Hydrographic Correlates of Winter Dunlin Abundance
and Distribution in a Temperate Estuary

JOHN P. KELLY

Cypress Grove Research Center, Audubon Canyon Ranch, P. O. Box 808, Marshall, CA 94940 USA
E-mail: kellyjp@nbn.com

Abstract.—From 1989 to 1999, I examined intra-seasonal and annual changes in the abundance and local distribution of two groups of wintering Dunlin (*Calidris alpina*) occupying different positions along hydrographic gradients in the Tomales Bay estuary, California. Reciprocal translocation of color-banded Dunlin indicated a discrete separation of wintering Dunlin between the north and south of Tomales Bay. Local abundance in both groups was significantly associated with cumulative seasonal rainfall within and among years. Increased variation in annual and intra-seasonal abundance was related to reduced tidal circulation, greater freshwater stream flow, and increased salinity variation. On average, winter Dunlin use peaked later but declined earlier in the southern part of the bay (near the head of the bay) than in the northern part of the bay (near the mouth of the bay). Shifts in distribution associated with changes in hydrographic conditions and weather revealed consistent intra-seasonal changes in habitat preference on temporal scales other than tidal cycles. In the northern part of the bay, changes in habitat preference by Dunlin corresponded to thresholds of 20-25 cm cumulative rainfall and 0.5-1.0 m^3 sec^{-1} stream flow, whereas in the south bay changes were relatively continuous. Rainfall, wind velocity and direction, and temperature also influenced habitat preferences. Flocking behavior dominated over habitat choice at low levels of Dunlin abundance, resulting in contrasting patterns of habitat use relative to overall trends. These patterns suggested the loss of habitat quality as the criterion for patch use. In general, this study indicates that winter shorebird use of temperate estuaries can be predicted by differences in weather and hydrographic regimes, including rates and variances of freshwater inflow, estuarine circulation, and water residence times unique to each system. *Received 4 February 2001, accepted 15 June 2001.*

Key words.—Allee's principle, *Calidris alpina*, habitat selection, intra-seasonal, Pacific coast, patch, seasonal, shorebird, Tomales Bay, weather.

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Ecosystems important to shorebirds wintering on the Pacific coast of North America include large bays, such as San Francisco Bay, and river estuaries, exemplified by the Columbia and Eel Rivers. Large bays exhibit relatively stable patterns of food availability and shorebird use that vary predominantly with tidal regime (Nichols 1977; Recher 1966) and contrast with seasonally dynamic patterns in estuaries dominated by changes in river discharge (Colwell 1993). Between these extremes, estuarine systems vary widely. in terms of freshwater runoff, estuarine circulation, water residence times, weather, and salinity patterns (Kjerfve 1989). Such variation is likely to influence patterns of shorebird use. In addition, abiotic influences vary according to annual, seasonal, intra-season-al, circadian, and tidal patterns. Therefore, temporal scales of variation in shorebird use of feeding areas may differ among estuarine systems. However, little attention has been given to the effects of hydrographic regimes in estuaries on local shorebird distribution.

Habitat patch use by foraging shorebirds reflects spatial and temporal patterns of prey density (Goss-Custard *et al.* 1977; Puttick 1984; Bryant 1979) or availability (Recher 1966; Goss-Custard 1984), as well as density-dependent processes such as competition, interference, prey depletion, or predation pressure (Goss-Custard 1980; van der Have 1984). When foraging profitability is substantially altered by weather-related factors such as temperature, wind, or rain, or other abiotic factors such as tides (Connors *et al.* 1981),

sediment runoff (Gerstenberg 1979), or sa-
linity (Wolff 1969; Velasaquez 1992), shore-
birds generally respond by changing their
choice of habitat patches (Burger 1984). Abi-
otic conditions may also affect shorebird be-
havior by influencing the amount of energy
required for thermoregulation or foraging
(Davidson 1981), or by serving as proximate
cues related to changing intake needs (Kelly
et al. 2001). Many density-dependent pro-
cesses operate within limits determined by
abiotic factors, which set and reset levels of
profitability or risk at various temporal scales.
The particular expression of weather and hy-
drographic effects in temperate estuaries
may therefore provide a framework by which
patterns of shorebird use can be compared.

Tomales Bay is one of the least disturbed
estuaries in California, and has been recog-
nized by the Western Hemisphere Shorebird
Reserve Network as important to Pacific coast
shorebirds (Harrington and Perry 1995; Page
et al. 1999). The bay is particularly well-suited
for studies of physical processes that might af-
fect winter shorebird distribution and use,
because it is geometrically and hydrographi-
cally simple, with an easily measured salinity
gradient and slow exchange with nearshore
coastal waters (Hollibaugh et al. 1988).

In this paper, I examine ten years of cen-
sus data for annual and intra-seasonal effects
of weather, runoff, and salinity on the distri-
bution and abundance of Dunlin (Calidris
alpina) in Tomales Bay (Fig. 1). I investigated
these effects in two wintering groups of Dun-
lin occupying parts of the estuary that corre-
spond to different positions along a hydro-
graphic gradient. Variation in food supply
was not measured directly. The study period
encompassed a range of seasonal weather
that included successive years of exceptional-
ly dry conditions followed by years of greater-
than-average rainfall. I focused on Dunlin
because it is the most abundant species on
Tomales Bay, reaching almost 13,000 birds in
late autumn and averaging 53% of total
shorebird abundance (Kelly 2001), and be-
cause this species exhibits local and regional
midwinter movements related to changing
foraging conditions (Page et al. 1979; Ruiz et
al. 1989; Warnock et al. 1995).
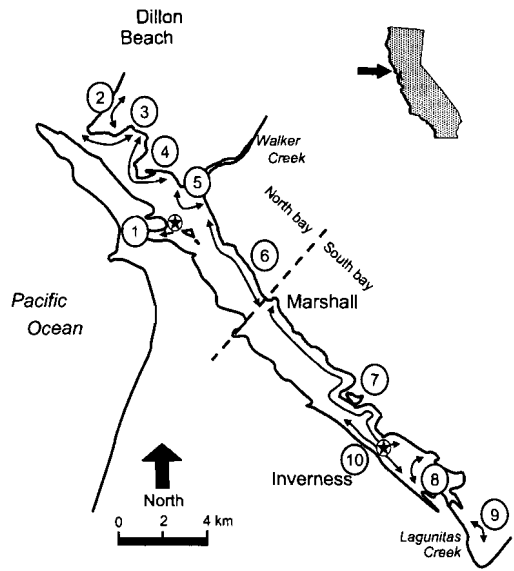
Figure 1. Shorebird count areas on Tomales Bay, Cali-
fornia. North bay count areas: 1 = White Gulch, 2 = Law-
son's Meadow; 3 = Sand Point, 4 = Tom's Point, 5 =
Walker Creek delta; south bay count areas: 6=North
Marshall, 7 = South Marshall, 8 = Lagunitas Creek delta,
9 = Giacomini Pasture, 10 = Inverness Shoreline. Stars
indicate locations of salinity measurements (Smith et al.
1991). Arrows indicate the extent of shoreline within
each count area.

STUDY AREA

Tomales Bay is long (20 km), narrow (1.4 km) and
straight, formed by the intersection of the San Andreas
Fault and the central California coastline, about 45 km
northwest of San Francisco (Fig. 1; Galloway 1977). Ap-
proximately 18% of the bay is intertidal, with sand and
mud flats concentrated primarily at the northern and
southern ends and to a lesser extent along the east
shore. Large tidal deltas suitable for foraging shorebirds
occur at two primary points of inflow, one at Walker
Creek near the north end of the bay and the other at La-
gunitas Creek at the south end (Fig. 1). Numerous oth-
er smaller perennial and ephemeral streams enter the
bay along the east and west shores, each associated with
smaller delta marshes and tide flats. Annual rainfall oc-
curs primarily (95%) from October through April, with
55% occurring from December through February (Au-
dubon Canyon Ranch, unpublished data).

Tidal circulation differs dramatically between the
northern and southern parts of Tomales Bay. Water in
the northern 6 km of the bay exchanges with nearshore
coastal water on each tidal cycle, while water in the
southern 14 km of the bay is resident for approximately
120 days during periods of low runoff (Hollibaugh et al.
1988). In winter, water residence time in the southern
part of the bay is determined by the extent of freshwater
inflow. Constrained tidal circulation and variably high
rates of inflow at the south end of the bay interact to cre-
ate a dynamic salinity gradient along the 20-km axis of
the bay. Thus, estuarine water circulation is driven pri-
marily by runoff and wind in the southern part of the

bay, and by tides in the northern part of the bay. Salinities in the southern part of the bay range from nearly fresh in winter after periods of heavy freshwater inflow, to slightly hypersaline in late autumn after seasonally low inflows and periods of high evaporation (Smith and Hollibaugh 1997). Salinities in the northern third of the bay more consistently reflect those of the nearshore coastal waters.

Intertidal sediments grade from coarse and fine sands to clayey silts in the northern half of the bay, with clayey silts and silty clays predominating on tide flats further south (Daetwyler 1966). Seasonal wetlands suitable for shorebirds are normally limited to about 15 ha of a 200-ha diked pasture adjacent to the south end of the bay and approximately 20 ha of wet meadow in a wide dune slack at the north end of the bay. During periods of heavy flooding, shorebirds use seasonal wetlands in agricultural areas, 5-15 km northeast of the bay. The tidal range is slightly greater at the south end of the bay (mean = 1.13 m; max. = 2.65 m) than at the mouth (mean = 1.06 m; max. = 2.43 m; U. S. National Oceanic and Atmospheric Administration harmonics and correction tables, Tides and Currents, Nautical Software, Inc.).

METHODS

Bird Counts

From 1989 to 1999, teams of observers counted Dunlin simultaneously in ten sub-areas of Tomales Bay, during 60-90-minute census periods (Fig. 1). The count areas included adjacent seasonal wetlands and almost all of the intertidal flats in the bay, with the exception of a few small areas at creek mouths along the west shore. Observers conducted all counts during rising tides, at tide levels between 0.76 m and 1.22 m above mean lower low water at Blake's Landing, near Marshall. Usually, six counts were completed annually, three in each of two intra-seasonal periods: early winter (1 November to 19 December) and late winter (15 January-4 March).

Reciprocal Translocation

Field observations of flock movements between feeding areas and high-tide roosting areas suggested that shorebirds frequently moved among habitat areas within the northern or southern subregions of Tomales Bay, but that movements were markedly restricted in either direction between areas 6 and 7 (Fig. 1). Therefore, to examine the possibility that different groups of wintering Dunlin use the northern and southern portions of the bay, I conducted a reciprocal translocation of color-banded birds. During November, December, and January, I translocated 21 of 44 Dunlin banded at Walker Creek delta to Lagunitas Creek delta, and 11 of 18 banded at Lagunitas Creek delta to Walker Creek delta. Birds were transported in well-ventilated holding boxes and released at night in groups of six or more individuals, 1-3 hours after capture. Uniquely marked individuals were subsequently resighted over the next twelve weeks, during ten low-tide feeding periods at Walker and Lagunitas Creek deltas. The results indicated that Dunlin moved frequently among habitat areas within the northern or southern subregions of Tomales Bay, but that little movement occurred between the two ends of the bay (see Results). Therefore, I analyzed results separately for subregions north (hereafter, "north bay") and south (hereafter "south bay") of Cypress

Point, Marshall (areas 1-6 and 7-10, Fig. 1). An additional 37 wintering Dunlin, captured before or after the translocation experiment, were included in testing differences in proportions of adults and juveniles in the north and south bay subregions.

Weather and Hydrography

To evaluate weather effects on Dunlin abundance, I used daily rainfall records at Cypress Point halfway along the east shore of Tomales Bay (Audubon Canyon Ranch, unpublished data) and additional weather data from the University of California Bodega Marine Reserve, 12 km northwest of Tomales Bay. Weather variables used in the analyses were daily rainfall (cm); cumulative rainfall in previous 3 days (cm); cumulative seasonal rainfall since 1 September (cm); daily barometric slope (mb hr^{-1}); minimum, maximum and average daily wind velocity (m sec^{-1}); minimum, maximum and average daily temperature (°C); and mean daily wind direction (coded 1 for northwest-to-northeast, 270°-45°, -1 for southwest-southeast, 90°-225°, and 0 for other directions). Salinity data (1989 to 1995) were obtained for two sites from the Tomales Bay LMER/BRIE Research Program, University of Hawaii (Stephen V. Smith, unpublished; Fig. 1). Stream flow data were obtained from U.S. Geological Survey gauges in the lower reaches of Walker and Lagunitas creeks (1989-1998, USGS Stations 11460750 and 11460600), and the flow rates were multiplied by 1.29 and 1.40, respectively, to adjust for ungauged portions within each watershed.

Statistical Analyses

To facilitate comparisons of Dunlin use of feeding areas of varying size, the abundance data were transformed into densities based on the extent of exposed mud flat in each count area estimated at mean low water with a planimeter from a bathymetric chart (U.S. National Oceanic and Atmospheric Administration Chart 18643, 16th Ed., Dec. 1995). Foraging Dunlin usually concentrated along the tide line, but also selected depressions in exposed tidal flats (Mouritsen and Jensen 1992). Therefore, estimates of habitat preference based on differences in density may be sensitive to the areal measurement used to assess habitat availability (Warnock and Takekawa 1995). However, the topography was similar among suitable habitats in Tomales Bay, and areas available for foraging along the tide line represented similar proportions of tidal exposure among count areas.

To examine effects of count area location, intra-seasonal period, and year on Dunlin abundance and density, mixed-model analysis of covariance was used, controlling for days since the beginning of each intra-seasonal period (early or late winter) and treating year as a random effect. Abundances and densities were log-transformed to improve normality and stabilize the variance of residuals. Significant count area effects within the northern and southern subregions of the bay were followed by multiple pairwise comparisons within each intra-seasonal period, using experimentwise error rates to evaluate significance.

Thresholds and nonlinear trends in shorebird abundance associated with intra-seasonal timing (days since 1 November), subregional abundance, cumulative seasonal rainfall, stream flow and salinity were looked for by inspecting bivariate scatterplots using Cleveland's ro-

bust locally weighted regression smoothing algorithm (LOWESS; Cleveland 1979; Chambers *et al.* 1983). This method was selected because it uses locally weighted least squares and a robust fitting procedure to define smoothed points that are relatively insensitive to outlying values, and allows a flexible degree of smoothing by adjusting the proportion of data used to calculate each fitted value.

To distinguish the effects of cumulative seasonal rainfall and weather on local distribution, stepwise multiple regression was used with cumulative rainfall and weather variables as predictors of proportional use in each count area. Proportional abundances were log- or arcsine-transformed to improve the normality and stability of residuals. Independent variables were used in regressions only if product-moment correlations with other variables in the models were less than 0.4. Local distributions were examined for evidence of density-dependence by testing residual associations (partial correlations) between the resulting models and local Dunlin abundance. Trends in annual abundance were estimated from linear regression coefficients. After removing the linear effects of cumulative seasonal rainfall in the current and previous year, underlying trends in mean numbers of wintering Dunlin were looked for by examining partial correlations and bivariate plots of residual abundance on year. In analyses of trends in maximum annual abundance, cumulative rainfall in the current year was based on November only. Yate's correction for continuity was used in chi-square analyses with one degree of freedom. All analyses were conducted using SYSTAT (Version 8.0, SPSS, Inc. Chicago, IL).

RESULTS

Reciprocal Translocation

I resighted 48 of 62 color-banded Dunlin. Nearly all translocated individuals (24 of 25) returned to their original banding sites, often within 1-2 days of release, and were subsequently resighted only in those locations during an 11-week period after release. All non-translocated individuals (23 of 23) were resighted only in the vicinity of their banding sites. These differences indicated significant separation of northern and southern wintering groups, whether tested against expected locations of non-translocated of birds (χ^2_1 = 44.1, P < 0.0001) or against an even chance (50%) of resighting translocated birds at either end of the bay (χ^2_1 = 17.7, P < 0.001).

These results corroborated field observations of separate routine, and tide induced flock movements in the northern or southern subregions of Tomales Bay, and a lack of movement in the middle section of the bay between areas 6 and 7 (Fig. 1).

Local Abundance

Annual abundance of Dunlin declined dramatically over the ten years of this study (Fig. 2, Table 1). Maximum annual Dunlin abundance was more variable in southern (CV = 68%) than in northern Tomales Bay (CV = 45%). Average early-winter numbers of Dunlin in the north bay and south bay were similar (Table 2), but declined more steeply in the south bay (b = -756 birds yr^{-1}) than in the north bay (b = -478 birds yr^{-1}; Table 1). These declines were significantly associated with cumulative seasonal rainfall in the current year and total seasonal rainfall in the previous year (rainfall effects between years were independent of each other, r_9 < 0.12; Table 1). Decreasing abundance was more strongly related to rainfall in the previous year in the south bay than in the north bay (Table 1). After removing the linear effects of seasonal rainfall in the current and previous years, changes in numbers over the ten years of study were not significant (partial correlations with year, Table 1), and residuals showed no evidence of nonlinear trends.

Intra-seasonally, Dunlin abundance was significantly more dynamic in the south bay (mean CV = 103%) than in the north bay (mean CV = 79%, $F_{1,9}$ = 12.6, P < 0.01; Table 2). Although north bay and south bay numbers covaried significantly within years (partial r_{46} = 0.76, P < 0.001), the proportion in the north bay relative to the south bay increased with seasonal date (partial r_{46} = 0.62, P < 0.001). Salinity was also more variable in
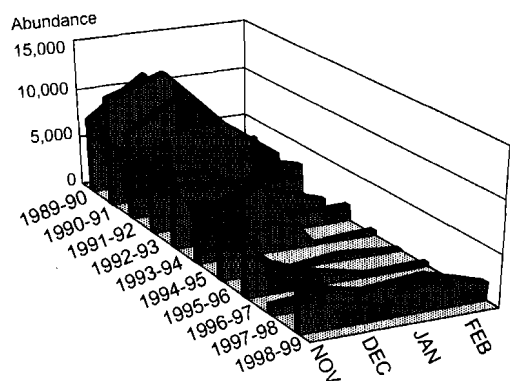

Figure 2. Annual and intra-seasonal baywide abundance of Dunlin in Tomales Bay, California.

Table 1. Multiple linear regressions of mean and maximum annual (autumn) Dunlin abundance, on mean cumulative seasonal rainfall on count days in the current year and total seasonal rainfall (through 30 June) in the previous year; partial correlations between residuals and year; standard and simple regression coefficients for annual trend in northern and southern Tomales Bay, California, 1989-90 to 1998-99 (N = 10). Variables for wind velocity and temperature did not enter the regressions.

	Mean abundance		Maximum abundance	
Independent variable	North Bay	South Bay	North Bay	South Bay
Mean cumulative seasonal rainfall, current year				
Standard partial coefficient	-0.71**	-0.75**	-0.87***[a]	-0.79**
Total seasonal rainfall, previous year				
Standard partial coefficient	-0.48*	-0.61**	-0.69**	-0.82**
R^2	0.85**	0.91**	0.86**	0.88**
Year				
Partial correlation	0.07	-0.06	-0.35	-0.18
Standard coefficient	-0.76**	-0.89***	-0.79**	-0.91***
Simple coefficient (birds per year)	-304**	-390***	-478**	-756***

*P < 0.05, **P < 0.01, ***P < 0.001.

southern (CV = 18%) than in northern Tomales Bay (CV = 9%; $F_{29,29}$ = 3.84, P < 0.001). The relative stability of north bay salinity was reflected in a significantly greater probability (0.33) of an increase in salinity the day after a decrease than in the south bay (0.12; χ^2_1 = 15.7, P < 0.001), presumably because of greater tidal circulation. Freshwater inflow was substantially greater from Lagunitas Creek (2.33 m³ sec⁻¹) than from Walker Creek (0.68 m³ sec⁻¹; t_{49} = 15.1, P < 0.001). Variation in stream flow was substantial in both Lagunitas Creek (CV = 236%) and Walker Creek (CV = 271%), but did not differ significantly between the two watersheds.

Arriving Dunlin reached maximum annual abundance, on average, twelve days later in the south bay than in the north bay, suggesting that arriving individuals may have filled the north bay before birds settled in the south bay. This difference was not significant based on the sample of ten years (paired t_9 = 1.40, n.s.), but was highly significant based on a bootstrap estimate of variability (paired t_{499} = 33.5, P < 0.0001). Dunlin abundance in winter declined significantly earlier in the south bay than in the north bay, with the decline beginning on average on 24 November ± 4.9 days (SE) in the south bay and 8 January ± 2.4 days in the north bay.

Proportional declines in winter abundance were significantly associated (P <

0.001) with greater cumulative winter rainfall (r_{55} = -0.62 in north bay and r_{55} = -0.75 in south bay), greater stream flow (r_{48} = -0.61, -0.64), and lower salinity (r_{28} = 0.48, 0.62). Hydrographic conditions produced more stable salinity in northern than in southern Tomales Bay (Fig. 3), which was associated with greater persistence of Dunlin in late winter (Table 2).

Feeding Distribution

Local shifts in the distribution of Dunlin among feeding areas were associated with weather and hydrographic conditions. At primary feeding sites on the deltas of Walker and Lagunitas Creeks, proportional use increased with subregional abundance of Dunlin, while at other sites such as Sand Point and South Marshall, proportional use declined (Fig. 4). In contrast, proportional use at Walker and Lagunitas Creek deltas declined with increasing cumulative seasonal rainfall and stream flow, and decreasing salinity, but increased at other sites such as Sand Point and South Marshall (Fig. 5).

At low numbers of Dunlin, trends in proportional abundance in south bay feeding areas were confounded by the flocking behavior. When south bay abundance dropped below 2,000 birds, individuals often concentrated into a single flock and occurred only

Table 2. Analysis of covariance[a] (ANCOVA) of abundance (ln) and density (ln) of Dunlin on Tomales Bay in relation to count area or north bay vs. south bay subregion (A), intra-seasonal period (S), and year (Y), and their interactions (AS, AY, SY). Multiple comparisons among transformed count area or subregional means are indicated columnwise by letters after untransformed means and standard errors: areas or subregions with the same letter within early or late winter period are not significantly different (Bonferroni adjustment for experimentwise error P > 0.05). Significant differences between early and late winter means are indicated by *P < 0.05, **P < 0.01, ***P < 0.001. See Fig. 1 for count area locations.

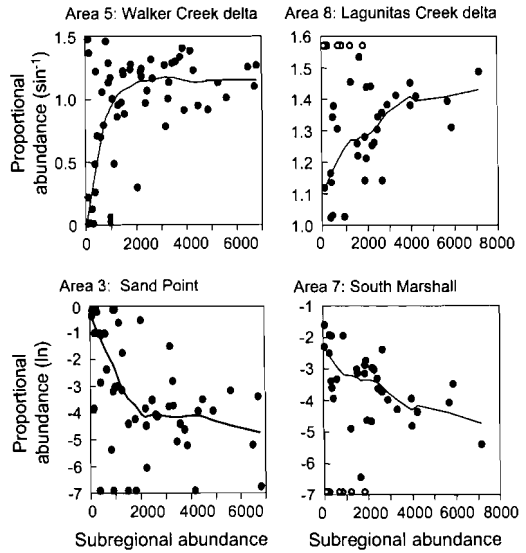| Count area or subregion	Area (ha)	Winter abundance				Winter density (birds·km⁻²)			
		Early		Late		Early		Late	
		$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
North bay		ANCOVA (N = 330)[a]: A**, Y**, AS**, AY**				ANCOVA (N = 330)[a]: A**, S, Y**, AS**, AY**			
1	8.7	2^C	0.9	2^D	1.0	0.20^C	0.10	0.22^C	0.11
2	8.7	10^{ABC}	9.6	13^{ABCD}	8.2	1.16^{ABC}	1.10	1.47^{ABC}	0.94
3	35.4	130^B	41.0	170^B	51.9	3.67^B	1.16	4.81^B	1.46
4	26.7	178^B	39.8	79***^{C}	25.2	6.66^B	1.49	2.97***^{B}	0.94
5	110.3	2968^A	336.9	868***^{A}	177.2	26.90^A	3.05	7.87***^{A}	0.94
6	31.9	23^C	11.3	17^D	6.7	0.72^C	0.35	0.53^C	0.25
South bay		ANCOVA (N = 202)[a]: A**, Y**, AS*, AY**, SY**, ASY**				ANCOVA (N = 202)[a]: A**, Y**, AS**, AY**, SY**, SY**			
7	55.7	60	10.7	20**^{B}	6.7	1.08^B	0.19	0.36**^{B}	0.12
8	215.4	2939	419.9	622***^{A}	148.9	13.64^A	1.95	2.89***^{A}	0.69
9	10.0	5	3.9	0^{AB}	0.0	0.52^{ABC}	0.39	0.00^{AB}	0.00
10	37.2	1	1.0	1^B	0.7	0.04^C	0.03	0.02^B	0.02
Tomales Bay		ANCOVA (N = 113)[a]: S*, Y**, AY**, SY**				ANCOVA (N = 113)[a]: A**, S*, Y**, AY**, AS, SY**			
North bay	221.8	3309	353.5	1149***^{A}	196.7	39.31^A	4.07	17.87***^{A}	2.68
South bay	318.3	3005	419.6	642***^{B}	152.6	15.28^B	1.94	3.26***^{B}	0.76

[a]Mixed-model analysis of covariance; covariate = days since beginning of early winter (November-December) or late winter (January-February); letter indicates effect with F-ratio significant at P < 0.05, *P < 0.01, **P < 0.001.
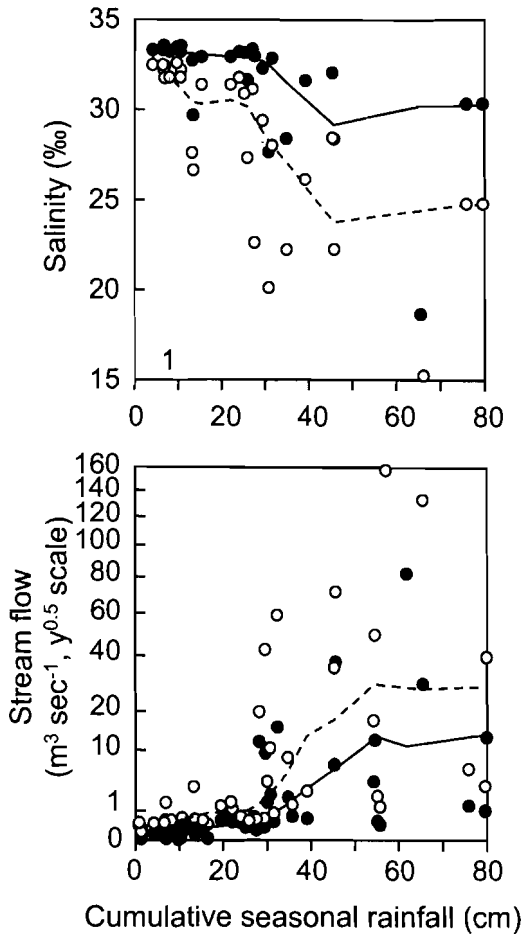
Figure 3. Relationships between cumulative seasonal rainfall, salinity and stream flow in Tomales Bay, California. Trend lines represent LOWESS smoothing (f = 0.5). Closed circles and solid line represent northern Tomales Bay; open circles and dashed line represent southern Tomales Bay.

Figure 4. Proportional use of key feeding areas in Tomales Bay by Dunlin, plotted against subregional Dunlin abundance in northern or southern Tomales Bay. Trend lines represent LOWESS smoothing (f = 0.5). Linear components of slope are significant in all plots ($P < 0.01$). Trends in proportional use of areas (7 and 8) do not include counts in which all south bay Dunlin occurred in a single flock at Lagunitas Creek delta (open circles, see text). Areas 5 and 8: $Y = \sin^{-1}(x)$, in radians; areas 3 and 7: $Y = \ln (x + 0.001)$. See Fig. 1 for area locations.

on the largest habitat patch—in spite of a contrasting shift toward other areas as subregional abundance declined (Figs. 4 and 5).

In the north bay, thresholds for shifts in relative use of feeding areas corresponded to a subregional abundance of 1,200-2,000 Dunlin (areas 3 and 5, Fig. 4), cumulative seasonal rainfall of 20-25 cm, and stream flow of about 0.5-1.0 m^3 sec^{-1} (areas 3 and 5, Fig. 5). In the south bay, relative use of feeding areas also changed with subregional abundance, cumulative seasonal rainfall, and stream flow, but no thresholds were apparent (Figs. 4 and 5). When cumulative seasonal rainfall reached 25-30 cm, stream flow

increased and salinity began to drop steeply at both ends of the bay, but more rapidly in south bay (Fig. 3). Dunlin distribution at both ends of the bay was associated with changes in salinity near the mouths of Walker and Lagunitas Creeks, with thresholds at about 33‰ in the north bay and 31‰ in the south bay (Fig. 5).

Regression analyses suggested a relationship between foraging density and Dunlin distribution (Fig. 4), but cumulative seasonal rainfall and weather accounted for these patterns (Table 3). Proportional use of several feeding areas declined with greater cumulative seasonal rainfall and post-storm conditions, including increasing barometric pressure, more northerly winds, and stronger winds (Table 3). In contrast, proportional use of Lawson's Meadow, Sand Point, and South Marshall (areas 2, 3, and 7) *increased* in response to such conditions (Table 3). Cumulative rainfall during three days prior to shorebird counts did not enter any models of weather effects because of a correla-

tion (r_{54} = 0.31) with cumulative seasonal rainfall, which was a more powerful predictor. Rainfall on count days entered as a significant term in two of the models (Table 3).

Feeding area preferences varied significantly between early and late winter and among years in both northern and southern Tomales Bay (Table 2). In most of the models (Table 3), weather variation accounted adequately for this variation. Exceptions were at White Gulch, Tom's Point, and North Marshall (areas 1, 4, and 6), where Dunlin use (independent of weather effects) varied significantly among years ($P < 0.05$). In all other models, intra-seasonal and annual effects of weather on Dunlin distribution were similar (modeling intra-seasonal effects independently, with year as random dummy variables, did not alter patterns of significant effects).

DISCUSSION

The general decline over years in number of wintering Dunlin observed in this study was correlated with a trend of increasing rainfall and storm activity. Consecutive years of heavy freshwater runoff can strongly reduce recruitment and abundance of estuarine bivalves, polychaetes, and amphipods (Boesch et al. 1975; Holland 1985), which predominate in the winter diets of Dunlin (Stenzel et al. 1983; Warnock and Gill 1996). Individual-based models of Oystercatcher (*Haematopus ostralegus*) abundance suggest that recurring winter food scarcity may reduce shorebird abundance by limiting recruitment of juveniles to the wintering area (Goss-Custard and West 1997). Alternatively, annual variation in winter Dunlin abundance might reflect the influences of other processes or seasons. Changes in Dunlin abundance on Tomales Bay are consistent with the hypothesis that numbers of wintering birds in more dynamic habitats are less stable across years. This suggests that winter shorebird use may be sensitive to changes in patterns of freshwater inflow into estuaries.

Warnock et al. (1995) provided evidence that intra-seasonal decreases in winter Dunlin abundance were associated with regional movements to inland habitats. It has been unclear whether such movements are driven by declining habitat suitability along the coast, by opportunities to exploit seasonally available wetlands in the interior, or by an interaction between these factors (Warnock et al. 1995). In Tomales Bay, the initiation of midwinter declines did not coincide in the two wintering groups of Dunlin, suggesting differential responses to local conditions.

Dunlin exhibited storm-related shifts in habitat preference away from sources of freshwater runoff and areas of wind exposure, to areas that offer relative protection from wind or more stable salinities. In the north bay, shifts in habitat preference coincided with thresholds of increasing stream flow and declining salinity. These thresholds occurred at 20-25 cm of cumulative seasonal rainfall, which is close to the point at which watershed soils become saturated by winter rains. Beyond this point, freshwater inflow responded quickly to rainfall events and remained elevated for about a week (Smith et al. 1991). Flooding events limited shorebird use by reducing tidal exposure of feeding areas, especially in the south bay where tidal drainage was restricted. Such events impose unpredictable limits on habitat use, indicated by consistent intra-seasonal shifts among habitat patches at temporal scales that contrast with the highly predictable cycles of tides (Connors et al. 1981; Barbosa 1997).

Because Dunlin and other shorebirds generally concentrate where the availability of their prey is greatest (Goss-Custard et al. 1977; Bryant 1979; Evans and Dugan 1984; Kelsey and Hassall 1989), the effects of salinity depression on the density and availability of benthic prey is a likely mechanism for midwinter changes in foraging distribution. Salinity depression in estuaries strongly reduces densities of benthic invertebrates, particularly during periods of heavy freshwater inflow or when salinities drop below 30‰ (Wolff 1983; Nordby and Zedler 1991). Differences in salinity tolerance, which are known to structure small-scale aggregated distributions and gradients in composition, richness, and seasonal abundance of invertebrates in estuaries (McLusky 1981; Wolff 1983), were suggested by changes in Dunlin
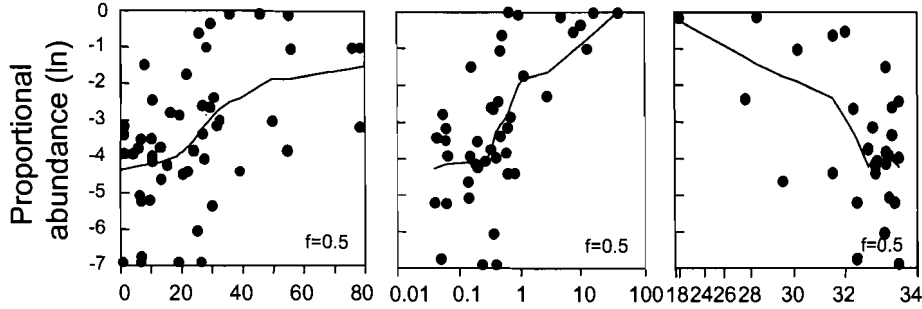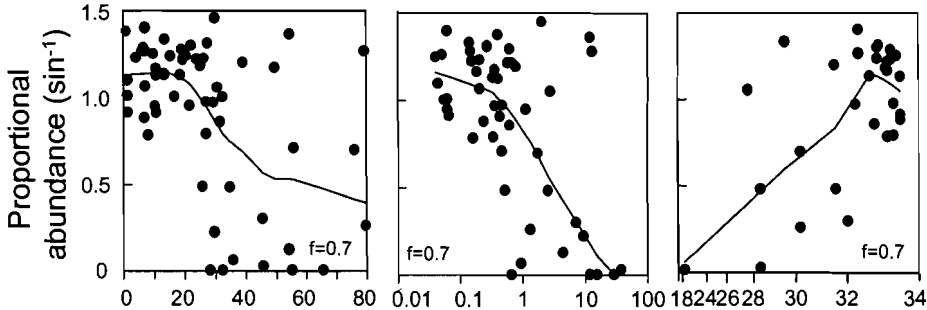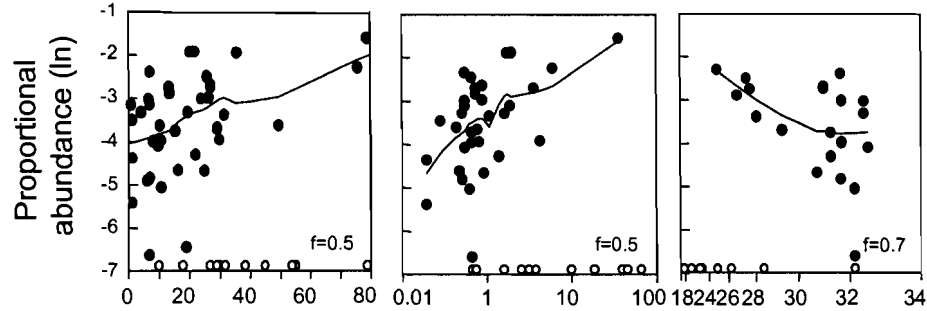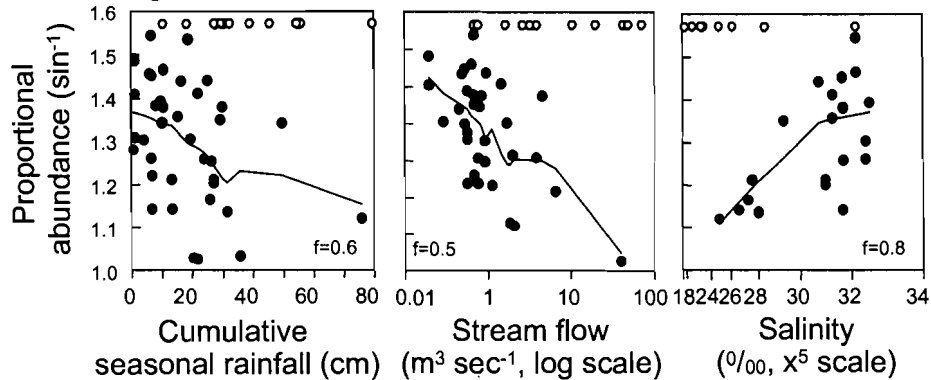
Figure 5. Proportional use of key feeding areas in Tomales Bay by Dunlin, plotted against cumulative seasonal rainfall, stream flow, and salinity. Salinities for areas 3 and 5 were measured near area 5; salinities for areas 7 and 8 were measure near area 8. Trend lines represent LOWESS smoothing. Linear trends are significant in all plots ($P<0.01$). Thresholds of abundance, suggested by consistent changes in slope across several scales of smoothing, are highlighted by the degree of smoothing (f) indicated in each plot. Trends in proportional use of south bay areas (7 and 8) do not include counts in which all south bay Dunlin occurred in a single flock at Lagunitas Creek delta (open circles, see text). Areas 3 and 7: $Y = \ln (x + 0.001)$; areas 5 and 8: $Y = \sin^{-1}(x)$, in radians. See Fig. 1 for area locations.

Table 3. Stepwise multiple regression of proportional Dunlin abundance by count area on daily weather variables (standard partial coefficients), partial correlations between residuals and subregional (north or south bay) abundance, and simple linear regression of proportional abundance on subregional abundance (standard coefficients), in Tomales Bay, California, 1989 to 1999 (N = 57). See Fig. 1 for area locations.

Independent variable	North bay count area						South bay count area		
	1	2	3	4	5	6	7	8	10
Cumulative seasonal rainfall	-0.30*	—[a]	0.57***	-0.59***	-0.60***	-0.31*	0.48**	-0.28	-0.49***
Rainfall	—	0.61***	—	—	—	—	—	-0.18	—
Barometric slope	—	—	—	—	-0.35***	—	—	—	—
Wind velocity, maximum	—	0.37***	0.21	—	-0.31**	—	—	—	—
Wind velocity, average	—	—	—	—	—	-0.30*	—	—	0.32*
Wind direction, average	—	—	—	—	—	—	—	—	-0.18
Temperature, average	—	—	—	-0.36***	-0.25**	—	—	-0.27*	—
Temperature, maximum	-0.54***	—	0.40***	—	—	-0.32*	—	—	—
Multiple regression R_{adj}^2	0.28***	0.66***	0.42***	0.50***	0.64***	0.17***	0.08*	0.25**	0.34***
Subregional abundance (partial correlation)	-0.02	-0.19	-0.16	0.23	0.13	-0.22	0.01	0.01	0.01
Subregional abundance (standard coefficient)	0.20	-0.29*	-0.41***	0.48***	0.71***	0.13	-0.28*	0.29*	0.30*

[a]Dash indicates that variable did not enter the regression (P > 0.15); *P > 0.05, **P < 0.01, ***P > 0.001.

habitat preference in Tomales Bay, which occurred at lower salinities in the south bay than in the north bay. Changes in Dunlin use may have been associated with lower salinity thresholds than indicated by the available data, because salinities were measured at mid-bay locations subject to greater mixing and unlikely to reflect direct effects of inflow from streams (Smith *et al.* 1991). In addition, salinities as low as 16‰ in the north bay and 0‰ in the south bay occurred between successive shorebird count days (Tomales Bay LMER/BRIE Research Program, Stephen V. Smith, unpublished).

In the north bay, the effects of runoff from Walker Creek on salinity tended to be smaller, more localized, and episodic, with lower inflow rates than at Lagunitas Creek in the south bay (Smith *et al.* 1971). Prey availability may decline as organisms recede deeper into substrates to avoid low salinities, and recover if runoff subsides and tidal circulation restores higher salinities (McLusky 1981). Heavy or persistent runoff, however, may severely reduce prey densities and prevent intra-seasonal recovery of suitable foraging conditions (Nordby and Zedler 1991). Consistent with these processes, Dunlin in the north bay exhibited relatively stable patterns of patch use until thresholds of cumulative seasonal rainfall, runoff, or salinity were reached. In the south bay, where water exchange depended primarily on runoff volume and wind-induced mixing rather than tides (Smith *et al.* 1971), salinity depression was greater, more extensive, and more persistent, corresponding to slower movement of freshwater through the system which can uncouple runoff patterns from immediate effects on tidal exposure and salinity. Under these conditions, patch use by Dunlin changed more continuously with stream flow and cumulative seasonal rainfall.

Rainfall, wind velocity and direction, and temperature were significantly associated with Dunlin distributions in Tomales Bay. Rainfall might affect patch use by reducing invertebrate activity and feeding rates of shorebirds (Pienkowski 1981; Goss-Custard 1984), or by forcing invertebrate prey to recede deeper into the substrate to avoid

reduced salinities. High winds have been shown to affect winter Dunlin distribution by propagating waves that mobilize fine sediments that, in turn, reduce invertebrate availability (Ferns 1983), and can result in higher tides that restrict access to feeding areas. Differences in wind exposure among patches can affect the thermal energy costs of foragers, the conspicuousness of prey, and selection of feeding areas (Evans 1976; Dugan *et al.* 1981; Davidson 1981). Although winter air temperatures on Tomales Bay were generally mild, with mean temperature on count days averaging $10.7 \pm 2.4°C$ (SD; N = 57), wind reduces the operative temperatures experienced by birds (Bakken 1990), and thermoregulatory costs in Dunlin change with wind-corrected (standard) operative temperatures below $19.8°C$ (Kelly 2000). Temperature-related shifts in habitat use were related to movements away from sources of freshwater inflow during warmer conditions associated with winter rainfall.

Dunlin may be able to respond to sediment cues rather than directly assessing differences in foraging success (Mouritsen and Jensen 1992). Deposition of flood-born sediment alters substrate texture and prey availability (Nordby and Zedler 1991), reducing use by foraging shorebirds (Gerstenberg 1979). In addition, high levels of turbidity trapped by slow exchange between the south bay and coastal waters may reduce or limit the abundance of benthic suspension feeders (Wolff 1983) consumed by shorebirds.

The relative abundance of a species between two habitat patches might be a poor indicator of habitat quality if patch use is influenced by Allee's principle (Fretwell 1972; Rangeley and Kramer 1998; Stephens and Southerland 1999), which states that per capita survival may decline at low population densities (Allee *et al.* 1949). Thus, at low abundance levels, individuals might settle preferentially in an occupied patch, irrespective of alternative foraging opportunities, if other advantages, such as the antipredation benefits of flocking (Page and Whitacre 1975; Kus 1985), outweigh differences in profitability among foraging sites. Results from southern Tomales Bay provide

evidence of this effect, where habitat use at low densities was determined by the location of a single flock, and was inconsistent with overall trends in proportional use. The apparent loss of foraging habitat quality as a criterion in habitat choice suggests reduced fitness in terms of winter survival.

Differences in Dunlin use of north and south Tomales Bay suggest that the strength and persistence of weather effects on local Dunlin distributions may depend on hydrographic parameters unique to each wintering area. These parameters include stream flow rates and variances, tidal prism (volume of tidal water exchange), water residence time, and circulation, and may be associated with topography, watershed soils and vegetation, land use, and climate (Kjerfve 1989).

Patterns of Dunlin abundance in Tomales Bay allow predictions about the dynamics of shorebird use in temperate estuaries. In areas where winter freshwater runoff varies substantially and tidal mixing is predominant, fast recovery times may result in relatively stable patterns of use by foraging shorebirds, interrupted by episodic shifts in habitat preference. In estuaries where pulses of winter freshwater runoff are slower or more continuous, or where water residence times are longer, recovery of suitable foraging conditions may be delayed and changes in habitat use may occur more continuously over longer intra-seasonal periods. In locations where winter flooding is intensive and persistent, as in river estuaries, shifts in habitat use may be limited to distinct seasonal reductions in foraging or overall use (Colwell 1993). Thus, the range of dynamic effects on winter shorebird abundance and distribution may extend from river estuaries to other intra-seasonally dynamic estuaries. The protection of coastal habitats for shorebirds can benefit from an understanding of how such processes influence habitat values within and among estuarine systems.

LITERATURE CITED

Allee, W. C., A. E. Emerson, O. Park, T. Park and K. P. Schmidt. 1949. Principles of Animal Ecology. W. B. Saunders, Philadelphia.

Bakken, G. S. 1990. Estimating the effect of wind on avian metabolic rate with standard operative temperature. Auk 107: 587-594.

Barbosa, A. 1997. Foraging habitat use in a Mediterranean estuary by dunlin, Calidris alpina. Journal of Coastal Research 12: 996-999.

Boesch, D. F., R. J. Diaz and R. W. Virnstein. 1975. Effects of Tropical Storm Agnes on soft-bottom macrobenthic communities of the James and York estuaries and the Lower Chesapeake Bay. Chesapeake Science 17: 246-259.

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

Burger, J. 1984. Abiotic factors affecting migrant shorebirds. Pages 1-72 in Behavior of marine animals, Vol. 6. Shorebirds: migration and foraging behavior (J. Burger and B. L. Olla, Eds.). Plenum Press, New York.

Chambers, J. M., W. S. Cleveland, B. Kleiner and P. A. Tukey. 1983. Graphical methods for data analysis. Wadsworth & Brooks/Cole Publishing Co., Pacific Grove, CA.

Cleveland, W. S. 1979. Robust locally weighted regressions and smoothing scatterplots. J. American Statistical Association 74: 829-836.

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

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

Daetwyler, C. C. 1966. Marine geology of Tomales Bay, central California. Pacific Marine Station Research Report 6: 1-169.

Davidson, N. C. 1981. Survival of shorebirds (Charadrii) during severe weather: the role of nutritional reserves. Pages 231-249 in Feeding and survival strategies of estuarine organisms (N. V. Jones and W. J. Wolff, Eds.). Plenum Press, New York.

Dugan, P. J., P. R. Evans, L. R. Goodyer and N. C. Davidson. 1981. Winter fat reserves in shorebirds: disturbance of regulated levels by severe weather conditions. Ibis 123: 359-363.

Evans, P. R. 1976. Energy balance and optimal foraging strategies in shorebirds: some implications for their distributions and movements in the non-breeding season. Ardea 64: 117-139.

Evans, P. R. and P. J. Dugan. 1984. Coastal birds: numbers in relation to food resources. Pages 8-28 in Coastal waders and wildfowl in winter (P. R. Evans, J. D. Goss-Custard and W. G. Hale, Eds.). Cambridge University Press, Cambridge.

Ferns, P. N. 1983. Sediment mobility in the Severn Estuary and its influence upon the distribution of shorebirds. Canadian Journal of Fisheries and Aquatic Science. 40 (Suppl. 1): 331-340.

Fretwell, S. D. 1972. Populations in a seasonal environment. Monographs in Population Biology 5. Princeton University Press, Princeton, NJ.

Galloway, A. J. 1977. Geology of the Point Reyes Peninsula, Marin County. Geological Bulletin 202. California Division of Mines, Sacramento.

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

Goss-Custard, J. D. 1980. Competition for food and interference among waders. Ardea 68: 31-52.

Goss-Custard, J. D. 1984. Intake rates and food supply in migrating and wintering shorebirds. Pages 233-270 in Behavior of marine animals, Vol. 6. Shorebirds: migration and foraging behavior (J. Burger and B. L. Olla, Eds.). Plenum Press, New York.

Goss-Custard, J. D. and A. D. West. 1997. The concept of carrying capacity and shorebirds. Pages 53-62 in Effect of habitat loss and change on waterbirds. ITE Symposium no. 30, Wetlands International publication no. 42 (J. D. Goss-Custard, R. Rufino and A. Luis, Eds.). Centre for Ecology and Hydrology, Natural Environment Research Council, London.

Goss-Custard, J. D., D. G. Kay and R. M. Blindell. 1977. The density of migratory and overwintering redshank, Tringa totanus (L.) and curlew, Numenius arquata (L.), in relation to density of their prey in south-east England. Estuarine and Coastal Marine Science 5: 497-510.

Harrington, B. and E. Perry. 1995. Important shorebird staging sites meeting Western shorebird Reserve Network criteria in the United States. Report of the U. S. Fish and Wildlife Service, Washington, D.C.

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

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

Kelly, J. P. 2001. Distribution and abundance of winter waterbirds on Tomales Bay, California: implications for conservation. Waterbirds. In press.

Kelly, J. P., N. Warnock, G. W. Page and W. W. Weathers. 2001. Effects of weather on body mass regulation in wintering Dunlin. Journal of Experimental Biology. In press.

Kelsey, M. G. and M. Hassall. 1989. Patch selection by Dunlin on a heterogeneous mudflat. Ornis Scandinavica 20: 250-254.

Kjerfve, B. 1989. Estuarine geomorphology and physical oceanography. Pages 47-78 in Estuarine Ecology (Day, J. W., C. A. S. Hall, W. M. Kemp and A. Yanez-Arancibia, Eds.). John Wiley & Sons, New York.

Kus, B. E. 1985. Aspects of flocking behavior and predator avoidance in wintering shorebirds. Ph.D. dissertation, University of California, Davis.

Manly, B. F. J. 1998. Randomization, bootstrap, and Monte Carlo methods in biology. Second edition. Chapman and Hall, London.

McLusky, D. 1981. The estuarine ecosystem. John Wiley and Sons, New York.

Mouritsen, K. N., and K. T. Jensen. 1992. Choice of microhabitat in tactile foraging Dunlins Calidris alpina: the importance of sediment penetrability. Marine Ecology Progress Series 85: 1-8.

Neter, J., M. H. Kutner, C. J. Nachtscheim, and W. Wasserman. 1996. Applied linear statistical models. IRWIN, Chicago.

Nichols, F. H. 1977. Infaunal biomass and production on a mudflat, San Francisco Bay, California. Pages 339-357 in Ecology of marine benthos (B. C. Coull, Ed.). University of South Carolina Press, Columbia, SC.

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

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

Page, G. W., and D. F. Whitacre. 1975. Raptor predation on wintering shorebirds. Condor 77: 73-83.

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

Pienkowski, M. W. 1981. How foraging plovers cope with environmental effects on invertebrate behavior and availability. Pages 179-192 in Feeding and Survival Strategies of Estuarine Organisms (N. V. Jones and W. J. Wolff, Eds.). Plenum Press, New York.

Puttick, G. M. 1984. Foraging and activity patterns in wintering shorebirds. Pages 203-231 in Behavior of marine animals, Vol. 6. Shorebirds: migration and foraging behavior (J. Burger and B. L. Olla, Eds.). Plenum Press, New York.

Rangeley, R. W. and D. L. Kramer. 1998. Density dependent anti-predator tactics and habitat selection in juvenile Pollock. Ecology 79: 943-952.

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

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

Smith, E. H., R. G. Johnson, and S. Obrebski. 1971. Physical, chemical, microbiological, and hydrographic characteristics of Tomales Bay. Pacific Marine Station Research Report 9: 1-70.

Smith, S. V., J. T. Hollibaugh, S. J. Dollar and S. Vink. 1991. Tomales Bay metabolism: C-N-P stoichiometry and ecosystem heterotrophy at the land-sea interface. Estuarine, Coastal and Shelf Science 33: 223-257.

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

Stenzel, L. E., G. W. Page and J. Young. 1983. The trophic relationships between shorebirds and their prey on Bolinas Lagoon. Point Reyes Bird Observatory, Stinson Beach, CA.

Stephens, P. A. and W. J. Southerland. 1999. Consequences of the Allee effect for behaviour, ecology and conservation. Trends in Ecology and Evolution 14: 401-405.

van der Have, T. M., E. Nieboer and G. C. Boere. 1984. Age-related distribution of Dunlin in the Dutch Wadden Sea. Pages 161-176 *in* Coastal waders and wildfowl in winter (P. R. Evans, J. D. Goss-Custard and W. G. Hale, Eds.). Cambridge University Press, Cambridge.

Velasquez, C. R. 1992. Managing artificial saltpans as a waterbird habitat: species' responses to water level manipulation. Colonial Waterbirds 15: 43-55.

Warnock, N., and R. E. Gill, Jr. 1996. Dunlin (*Calidris alpina*). *In* The Birds of North America No. 203 (A. Poole and F. Gill, Eds.). The Academy of Natural Sciences, Philadelphia; The American Ornithologists' Union, Washington D.C.

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

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

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

Wolff, W. J. 1983. Estuarine Benthos. Pages 151-182 *in* Ecosystems of the World 26: Estuaries and Enclosed Seas (B. H. Ketchum, Ed.). Elsevier Scientific Publishing Company, Amsterdam.