

# Are population dynamics of shorebirds affected by El Niño/Southern Oscillation (ENSO) while on their non-breeding grounds in Ecuador?

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## Abstract

Declines in avian populations are a global concern, particularly for species that migrate between Arctic-temperate and tropical locations. Long-term population studies offer opportunities to detect and document ecological effects attributable to long-term climatic cycles such as the El Niño/Southern Oscillation (ENSO). In this study, we report possible population-level effects of such climatic cycles on shorebird species that use two non-breeding season sites in Ecuador (Santa Elena peninsula area, near La Libertad). During our 9-year study period (1991/1992–1999/2000), there was a particularly strong ENSO warm phase event during 1997/1998. Population trend data for three species of shorebird, Western Sandpipers (*Calidris mauri*), Semipalmated Sandpipers (*C. pusilla*), and Least Sandpipers (*C. minutilla*), indicated abundances generally declined during the 1990s, but there was an increase in the proportion of first-year birds and their abundance in the years following the 1997/1998 ENSO warm phase. There was some support for variation in apparent survivorship associated with the onset of the ENSO warm phase event in our population models, based on capture–mark–recapture data. Following the 1997/1998 ENSO event onset, individuals for all three species were significantly lighter during the non-breeding season ( $F_{1,3789} = 6.6$ ,  $p = 0.01$ ). Least-squares mean mass (controlling for size, sex and day of capture) for first-year birds dropped significantly more than for adults following ENSO (first-year mass loss =  $0.69 \pm 0.12$  g; adult mass loss =  $0.34 \pm 0.11$  g,  $F_{1,3789} = 5.31$ ,  $p = 0.021$ ), and least-squares mean mass dropped most during the period when sandpipers prepare for northward migration by gaining mass and moulting into breeding plumage. Least Sandpipers may have declined the most in mean mass following ENSO ( $0.76 \pm 0.19$  g), whereas Semipalmated Sandpipers were  $0.52 \pm 0.12$  g lighter, and Western Sandpipers  $0.40 \pm 0.13$  g lighter, but overall variation among species before (1992/1993–1996/1997) and after (1997/1998–1999/2000) ENSO was not significant ( $F_{2,3787} = 1.52$ ,  $p = 0.22$ ). Anomalously warm and wet conditions associated with strong ENSO warm phases during the non-breeding season may either act directly on shorebirds (increasing metabolic demands) and/or indirectly through reductions in prey availability. Reduced mass and mass gain may explain lower survivorship, particularly in adults, which are more likely to migrate northward in the spring than are first-year birds, at least in Western Sandpipers. Our results suggest a potential mechanism selecting for life history strategies suitable for withstanding long-term fluctuating climatic cycles such as ENSO.

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## 1. Introduction

Declining populations of migratory birds are a major conservation issue worldwide, particularly for temperate-tropical migratory species. Long-term monitoring programmes have provided convincing evidence for these declines, and clearly documented examples come from passerine species, particularly

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songbirds (Robbins et al., 1989; Terborgh, 1989; Askins et al., 1990). Earlier research focused on changes on the breeding grounds, such as reduced available nesting habitat, as factors limiting global songbird populations and explaining contemporary global trends. More recently many have argued that factors affecting fitness (i.e., survivorship or body condition) during other stages of the annual life cycles can be as, or more, important for limiting global populations (Rappole and McDonald, 1994), especially since migrant birds can spend as little as 25% of the year on breeding grounds (Silllett and Holmes, 2002). Global populations of nearctic breeding shorebirds are also apparently declining (e.g., Donaldson et al., 2000; Lanctot et al., 2002; IWSG, 2003; CHASM, 2004; Morrison et al., 2004), but less work has focused on population limiting factors and reasons for current population trends in this group of birds than for migrant songbirds. It is unclear where and when during their annual or life cycles these population limiting factors occur and whether changes to these factors are principal causes of the population declines that are being currently documented for Nearctic breeding shorebirds.

The overwhelming number of cases of declining populations are reason for concern despite suggestions that some of these reported declines may result from procedural errors (Rappole and McDonald, 1994). These declines may reflect natural large-scale climatic cycles such as El Niño/Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO as per Mantua and Hare, 2002) and interpretations of abundance trends are increasingly incorporating potential impacts from these cycles. There has been recent development of more precise instrumentation, wider temporal coverage and proxy measures, such as tree ring measures and records of isotope ratios in coral. These, along with an expansion of long-term monitoring programmes and improved analytical techniques, can help resolve normal long-term climatic variability and ascribe resulting biological and ecosystem level effects (Fiedler, 2002). Both PDO and ENSO are important organizing structures for the Pacific Basin (Gedalof et al., 2002), and these large scale cycles likely are reflected in population processes and ultimately in the evolution of life history strategies for organisms that are part of ocean-linked ecosystems.

El Niño is defined as a persistent surface layer of anomalously warm water in the Eastern Tropical Pacific (ETP) along the Ecuadorian and Peruvian coastlines (Barber and Chavez, 1983), and is a manifestation of the global-scale ENSO phenomenon (Barber and Chavez, 1986). Oceanic warm phases associated with strong ENSO events typically result in reduced upwelling leading to lower nutrient levels in surface waters (Wooster, 1978) and deeper thermoclines and nutriclines in areas normally characterized by strong upwelling currents (Barber and Chavez, 1983). Partly due to reduced nutrient levels, primary productivity in the euphotic zone is typically constrained during ENSO (Barber and Chavez, 1983), leading researchers to investigate the effects of these climatic cycles on higher trophic level taxa in marine ecosystems, as well as to explore linkages within ecosystems (e.g., Ticktin, 2003).

The coastline of Ecuador and Peru is associated with ecosystems characterized by ocean upwelling that can be affected

by strong ENSO warm phases. Bottom-up regulation can be important in the regulation of intertidal communities that lie adjacent to regions of strong upwelling (i.e., benthic–pelagic coupling as described by Menge, 2000). Intertidal productivity can depend on winds that favor upwelling, which tend to be suppressed during ENSO warm phases (Takesue et al., 2004). Suppression of intertidal productivity likely affects top trophic level organisms (bottom-up regulation). Strong ENSO warm phases occurred during the boreal winters of 1982/1983 and 1997/1998. Before 1982, the closest ENSO of similar strength occurred in 1877 (Arkin et al., 1983; Kiladis and Diaz, 1984). Both of these recent ENSO events are considered similar in terms of signal strength but the ecological effects of the second may have been mitigated by a climatological change that was originally classified as a regime shift to the cooler phase for the longer phase PDO climatic cycle (Chavez et al., 2002). Nevertheless, coastal rainfall increased by nearly an order of magnitude in 1997/1998 in our study area in Ecuador (Fig. 1), which is typical of heavy rainfall along the eastern coast of the tropical Pacific associated with a warm phase ENSO event (Kalmbach et al., 2001).

A shorebird survey program that began in 1989 has provided an opportunity to measure potential effects of large scale climate cycles such as ENSO on shorebird species that spend their non-breeding season in Ecuador. In general, population trends estimated for migratory arctic and sub-arctic breeding shorebirds captured in Ecuador should be representative of global trends as shorebird species are often characterized by a high degree of site fidelity to non-breeding sites, as well as to breeding sites and probably also to sites used throughout their annual life cycles (e.g., Middlemiss, 1961; Holmes, 1971; Oring and Lank, 1982; Gratto et al., 1985; Thomas, 1987; Warnock and Takekawa, 1996). Furthermore, processes resulting in abundance trends for non-breeding populations at a local or regional scale may carry global population implications given the variation in sex and age proportions that apparently occur with latitude in wintering populations of some shorebird species (e.g., Western Sandpiper; Nebel et al., 2002).

Long-term population monitoring programmes for species found in Eastern Tropical Pacific ecosystems have provided evidence for negative impacts associated with warm phases of both ENSO and PDO (e.g., Laurie, 1990; Kalmbach et al., 2001; Vargas-Angel et al., 2001; Fiedler, 2002). In this study, we estimated population trends for three shorebird species that spend their non-breeding seasons in Ecuador: Western Sandpipers (*Calidris mauri*), Semipalmated Sandpipers (*C. pusilla*), and Least Sandpipers (*C. minutilla*). Using capture data from 1991/1992 to 1999/2000 (9 years), we estimated relative annual abundances, apparent survivorship patterns, and changes in mass potentially associated with the ENSO warm phase event that occurred in 1997/1998. Also, we estimated trends in recruitment using age–class ratios (i.e., the proportion of first-year birds, or birds in their first non-breeding season in Ecuador) as indices of recruitment into non-breeding populations at our survey sites. We expected to detect negative impacts associated with ENSO warm phases on our three shorebird species for two reasons. First, increased

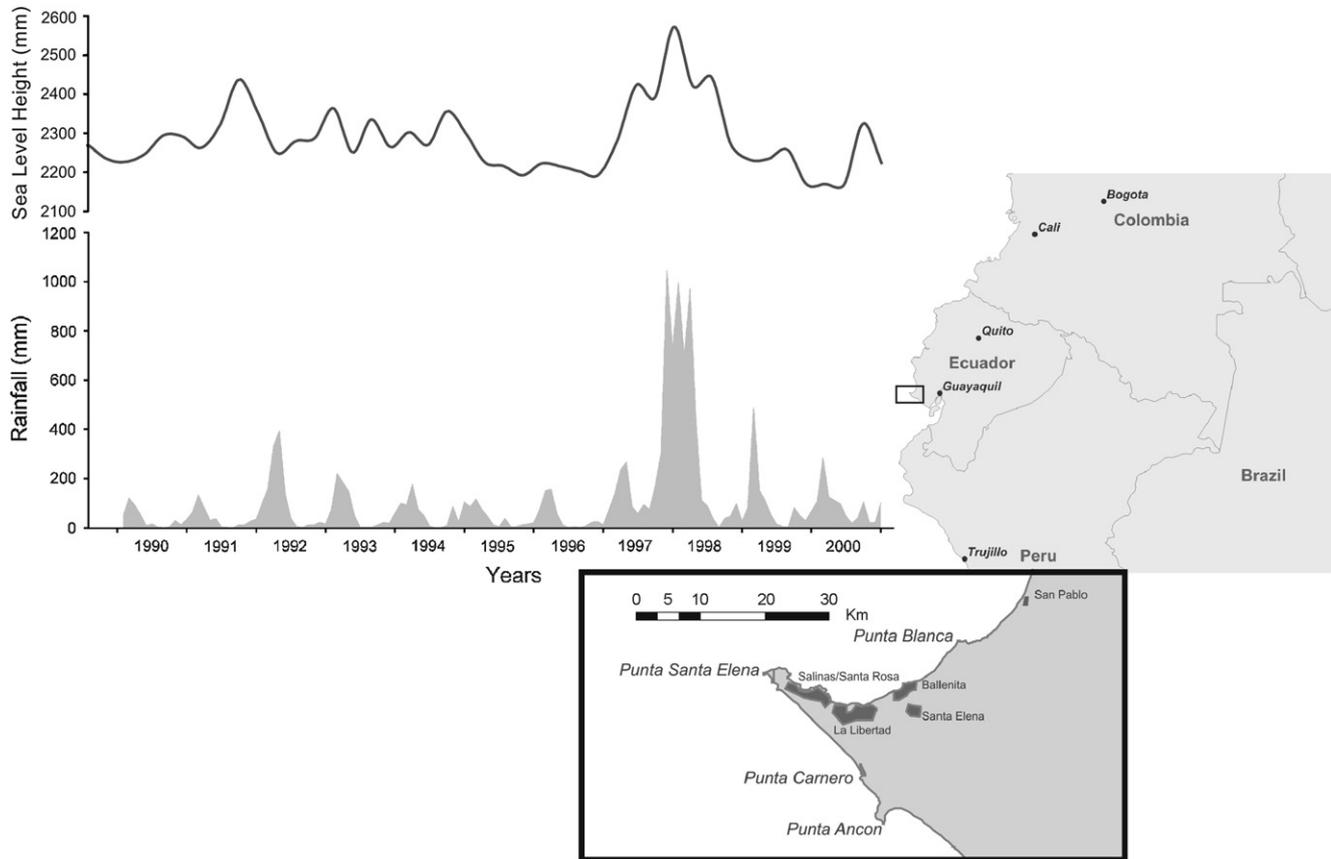


Fig. 1. Sea level changes and mean rainfall patterns in the Punta Santa Elena Peninsular region of Ecuador. Mean sea level (mm) were estimated from sea level data collected from 1990 to 2000 ( $02^{\circ}12' S$ ,  $80^{\circ}55' W$ ; data from <http://www.pmel.noaa.gov/tao/elnino/sea-level.html>). Mean rainfall for the same region was estimated from coastal grid centroids ( $5 \times 5$  km) within 10 km north and south of La Libertad (see map) for the same period as the estimated mean sea level. Grid data were downloaded from URL: <http://www.dwd.de/vaslimo>.

precipitation associated with ENSO warm phases may reduce invertebrate prey populations or drive them deeper into the substrate, making them less available to foraging shorebirds. Second, a linkage may exist between reduced nutrient/primary productivity in marine ecosystems and the productivity of adjacent mudflat foraging areas. Both warm-phase associated effects could result in reduced prey availability to foraging shorebirds, potentially leading to (a) reduced mean mass during the non-breeding season, and/or (b) slower rates of mass gain during the premigratory period, and (c) lower apparent annual survivorship (combined probabilities of true survivorship and permanent emigration). Individuals may compensate for reduced prey availability by devoting larger proportions of their daily time budget to foraging, at the expense of other possibly important activities such as preening, thermal regulation and vigilance.

## 2. Materials and methods

### 2.1. Site description

The Punta Santa Elena peninsula (Fig. 1) is a hilly region of low, open, dry scrub fringed by extensive sand beaches. The climate is tropical with a wet, hot season from December to

July, and a cooler, dry season from August to November. Shorebirds are found in all habitats, but the three focal species in this study typically forage in and around salt and shrimp production ponds in two coastal areas (both areas include approx. 610 hectares of salt or shrimp ponds); Mar Bravo ( $2^{\circ}14' S$ ,  $80^{\circ}57' W$ , near Punta Carnero) and San Pablo ( $2^{\circ}06' S$ ,  $80^{\circ}45' W$ ). The Mar Bravo area supports an overwintering population in excess of 20,000 shorebirds.

Although salt and shrimp production ponds are not natural habitat, sandpipers occur at all but the most saline ponds, feeding in the shallows and on the ribbon of mudflat along dikes bordering salt ponds. Shorebirds prey heavily on brine fly (Family Ephydriidae) larvae and pupae, and also catch adults (B.J.M. Haase, unpublished data). Brine shrimp (Genus *Artemia*) and small infaunal invertebrates are usually plentiful as prey items. We used mean sea level (data downloaded from National Oceanic and Atmospheric Administration (NOAA) Atlantic Oceanographic and Meteorological Laboratory: <http://www.pmel.noaa.gov/tao/elnino/sea-level.html>) and mean rainfall as indicators of local environmental effects of climatic cycling (Fig. 1). Mean rainfall for the region was estimated from globally gridded datasets of observed station precipitation, using coastal grid centroids ( $5 \times 5$  km) for 1990–2000. These datasets were prepared by Dr C. Beck and Dr J. Grieser

at the Global Precipitation Climatology Centre (GPCC) as part of the project VASCLIMO and can be downloaded from URL: <http://www.dwd.de/vasclimo>.

## 2.2. Survey methods

Three species of shorebirds were captured and recaptured at our sites over a 9-year period from 1991/1992 to 1999/2000; Least Sandpipers (*C. minutilla*), Semipalmated Sandpipers (*C. pusilla*), and Western Sandpipers (*Calidris mauri*). Birds were captured using mist nets erected over shallow pools fed by outflows from shrimp ponds in the San Pablo area and by mist nets erected perpendicular to dikes along the salt production ponds in the Mar Bravo area. Capture periods occurred between 20 August and 30 April for each non-breeding season; however, we only included data from individuals captured between September and December for our recruitment and apparent survivorship analyses (see below). We measured mass (to the nearest gram using hand-held *Pesola* brand spring scales), and length of exposed culmen (a.k.a. bill, to the nearest 0.1 mm). Sex determination was based on length of exposed culmen as described in Page et al. (1972) and Prater et al. (1977). Individuals of unknown sex were eliminated from analyses that tested for sex effect and re-included if the sex effect was non-significant. We classified captured individuals into two age categories (first-year, first non-breeding season; adults, second non-breeding season or older) based on plumage (see Prater et al., 1977) and banding histories. All newly captured individuals were banded with uniquely numbered USFWS aluminum bands.

## 2.3. Analyses

### 2.3.1. Interannual trends in abundance and recruitment

We explored interannual abundance trends for the above-defined capture period using the annual proportion of the total number individuals captured within species, while controlling for annual variation in effort. We used the product of total length of all mist nets and total hours that the nets were deployed during capture periods (net m-h) as an index of effort. Annual proportions captured per species were corrected using net m-h (Fig. 2, corrected proportion of total captured). We tested for decline in capture rates following the 1992/1993 capture period among and within species by fitting a general linear model with maximum likelihood estimation (Proc Genmod; SAS, 1999), while controlling for variation attributable to sex and including sampling effort (m-h) as an offset variable.

We estimated the age–class ratio for each species during the non-breeding seasons and used this as an index of recruitment. We tested for the effect of the 1997/1998 El Niño/Southern Oscillation (ENSO) warm-phase event on annual recruitment by dividing our dataset into two periods: before (1992/1993–1996/1997) and during/after (1997/1998–1999/2000) this ENSO event (the latter hereafter referred to as “after the onset of ENSO”). For the recruitment analyses, we used data from individuals captured between August 20 and January 31, since first-year birds were increasingly difficult to identify as

feathers used for age identification wore during the capture period. We tested for differences in recruitment before and after onset of the ENSO warm phase using a general linear model fitted with maximum likelihood and a logit link function (Proc Genmod; SAS, 1999), while controlling for variation among species and sex categories. Also, we compared counts within species and age categories using the same modeling techniques, but with log link functions, and used *post hoc* comparisons to test for significant differences in numbers captured before and after ENSO onset within age categories (LS-means differences Proc Genmod; SAS, 1999). We did this comparison to determine if age-ratio changes were due to variation in numbers captured before and after ENSO onset for adults, first-year birds, or both. To control for overdispersion and clustering in our data, we included SCALE = deviance in our Proc Genmod model statement (SAS, 1999). All  $\chi^2$ -values are reported with both numerator and denominator degrees of freedom as subscripts.

### 2.4. Apparent survivorship

Recapture rates are the probability product of apparent annual survivorship ( $\phi$ , true survivorship and return rate) and probability of recapture ( $\rho$ ). We used the standard Cormack–Jolly–Seber (CJS) model (e.g., Lebreton et al., 1992) incorporated in *Program Mark* developed by G.C. White at the University of Colorado (for a general introduction see Cooch and White, 2006). We selected models based on relative fit and parsimony using quasi-likelihood adjusted AIC (Akaike's Information Criterion, QAIC), which indicate relative plausibility or support for each posed model (Burnham and Anderson, 2002). QAIC is derived from AIC that has been corrected for extra-binomial variation (overdispersion) using  $\hat{c}$  as an index of overdispersion. We estimated  $\hat{c}$  by dividing the observed deviance of the global model by the mean deviance estimated in the bootstrap goodness-of-fit (GOF, as described in Cooch and White, 2006). We constrained our apparent survivorship analyses by using data only from individuals captured between 1 September and 31 December, in order to reduce potential variation in intervals between capture events.

We could not test for overdispersion in a fully saturated global model (i.e., incorporating both sex-based and age-based structure that varies annually) because of sparse recapture data. In order to estimate  $\hat{c}$ , we had to first eliminate some structure in our global model (i.e., pool data between one of our categories). In our preliminary analyses (i.e., not corrected for overdispersion), we found that for all three species, sex-based structure was least supported in all models tested. Some of the models we tested that incorporated sex structure also included age structure and/or before (1992/1993–1996/1997) and after (1997/1998–1999/2000) ENSO onset as a covariate. All models incorporating sex structure had AIC weights of less than 0.048, indicating support for any sex structure model was less than 5% relative to all other models. Thus, our global or most saturated model, which we tested for overdispersion, incorporated structure based on age and capture period (models with capture periods before

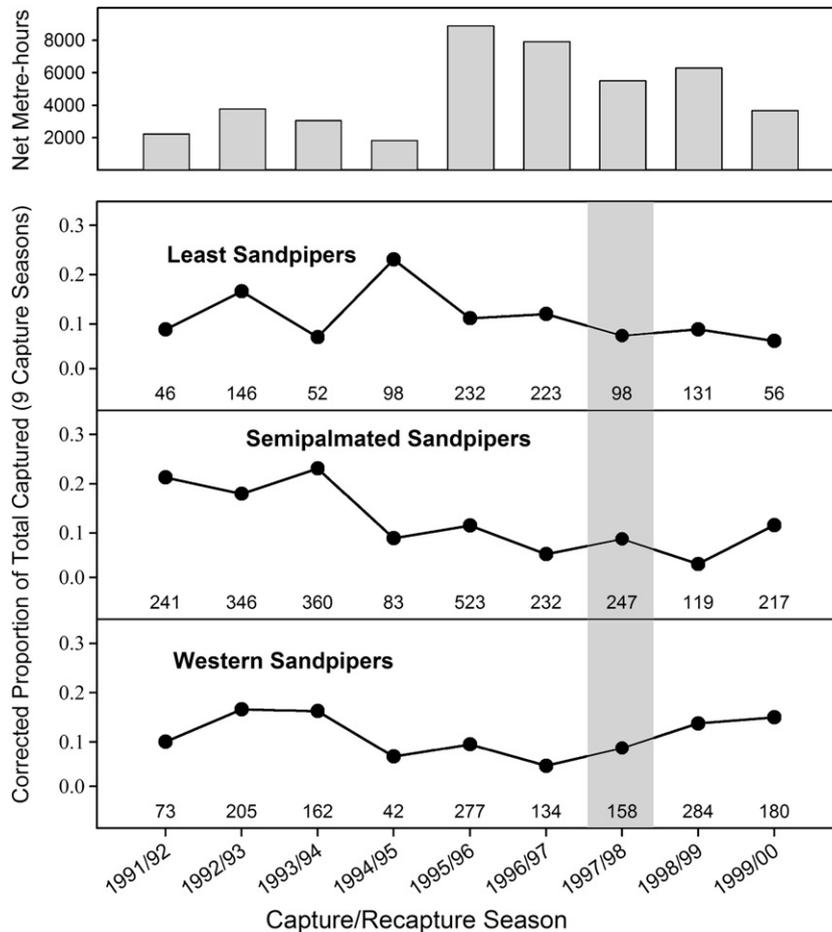


Fig. 2. Population trends for all three species of shorebirds. Sampling effort per capture season is expressed as net meter-hours in the top panel. The following three panels show population trends expressed as both effort-corrected proportion captured each year of total individuals captured over the study period (corrected percent of total captured (9 capture seasons)) and as uncorrected total number caught per capture season (total captured per capture season). Grey bar indicates a period of a strong El Niño/Southern Oscillation (ENSO).

and after onset of ENSO are nested within models that varied freely with capture period), with data pooled between sex categories.

### 2.5. Mass variation

We tested for ENSO effects by comparing mass data collected during years categorized as before (1992/1993–1996/1997) and after (1997/1998–1999/2000) the onset of the 1997/1998 ENSO warm-phase event. To control for non-linear variation in mean mass within non-breeding seasons (i.e., premigratory mass gain in preparation for migration; see Results), we derived mass residuals from a daily mean mass estimated by fitting a semi-non-parametric spline curve (Proc TPSPLINE; SAS, 1999) for data pooled among species and capture seasons. We also included culmen length as an index of sandpiper structural size to reduce variation at the population level (i.e., movements of individuals between non-breeding sites during the capture periods). The spline curve was fitted using a smoothing factor ( $\lambda_{0.0}$ ) that minimized the generalized cross-validation function (GCV in Proc TPSPLINE; SAS, 1999). Because we used

culmen length as a continuous cofactor, the thin-plate spline fit was considered semi-non-parametric (SAS, 1999).

Using these residuals, we tested for ENSO effects by comparing intercepts, slopes, and least-squares means (LS-means) for data collected during capture periods before and after ENSO onset with a General Linear Model ANOVA (Proc GLM; SAS, 1999). ANOVA of derived mass residuals controlled for interannual variation among species, and sex–age categories. We used LS-mean mass (LS-MEANS statements in Proc GLM; SAS, 1999) to show differences before and after ENSO onset for all three species, and to show differences before and after ENSO onset during the mass maintenance period and during the premigratory mass gain period for data pooled among species. The mass maintenance period was defined as the non-breeding months (November to January inclusive) when sandpipers maintained a relatively stable mass (see Section 3 and O'Hara et al., 2005), before the onset of mass gain in preparation for migration (February to April inclusive). Differences in LS-means are *a posteriori* comparisons that controlled for variation associated with sex–age category and species, and also controlled for date of capture and culmen length because the LS-means were

derived from residuals from the semi-non-parametric curve as described in the previous paragraph. However, LS-means shown in Fig. 6 do not control for variation among species, where we compared before and after ENSO onset variation among species. All tests with a *p*-value of less than 0.05 were considered significant.

### 3. Results

#### 3.1. Interannual trends in abundance and recruitment

In total, we captured and recaptured 1036 Least Sandpipers, 2127 Semipalmated Sandpipers, and 1442 Western Sandpipers between 20 August and 30 April within a capture period (not including repeat recaptures). We found that our indices of population abundances (individuals captured per season while controlling for effort (m-h)) fluctuated similarly among

species interannually with peaks occurring during the mid 1990s and decreasing towards the end of the decade (Fig. 2). Following the third capture period (Fig. 2; 1992/1993), there was an overall decrease in individuals captured per season ( $\chi^2_{1,69} = 6.60, p = 0.010$ ) and this trend was consistent between sex classes ( $\chi^2_{1,46} < 0.01, p = 0.99$ ). Although these interannual trends in capture rates were statistically consistent among species ( $\chi^2_{2,65} = 0.03, p = 0.98$ ), the timing of the peak in abundance was earliest for Western Sandpipers, with Semipalmated Sandpiper numbers peaking 1 year later, followed by Least Sandpipers peaking 2 years after the Western Sandpiper maximum.

We found that there was a significant increase in proportion of first-year birds after ENSO onset (Fig. 3; ENSO:  $\chi^2_{1,23} = 41.3, p < 0.001$ ) that was consistent between sex-classes in general (sex  $\times$  ENSO:  $\chi^2_{1,34} < 0.01, p = 0.99$ ), and between sex classes and species (sex  $\times$  ENSO  $\times$  species:

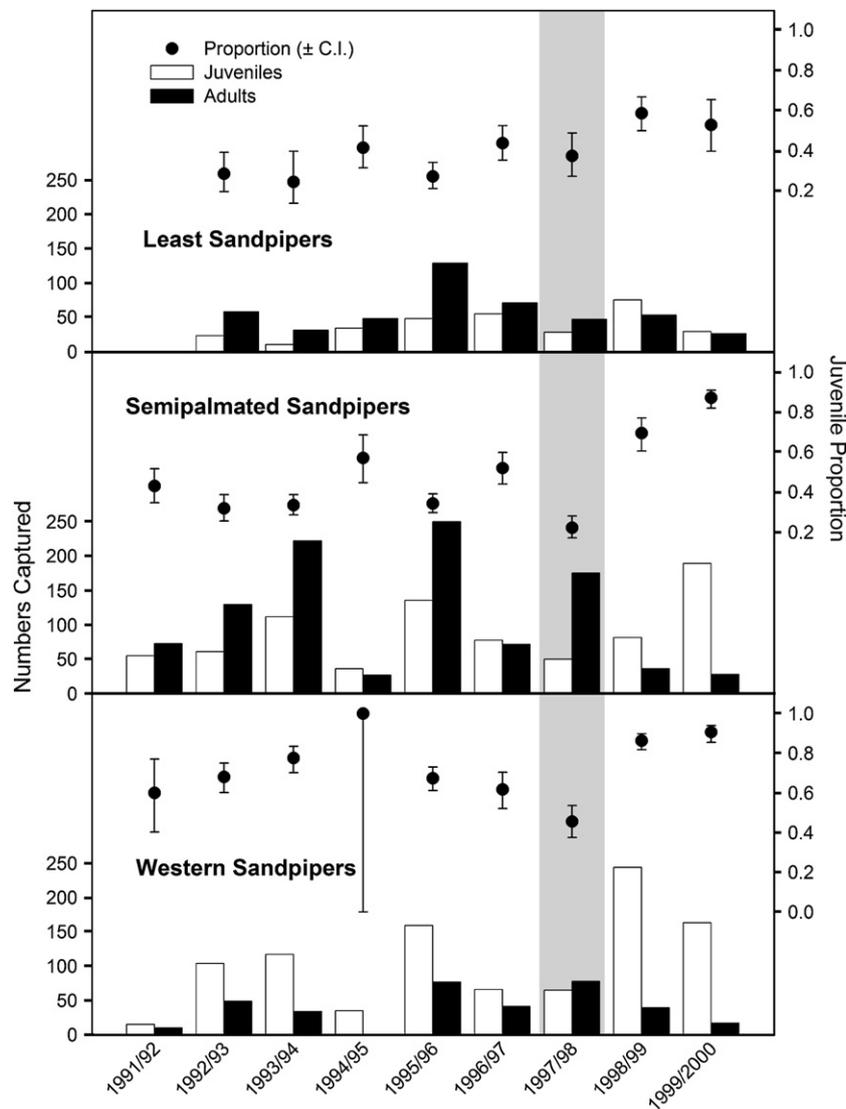


Fig. 3. Seasonal capture rates and proportion of first-year birds. Grey bar represents ENSO event. Age–class ratio also varies significantly before and after ENSO, and varies consistently between sexes and among species (see text for statistical results). From the 1995–1996 season to the end of study period, there was a significant decline in adult seasonal capture rates (controlling for capture effort:  $F_{1,73} = 3.92, p = 0.0069$ ) that was consistent between sexes ( $p > 0.62$ ) and among species ( $F_{1,71} = 0.94, p = 0.40$ ).

$\chi^2_{2,34} = 0.73, p = 0.69$ ). For data pooled across sexes, the degree of increase in the first-year proportion did not vary significantly with species (ENSO  $\times$  species:  $\chi^2_{2,21} = 3.38, p = 0.18$ ). We found that numbers per capture period varied with ENSO differently between age categories (age  $\times$  ENSO:  $\chi^2_{1,46} = 14.8, p < 0.001$ ), and this age-dependent difference was consistent among species (age  $\times$  ENSO  $\times$  species:  $\chi^2_{2,42} = 0.89, p = 0.64$ ). Within age categories, higher numbers of first-year birds were netted per capture season following ENSO onset (LS-means difference  $\chi^2 = 10.3, p = 0.001$ ) with fewer adults (LS-means difference  $\chi^2 = 4.83, p = 0.03$ ). Because the number of individuals netted per capture period varied among species (Fig. 3; species:  $\chi^2_{2,46} = 16.6, p < 0.001$ ) and age categories (age:  $\chi^2_{1,46} = 5.79, p = 0.016$ ), and the numbers within age categories also varied among species (age  $\times$  species:  $\chi^2_{2,46} = 13.3, p < 0.001$ ), we had to control for age by species variation in our analyses above.

### 3.2. Apparent survivorship

Overall, we captured and recaptured 803 Least Sandpipers (46 recaptures), 2038 Semipalmated Sandpipers (95 recaptures), and 1387 Western Sandpipers (46 recaptures) between 1 September and 31 December. As goodness-of-fit (GOF) tests ( $n = 1000$ ; see Section 2) indicated that capture–mark–recapture (CMR) data for Least and Semipalmated Sandpipers were overdispersed, we estimated quasi-likelihood adjusted AIC (QAIC) using our estimated c-hat values for all data sets (c-hat = 1.71, 1.53, and 1.00 for Least Sandpipers, Semipalmated Sandpipers, and Western Sandpipers, respectively). We reduced parameterization for  $\rho$  (recapture probability), using c-hat adjusted QAICs, from the saturated model where both  $\phi$  (apparent survivorship) and  $\rho$  were free to vary with capture season independently within age categories (Table 1). For both Least and Semipalmated Sandpipers, the most parsimonious submodel had constant  $\rho$  among years and between age categories ( $\rho_c$ ), and for Western Sandpipers,  $\rho$  varied among years consistently between age categories ( $\rho_t$ ).

Allowing apparent survivorship ( $\phi$ ) to differ before and after onset of the 1997/1998 ENSO was the most supported model for Least Sandpiper (Table 2). The most supported model for Semipalmated Sandpipers varied  $\phi$  with time and for Western Sandpipers  $\phi$  was constant, but for both these

Table 2

Submodels for parameterization of annual apparent survivorship ( $\phi$ ). Models are ordered with respect to weighted QAIC or support (see Section 2). QAIC is Akaike's information criteria corrected for overdispersion using c-hat (see Section 2). QAIC weights indicates the relative importance of each model (with species). For both Least and Semipalmated Sandpipers, the probability of recapture ( $\rho$ ) is held constant among capture periods and age categories ( $\rho_c$ ), and for Western Sandpipers,  $\rho$  varies with capture period similarly between age categories ( $\rho_t$ ) (see Table 1). In this table we show model fit for  $\phi$  that is constant among capture periods within age categories but varies between age categories ( $\phi_a$ ), for  $\phi$  that varies among capture periods similarly between age categories ( $\phi_t$ ), and for  $\phi$  that varies among age categories and capture periods ( $\phi_a \times t$ ). Also, we show fit for  $\phi$  that can vary before and after the 1998 ENSO, similarly ( $\phi_{\text{enso}}$ ) or differently between age categories ( $\phi_a \times \text{enso}$ )

	Model structure	QAIC	QAIC weight	No. of par.	Q Dev.
Least Sandpipers	$\phi_{\text{enso}}, \rho_c$	117.4	0.600	3	28.03
	$\phi_c, \rho_c$	120.1	0.157	2	32.74
	$\phi_t, \rho_c$	121.1	0.095	9	19.44
	$\phi_a \times \text{enso}, \rho_c$	121.2	0.091	5	27.74
	$\phi_a, \rho_c$	122.1	0.058	3	32.70
	$\phi_a \times t, \rho_c$	133.8	0.000	16	17.44
Semipalmated Sandpipers	$\phi_t, \rho_c$	320.2	0.645	9	39.36
	$\phi_{\text{enso}}, \rho_c$	321.8	0.295	3	53.04
	$\phi_a \times \text{enso}, \rho_c$	325.0	0.059	5	52.23
	$\phi_a \times t, \rho_c$	334.2	0.001	17	37.00
Western Sandpipers	$\phi_c, \rho_c$	335.8	0.000	2	69.01
	$\phi_a, \rho_c$	337.8	0.000	3	69.01
	$\phi_c, \rho_t$	278.6	0.460	9	25.41
	$\phi_{\text{enso}}, \rho_t$	279.7	0.264	10	24.47
	$\phi_a, \rho_t$	280.5	0.176	10	25.28
	$\phi_t, \rho_t$	282.9	0.052	14	19.54
	$\phi_a \times \text{enso}, \rho_t$	283.1	0.047	12	23.82
$\phi_a \times t, \rho_t$	292.3	0.001	21	14.35	

species, there was little or no support for  $\phi$  variation between age categories. For Semipalmated and Western Sandpipers allowing  $\phi$  to differ before and after ENSO onset was the second most supported model based on QAIC values. However, in all three species,  $\phi$  differed before and after ENSO onset, and  $\phi$  differed similarly between age categories (i.e., little or no support for model  $\phi_a \times \text{enso}$  in Table 2).

### 3.3. Mass variation

Typically, for all three species, mean mass dropped during the non-breeding season every year following arrival at our

Table 1

Sub-models for reducing parameterization of the probability of recapture ( $\rho$ ). In all cases, the apparent survivorship ( $\phi$ ) varies among age categories and capture periods ( $\phi_a \times t$ ). Subscripts for  $\rho$  indicate that  $\rho$  is constant (c) among capture periods and age categories, varies between age categories but is constant among capture periods within age categories (a), varies among capture periods consistently between age categories (t), and varies among age categories and capture periods (a  $\times$  t). QAIC is Akaike's information criteria corrected for overdispersion using c-hat (see Section 2)

Model structure	Least Sandpipers				Semipalmated Sandpipers				Western Sandpipers			
	QAIC	QAIC weight	No. of par.	Q Dev.	QAIC	QAIC weight	No. of par.	Q Dev.	QAIC	QAIC weight	No. of par.	Q Dev.
Global ( $\phi_a \times t, \rho_a \times t$ )	144.1	0.004	25	8.24	340.1	0.034	26	24.29	297.7	0.023	25	11.45
$\phi_a \times t, \rho_a$	135.8	0.249	17	17.31	336.3	0.232	18	37.00	292.4	0.334	18	20.69
$\phi_a \times t, \rho_t$	138.3	0.072	22	9.05	338.2	0.087	22	30.71	292.3	0.352	21	14.35
$\phi_a \times t, \rho_c$	133.8	0.675	16	17.44	334.2	0.647	17	37.00	292.6	0.290	17	23.05

Ecuadorian sites, and increased again prior to migration in the spring (Fig. 4). The relationship between mean mass and day captured during the capture period, while controlling for culmen length (residual mass; see Section 2), differed before and after ENSO onset (ENSO:  $F_{1,3789} = 6.6$ ,  $p = 0.01$ ). This ENSO associated variation in the relationship between mean mass and day captured variation was consistent between sex category (ENSO  $\times$  sex:  $F_{1,3788} = 0.03$ ,  $p = 0.88$ ) and among species (ENSO  $\times$  species:  $F_{2,3787} = 1.52$ ,  $p = 0.22$ ), but varied among age categories (ENSO  $\times$  age:  $F_{1,3789} = 5.31$ ,  $p = 0.021$ ). Also, mass differences before and after ENSO were greater towards the end of the non-breeding season

(ENSO  $\times$  day:  $F_{2,3789} = 6.60$ ,  $p = 0.010$ ; before ENSO mass (g) =  $0.18 - 0.00013 \times \text{day}$ ,  $t = 0.24$ ,  $p = 0.81$ ; after ENSO mass (g) =  $0.21 - 0.0041 \times \text{day}$ ,  $t = 2.83$ ,  $p = 0.005$ ) suggesting that individuals were not as able to gain mass in preparation for migration during the period of premigratory mass gain (Fig. 4, period of mass gain between February to end of April) in the years following the onset of ENSO.

Using derived residual mass (controlling for culmen length and day captured during the non-breeding season) and least-squares means (controlling for sex, age and species), we found that individuals were  $0.52 \pm 0.08$  g ( $\pm$ SE) lighter during the non-breeding seasons following the onset of ENSO (Figs. 5

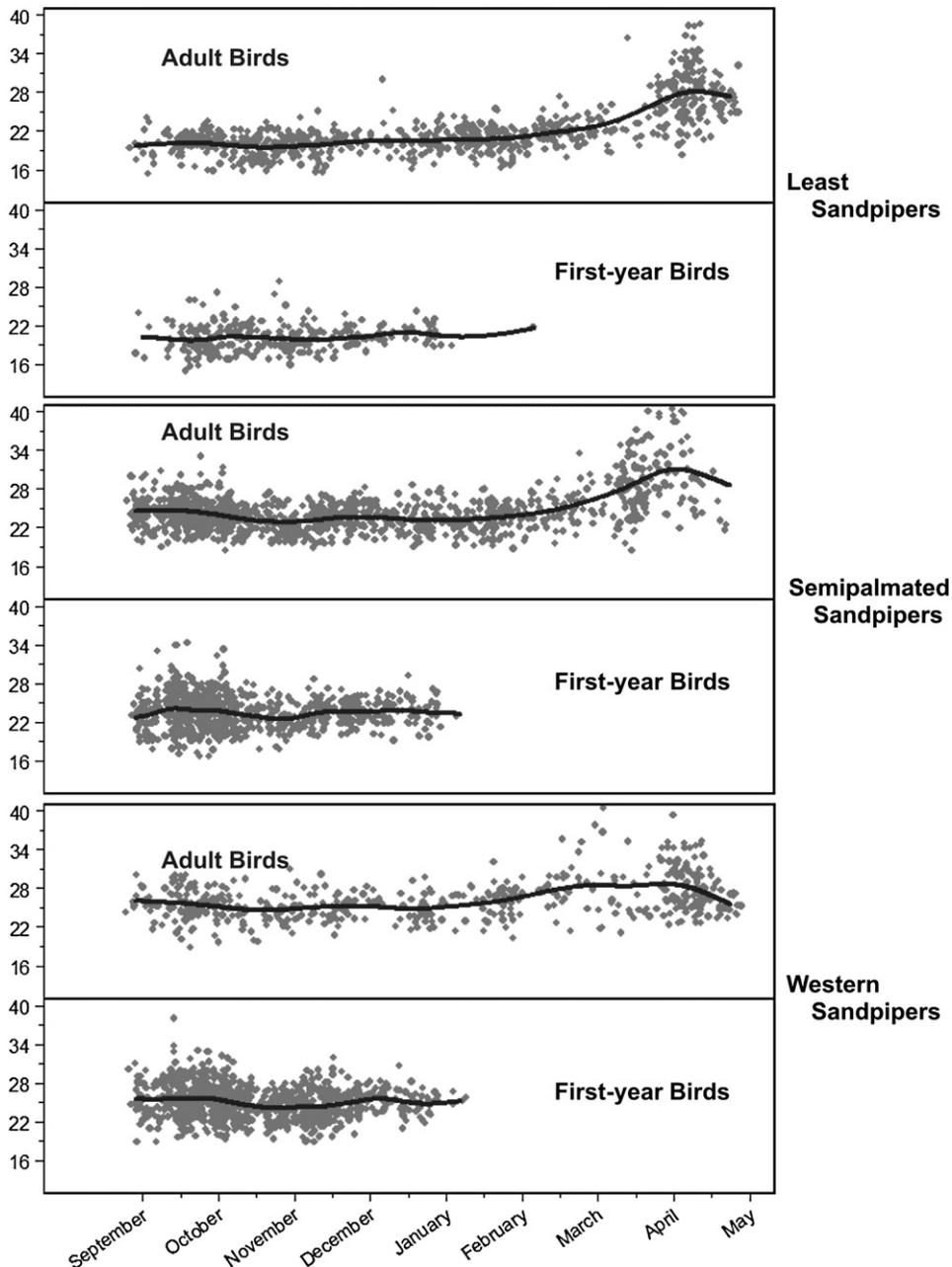


Fig. 4. Individual mass and smoothing curves to emphasize trends for both age categories and each of the three species that we aged. Data have been pooled over sex categories and among years. Curves are smoothed with a locally weighted cubic spline function that minimizes a penalized residual sum of squares (S-PLUS, 2005).

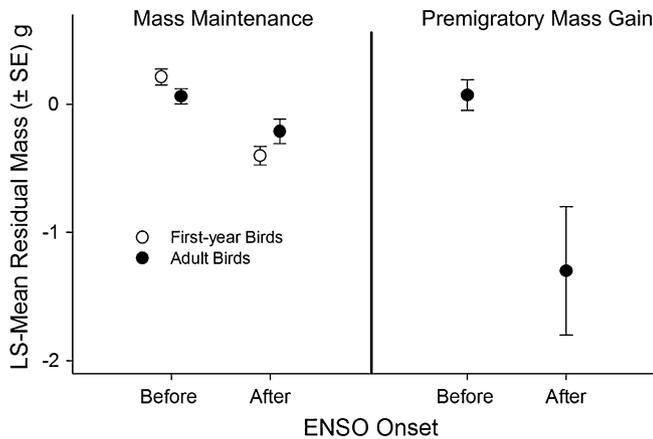


Fig. 5. LS-means ( $g \pm SE$ ) of mass residuals (from spline curve; see Section 2) before and after ENSO onset for age categories during mass maintenance and premigratory periods (see Section 2) for data pooled among all three species. LS-means of mass residuals control for variation associated with date of capture, culmen length (as a proxy for structural size), and sex–age category (see Section 2).

and 6: LS-means,  $t$ -value = 6.63,  $p < 0.0001$ ). This trend was more exaggerated for first-year birds than for adult birds during the mass maintenance period, with first-year LS-means (controlling for sex and species) dropping by  $0.69 \pm 0.12$  g (Fig. 5; approximately 2.9% of mean mass for data pooled over all capture periods and species) and adult LS-means dropping by  $0.34 \pm 0.11$  g (Fig. 5, approximately 1.4% of mean mass). However, during the premigratory mass gain, LS-mean mass for adults (including unidentified juveniles) dropped the most following the onset of ENSO (Fig. 5;  $1.37 \pm 0.52$  g). Least Sandpipers may have declined the most in mean mass following

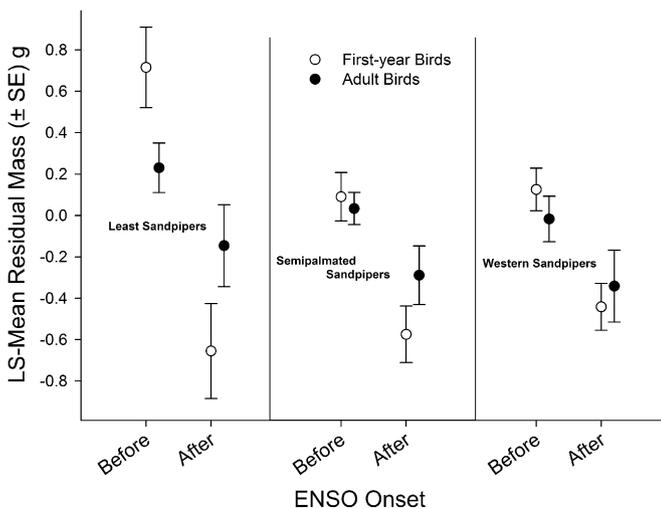


Fig. 6. LS-means ( $g \pm SE$ ) of mass residuals (from spline curve; see Section 2) before and after ENSO onset for all three species. LS-means of mass residuals control for variation associated with date of capture, culmen length (as a proxy for structural size), and sex–age category (see Section 2). Overall, LS-means differed before and after ENSO onset within both adults and first-year birds (see Section 3), and this age-dependent difference was significant within each species (Least Sandpipers:  $t$ -value = 8.3,  $p < 0.0001$ ; Semipalmated Sandpipers:  $t$ -value = 6.5,  $p = 0.0002$ ; Western Sandpipers:  $t$ -value = 6.4,  $p = 0.0003$ ).

ENSO (Fig. 6;  $0.76 \pm 0.19$  g; approximately 3.4% of mean mass for data pooled over all capture periods and age categories), whereas Semipalmated Sandpipers were  $0.52 \pm 0.12$  g (Fig. 6; approximately 2.1% of mean mass) lighter, and Western Sandpipers  $0.40 \pm 0.13$  g (Fig. 6; approximately 1.5% of mean mass) lighter, but overall variation among species before and after ENSO was not significant (see above).

## 4. Discussion

### 4.1. Annual population abundance and recruitment

Our capture data, controlling for effort, indicate an average decline in relative abundance over the study period for non-breeding Least Sandpiper, Semipalmated Sandpiper, and Western Sandpiper populations in Ecuador during the 1990s (Fig. 2). Our results are consistent with reports concluding similar declining trends in shorebird populations world-wide, particularly for arctic breeding species (e.g., IWSG, 2003; CHASM, 2004). In a summary of monitoring programs for migrating and breeding shorebird populations throughout Canada and the east coast of the US, Donaldson et al. (2000) concluded that 25 of 31 species showed negative population trends (19 were significant,  $p < 0.05$ ). In addition, substantial population declines have been detected for shorebird species such as the Red Knot (*Calidris canutus rufa*) (Morrison et al., 2004) and the Buff-breasted Sandpiper (*Tryngites subruficollis*) (Lanctot et al., 2002) during non-breeding seasons in central and southern South America. However, we stress that there is some indication of population recoveries occurring in at least two of our shorebird species (Semipalmated and Western Sandpipers) following the onset of the ENSO warm phase, inviting a hypothesis that long-term population dynamics may reflect larger scale climatic cycles.

Variation in relative abundance at our sites probably reflects actual abundance trends given that shorebird species in general express a high degree of fidelity to sites throughout their annual life cycles (e.g., Oring and Lank, 1982; Summers et al., 1990; Smith et al., 1992; Handel and Gill, 2000). Specifically, strong natal nest philopatry or site fidelity has been shown for Semipalmated and Western Sandpipers (Holmes, 1971; Gratto et al., 1985; Sandercock and Gratto, 1997), and strong site fidelity for migratory stopover and non-breeding sites has been shown for Western and Least Sandpipers (Middlemiss, 1961; Thomas, 1987; Warnock and Takekawa, 1996). Nevertheless, it remains unclear whether population dynamics at our sites reflect dynamics at the global level. Site specific declines could be a result of local movement patterns (Warnock et al., 1995; Butler et al., 2002); however, capture–mark–recapture analyses for data collected from non-breeding populations of Red Knots (*C. canutus rufa*) in Patagonia (southern South America) suggest that declines detected there were not from local movement or temporary emigration (Baker et al., 2004). Population declines detected at non-breeding sites also may be a result of perturbations that occur locally during the non-breeding season, leading to locally increased mortality, and may not affect populations of the same species on a global

scale. Conversely, factors impacting non-breeding population dynamics at a local scale can be manifestations of larger scale phenomena such as climatic cycles or global warming. These larger scale impacts could lead to general increases in mortality throughout the non-breeding range of a species, and/or affect shorebirds during other parts of their life cycles (i.e., during migration or breeding).

Following the 1997/1998 ENSO warm phase, the proportion of first-year birds increased significantly in the non-breeding populations at our sites for all three species. The proportion of first-year birds for both Least and Semipalmated Sandpiper populations approximately doubled following ENSO, whereas the first-year proportion for Western Sandpiper populations increased by approximately 30% (Fig. 3). These changes in age–class ratio were apparently a result of increasing numbers of first-year birds coupled with declining adult numbers after the onset of ENSO for all species. However, we point out here that the increase in the proportion of first-year birds for Least Sandpipers could also be explained by increasing first-year proportions with year that was apparent throughout the study. This trend for Least Sandpipers notwithstanding, our results suggest that overall declines are not necessarily related to factors affecting breeding success only and point to factors affecting survivorship. However, if local movement patterns are associated with ENSO phase shifts, our estimated declines in adult abundances may not result directly from decreases in survivorship. In particular, older more experienced adults may be seeking secondary areas if conditions are poor at the primary sites (e.g., Warnock et al., 1995).

#### 4.2. Apparent survivorship and mass variation

Overall, there was some support (i.e., QAIC weights) for ENSO affecting apparent survival ( $\phi$ , Table 2). Variation in  $\phi$  with ENSO was clearest in the Least Sandpiper models. Models for Semipalmated Sandpipers indicate that  $\phi$  varies more with capture period (interannually), whereas for Western Sandpipers, a constant  $\phi$  fit the capture–mark–recapture data better (i.e., more parsimoniously). Given that the proportion of first-year birds increased in all three species following ENSO because of both declining adult and increasing first-year bird abundances, we expected  $\phi$  to vary with age. However, we found little support for models with ENSO dependent variation in  $\phi$  that also differed between age categories (i.e.,  $\phi_{a \times \text{enso}}$ ). Generally weak support for ENSO structure in our  $\phi$  models, especially when coupled with age-dependence, may be a result of a lack of capture periods following the onset of the 1997/1998 ENSO warm-phase event as well as low recapture rates.

Other critical issues need to be considered in interpreting our apparent survivorship analyses and results. Apparent survivorship models for first-year birds are based on survivorship estimates that are confounded by young adult survivorship to an unknown extent, as we could not control for time interval between first capture (when identified as a first-year bird) and subsequent recapture of the same individual (which may have occurred two or more capture periods following first capture). Also, temporal variation of capture effort during

the non-breeding season may lead to variation in the intervals between annual capture periods (i.e., length of period between years). In an attempt to address this concern, we used only data from individuals captured between 1 September and 30 December for each capture period. However, temporally constraining data used in our analyses does not completely eliminate variation in interval length, and interval length variation must be considered in the interpretation of our survivorship model results. Finally, due to lack of capture periods and generally low recapture rates, it was not possible to estimate actual  $\phi$  (apparent survivorship) values during the period following ENSO onset.

Residual mean mass was lower in the years following the onset of ENSO, for both adults and first-year birds. Our spline curve accounts for variation in mass during the non-breeding season for data pooled among species and non-breeding seasons. Thus, a decline in our derived residual masses with capture day during non-breeding seasons following ENSO onset indicates that individuals were either losing mass or not gaining mass as quickly during the period just prior to migratory departure, relative to seasons prior to the ENSO onset. This pattern is more apparent when we constrained our LS-mean mass estimates to months when sandpipers theoretically maintain their mass trading off environmental unpredictability and risk of predation (Fig. 5; mass maintenance period) and to months when individuals prepare for migration northward by increasing in mass and moulting into breeding plumage (Fig. 5; premigratory mass gain period). Although our results do not distinguish between adult and first-year birds during the premigratory mass gain period, Western Sandpiper adults are more likely to migrate in the spring than are first-year birds (O'Hara et al., 2005), and for this reason reduced mass gain in preparation for migration in the spring may result in increased mortality during migration in this species and age category. Consistent patterns among species for both interannual mass variation and age–class ratios suggest that adult Least and Semipalmated Sandpipers may also face greater risk of mortality following ENSO as a consequence of lower mass prior to migratory departure.

At this point, we emphasize that we describe abundance, recruitment, survivorship and mass patterns that are associated with climatic variation due to ENSO. However, in order to clearly couple these patterns with long-term climatic oscillations, we need longer term population studies that extend over multiple phases of climate cycles such as ENSO and the Pacific Decadal Oscillation. These longer term population studies would not only help us understand the evolution of migratory patterns in long-distance migrant shorebirds but would help us to distinguish between population effects associated with cyclic climatic fluctuations and anthropogenically induced climate change.

#### 4.3. Factors limiting populations of migrant birds

The identification of factors limiting populations of migrant bird species, and where and when they occur during the annual cycle is crucial to their conservation. Early research on declining

migrant songbird population focused on factors that occur during the breeding season such as availability of suitable nesting habitat and survivorship during breeding (e.g., Hagan and Johnston, 1992; Degraaf and Rappole, 1995). In a seminal paper, Rappole and McDonald (1994) used results from the literature to evaluate the hypothesis that declines in populations of Nearctic breeding migrant birds are a result of changes to breeding ground factors (i.e., reduced available nesting habitat), and concluded that many of these populations are limited by factors occurring during other phases of the annual cycle, such as reduced survivorship during the non-breeding season. Sillett and Holmes (2002) decomposed annual apparent survivorship in the Black-throated Blue Warblers (*Dendroica caerulescens*) and estimated that mortality rates were at least 15 times higher during migration than during other phases of the annual cycle. Thus, populations of these warblers may be sensitive to changes in factors affecting adult survivorship during migration (such as availability of important stop-over sites). Shorebirds tend to have lower annual reproductive rates, reach reproductive age later, and live longer than songbirds. This suggests that variation in adult survivorship determining shorebird population dynamics is at least as important as it appears for songbirds.

In Ecuador, anomalously warm and wet conditions associated with ENSO warm phases can act directly on individual shorebirds, affecting their survivorship. Shorebirds can suffer increased physiological stress associated with heat (i.e., evaporative water loss: Klaassen, 1990; Verboven and Piersma, 1995). Thus, increased temperatures in Ecuador during ENSO may lead to increased physiological stress, and managing heat load can become more difficult as the date for migratory departure nears (Battley et al., 2003). ENSO can also affect shorebird food supply. For example, increased precipitation along the Pacific coast of Colombia during the cold phase of the 1997/1998 ENSO resulted in an increased riverine flow into an estuarine system in the Buenaventura Bay region (near Calí, Colombia). Increased riverine flow apparently affected salinity, temperature, oxygen load and sedimentation rates in associated mangroves and mudflats areas, and presumably, this led to documented variation in the structure of associated macrobenthos communities (Lucero et al., 2006). There was increased precipitation associated with warm-phase ENSO in our study area in Ecuador, such that we would expect similar changes to physical conditions in the sediments and macrobenthic community structure associated with increased precipitation as found in Colombia during the ENSO cold phase.

Pelagic-benthic linked bottom-up regulation can be an important determinant of community structure in some marine coastal ecosystems, such as rocky intertidal communities that lie adjacent to regions that experience oceanographic anomalies (Menge, 2000). Similarly, there may be a link between mudflat productivity in Ecuador and adjacent upwelling, but we are currently not aware of direct evidence supporting this link. If mudflat productivity is associated with nearshore upwelling activity in this region, then increased sea-surface temperatures during an ENSO warm phase, typically associated with decreased upwelling and generally lower oceanic productivity, could depress productivity in adjacent mudflats.

Pectoralis muscle size, fat load or mass as indices of body condition have been linked to survivorship in both passerines and shorebirds during the non-breeding season (Davidson, 1990; Castro et al., 1992; Sherry and Holmes, 1996; Burton et al., 2006) as well as during migration for shorebirds (Dinsmore and Collazo, 2003; Baker et al., 2004). Presumably body condition can be affected by physiological stress associated with heat, or through variation in food supply. A direct link between maintaining mass and food supply has been shown in Ovenbirds (*Seiurus aurocapilla*), however; mass variation may also result from trading off lipid storage with vulnerability to predation (Dugan et al., 1981; Lima, 1986; Rogers, 1987; Castro et al., 1992; Gosler et al., 1995). Our data suggest that it is more difficult to maintain mass during the non-breeding season following ENSO, and perhaps more importantly, mass gain during the period of preparation for migration is lower. Since we have no data on predation rates, we are unable to determine if lower mean mass following ENSO is simply an adaptive response to increased rates of predation, although B.J.M. Haase (unpublished data) did not document increased predation rates during this period. Rates of mass gain prior to migratory departure may be important for two reasons: (1) survivorship during migration (Dinsmore and Collazo, 2003; Baker et al., 2004), and (2) overall speed of migration, which can ultimately affect the likelihood of a successful reproductive year (migration time minimization strategies, Lindstrom, 1991; Hedenström and Alerstam, 1997). However, fat/mass deposition rates can be modified if shorebirds are trading off lipid storage with risk of predation during migration (Ydenberg et al., 2002).

In summary, we have demonstrated a pattern in the demographics of three species of shorebirds spending their non-breeding seasons in Ecuador, with a shift towards greater numbers and proportions of first-year birds following the 1997/1998 ENSO warm-phase event. Reduced numbers of adults captured at our sites in Ecuador could indicate a larger scale decline in adult abundance, as opposed to changes in local movement patterns during the non-breeding season, given that these species likely express a high degree of site fidelity. We have found limited support for ENSO structure in our apparent survivorship analyses, but more compellingly, we have found that mean mass and mass gain was lower in years following ENSO than before. Lower mean mass and mass gain may have implications with respect to survivorship. ENSO associated factors could impact these species of shorebirds at any point during the annual life cycle. Variation in prey availability (both timing and abundance) during migration could affect survivorship as well as reproductive outcomes. Since we have shown that numbers of first-year birds increased with an ENSO warm phase it seems unlikely that factors affecting reproductive outcomes are important. However, because Western Sandpiper adults are more inclined to migrate in the spring than are first-year birds (Fernández et al., 2004; O'Hara et al., 2005), which may be true for the other two species as well, adult survivorship is more likely to be impacted if adults have to cope with reduced prey availability during premigratory preparation at non-breeding sites, as

well as at migration stop-over sites. This example of a potential age-dependent impact of varying climate illustrates how long-term climatic cycles such as ENSO can potentially interact with life history strategies, and in turn, provide a potential mechanism through which life history strategies evolve in response to these cycles.

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