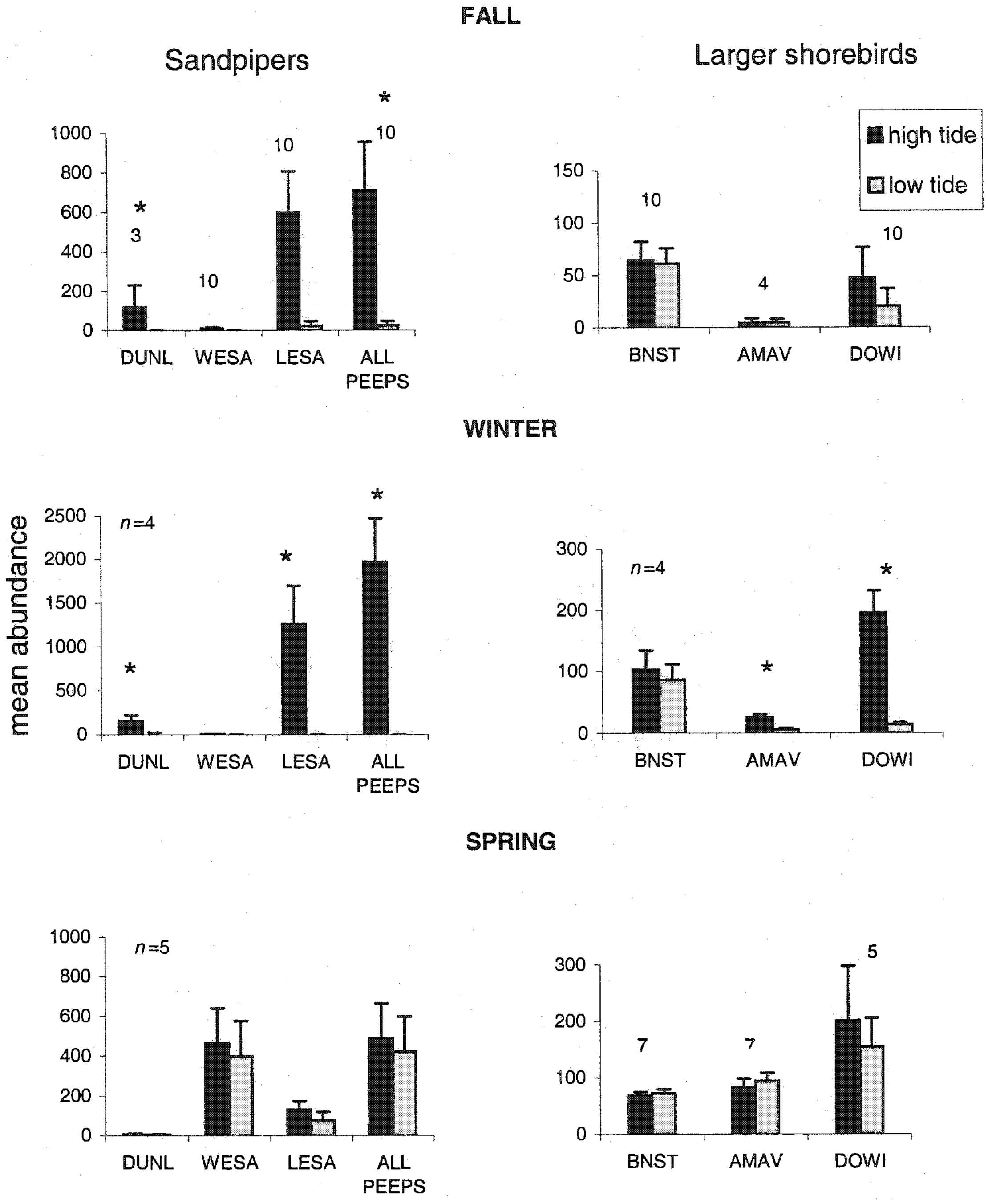


Figure 18. Comparison of shorebird abundance at high and low tide (± SE) within a tide cycle at Moro Cojo Slough, spring 1999 through spring 2000. Bars with asterisk (*) were significant ($P<0.05$); sample size is noted above bars. Note differences in y-axis values. See Appendix 1 for species abbreviations.

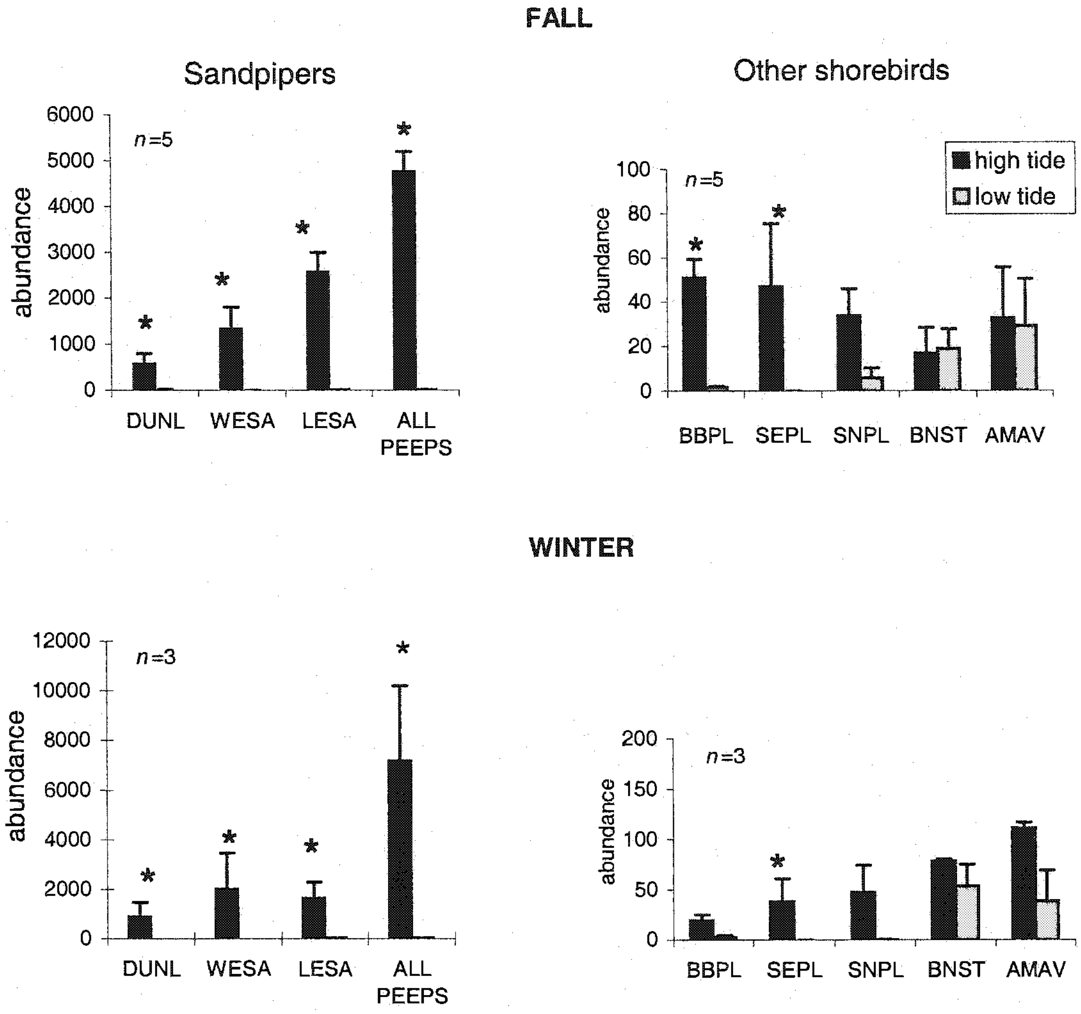


Figure 19. Comparison of shorebird abundance at high and low tide (± SE) within a tide cycle at the salt ponds, fall 1999 and winter 1999-2000. Bars with asterisk (*) were significant ($P<0.05$). Note differences in y-axis values. See Appendix 1 for species abbreviations.

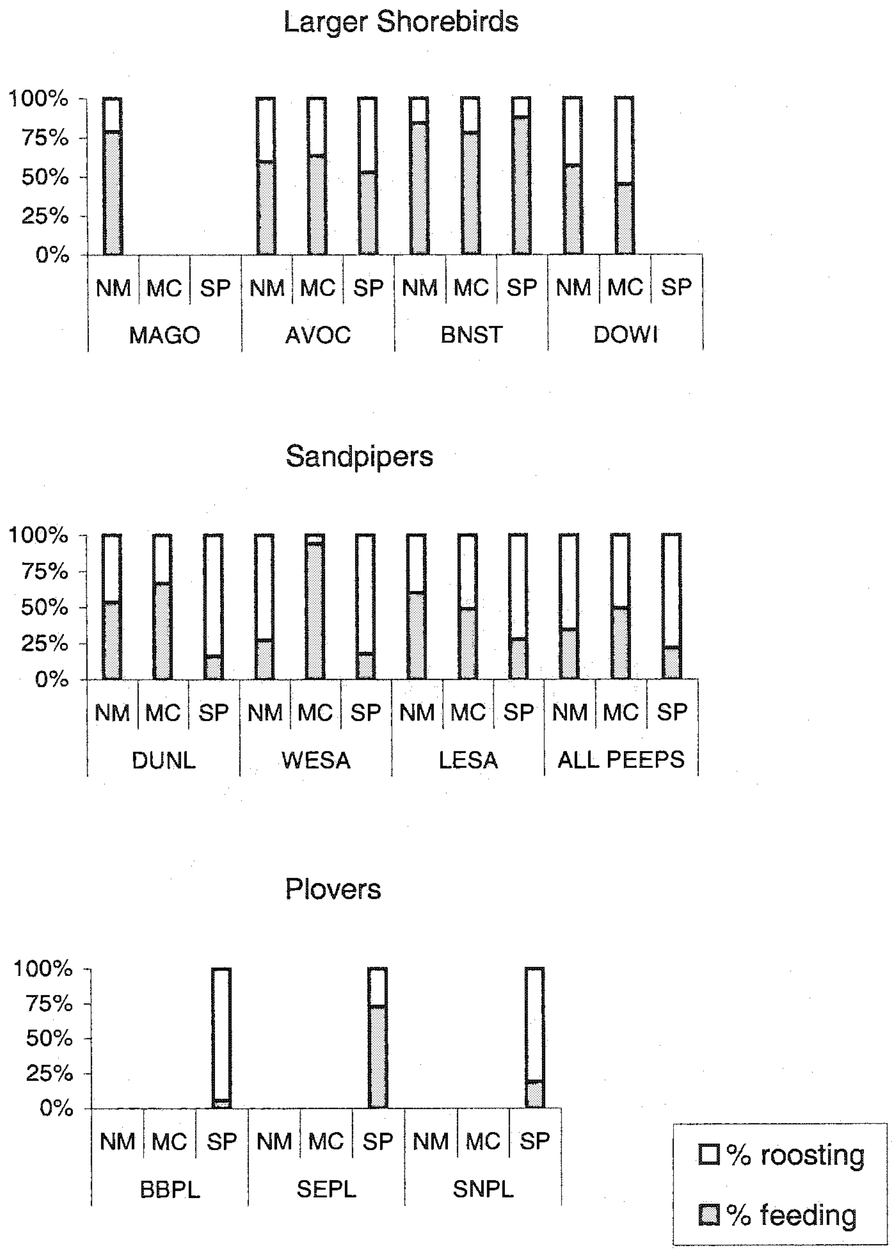


Figure 20. Behavior of most abundant shorebirds at North Marsh (NM), Moro Cojo Slough (MC), and salt ponds (SP) during high tide surveys from spring 1999 through winter 2000. See Appendix 1 for species abbreviations.

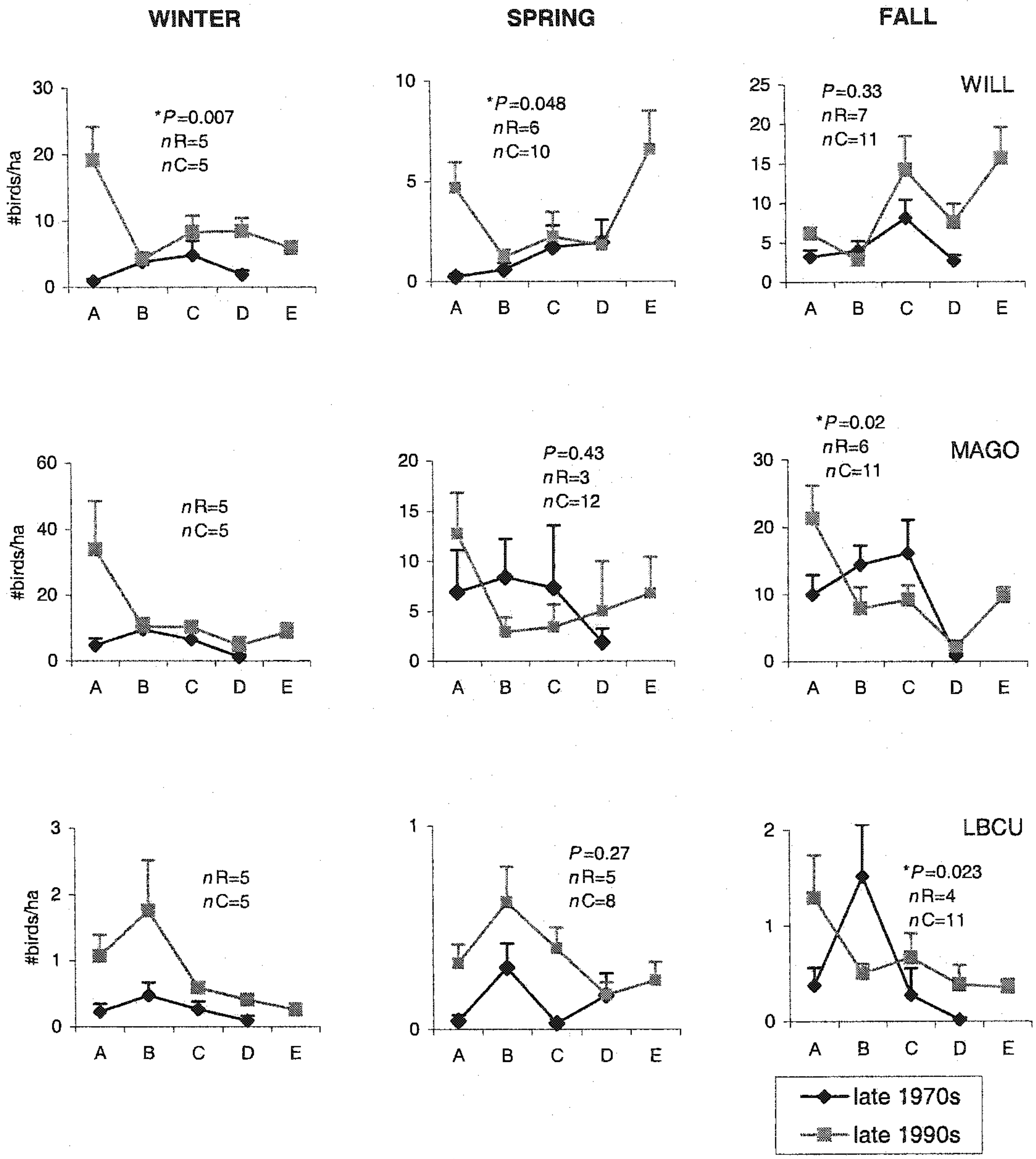
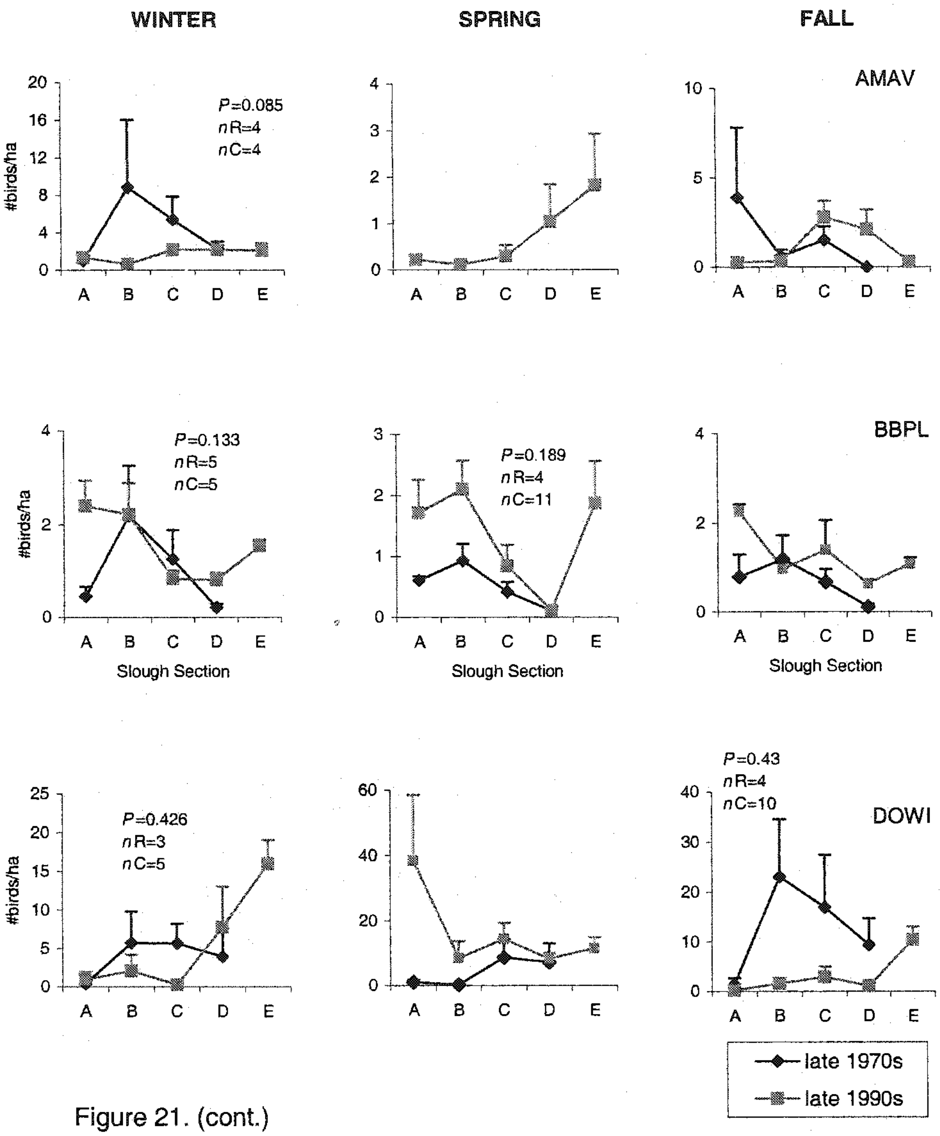


Figure 21. Comparison of shorebird distribution between the late 1970s and late 1990s on the main channel of Elkhorn Slough (A=slough mouth; E=slough head). Graphs without *P* values had unequal variances; 1970s data was not available for some species in spring; *n*R: 1970s sample size; *n*C: 1990s sample size . See Appendix 1 for species abbreviations.



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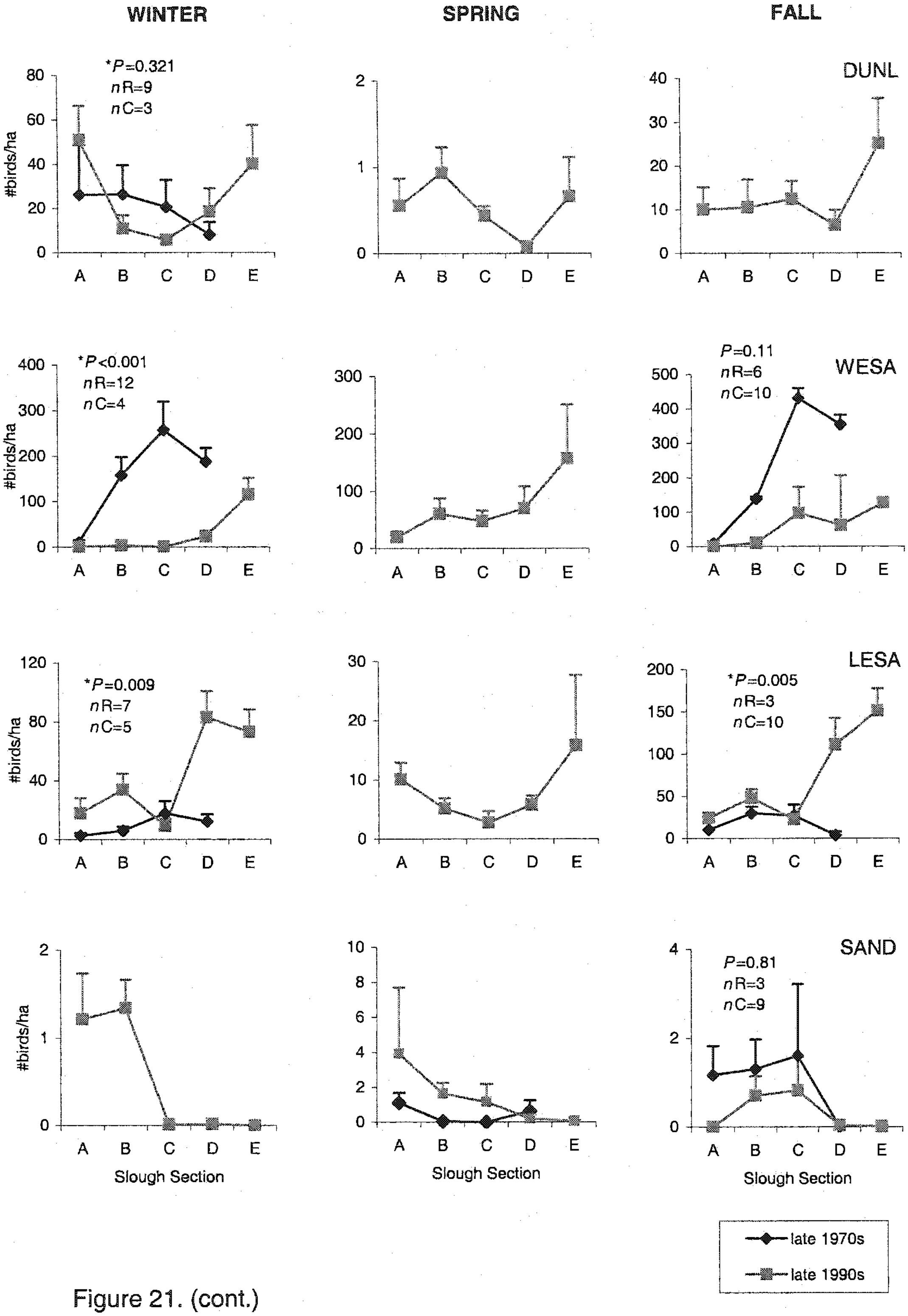

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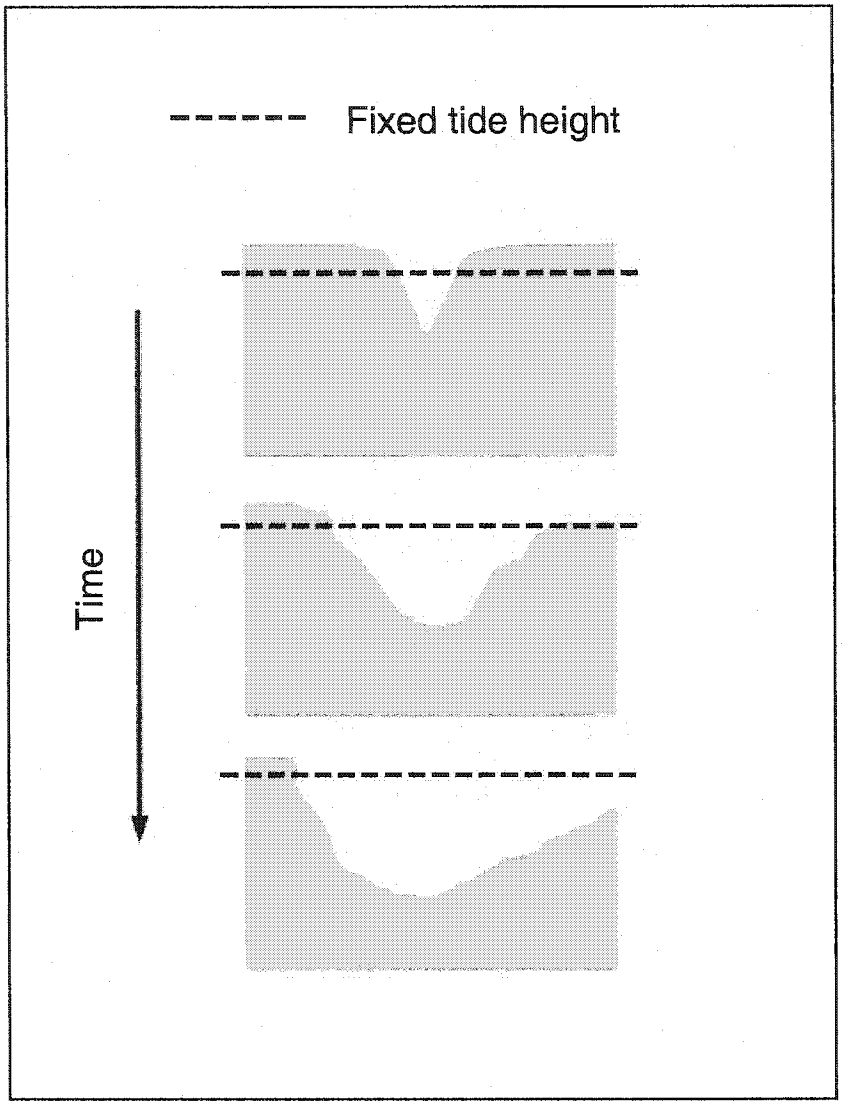

Figure 22. Depiction of cross-sectional area of lower slough channel in Elkhorn Slough and the progression of tidal scour; modified from Malzone (1999).

Appendix A. Common names, scientific names, and abbreviations of shorebird species addressed in this study.

Black-bellied Plover	(*Pluvialis squatarola*)	BBPL
Semipalmated Plover	(*Charadrius semipalmatus*)	SEPL
Snowy Plover	(Charadrius alexandrinus)	SNPL
American Avocet	(*Recurvirostra americana*)	AMAV
Black-necked Stilt	(*Himantopus mexicanus*)	BNST
Willet	(*Catoptrophorus semipalmatus*)	WILL
Long-billed Curlew	(*Numenius americanus*)	LBCU
Marbled Godwit	(*Limosa fedoa*)	MAGO
Sanderling	(*Calidris alba*)	SAND
Dunlin	(*Calidris alpina*)	DUNL
Western Sandpiper	(*Calidris mauri*)	WESA
Least Sandpiper	(*Calidris minutilla*)	LESA
Long-billed Dowitcher	(*Limnodromus scolopaceus*)	LBDO
Short-billed Dowitcher	(*Limnodromus griseus*)	SBDO