

EFFECTS OF RESTORATION ON THE SMALL SHOREBIRD
CARRYING CAPACITY OF A SOUTH BAY MUD FLAT

A thesis submitted to the faculty of
San Francisco State University
In partial fulfillment of
The Requirements for
The Degree

Master of Arts
In
Geography Resource Management Environmental Planning

by
Aariel Rowan
San Francisco, California
January, 2012

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CERTIFICATION OF APPROVAL

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EFFECTS OF SALT POND RESTORATION ON THE SMALL SHOREBIRD
CARRYING CAPACITY OF A SOUTH BAY MUD FLAT

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2012

A major question challenging the South Bay Salt Pond Restoration Project is whether conversion of existing salt ponds to tidal marsh will result in decreased numbers of migratory birds supported in the region. We used elevation, water level, invertebrate density, and avian abundance data collected from August 2009 to May 2010 at an intertidal mud flat. We developed a foraging model for Western Sandpipers and Dunlin based on their energy balance with their invertebrate prey and evaluated how a loss of foraging area (from sediment transport into restored subsided salt ponds) might impact the carrying capacity of the site.

We found that reducing the intertidal foraging area by one-third reduced bird use-days supported by the site in all months, and this most impacted the birds in April. To anticipate such losses, managers should ensure that foraging habitat remains available within shallow salt ponds during spring migration.

I certify that the Annotation above is a correct representation of the content of this written creative work.

Chair, Thesis Committee

Date

ACKNOWLEDGEMENTS

This work was supported by the South Bay Salt Pond Restoration Project, the Coastal Conservancy, the Resource Legacy Fund and the U.S. Geological Survey Western Ecological Research Center (WERC). The study benefited from the permissions to use unpublished data provided by the USGS San Francisco Bay Estuary Field Station (Isa Woo and John Takekawa), USGS Pacific & Marine Science Center (Bruce Jaffe and Amy Foxgrover), and the USGS Water Resources (Greg Shellenbarger and Dave Schoellhamer). James Lovvorn (Southern Illinois University) provided extensive assistance.

Many thanks go to Ashley Smith, William Chan, Andrew Perry, Alex Westhoff, Brian Hess, Brittany Stieg, Carmen Daggett, Derek Drolette, Daniel Porton, Erin Flynn, Elana Garfinkle, Eric Palm, Harlan Vaska, Jonathan Felis, Joel Shinn, Kristin Brailsford, Kristin Hirsch, Katherine Powelson, Margaret Schaap, Maria Villagrana, Polly Gibson, Stephanie Bishop, Seth Lanning, Stacy Moskal, Sara Piotter, Sylvia Major, Tina Mathews, Toby Rohmer, Cliff Rocha and Marta Rocha.

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INTRODUCTION

The San Francisco Bay Estuary is the largest estuary in the western United States and supports a tremendous diversity of flora and fauna, including many special status species and millions of migrating and wintering waterbirds. This estuary is of key importance to shorebird populations and hosts an average of 67% of all shorebirds travelling along the west coast (Page et al. 1999). Extensive urban and agricultural developments in the last 200 years have resulted in loss of 80% of this estuary's historic tidal salt marshes and 40% of its intertidal mud flats (Foxgrover et al. 2004, Goals Project 1999).

Recent transfer of over 5,400 ha of salt evaporation ponds to government management in the South San Francisco Bay (hereafter South Bay) has resulted in the largest tidal restoration effort on the North American West Coast (Goals Project 1999). A primary goal of the South Bay Salt Pond Restoration Project (SBSRP) is to conserve populations of migrating and wintering bird species while providing additional resources for endangered species that rely on intertidal salt marsh. Most shorebirds feed on the intertidal mud flats adjacent to the salt ponds and in the salt ponds themselves (Takekawa et al. 2001, Warnock et al. 2002, Masero 2003). The effect that marsh restoration will have on South Bay shorebird populations is largely unknown because salt marsh currently supports a much lower density of shorebirds than the existing tidal salt pond habitat (Takekawa et al. 2001). Attempts have been made to identify management strategies to maximize waterbird populations, and the availability of food and carrying

capacity of mudflats will be primary concerns for conservation of shorebirds as salt ponds are converted to tidal marshes (Stralberg *et al.* 2009).

Because many birds currently use these salt ponds, there is concern about whether alternative feeding grounds elsewhere in the estuary will be able to meet the birds' energy needs (Stralberg *et al.* 2006). Determining the carrying capacity of South Bay intertidal mud flats is critical to the SBSPRP because it will help describe how changes to the sediment profiles of mudflats will impact the energy budgets of foraging shorebirds (Bearman *et al.* 2010, Brew & Williams 2010).

Elevation controls the schedule and extent of tidal exposure of mud flats and influences the distribution of intertidal macroinvertebrates (Baldwin and Lovvorn 1994). Tidal exposure changes the salinity, pH, temperature, and degree of desiccation experienced by these invertebrates (Nichols and Pamatmat 1988). Effects of mud flat elevation and tidal exposure on macroinvertebrates may vary with season and with sediment grain size, organic content, and microtopography (Wolff and de Wolf 1977, Quammen 1982, Hicklin and Smith 1984, Baldwin and Lovvorn 1994). The sediment flux experienced by South Bay mud flats will be an important predictor of their ability to buffer possible changes due to sea level rise and sediment transport into breached subsided salt ponds (South Bay Salt Pond Restoration Project 2007). Prey availability or shorebird foraging efficiency may be directly affected by a change in mud flat characteristics or extent resulting from restoration, so this study provides an important

baseline estimate of habitat quality for foraging shorebirds (Quammen 1982, Shepherd and Boates 1999, Poulton *et al.* 2004).

Foraging shorebirds consume amphipods, bivalves, cumaceans, polychaete and oligochaete worms in the South Bay mud flats. Factors that drive the distributions of these invertebrates are poorly understood, but a recent study conducted by the USGS San Francisco Bay Estuary Field Station is beginning to provide detailed information on the seasonal abundance and dispersion of invertebrates on a South Bay mud flat, the Dumbarton Shoals (Takekawa & Woo, USGS Shoals Study, unpublished data).

Our carrying capacity model focuses on the most abundant small shorebirds in the South Bay, Western Sandpiper (WESA, *Calidris mauri*) and Dunlin (DUNL, *Calidris alpina*) (Page *et al.* 1999, Stenzel *et al.* 2002, Takekawa *et al.* 2006). During the November 2008 SFB Shorebird Census (Wood *et al.* 2010), Western Sandpipers were the most abundant shorebird comprising 30% of all birds, followed by DUNL with 29% (about 100,000 of each). These two species have prey size overlap (Appendix 2), and so were considered together in the foraging analysis of the Dumbarton Shoals.

The main objectives of this study were to estimate the carrying capacity (which we define as the maximum number of bird use-days that a site can support) of a South Bay mud flat during different seasons, and to describe the potential impact to foraging small shorebirds if one-third of the mud flat were to erode into the channel.

METHODS

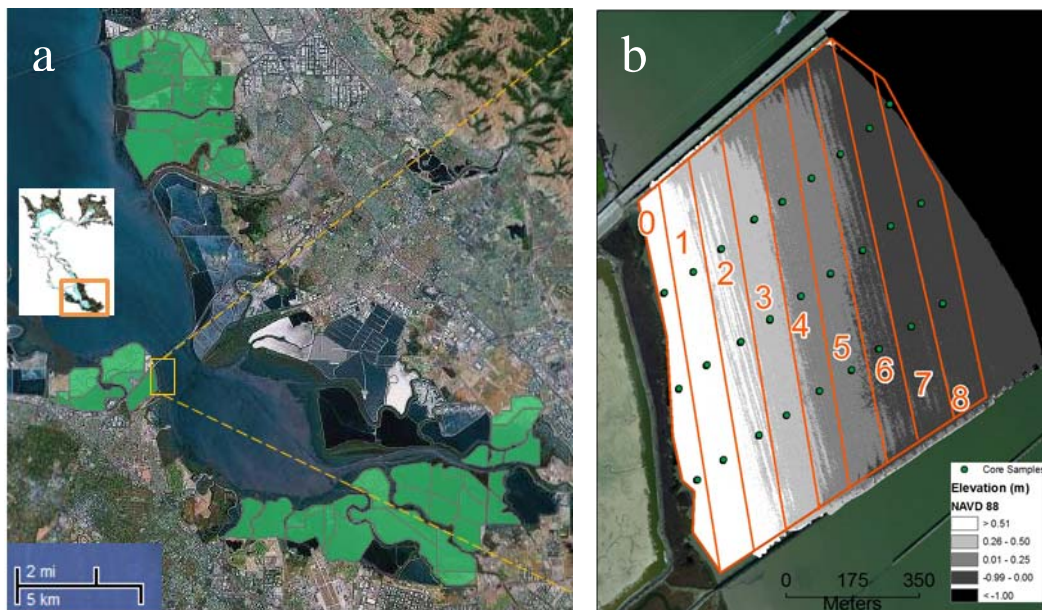
Study Site

The study site (Fig. 1a) was located on an intertidal mud flat, the Dumbarton Shoals, adjacent to pond RSF2 in the Ravenswood complex of the SBSPRP in the South San Francisco Bay, California. The site has a surface area of about 8.48 ha and is bounded by the Dumbarton Bridge to the north and the Southern Pacific Railroad Bridge to the south. The shoal extends about 1km from shore to the channel, and has a width of about 0.8km. We divided the site into nine zones (Fig. 1b) at incremental distances from shoreline. The mud flat ranges in elevation from -0.80 m to 0.97 m NAVD88 (North American Vertical Datum 1988) and a deep channel cuts across the northeastern side of the site (Fig. 1c). Water-column salinity during flood tides on the site ranged from 18‰ in March and April to 32‰ in late August and September. Total organic carbon in sediments ranged from (mean \pm 1SD) $1.6 \pm 0.3\%$ dry mass in January to $2.2 \pm 0.4\%$ in July. Water temperatures during flood tides ranged from 11.1 ± 0.7 °C in January to 21.3 ± 1.5 °C in June (Shellenbarger & Schoellhamer, USGS Shoals Study, unpublished data).

Model structure

To estimate shorebird use-days supportable on the existing prey, we employed a daily ration model (Goss-Custard et al. 2003). Our model used estimates of daily bird energy needs, the energy content of prey standing stocks, and the efficiency with which

Figure 1. (a) Mudflat study site located south of the Dumbarton Bridge on west side of South SF Bay. Restoration on SBSPRP ponds (shown in green) are expected to dramatically change the South Bay landscape. (b) Zones for sampling included an irregularly-shaped near shore area (Zone 0) and 8 strips at 100 m increments extending out from shoreline (Zones 1–8) to the edge of the deep-water channel. Elevations (NAVD88 m) were collected with side-scan bathymetry.



birds convert ingested prey to metabolic energy to estimate the carrying capacity of our study site for small shorebirds (Table 1). Total energy content in prey stocks divided by the energy requirements of an individual shorebird equals the carrying capacity of the area for shorebirds (Fig. 2). This model assumes that small shorebirds are able to consume prey fast enough to meet their daily energy needs on this site alone, i.e. that intake rate is limited by handling time and not prey density over all prey densities until prey are abruptly depleted (Goss-Custard et al. 2006).

Sampling

From August 2009 to May 2010, the USGS Shoals Study (Takekawa and Woo, unpublished data) sampled benthic macroinvertebrates monthly by taking cores along three transects (Fig. 1b). At each of 9 stations spaced at 100 m intervals along each transect, we took triplicate sediment cores 10 cm deep and 10 cm wide ($n = 81$ cores for each sampling date). In the field, we rinsed the core samples through a 0.5 mm sieve and preserved them in an ethanol and Rose Bengal solution. Then in the laboratory, we identified invertebrates to lowest taxonomic level possible, and counted, weighed, measured, and dried them to constant mass at 60°C. We converted dry mass to ash-free dry mass based on conversion factors taken from the literature (AFDM, Ricciardi and Bourget 1998).

We surveyed avian abundance biweekly during falling tides and recorded the spatial locations of birds relative to the tide line and shore. For the more numerous

shorebirds, we estimated the prey biomass needed to satisfy the daily energy needs of the average number of shorebirds detected on the site.

USGS scientists (B. Jaffe, R. Kayen, G. Shellenbarger, D. Schoellhamer) in the collaborating Shoals Study mapped the channel and deeper shoal habitat with side-scan sonar and an interferometer (± 6 cm), and the shallow mud flat habitat with terrestrial light detection and ranging (LiDAR) surveys (± 3 cm). A high-accuracy pressure transducer (Sea-Bird Electronics, Bellevue, WA) recorded water levels every 15 min throughout the study period. Surface sediment samples were collected monthly at all invertebrate coring locations ($n = 27$). Water quality information (water-column salinity, temperature, dissolved oxygen, pH) was also collected from a boat during flood tides for each coring session.

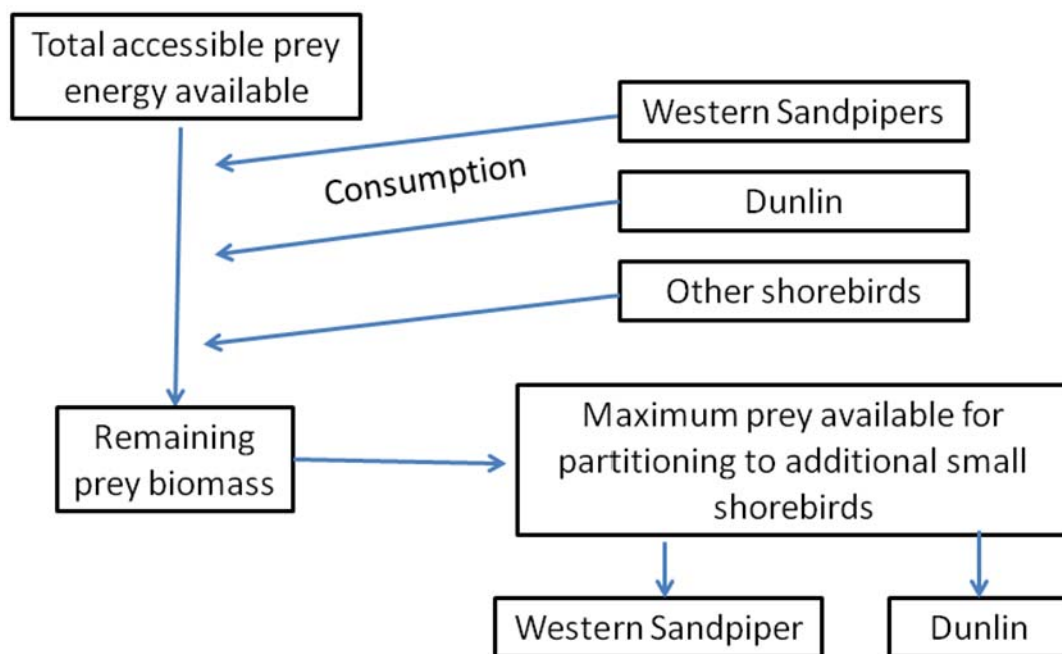
Accessible (and profitable) prey

Amphipods, bivalves (<12 mm), cumaceans, gastropods, oligochaetes, and polychaetes have been known to be prey items exploited by migrating shorebirds (Appendix 1). Bivalves and polychaetes were the most abundant prey items on the site, and other possible prey items were not detected in densities great enough to be important foods. Since shorebirds avoid prey items too small to be profitable, we estimated the minimum size taken ($\text{mg AFDM} = 0.0012M^{1.20}$ ($M = \text{body mass}$, Zwarts & Wanink 1993) for each species. WESA take prey items that are at least 0.06 mg AFDM, and DUNL focus on

Table 1. Estimated energy budget of Western Sandpipers (WESA) and Dunlin (DUNL).

Measurements	WESA Value (mean \pm SD)	DUNL Value (mean \pm SD)	Reference
Average body mass (g); A	26.8 \pm 3.0	57.0 \pm 4.5	Takekawa, unpublished data, Warnock & Gill 1996
Assimilation efficiency (%); B	73.9 \pm 2.28	73.9 \pm 2.28	Castro et al. (1989)
Macroinvertebrate energy content (J/mg AFDM); C	22.99 \pm 0.26	22.99 \pm 0.26	Brey et al. (1988)
Fattening rate (kJ/d); D	16	33	Warnock & Bishop (1998), Williams et al. (2007), Masero (2003)
Daily energy expenditure (kJ/d)			
Wintering; $E_w = 10 \cdot \exp(0.969$ $+ 0.676 \log A$ (g))	86	143	Tieleman & Williams (2000)
Migration; $E_m = E_w + D$	102	176	

Figure 2. Schematic of carrying capacity model.



prey greater than 0.15 mg AFDM. Bill size limits the ability of small shorebirds to consume large bivalves. We assumed that all sizes of polychaetes were available, and that bivalves larger than 12 mm were unavailable (Appendix 2). We assumed that invertebrate consumption by fish or other predators such as waterfowl was negligible, since we lacked estimates of their foraging rates. Thus, our estimates of carrying capacity for shorebirds are conservative, since other predators may reduce the overall food resources available for shorebirds.

We assumed a macroinvertebrate energy content of $22.99 \pm 0.26 \text{ J mg}^{-1}$ AFDM (Brey *et al.* 1988) and an assimilation efficiency of $73.9 \pm 2.28\%$ (Castro *et al.* 1989).

Generating prey maps from benthic samples

To better visualize the spatial distribution of prey biomass, we interpolated macroinvertebrate densities on the Dumbarton Shoals using values from the nearest sampling stations. For each core, we summed all accessible prey of the proper size class. Then we averaged total biomass from the triplicate cores to estimate a mean prey density for each station (n=27).

Interpolation with the inverse multi-quadratic radial basis function, (RBF, ArcGIS Geostatistical Analyst, ESRI, Redlands, CA) yielded the lowest root mean square error during cross validation. Cross validation compared the predicted value at each sampling point (while omitting that point) with the actual sampled value. The RBF method took into account the anisotropy present due to the environmental gradients in the site

(namely, the increasing water depth extending perpendicular to shore). All settings were selected to minimize the root mean square error (neighbors: 10, at least: 5; sector: 4 and 45°; angle: 347.5°; major semiaxis: 300, minor semiaxis: 100).

Chronology of shorebird use

To analyze prey availability before fall migration and after spring migration, the analysis focuses on the ‘shorebird year’ from Aug 2009 to May 2010. This time period represents the overwintering period and before versus after the spring migration. Also, construction on salt pond RSF2 (adjacent to study site) began altering the mud flat in May 2010, so the study period reflects the habitat quality of the mud flat immediately before restoration.

Daily Energy Needs

Total energy needs of small shorebirds on the study site were equal to their abundance times their estimated daily energy expenditure (DEE). The DEE in winter was assumed to be equal to the field metabolic rate (*FMR*), which is the average rate of energy use as an animal goes about its normal activities including resting, foraging, and flying.

$$\log FMR \text{ (kJ/d)} = 0.969 + 0.676 \log M \text{ (g)}$$

where M = Body mass (Tieleman & Williams 2000). We estimate winter DEE to be 86 kJ/d for WESA and 143 kJ/d for DUNL. Additional energy was needed for migration, so

a fattening rate was included in April estimates of DEE (Warnock and Bishop 1998, Williams *et al.* 2007, Masero 2003), where:

$$\text{Migration DEE (kJ/d)} = \text{FMR (kJ/d)} + \text{fattening rate (kJ/d)}$$

We estimated migration DEE to be 102 kJ/d for WESA and 176 kJ/d for DUNL. We multiplied the mean daily number of each species by their DEE to estimate the total prey energy that shorebirds would have to consume to meet their energy needs during each month from October 2009 to April 2010.

Estimation of potential shorebird use-days

The carrying capacity of shorebirds in the study site was based on the daily ration model (Goss-Custard *et al.* 2003). In the basic model the total number of bird use-days S are estimated as $S = F_{cons}/r$, where F_{cons} is equal to the total amount of consumable food above the profitability threshold and r is the daily ration of an average animal (DEE).

We assumed that shorebirds met 100% of their energy needs from this site, were ideal foragers with equal ability to obtain foods, and had no extra energy expenditures from weather or predator avoidance. We multiplied the mean daily number of WESA (from area surveys) by the number of days in each month and their DEE to yield the total prey energy consumed by WESA over this period. After subtracting that value from the total energy available, we subtracted consumption by DUNL. The remaining energy was allocated among the two species according to their relative consumptions to estimate the amount of energy available to support additional numbers of each species. These energy

estimates were divided by their respective DEEs to estimate the number of shorebird use-days supported per month.

Uncertainty analysis

We evaluated the effects of different parameters on use-day estimates. For parameters impacting the energy intake of small shorebirds for which we had no empirical measurements, we selected a range of likely values that are discussed below. The range of daily energy expenditures was calculated from ± 1 SD of body mass during the wintering (Oct to Mar) and migration (Apr) periods from birds measured in San Francisco Bay (Holmes 1966, Takekawa, unpublished data). Much of this range reflected difference in body mass between sexes. For each parameter obtained from the literature (energy content, assimilation efficiency), the uncertainty analysis used a range of values within one standard deviation from the mean.

Results of the uncertainty analysis showed that variability in energy content and assimilation efficiency had little impact on output of the model (1% and 3% respectively). Variation in body mass had the most impact on daily energy intake (11% for WESA and 17% for DUNL), as both WESA and DUNL exhibit a wide range of body size.

Scenario of mud flat change

Lastly, we calculated how the loss of the mud flat due to erosion into the channel would impact shorebird use-days by decreasing mud flat area by one third to reflect a historical (1931) low in mud flat width (Foxgrover et al. 2004). To simulate the loss of the outer mud flat, we omitted the outer 300m (zones 6, 7, and 8) from the analysis. We compared the resulting changes in shorebird use-days to the original model.

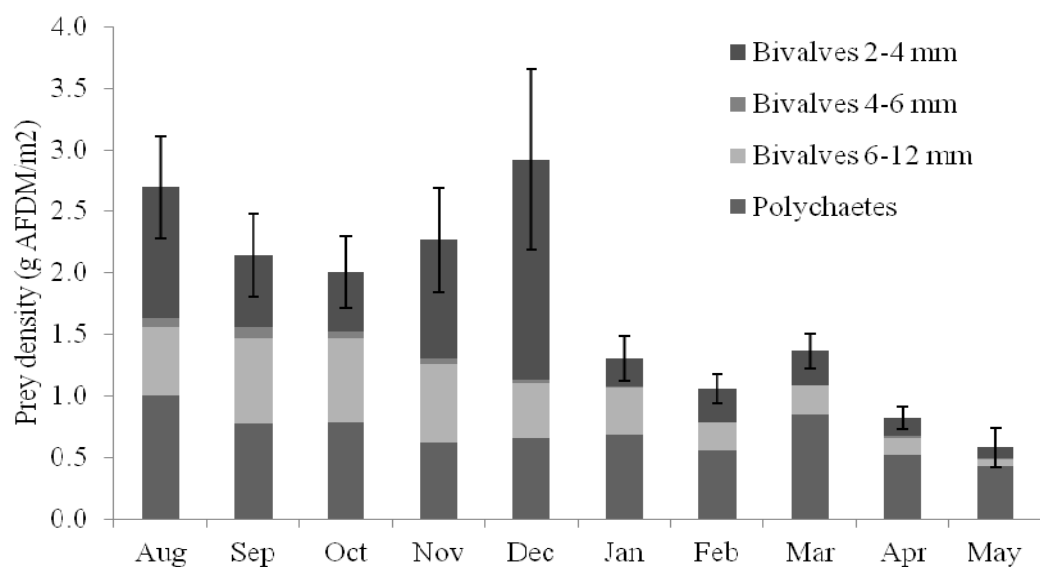
RESULTS

Chronology of prey biomass and shorebird densities

After summer recruitment and growth, invertebrate prey densities were high (mean \pm 1SD, 2.14 ± 0.34 g AFDW/m² in September 2009) and remained so through December (2.92 ± 0.74 g AFDW/m², Fig. 3). However, prey density dropped abruptly in January (1.30 ± 0.18 g AFDW/m²), remained low through the spring and declined through May (0.58 ± 0.16 g AFDW/m²). In January, overall prey stocks were reduced by roughly half due to the decline of 2–4 mm long *Gemma gemma*. This is a clam that does not generally grow larger than 5 mm (Sellmer 1967). However, bivalves in the 4–6 mm range were noticeably absent from the samples, even during the summer when small shorebirds did not use the site.

Bivalves 6–12 mm reached peak density during summer (when shorebirds are mostly absent) and their biomass diminished through May 2010 (Fig. 3). A large

Figure 3. Density of prey (mean ± 1 SE, g AFDM/m²) available to foraging WESA and DUNL from Aug 2009 to May 2010. Error bars represent the standard deviation of all prey items combined ($n = 81$). Three replicate cores were collected from nine stations 100 m apart along three transects lines perpendicular to shore and separated from each other by 200m. The total area of the site is 847,700 m².



increase in 2–4 mm bivalves (mostly *Gemma gemma*) in November and December appeared to reflect a pulse of recruitment from a fall breeding period. Polychaetes on the site maintained relatively constant biomass through the year, as various species reproduced during different months.

Densities of small shorebirds varied greatly between surveys because large flocks travel through the site while utilizing a much larger area to forage and roost. Winter small shorebird density was greatest in December (mean \pm 1 SD, 89.1 ± 25.7 WESA/ha and 122.6 ± 35.4 DUNL/ha, Fig. 4) and lowest in February (57.6 ± 40.5 WESA/ha and 14.7 ± 17.2 DUNL/ha). April was the month of highest annual bird density (248.5 ± 130.3 WESA/ha and 57.0 ± 42.4 DUNL/ha) due to spring migration. Although April counts had high standard deviations, similar avian densities were detected in 2008 (212.2 ± 128 WESA/ha and 112.1 ± 8.1 DUNL/ha). These surveys were collected during different parts of the month (from April 1st to April 28th). So, average densities take into account the variation in avian abundance as migrants pass through the region.

Spatial distribution of prey biomass vs. shorebirds

Prey densities were much greater closer to shore, especially in late summer. Only 13% of the prey biomass was found on the mud flat 600 m to 900 m from shore. Sixty-eight percent of the prey biomass on the site was found within 300 m from shore (Figs. 5, 6). Accordingly, shorebirds used the site most heavily just after the falling tide exposed Zones 0 and 1 (within 200m from shore, Fig. 1b). For example, nearly 28,000 WESA

Figure 4. Density of WESA and DUNL detected in ground surveys (mean \pm 1 SD for two counts per month). The total area of the site is 84.8 ha.

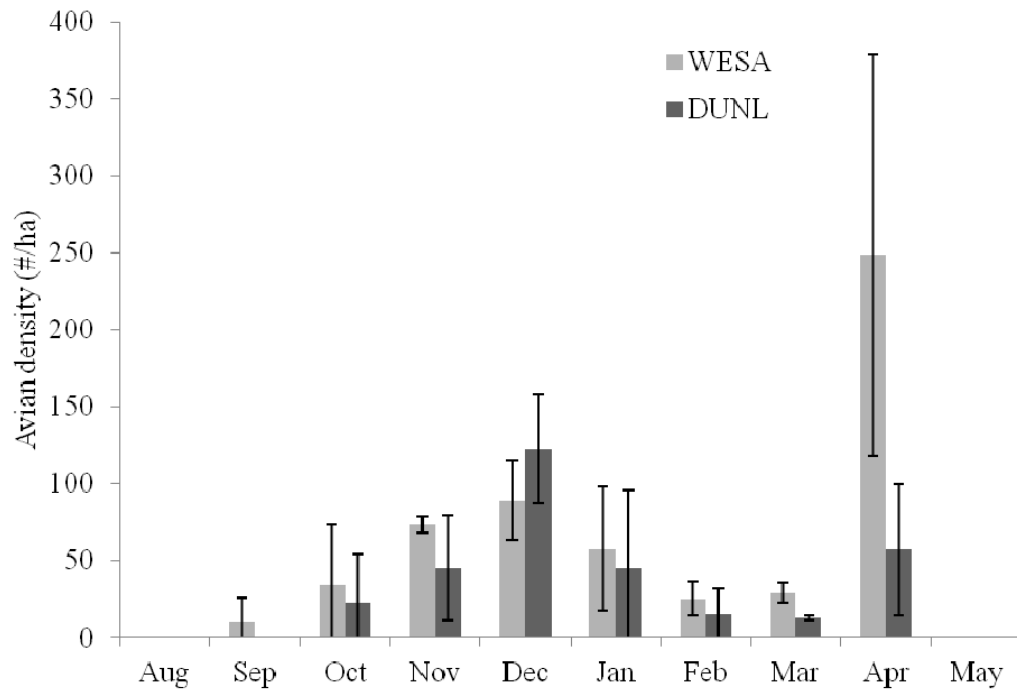


Figure 5. Density of prey (mean \pm 1 SE, g AFDM/m² for 9 cores per zone) available to foraging WESA and DUNL by elevation zone (Fig. 1) for all months combined. Greatest prey densities were closer to shore. Each month, nine cores were collected from each zone (three replicate cores for each of three transects). Zones extending from shore were 100 m wide and the three transects lines were separated from each other by 200m. The total area of the site is 847,700 m².

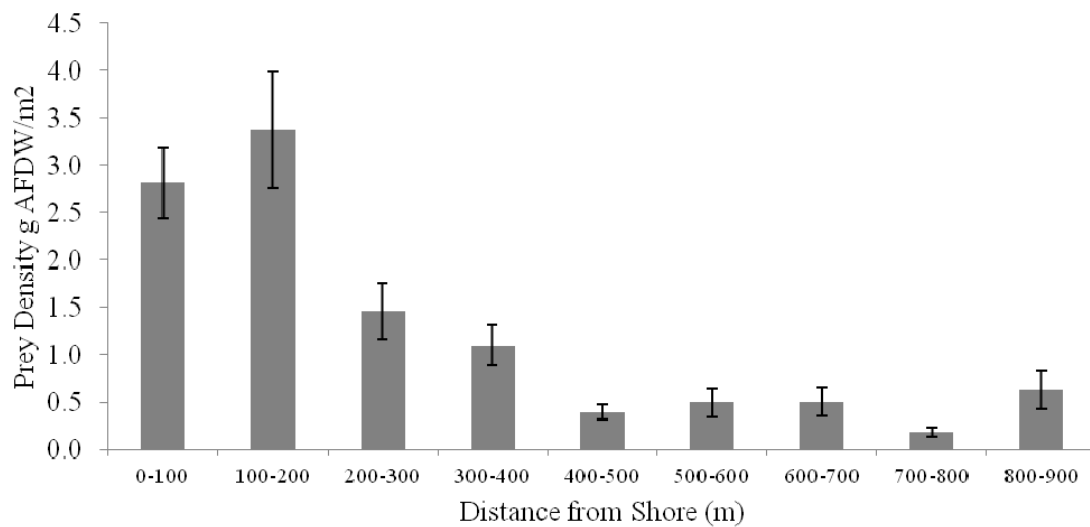
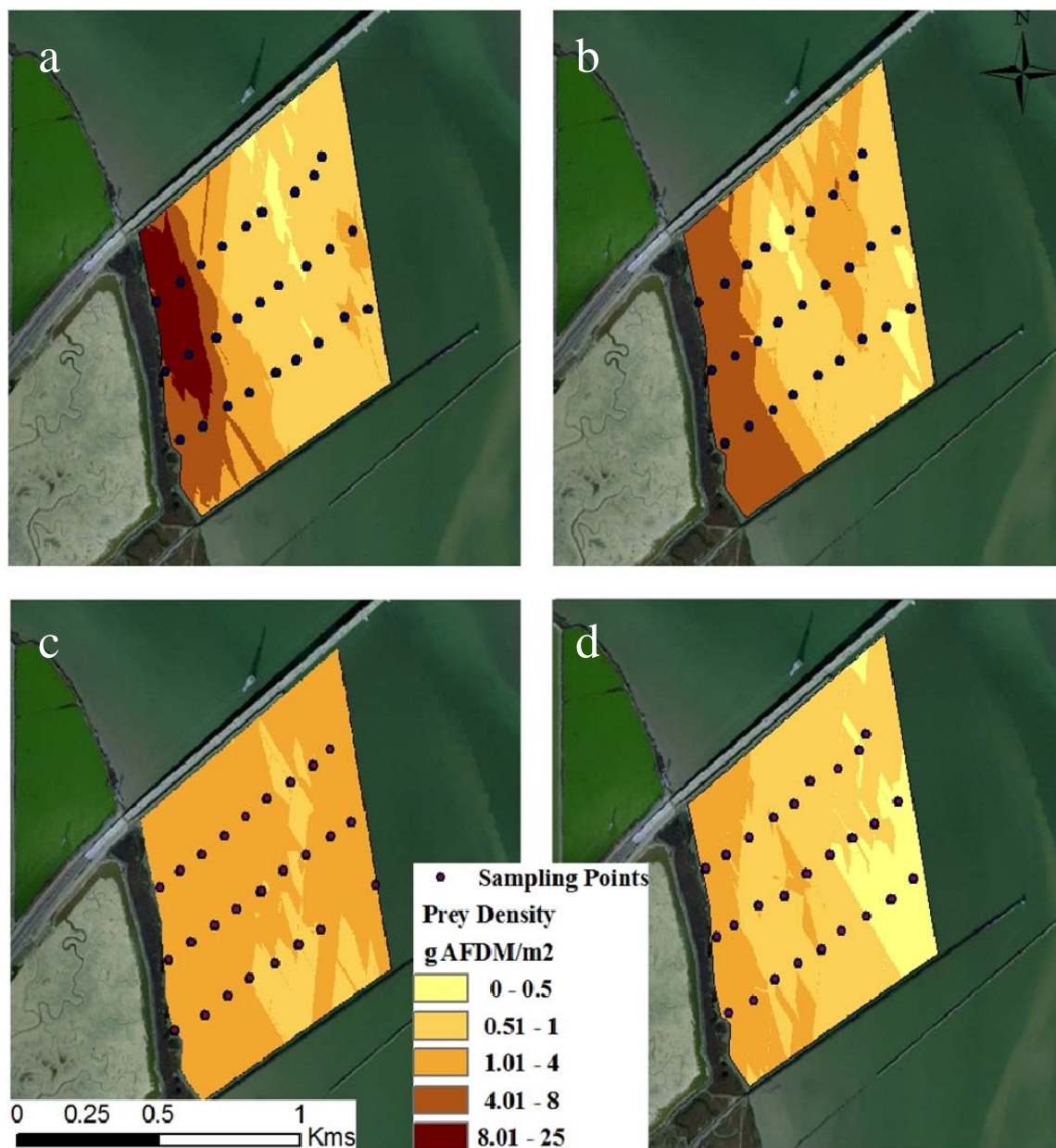


Figure 6. Prey densities (g AFDM/m²) on the study site during (a) December 2009, (b) January 2010, (c) March 2010, and (d) and April 2010 (USGS Shoals Study, Takekawa and Woo, unpublished data).



were detected during a single survey in April 2010, and over 24,000 (86%) of these WESA were in Zone 1 (100m to 200m from shore) where high densities of prey were found (Fig. 6d). This feeding pattern may partly reflect the foraging needs of shorebirds when mud flats first become available after a period of tidal inundation. Nevertheless, patterns of both bird feeding and prey density emphasize the high importance of foraging areas near shorelines despite steady declines of prey densities in that zone from August through April.

Shorebird use-days for WESA and DUNL

From September through March (but not in April), estimated consumption by WESA and DUNL (Fig. 7) was less than the total amount of prey available (Fig. 3). As prey biomass available exceeded that consumed by small shorebirds, we determined that additional small shorebirds could be supported on the site during the wintering period but not during spring migration (Fig. 8). Since small shorebirds are most successful when foraging at the tide line (Dierschke *et al.* 1999, Granadeiro *et al.* 2006), there were very few periods of the most favorable foraging conditions when the tide passed through the near shore mud flats.

Shorebird energy demand depends on the timing of available prey (Fig. 3) and shorebird abundance (Fig. 4). Prey biomass peaked twice during 2009–2010. One peak occurred during late summer when few shorebirds were present. Prey density then diminished gradually until biomass began to increase again in November to a second

Figure 7. Expected consumption (kg ash-free dry mass/month) of invertebrates by WESA and DUNL observed on the site. Estimates were calculated as the average of two bird counts per month (Fig. 3) multiplied by average DEE values for each bird species.

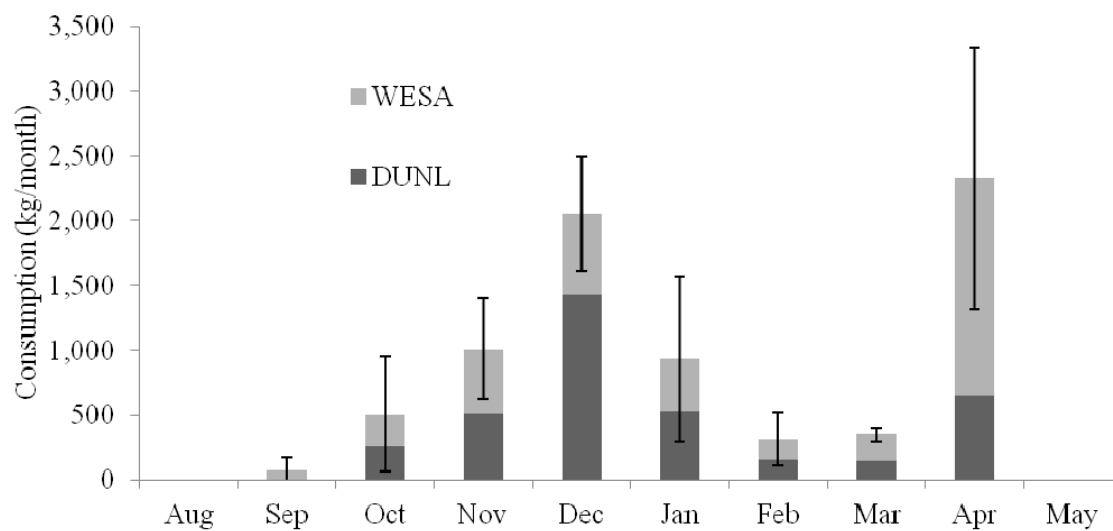
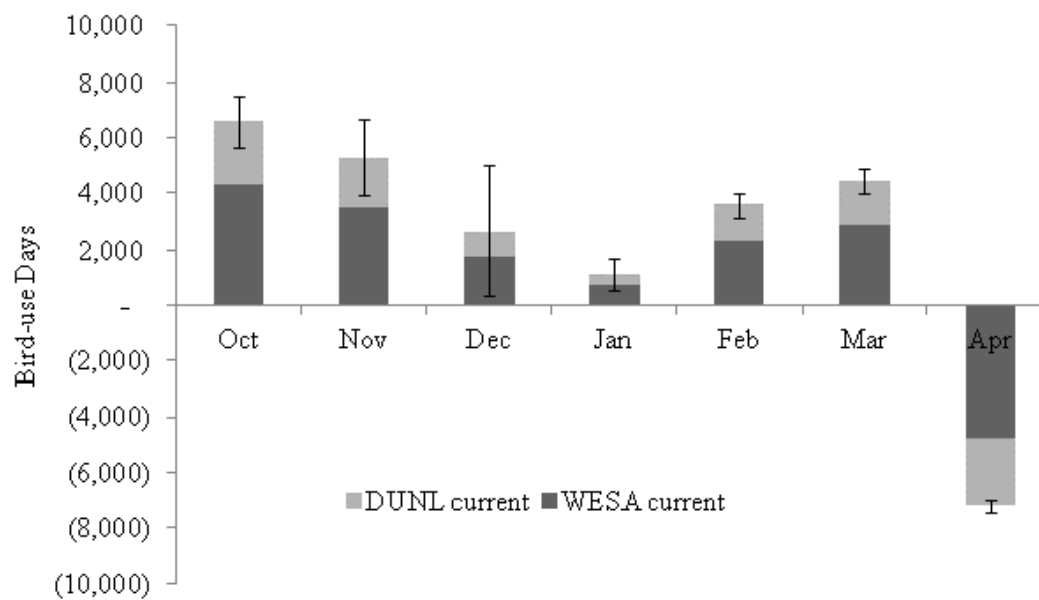


Figure 8. Additional bird-use days (mean \pm 1 SE) available each month, after consumption by the observed small shorebird population was subtracted from total prey biomass at the site.



peak in December. In December, small shorebirds were abundant at the same time that prey biomass was high. Prey biomass dropped off sharply in January but so did bird numbers, so prey resources were still adequate to meet demand through March (Fig. 8). However, synchrony of prey biomass and bird numbers broke down during spring migration, when our study site lacked the foraging resources to fully support the large flocks of small shorebirds visiting the site. In fact, prey stocks on the Dumbarton Shoal were only able to provide 31% of the energy needed by small shorebirds visiting in April. These large flocks must find prey elsewhere in the region to meet their energy needs. In recent decades, these additional foods have been provided by nearby salt ponds, which may soon be converted to tidal marsh and support much lower shorebird densities (Takekawa *et al.* 2006, Warnock & Takekawa 1996).

Shorebird use-days with loss of outer mud flat

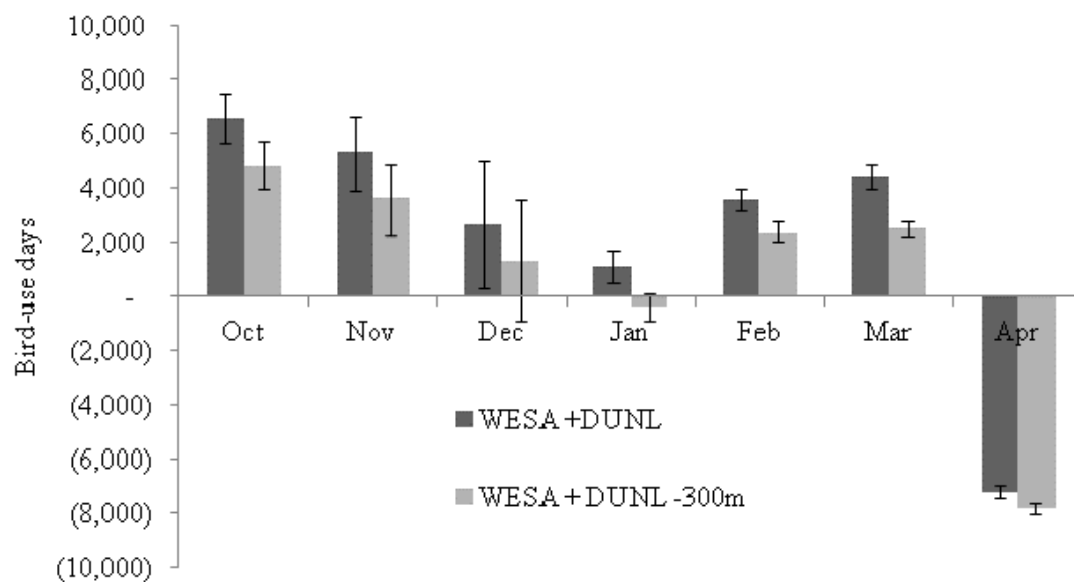
We considered how the erosion of outer mudflat to 1931 levels (Foxgrover *et al.* 2004) would affect the carrying capacity of the Dumbarton Shoals for small shorebirds. With 300m of erosion, potential bird use-days declined by 640 to 1940 bird use-days (mean \pm 1SD: 1,427 \pm 420) but remained positive (signifying the ability for the site to support additional birds) in all months but January and April (Fig.9). With this scenario, the mud flat would be at carrying capacity in January and would only be able to support 25% of the migrating small shorebirds visiting the site during April.

DISCUSSION

While the mid-winter invertebrate population crash may have been caused by the large numbers of shorebirds on the site in the winter, it is also possible for bivalve populations to die off in response to fresh water or sedimentation events (Jan Thompson, personal communication). However, an earlier study found *Gemma* clams to be an important diet item (present in 47% of gizzards, $n = 32$) for WESA foraging in South Bay mud flats (Takekawa & Warnock, unpublished data), and it is not uncommon for predators to cause declines in intertidal prey (Rosa *et al.* 2008). So, the correlation between high bird numbers in December and the prey decline between December and January may well have resulted from high levels of bird predation. Diet studies (Appendix 2) suggest that 4–6 mm bivalves should be preferred by foraging WESA. Bivalves of this size would be most profitable without being too large to consume, and the absence of these clams strongly implies that shorebird predators are applying top-down controls in the intertidal ecosystem.

The avian and invertebrate communities using intertidal habitats are highly variable, and predicting future population trends is difficult. Our intensive sampling regime provides a snap shot of this community during survey periods. Thus, this carrying capacity model provides a simplified carrying capacity estimate of how prey resources may support two species of shorebirds. Many other factors affect their population dynamics, including risk of predation, weather, extreme tide events, foraging and breeding conditions on other parts of their migration pathway.

Figure 9. Number of bird use-days available on the site after prey consumption by current numbers of shorebirds (WESA + DUNL) compared to the estimated bird use-days that may be available on the site if the mud flat receded 300 m shoreward (WESA + DUNL - 300m)



An important caveat to our carrying capacity estimates is that we assume that a density below does not exist below which negative profitability (energy gain minus cost) causes the birds to go elsewhere before depleting all prey. Departure from foraging habitats before available prey has been depleted has commonly been observed in shorebirds (Goss-Custard et al. 2006, Stillman and Goss-Custard 2010). Consequently, assuming that all prey can be exploited profitably may lead to substantial overestimates of carrying capacity. To counter this, we omitted any prey item less than the critical mass needed to obtain a positive energy balance from our analysis (Zwarts and Wanink 1993).

Additionally, this model likely overestimates shorebird use-days by omitting stock depletion from competing shorebirds, fish, waterfowl and other ectothermic predators, as their consumption rates are unknown. Our estimates of supportable shorebird use-days should be considered maximum estimates with actual values likely being appreciably lower. The strength of this analysis is not in the precision of shorebird use-day estimates but in the comparisons between current conditions and how existing systems may respond to environmental change.

Biofilm foraging has been observed on the site and could be an additional source of energy (Kuwaie, personal communication), but biofilm consumption was not included in this carrying capacity model. It may be an especially important food resource for shorebirds, and thus understanding the seasonality of biofilm productivity may be critical to fully estimate carrying capacity. If high volumes of biofilm become available in the

early spring, it may help support the vast numbers of small shorebirds staging in the South Bay on their northward migration (Kuwae *et al.* 2008, Kuwae *et al.* 2010).

Management implications

Beyond the impacts of salt marsh restoration in the South Bay Salt Ponds, shorebirds will be facing numerous other challenges in the coming decades. Invasive plants such as *Spartina foliosa x alterniflora* hybrids threaten to reduce the foraging quality of mud flats (Stralberg *et al.* 2004). Mud flat habitat is expected to decline by at least 30% in the next 50 years with sea level rise and sediment flux into breached and subsided salt ponds (South Bay Salt Pond Restoration Project 2007). Macroinvertebrate communities are widely variable and subject to invasion by non-native species (Nichols *et al.* 1990) and changes in regional ecosystem states (Cloern *et al.* 2007). Since invertebrate prey are concentrated near shore, disturbance to the outer mud flats (at edge of channel) would have less of an impact to small shorebirds than disturbance to mud flats near shore.

Sediment transfer from the open bay into subsided salt ponds will likely cause an increase in mud flat loss, but that can be balanced through phasing pond conversion and the creating a progression of transitional mud flats in the ponds (Brew and Williams 2010). This approach still leaves a greatly reduced mud flat area once the elevation in transitional pond habitat rises above the intertidal zone and eventually becomes

vegetated. So, creative solutions will be needed to find upland habitat adjacent to current intertidal areas for wetland habitats to migrate upslope.

Since small shorebirds exist on our site below the estimated carrying capacity, they are likely not limited by prey density in South Bay mud flats except during the month (April) with peak numbers of migratory shorebirds. Western Sandpipers make greater use of salt ponds during spring migration (Warnock & Takekawa 1996) than other times, so suitable mid-winter foraging opportunities in salt ponds could be crucial to maintain regional numbers of migrating small shorebirds if the intertidal mud flat habitat declines in the future.

This study has been an initial step toward addressing a number of key uncertainties regarding shorebird populations and mud flat habitat. Small shorebirds use a combination of habitats in the region, and estimates of relative contributions of foraging resources on mud flats will help managers to maintain existing populations as the South Bay changes with salt pond conversions.

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APPENDICES

Appendix 1. Sources of diet information used in Appendix 2.

Species		n	Location	Reference	Sample Type
Western Sandpiper	<i>Calidris mauri</i>	21	San Francisco Bay, CA	Takekawa <i>et al.</i> (unpublished)	esophogus, gizzard
		160	Playa Lakes Region, TX	Davis & Smith (2001)	esophogus
		30	Elkhorn Slough, CA	Ramer <i>et al.</i> (1991)	stomach
		-	Frasier River Delta, Canada	Sutherland <i>et al.</i> (2000)	exclosure
Dunlin	<i>Calidris alpina</i>	36	Langenwerder, Germany	Dierschke <i>et al.</i> (1999)	stomach
		244	Tagus Estuary, Portugal	Santos, Granadeiro, Palmeirim (2005)	pellets
		178, 93	Cadiz Bay, Spain	Masero (2003)	obervation, pellets
		17	Nesseby, Norway	Lifjeld (1984)	esophogus
		811, 179	Severn estuary, Europe	Worrall 1984	pellets, gizzards

Appendix 2. Summary of diet items and size class (mm) consumed by Western Sandpiper and Dunlin.

	Cumacea	Crustacea	Sepsid larvae	Dipteran larvae	<i>Bivalvia</i>	Polychaeta	All, excluding Polychaetes
Western Sandpiper	<1	<1- 6				>20	0-5
Dunlin		all	4-11	7-17	2-12	7-66	