

## LATITUDINAL CLINES IN FOOD DISTRIBUTION CORRELATE WITH DIFFERENTIAL MIGRATION IN THE WESTERN SANDPIPER

KIMBERLEY J. MATHOT,<sup>1,3</sup> BARRY D. SMITH,<sup>1,2</sup> AND ROBERT W. ELNER<sup>1,2</sup>

<sup>1</sup>Centre for Wildlife Ecology, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6 Canada

<sup>2</sup>Pacific Wildlife Research Centre, Canadian Wildlife Service, Environment Canada, RR1, 5421 Robertson Road, Delta, British Columbia V4K 3N2 Canada

**Abstract.** We report that a latitudinal cline in intertidal food distribution is associated with the nonbreeding distribution of the Western Sandpiper (*Calidris mauri*). This novel result is the first to demonstrate a clear relationship between patterns of differential nonbreeding distribution and food availability for any shorebird species. Within each age class and sex, longer-billed Western Sandpipers winter further south. Moreover, females, the longer-billed sex, tend to winter south of males. Thus, both inter- and intra-sexual clines in bill morphology result in an overall gradient of increasing bill length from north to south. Longer-billed birds are able to extract prey that are buried more deeply in the sediment; therefore, we predicted shifts in the vertical distribution of food resources to coincide with the clines in bill morphology across the nonbreeding range. We tested our prediction by measuring biofilm density and the vertical distribution of macrofaunal invertebrates at six nonbreeding sites. Although no latitudinal trend was observed for biofilm, the vertical distribution of invertebrates was consistent with our prediction and revealed that the greatest relative abundance of surface prey occurred at northern nonbreeding sites and declined with decreasing latitude. We discuss the potential implications of these findings in the context of competing evolutionary hypotheses of differential migration and bill dimorphism in shorebirds.

**Key words:** *biofilm*; *Calidris mauri*; *differential migration*; *intertidal invertebrates*; *latitudinal gradients in resource distribution*; *nonbreeding distribution*; *shorebird*; *Western Sandpiper*.

### INTRODUCTION

Differential migration, in which the migration of some discernible classes of individuals (e.g., age, sex, or race) differs with respect to timing, distance, or both (Terrill and Abele 1988), is common in avian systems. When spatial segregation of a population occurs during the nonbreeding season, members of a population occupying different nonbreeding sites may be subject to different food regimes, weather conditions, levels of competition, and predation danger, all of which may affect survivorship (Cristol et al. 1999). Consequently, differential migration can have major demographic consequences with relevant implications for the design of conservation plans.

Three hypotheses are commonly evoked to explain differential migration, though empirical support for these hypotheses has been equivocal (for review see Cristol et al. 1999). The body size hypothesis (also

known as Bergmann's rule) proposes that larger individuals have greater cold-weather tolerance when compared with smaller individuals and therefore predicts that larger individuals should winter at higher latitudes or altitudes (Ketterson and Nolan 1976). The dominance hypothesis states that dominant individuals occupy areas closest to the breeding grounds and force subordinates to more distant areas (Gauthreaux 1978). Finally, the arrival time hypothesis proposes that the distance migrated affects the arrival time on the breeding grounds and predicts that the class of individuals that benefits most from early arrival to the breeding grounds should winter closest to the breeding grounds (Myers 1981). Despite the well-recognized role of patterns of food abundance for both migration (Lack 1960, Schneider and Harrington 1981, Alerstam 1993) and habitat selection processes (Stephens and Krebs 1986), food distribution has only recently been considered as a factor associated with patterns of differential nonbreeding distributions in avian systems (Elner and Seaman 2003, Katti and Price 2003, Nebel 2005).

Sexual dimorphism in body size and bill morphology is common among birds (Shine 1989, Figuerola 1999), and differences in bill structure are often associated with differences in feeding technique and diet (Durell 2000, Nebel et al. 2005). Therefore, differences in prey distribution may be expected to coincide with patterns of

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<sup>3</sup> Present address: Faculté des sciences, Département des sciences biologiques, Université du Québec à Montréal, Case postale 8888, Succursale Centre-ville, Montréal, Québec H3C 3P8 Canada.

E-mail: mathot.kimberley@courrier.uqam.ca

differential migration in sexually dimorphic species (the latitudinal gradients in prey availability hypothesis [Elner and Seaman 2003] and the resource-partitioning hypothesis [Nebel 2005]). In shorebirds that feed in soft substrates, shorter-billed birds rely more heavily on prey from the sediment surface compared with longer-billed birds, which are able to probe more deeply into the sediment to extract buried prey (Durell 2000). Therefore, in these shorebirds, a food-based hypothesis for differential migration would predict that the class of individuals with shorter bills should winter at sites with a higher proportion of food available at or near the surface, while the class of individuals with longer bills should winter at sites with a higher proportion of food available below the surface (Elner and Seaman 2003, Nebel 2005).

The Western Sandpiper (*Calidris mauri*) is an ideal species to test for a relationship between latitudinal patterns of food distribution and differential migration because they are highly sexually dimorphic with a well-documented pattern of differential migration. Females are ~5% larger than males with respect to most body measures, but 12% longer-billed (Cartar 1984). During the nonbreeding season, Western Sandpipers are distributed primarily along the west coast of the Americas between northern California and Peru, where they forage on intertidal mudflats (Wilson 1994). Western Sandpipers use two broad categories of feeding behaviors: pecking and probing (Sutherland et al. 2000), and there are sex-related differences in feeding behavior, with females using probing (subsurface) feeding modes more than males, the latter feeding almost exclusively by pecking (Mathot and Elner 2004). Females winter further south than males, and there is a pattern of increasing bill length from north to south within each age and sex class (Nebel et al. 2002, O'Hara 2002). Juveniles are underrepresented in the center of the nonbreeding range (Nebel et al. 2002).

Of the three hypotheses commonly evoked to explain differential migration, only the arrival time hypothesis has received empirical support in Western Sandpipers (Nebel et al. 2002, Nebel 2005). However, Nebel et al. (2002) have argued that the arrival time hypothesis is insufficient to explain differential migration by sex in Western Sandpipers because males wintering further south can and do initiate northward migration earlier (Fernández et al. 2001), possibly offsetting the cost of migrating a longer distance. Therefore, testing alternative hypotheses to explain the patterns of differential migration observed in this species seems prudent. Accordingly, O'Hara (2002) and Nebel and Ydenberg (2005) have proposed and tested two additional hypotheses for differential migration in the Western Sandpiper: (1) differential costs of flight associated with differences in body size and wing morphology, predicting larger and longer-winged individuals to migrate further south (O'Hara 2002) and (2) differential risk of predation among individuals, which predicts that more vulnerable

individuals should winter further south because it allows them to carry less fat, thereby reducing wing-loading and improving escape performance (Nebel and Ydenberg 2005). Here we test a food-based hypothesis for differential migration. Based on the overall trend of increasing bill length from north to south, we predict a shift from surface-biased food distributions in the north to subsurface-biased food distributions in the south of the Western Sandpiper nonbreeding range.

## METHODS

### *Study sites*

This work was carried out at six Western Sandpiper nonbreeding sites spanning 5000 km and 30° of latitude. Humboldt Bay (40°50' N, 124°05' W), Bodega Bay (38°19' N, 123°02' W), and San Francisco Bay (37°30' N, 122°06' W) in California were sampled in January and February 2003. Punta Banda (31°45' N, 116°37' W) and La Paz (24°06' N, 110°22' W) in Mexico were sampled in January 2004, and Costa del Este (09°00' N, 79°27' W) in Panama was sampled between September and December 2003.

### *Food sampling*

We collected invertebrates by means of sediment cores using a haphazard sampling design immediately following tidal exposure. Intertidal zones are notoriously heterogeneous (Sewell 1996), with invertebrate densities varying as a function of distance from the shoreline (Swennen et al. 1982, Pomeroy 2006), time since tidal exposure (Boaden and Platt 1971), and weather conditions (Pienkowski 1983). Therefore, invertebrate sampling was conducted at similar times following tidal exposure and at similar distances from the shoreline for all latitudes sampled in order to minimize the within-site variance arising due to these factors. The lower intertidal areas at three of our sites (9°, 24°, 37° N) were inaccessible due to the high penetrability of the sediment; therefore, we restricted our sampling and observations to the upper intertidal at all sites.

We used a modified syringe (with the apex sliced off and the edges beveled) with a 26-mm internal diameter and sampled to a depth of 40 mm to collect cores. These core dimensions were used because they allowed comparability with other studies (Sutherland et al. 2000, Mathot and Elner 2004, Pomeroy 2006) and because the depth is appropriate for sampling prey accessible to Western Sandpipers. Although the lowest depth at which prey was sampled exceeds the length of the longest Western Sandpiper bills by ~10 mm, these samples likely represent prey that would be accessible to the longest-billed Western Sandpipers prior to retraction into the sediment during sampling (Wolf 2001, Seaman 2003). Thus, depth intervals for sampled prey do not correspond directly to bill length, but increasing prey depth corresponds to prey accessible to increasingly longer-billed individuals.

We collected 20 invertebrate core samples at each of the first three sites sampled (37°, 38°, 40° N). One depth fraction from a sample collected at San Francisco Bay (37°) was lost prior to processing, resulting in a sample size of 19 for that site. Following the processing of these samples, power analysis using the most conservative (i.e., highest) estimate of variance indicated that a total sample size of 84 would be required to detect an overall decline of 25% in the uppermost layer of sediment across six nonbreeding sites with an  $\alpha = 0.05$  and  $\beta = 0.95$ , corresponding to a sample size of 14 per site. Accordingly, we reduced our sampling effort at the three remaining sites to 15 samples, of which one sample was lost from Costa del Este (9°) and one from La Paz (24°). Therefore, sample sizes for invertebrate cores at each site were: 9°,  $N = 14$ ; 24°,  $N = 14$ ; 31°,  $N = 15$ ; 37°,  $N = 19$ ; 38°,  $N = 20$ ; and 40°,  $N = 20$ .

Immediately following collection, each core for invertebrate estimates was sliced at 5-mm intervals, and each fraction was stored in an individually labeled plastic bag, placed in a cooler, and later preserved in 10% formalin in sea water. Core sampling and slicing took less than five minutes for each sample, which is within the range of times required for other invertebrate vertical profiling methods (range 4–8 min; Tita et al. 2000). Invertebrate samples were washed with filtered sea water through a 500- $\mu\text{m}$  sieve to separate the macrofaunal fraction of invertebrates. The fauna retained on the sieve were then identified and enumerated on a scored petri dish under a binocular microscope at 40 $\times$  magnification. Nematodes have previously been excluded from prey counts for other shorebirds, including Dunlin (*Calidris alpina*; Yates et al. 2000), a species closely related to the Western Sandpiper. Although Western Sandpipers are considered to be generalist foragers, opportunistically feeding on a variety of macroinvertebrates (Wilson 1994), we believe that excluding nematodes from prey counts in Western Sandpipers is also justified for the following reasons: (1) nematodes have been demonstrated to be absent from the stomach contents (Reeder 1951, Recher 1966, Senner 1979, Baldassarre and Fischer 1984, Quammen 1984, Senner et al. 1989, Davis and Smith 2001) and fecal droppings (Quammen 1984, Wolf 2001, Seaman 2003) of Western Sandpipers, despite being among the most numerically dominant taxa of invertebrate on intertidal mudflats (Heip et al. 1985), and (2) exclosure experiments that have detected the depletion of several invertebrate taxa following periods of high-intensity foraging by Western Sandpipers have failed to detect any depletion of nematodes (Sutherland et al. 2000).

We compare both the vertical distribution of biomass (ash free dry mass [AFDM]) across latitudes and the vertical distribution of individuals (counts). We calculated AFDMs by subtracting the mass of invertebrates after being combusted at 575°C for 6 h from their dry mass obtained after 72 h in a drying oven at 65°C (Swennen et al. 1982).

Biofilm was sampled as a food resource based on a recent study suggesting that it is a selected component of Western Sandpiper diets, particularly that of males (Elner et al. 2005). Biofilm consists of a thin layer of diatoms, bacteria, and muco-polysaccharides on the sediment surface (Cognie et al. 2001) and is rich in carbohydrates and proteins (Decho and Lopez 1993). Haphazardly collected core samples were used for biofilm estimates.

We collected 20 biofilm samples at each of the first three sites sampled (37°, 38°, 40°), with one sample being lost from site 40°. Power analysis based on the first three sites indicated that a total sample size of 120 (20 samples per site) would be required to detect an overall decline of 25% in the uppermost layer of sediment across six nonbreeding sites with an  $\alpha = 0.05$  and  $\beta = 0.95$ . However, we were forced to reduce our sampling effort at the final three sites sampled due to limited access to freezer space for our samples and collected 15 samples at each of the final three sites. This sampling effort gave us a predicted power of 0.90. Therefore, sample sizes for biofilm cores at each site were: 9°,  $N = 15$ ; 24°,  $N = 15$ ; 31°,  $N = 15$ ; 37°,  $N = 20$ ; 38°,  $N = 20$ ; and 40°,  $N = 19$ .

Cores sampled for biofilm were frozen immediately following collection, and then the top 2 mm were sliced off the frozen core. Chlorophyll is a major component of biofilm and can be used as a predictor of biofilm density (Underwood and Smith 1998). We therefore used chlorophyll concentration as an index of biofilm abundance. Chlorophyll concentration was determined fluorometrically according to the method outlined in Sutherland et al. (1998).

#### *Latitudinal patterns in the vertical distribution of food*

We used a model selection approach (Burnham and Anderson 2002) to rank competing hypotheses that the vertical distribution of invertebrates (counts and biomass) varied with latitude. At each of six north latitude (9°, 24°, 31°, 37°, 38°, 40°) sites we measured the number and biomass of invertebrates in each of eight depth categories from 0 to 40 mm (i.e., 5-mm categories) in each sample. The number of samples ( $s$ ) collected at each latitude varied (see Methods and Table 1), but yielded a total of 816 invertebrate counts and biomass measurements.

Our hypothesis that the distribution of invertebrates by depth changes predictably with latitude leads to a global explanatory regression model to predict the mean proportion of biomass or counts for each depth  $\times$  latitude cell that treats latitude as a continuous variable ( $L$ ) of degree units and depth as eight categorical variables ( $D_1$  to  $D_8$ ,  $D_d = 0$  or 1) increasing with depth. Since our key hypothesis is that the distribution of invertebrates among depth categories varies with latitude, our model also requires seven interaction terms ( $L \times D_1$  to  $L \times D_7$ ). Note that the variable  $L$  does not occur independently in our set of hypothetical models since the total of the proportions over all depths in each

TABLE 1. Summary of differences among six Western Sandpiper nonbreeding sites spanning 5000 km on the west coast of the Americas.

Location	Sex bias	Prey density		Prey biomass		Biofilm	
		Mean ± SE	N	Mean ± SE	N	Mean ± SE	N
Costa del Este, 09° N	female	1363 ± 348	14	0.34 ± 0.09	14	2736 ± 884	15
La Paz, 24° N	male	1279 ± 348	14	0.23 ± 0.09	14	11899 ± 884	15
Punta Banda, 31° N	male	1354 ± 336	15	0.33 ± 0.09	15	1382 ± 884	15
San Francisco Bay, 37° N	male	3801 ± 299	19	0.99 ± 0.08	19	1319 ± 765	20
Bodega Bay, 38° N	male	3321 ± 291	20	0.44 ± 0.08	20	5565 ± 785	19
Humboldt Bay, 40° N	male	1807 ± 291	20	0.22 ± 0.07	20	4940 ± 785	19

Notes: Prey density is expressed as number of prey individuals per liter of sediment; biomass is expressed as grams ash-free dry mass per liter of sediment; and biofilm density is expressed as micrograms chlorophyll *a* per liter of sediment. Invertebrates were sampled to 40 mm depth; biofilm was sampled to 2 mm depth.

sample (*s*) and at all latitudes sums to unity (1), so by definition the total of the proportions cannot logically vary with latitude. Thus our linear global model is

$$\tilde{P}_{l,d} = \sum_{d=1}^7 D_d(\beta_d + \beta_{7+d}L_l) \tag{1a}$$

using *l* as an index for *L*, and where we use the logit link

$$P_{l,d} = \frac{1}{1 + e^{-P_{l,d}}} \tag{1b}$$

to map the linear predictor  $\tilde{P}_{l,d}$  of the mean proportion for each depth and latitude,  $P_{l,d}$ , to the range (0, 1). Note also that

$$P_{l,8} = 1 - \sum_{d=1}^7 P_{l,d}. \tag{1c}$$

We obtained the maximum likelihood model fits by calculating the negative ln-likelihood of our observed biomass proportions, given the model predictions, assuming a normal distribution of model residuals for the biomass data. Modeling the variance associated with each depth by latitude biomass proportion prediction ( $P_{l,d}$ ) as a scaled (*V*) function of that prediction ( $VP_{l,d}^2$ ) was effective for empirically achieving homoscedastic and approximately normally distributed residuals. Model likelihood ( $\ell$ ) for the biomass model was therefore defined by

$$\ell = \sum_{l=1}^6 \sum_{d=1}^8 \sum_{s=1}^{S_l} \ln \sqrt{2\pi VP_{l,d}^2} + 0.5 \left[ \frac{(M_{l,d,s} - P_{l,d})^2}{VP_{l,d}^2} \right] \tag{2}$$

where  $S_l$  are the sample sizes for each latitude, and  $M_{l,d,s}$  are the measured proportions.

For our count data we used ordinal logistic regression with a multinomial error distribution, the multinomial likelihood being defined by

$$\ell = \sum_{l=1}^6 \sum_{d=1}^8 \sum_{s=1}^{S_l} C_{l,d,s} \ln \left( \frac{C_{l,d,s}}{E_{l,d,s}} \right) \tag{3a}$$

where  $C_{l,d,s}$  is the actual invertebrate count and  $E_{l,d,s}$  is the expected count, for each sample subject to the constraint that

$$\sum_{d=1}^8 C_{l,d,s} = \sum_{d=1}^8 E_{l,d,s}. \tag{3b}$$

The expected count ( $E_{l,d,s}$ ) is calculated as

$$E_{l,d,s} = P_{l,d} \sum_{d'=1}^8 C_{l,d',s}. \tag{3c}$$

Because of the need to code a nonstandard statistical design (Eqs. 1 and 2), both models were coded in Microsoft EXCEL. For each posed model the maximum likelihood parameter estimates for  $\beta_1$  to  $\beta_{14}$  and *V* were obtained by minimizing the negative ln-likelihood using EXCEL's Solver tool. Each model's Akaike Information Criterion (AIC<sub>c</sub>, or QAIC<sub>c</sub>) was subsequently calculated, and statistical significance was calculated using likelihood ratios. Model selection protocols were followed as described in Burnham and Anderson (2002), with the best-supported model being chosen on the basis of lowest AIC<sub>c</sub>, or in the case of the invertebrate counts, QAIC<sub>c</sub>, using a value for  $\hat{c}$  obtained from a goodness-of-fit randomization.

We tested for trends in biofilm abundance using a linear regression with latitude as the explanatory variable.

*Feeding behavior*

In Western Sandpipers, sex-related differences in bill morphology are associated with sex-related differences in foraging behavior (Mathot and Elnor 2004). We took advantage of the intra-sexual clines in bill morphology across the nonbreeding range to test whether intra-sexual differences in bill morphology conferred differences in feeding behavior. Observations were made using a spotting scope in the open among flocks of foraging sandpipers. We classified individuals as either male or female by eye (see Mathot and Elnor 2004) based on the high degree of sexual dimorphism in bill length in this species (Page and Fearis 1971, Cartar 1984). Intermediate-sized individuals were not assigned to a sex and are excluded from the analyses.

Individuals were randomly selected for one-minute observations, except in La Paz, where uniquely color-banded individuals were preferentially observed in order

TABLE 2. Independent verification of visual sex assignment to individually color-banded birds in La Paz, Mexico, whose sex, based on Page and Fearis (1971) classification scheme, was known.

Page and Fearis (1971) assigned sex†	Visually assigned sex			Error rate‡
	Male	Intermediate	Female	
Male (24)	21	3	0	1/22; 4.5%
Indeterminate (1)	1	0	0	NA
Female (10)	0	6	4	0/4; 0%

† Values in parentheses indicate sample sizes.

‡ Error rates were calculated as the percentage of individuals that were falsely assigned to a sex category out of the total number of individuals assigned to that sex category. For example, a total of 22 birds were visually assigned the sex of male. Of these, one bird was not assigned to the male sex according to the Page and Fearis (1971) sexing criteria. Therefore, the error rate in the assignment of the male sex is 1/22, or 4.5%. Similarly, a total of four individuals were visually assigned the sex of female. Of these, all four were assigned the female sex based on Page and Fearis' (1971) sexing criteria. Therefore, the error rate in assignment of the female sex is 0/4, or 0%. No error rate is estimated for the assignment of the intermediate sex category, because this category was used to avoid misclassification of individuals to either sex and not to approximate the number of individuals that would remain unclassified using the Page and Fearis (1971) sexing criteria.

to independently verify the accuracy of the visual sexing method. Results indicate that the visual sexing technique was accurate, with a 0% error rate in the assignment of the female sex category and a 4.5% error rate in the assignment of the male sex category (see Table 2). We recorded the occurrence of two major feeding modes: "pecks" and "probes." "Pecks" included all behaviors that involved contact of the bill to the sediment surface. "Probes" included all behaviors involving insertion of the bill into the sediment, usually >1/3 the length of the bill. Percentage of probing was used as an index of feeding mode. A single observer (K. J. Mathot) made all focal observations.

Because no females were observed at the two northernmost nonbreeding sites, we could not test for

a sex × latitude interaction. Therefore, we tested for patterns in feeding mode within each sex using separate linear regressions with latitude as the explanatory variable. We used both normal and binomial regressions for each sex.

RESULTS

Sites

The invertebrate communities were dominated by nematodes and polychaetes at all sites, except at San Francisco Bay (37°) and Humboldt Bay (40°), where small bivalves (<1 cm across) and coropheum, respectively, were also abundant (Fig. 1). Site differences in total food abundance measures are summarized in Table 1. Latitude was a significant factor associated with inter-

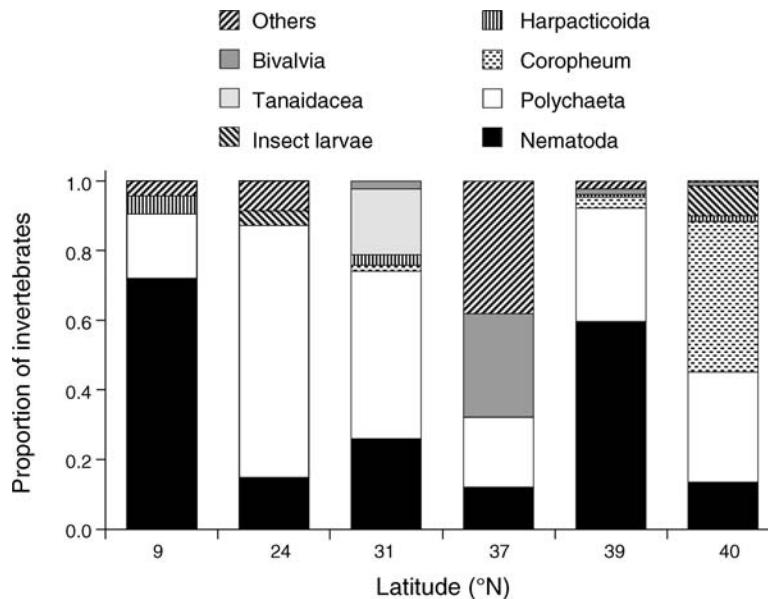


FIG. 1. Proportional representation of invertebrate taxa for each site. "Others" consists of the following taxa: amphipoda, arthropoda, brachiopoda, brachyura, cumaceans, foraminifera, gastropoda, ostracoda, and tanaidaceans. This work was carried out at six Western Sandpiper nonbreeding sites spanning 5000 km on the west coast of the Americas.

TABLE 3. Regression model rankings for the global model and less-parameterized models posed to explain the variance in invertebrate counts and biomass proportions at depth ( $D$ ) and in relation to north latitude ( $L$ ) and the  $D \times L$  interaction.

Model	Rank	$\Delta\text{QAIC}_c$ or $\Delta\text{AIC}_c^\dagger$	$K$	$\ell$	$P$	$r^2$
Invertebrate counts						
$L + D + D(L)$	1	0.00	9	1231.57	<0.0001	0.46
Global model $D + D \times L$	2	4.93	14	1223.51	<0.0001	0.46
$D$	3	38.15	7	1297.98	<0.0001	0.45
Null model (all $P_{i,d} = 0.125$ )	4	868.93	1	2625.39	...	0.00
Invertebrate biomass proportions						
Global model $D + D \times L$	1	0.00	15	-921.59	<0.0001	0.51
$L + D + D(L)$	2	3.19	10	-914.84	<0.0001	0.51
$D$	3	182.28	8	-823.24	<0.0001	0.47
Null model (all $P_{i,d} = 0.125$ )	4	1099.34	2	-358.62	...	0.00

Notes: The corrected Akaike Information Criterion ( $\text{AIC}_c$ ) for the best-supported biomass models (rank = 1) is -1812.59.  $\text{QAIC}_c$  for the best-supported invertebrate counts is 804.92, based on a  $\hat{c} = 3.15$ .  $K$  is the number of estimated parameters,  $\ell$  is the model likelihood. Statistical significance ( $P$ ) is expressed relative to the null model.

$^\dagger$  Values are  $\Delta\text{QAIC}_c$  for the invertebrate counts and  $\Delta\text{AIC}_c$  for the biomass proportions.

site variation in the count distribution of invertebrates ( $F_{1,100} = 14.62$ ,  $P = 0.0002$ ,  $r^2 = 0.13$ ), but not with inter-site variation in invertebrate biomass densities ( $F_{1,100} = 2.74$ ,  $P = 0.10$ ,  $r^2 = 0.03$ ). Biofilm abundance varied significantly between sites ( $F_{5,97} = 21.19$ ,  $P < 0.0001$ ).

#### Latitudinal patterns in the vertical distribution of food

Our regression analyses provide unequivocal statistical evidence that the depth profiles of invertebrates varied with latitude (Table 3). For both invertebrate counts and invertebrate biomass, the difference in  $\text{AIC}_c$  ( $\text{QAIC}_c$ ) between the two best-supported models and their competitors clearly removes the lesser-supported models from consideration. The top two ranked models in both analyses show a shift in the distribution of invertebrate counts and invertebrate biomass with depth consistent with our prediction that at lower latitudes, invertebrate counts (Fig. 2) and invertebrate biomass (Fig. 3) tend to be concentrated deeper in the sediment. The " $L + D + D(L)$ " model, in which the depth effect is a function of latitude (i.e., all values of  $\beta_{7+d}$  are equal), is a more parsimonious representation of the global model, though both the global and " $L + D + D(L)$ " models present similar depth distribution patterns with latitude.

There was no effect of latitude on biofilm abundance across the nonbreeding distribution of Western Sandpipers ( $F_{1,101} = 0.40$ ,  $P = 0.53$ ,  $r^2 = 0.004$ ; Table 1).

#### Feeding behavior

Across all sites, females used a higher percentage of probing feeding behaviors than males ( $F_{1,499} = 173.35$ ,  $P < 0.0001$ ), and there was no effect of latitude on feeding behavior within females ( $F_{1,119} = 0.53$ ,  $P = 0.47$ ,  $r^2 = 0.004$ ; Fig. 4) using normal regression. Though binomial regression indicated a weak increase in probing with increasing latitude ( $P = 0.001$ ) we are not confident in this conclusion since our data no doubt include more than just binomial sampling error. Using normal regression, and corroborated with binomial regression,

there was a small (from 0.2% to 0.9% probing) but significant increase in the percentage of probing in males with decreasing latitude ( $F_{1,379} = 5.01$ ,  $P = 0.019$ ,  $r^2 = 0.014$ ; Fig. 4).

#### DISCUSSION

Ours is the first study to relate clines in the distribution of food to patterns of differential migration in a shorebird system and, to our knowledge, also the first to document latitudinal clines in the vertical distribution of marine invertebrates in soft sediments. We recorded higher counts of prey at more northerly nonbreeding sites. We also recorded differences in the vertical distribution of food, independently of total food abundance, which were consistent with predictions from a food-based hypothesis for differential migration. No latitudinal trends in mean biofilm density were observed; however, the vertical distribution of invertebrate prey, both in terms of biomass and counts, differed across latitudes. The greatest relative abundance of surface prey occurred at northern nonbreeding sites and showed linear declines with decreasing latitude.

We are aware of only one other study that has investigated food availability in a shorebird system across a broad geographic range. In that study, Piersma et al. (1993) compared prey biomass and the harvestable fraction of prey for Red Knots (*Calidris canutus*) across several nonbreeding sites spanning  $>90^\circ$  of latitude. As in our study, they were unable to detect any relationship between total prey biomass and latitude. However, they did not test for latitudinal patterns in the vertical distribution of prey.

Male and female Western Sandpipers showed consistent differences in their feeding behavior across the six nonbreeding sites sampled. Females had a higher use of probing feeding modes compared with males, the latter feeding almost exclusively using pecking modes. The magnitude of difference between males and females ( $\sim 1\%$  probing and  $10\text{--}15\%$  probing, respectively) was comparable to previous observations at a migratory

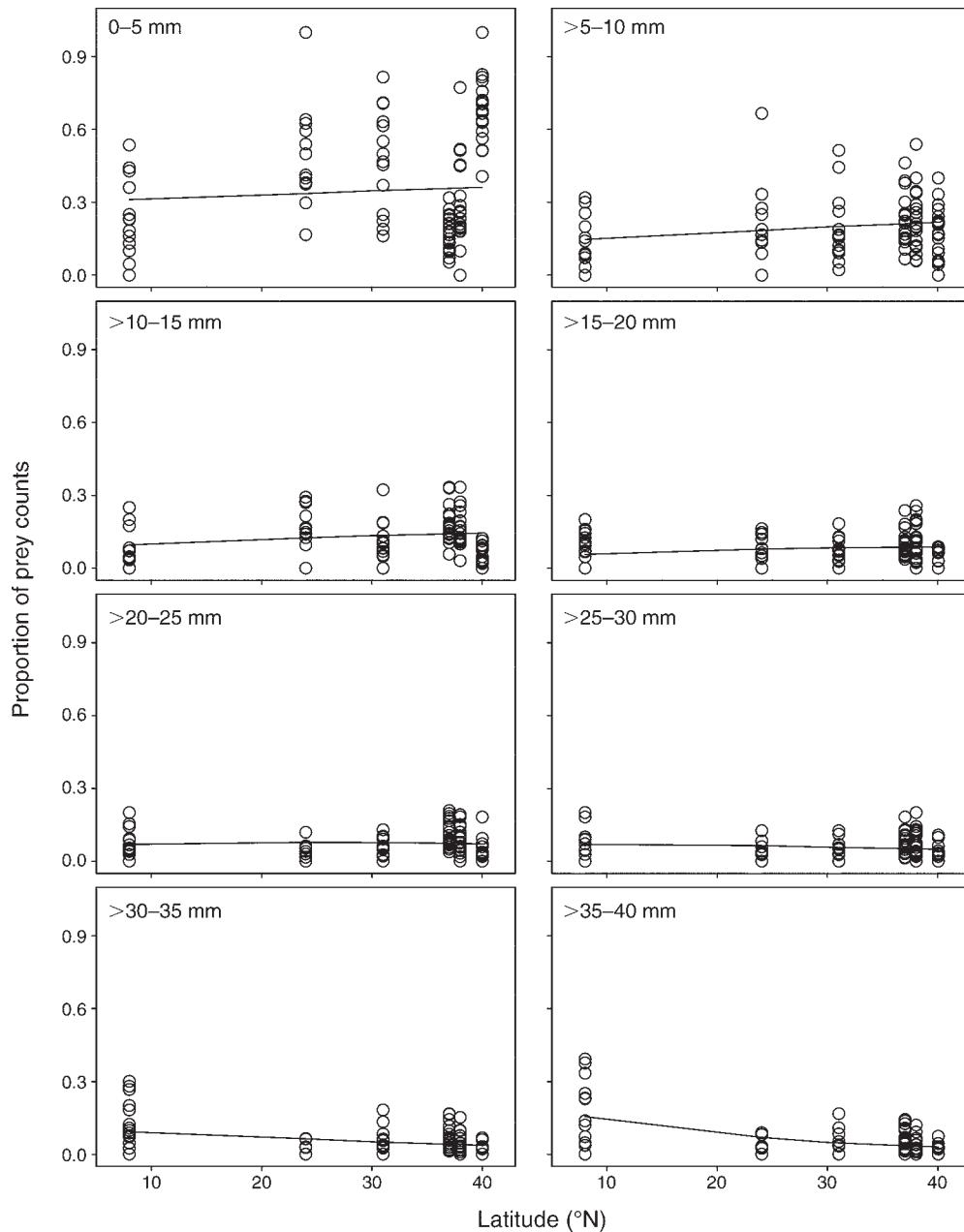


FIG. 2. Changing proportions of prey counts in each depth range in relation to latitude for eight 5-mm sediment depth ranges between 0 and 40 mm. The model fit lines from the best-supported model ( $D + L + D(L)$ ;  $P < 0.0001$ ) demonstrate a shift in prey count depth distribution from deep to shallow as latitude increases (south to north). Sample sizes for each latitude are as follows: 9°,  $N = 14$ ; 24°,  $N = 14$ ; 31°,  $N = 15$ ; 37°,  $N = 19$ ; 38°,  $N = 20$ ; 40°,  $N = 20$ . The sample sizes indicate the number of samples collected at each site (i.e., at each latitude). Each sample in turn is composed of eight depth intervals.

stopover site (Mathot and Elnor 2004). However, we detected no strong shifts in feeding mode across latitudes for female Western Sandpipers. Latitudinal trends in feeding mode were observed for males, with a fourfold increase in the use of probing recorded from north to south in the nonbreeding range.

Our results differ from those reported by Nebel (2005), in which no latitudinal trends in foraging

behavior were apparent for male or female Western Sandpipers, but significant among-site differences were observed for females. We suggest that differences between our results and those reported in Nebel (2005) may be largely attributable to differences in power. We had relatively large sample sizes for males, sampled more sites, and included sites at more intermediate latitudes compared with Nebel (2005),

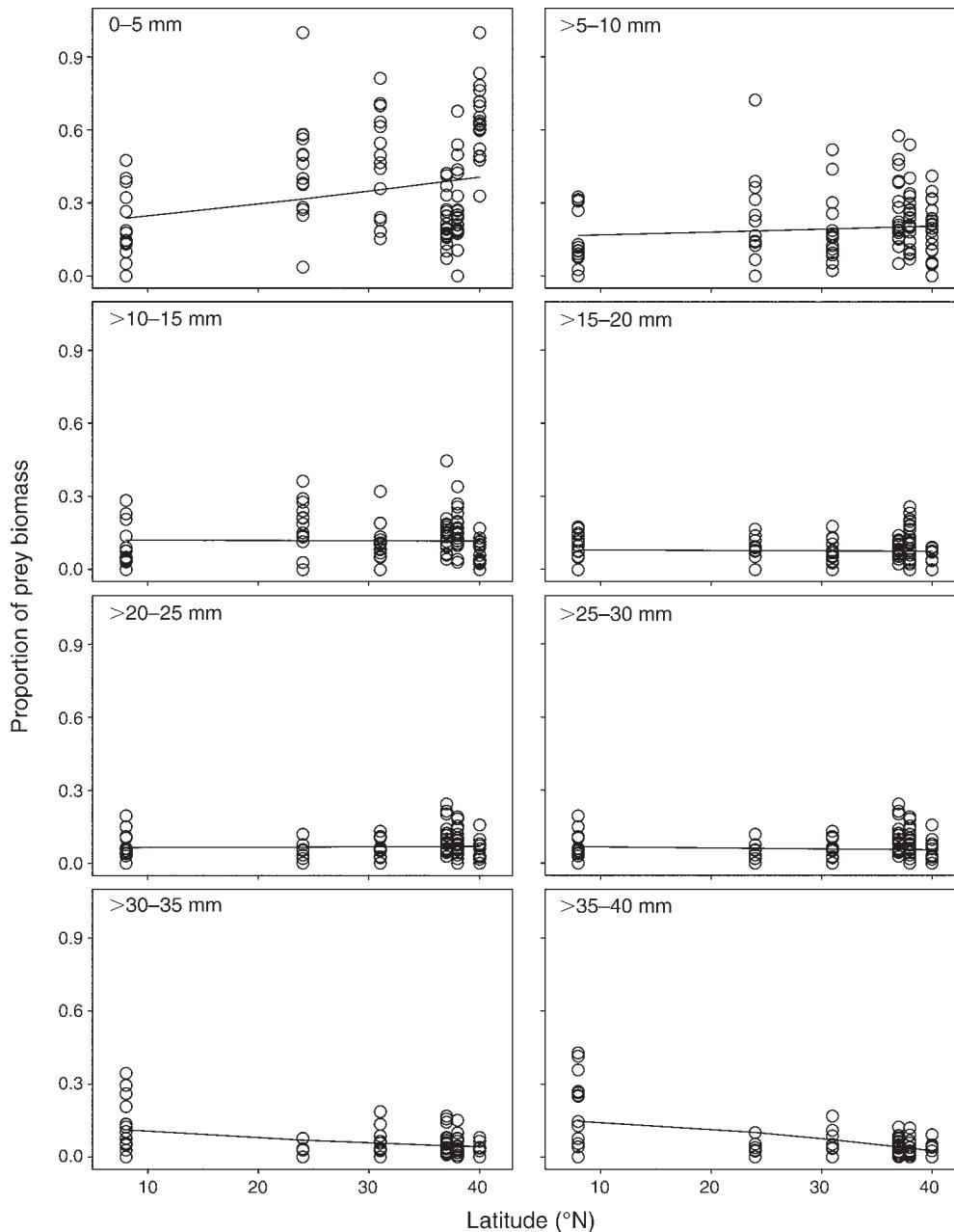


FIG. 3. Changing proportions of prey biomass in each depth range in relation to latitude for eight 5-mm sediment depth ranges between 0 and 40 mm. The model fit lines from the best-supported (global) model ( $D + D \times L$ ;  $P < 0.0001$ ) demonstrate a shift in biomass depth distribution from deep to shallow as latitude increases (south to north). Sample sizes for each latitude are as follows: 9°,  $N = 14$ ; 24°,  $N = 14$ ; 31°,  $N = 15$ ; 37°,  $N = 19$ ; 38°,  $N = 20$ ; 40°,  $N = 20$ .

giving us greater power to detect latitudinal trends in the foraging behavior of males. In contrast, the sample sizes for females in Nebel's (2005) study were generally larger compared with ours. However, although Nebel (2005) recorded significant differences in the foraging behavior of females between two sites, as in our study, no latitudinal trend in female feeding behavior is evident. We conclude that the trend in feeding behavior observed among males in this study corre-

sponds with increasing proportions of food available below the surface and increasing mean male bill length from north to south. While the absence of a trend in foraging behavior for females is difficult to interpret, high variance and low sample size may have obscured patterns and the case should not be considered resolved.

Our results demonstrate correlations between the patterns of bill morphology and food distributions

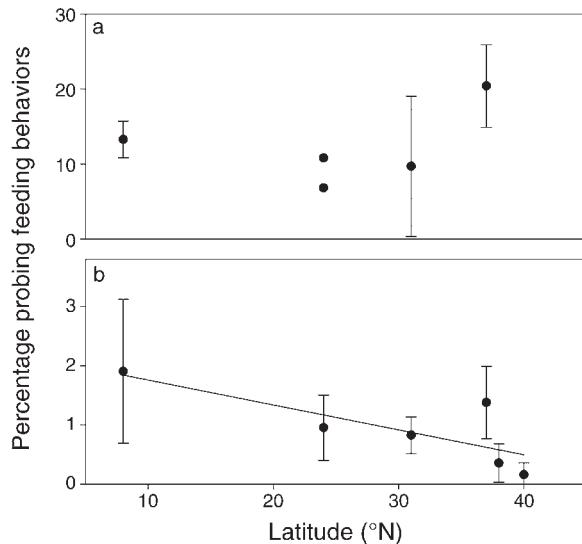


FIG. 4. Latitudinal trends in feeding mode for (a) female and (b) male Western Sandpipers using normal regression. Sample sizes for each latitude are as follows (male, female): 9°,  $N = 22$ , 107; 24°,  $N = 68$ , 2; 31°,  $N = 65$ , 7; 37°,  $N = 110$ , 8; 38°,  $N = 52$ , 0; 40°  $N = 65$ , 0. Error bars (95% CI) for females at La Paz, Mexico (latitude 24° N), are not presented because only two observations of females were made; raw data are presented instead.

across the nonbreeding range of Western Sandpipers. At least two mechanisms can be hypothesized to generate such correlations: (1) latitudinal patterns in the vertical distribution of food drive differential migration, resulting in overall clines in bill morphology across the nonbreeding range or (2) clines in bill morphology across the nonbreeding range result from adaptation of bill morphology to local patterns of food availability secondary to the evolution of differential migration.

Differentiating between these alternative hypotheses will require comparative analysis; however, there is insufficient information available on gradients in bill morphology and prey distribution patterns across the nonbreeding ranges of other shorebird species to allow for use of this method. Nonetheless, we argue that gradients in bill morphology appear more parsimoniously explained as a consequence rather than a cause of differential migration. Firstly, while a food-based hypothesis clearly predicts that males should be restricted to the northern part of the nonbreeding range, it is less evident why the longer bill of females should preclude them from wintering further north. Exclusion of females from northern nonbreeding sites resulting from the surface-biased distribution of food would require that females be less efficient at pecking compared with males or that the prey available via pecking be less profitable. Although females probe significantly more than males (Mathot and Elnor 2004), they nonetheless use pecking modes ~80% of the time, which suggests both that females are able to use the pecking mode effectively and that pecking is a profitable feeding mode

for females. Given this, and that invertebrate counts are higher and the cost of migration lower (O'Hara 2002) in the northern part of the nonbreeding range, additional factors other than food distribution seem necessary to explain the southerly distribution of females. A food-based hypothesis for differential migration also fails to easily account for age-related differences in migratory distance, which is common among shorebirds (Cristol et al. 1999) and has important life history consequences because the propensity for yearlings to attempt to breed in their first year declines with increasing migration distance (Summers et al. 1995, O'Hara et al. 2005). Therefore, we suggest that other factors are likely responsible for the differential migration by sex and age in Western Sandpipers and that secondary adaptation of bill morphology to local nonbreeding site conditions is responsible for the latitudinal gradient in bill length observed in this species.

Latitudinal variation in resource distribution and availability have previously been cited as factors driving inter- and intraspecific latitudinal gradients in body size in carnivorous and granivorous mammals (McNab 1971) and bill morphology in insectivorous birds (Schoener 1971) and leaf warblers (Katti and Price 2003). Adaptation of bill morphology to local nonbreeding conditions in shorebirds may provide a mechanism for the evolution of extreme bill dimorphism observed in some species. Sexual selection is the major selective pressure driving body size dimorphism in shorebirds (Székely et al. 2000). However, many species show disproportionately greater dimorphism in bill morphology, and there is no evidence that niche partitioning on the breeding grounds underlies dimorphism in feeding structure (Székely et al. 2000). Thus, for species such as the Western Sandpiper, where intersexual differences in bill morphology far exceed intersexual differences in most body size measures (~12% vs. 5%; Cartar 1984), differences in selective pressures on the nonbreeding grounds remain the most likely explanation for further divergence of bill morphology (Elnor and Seaman 2003).

Our finding of latitudinal trends in the depth distribution of invertebrates adds a third dimension to current understanding of latitudinal gradients of species distributions. While latitudinal gradients in species distributions have been documented in both terrestrial and marine systems (Rosenzweig 1995, Hillebrand 2004), most studies have focused on species richness gradients (Hillebrand 2004). To our knowledge, this study is the first to test for latitudinal gradients in the vertical distribution of macrofaunal invertebrates in marine soft-bottom sediments. However, latitude itself is not an environmental variable, but rather a surrogate for macro-ecological patterns (Rex et al. 2005) and consequently does not indicate the mechanism responsible for generating the patterns observed here. Although the mechanism underlying the vertical distribution patterns recorded in this study are unre-

solved, two mechanisms can be hypothesized: (1) increasing densities of surface-feeding crabs through temperate, subtropical, and tropical intertidal zones result in depletion of surface food types at lower latitudes (Elner and Seaman 2003) and (2) increasing mean ambient temperatures with decreasing latitude result in deeper burial depths of invertebrates at lower latitudes as a means of avoiding desiccation and heat stress during tidal exposure (Nebel 2005). Future studies should aim to address this unresolved question.

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