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Site Selection by Migratory Shorebirds in Oregon Estuaries Over Broad and Fine Spatial Scales

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Site Selection by Migratory Shorebirds in Oregon Estuaries
Over Broad and Fine Spatial Scales

by

Aileen Kilpatrick Miller

A thesis submitted in partial fulfillment of the
requirements for the degree of

Master of Science
in
Environmental Science and Management

Thesis Committee:
Catherine de Rivera, Chair
Michael Murphy
Greg Ruiz

Portland State University
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Abstract

Many migratory shorebirds rely on estuaries as stop-over sites to refuel during migration, and the loss of stop-over sites is a primary threat to shorebird populations on the West Coast of the United States (e.g. *Calidris alpina pacifica*, *C. mauri*).

Conservation and research has focused on the largest of these sites; however, smaller estuaries also host thousands of migratory shorebirds. Furthermore, the reasons for site selection are largely unknown. Estuarine inter-tidal microhabitats are non-uniform and both abiotic and biotic factors may serve as predictors of whether an abundance of shorebirds will use a site. I investigated shorebird site selection on broad and fine scales within Oregon estuaries.

To identify factors that relate to shorebird abundance on large spatial scales, I compiled shorebird abundance data from estuaries throughout the Pacific Northwest as well as data on site quality factors. To investigate site selection on a finer scale I measured shorebird abundance, habitat characteristics, and food resources—invertebrates and a newly considered source, biofilm—within two Oregon estuaries during the fall migration period. Finally, I examined whether channels are preferentially used by foraging Calidrid shorebirds by conducting observations during the spring migration. I investigated whether channels may be superior foraging habitat possibly because prey are more abundant, are found at shallower depths, or because sediments are more penetrable (increasing the opportunity for shorebird probing) by

taking infauna cores and measuring force required to probe in the sediment at channel and open mudflat sites.

Among estuaries, shorebird densities in spring were best predicted by estuary size, as opposed to the amount of any one habitat. During fall migration, the amount of grassland in the surrounding watershed was also a good predictor, pointing to the probable importance of roost sites as well as feeding grounds. The amount of infauna also related to the density of shorebirds using a site. Within estuaries, shorebird distribution in the inter-tidal region was not generally predicted by prey abundance. Channels were used preferentially by shorebirds, and infauna abundance along channels was greater than in the surrounding mudflats. The more penetrable sediments of the channel also made it easier for shorebirds to probe and capture prey. Identification of these large-scale and fine-scale factors that influence site quality for migratory shorebirds will assist land and wildlife managers' efforts to protect these species.

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Shorebird abundance and distribution data that were the foundation of my analysis in Chapter 1 were provided by Lynne Stenzel and PRBO Conservation Science. I thank the staff at PRBO and the many volunteers who conducted these extensive shorebird surveys. I also appreciate access to environmental data collected by the US EPA Western Ecology Division including both previously published data and data supplied by Melanie Frazier and Walt Nelson. Early development of the project also benefitted from discussions with Janet Lamberson of the US EPA.

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Background and Objectives

Migration is a critical period for nearctic breeding birds. Migration itself is energy demanding, and energy needs are heightened by the need to prepare for or recover from the breeding season (Alerstam and Hedenström 1998). Most mortality occurs outside of the breeding season, therefore survival during migration is likely to be a strong driver of population dynamics (Colwell 2010).

Thousands of migratory shorebirds stop over to feed and refuel during migration on the mudflats in Oregon estuaries (Merrifield 1998, Page et al. 1999). Several of these species have populations of high conservation concern as identified by the U. S. Shorebird Conservation Plan (e.g., Western Sandpipers *Calidris mauri* and Dunlin *C. alpina pacifica*; Brown et al. 2000). Loss of migratory habitat is a primary threat to these shorebird populations (Brown et al. 2000). However, the proximate factors that migratory shorebirds use to accept or reject a particular site are largely unknown. More detailed information on the specific habitat requirements of shorebirds is needed so that land managers can make conservation and restoration decisions with greatest benefits to threatened shorebird populations.

The most abundant shorebirds that migrate through Oregon include Western Sandpipers, Dunlin, Least Sandpipers *Calidris minutilla*, Sanderlings *C. alba*, Dowitchers *Limnodromus* spp., Black-bellied Plovers *Pluvialis squatarola*, and Semipalmated Plovers *Charadrius semipalmatus* (Page et al. 1999). These species breed in the Arctic and

populations of each species migrate down the coast of Western North America, wintering from the U.S. through Central and South America (Wilson 1994, Warnock and Gill 1996). Migration is energetically demanding, and individuals must stop to feed and refuel by foraging in the mudflats of estuaries and wetlands. Radio-tracked Western Sandpipers and Dunlin were shown to make multiple stops along their migration path (Warnock and Bishop 1998, Warnock et al. 2004). Shorebirds forage primarily on benthic infauna in estuaries. For smaller shorebirds these include polychaete worms and amphipods (Wilson 1994, Warnock and Gill 1996). Western Sandpipers have also recently been found to forage on biofilms at some locations (Kuwaie et al. 2008).

Shorebirds make site selection decisions at multiple spatial scales from broad-scale choices of which estuary to stop in down to selecting a specific micro-habitat at the scale of a few meters. At all scales, shorebirds must select sites with adequate prey abundance and availability, but site quality may also relate to safety from predation, interactions with other birds (e.g., inter- or intra-specific competition), availability of roost sites, and absence of disturbance from humans. Shorebird density, as well as foraging success, has been shown to vary with factors such as the abundance of prey, the habitat or sediment type, the proximity to the tidal edge, and the presence or absence of predators (Colwell and Landrum 1993, Yates et al. 1993, Warnock and Takekawa 1995, Beauchamp and Ruxton 2008, Finn et al. 2008, Beauchamp 2009).

Research has focused on the largest of the West Coast stop-over sites; however, smaller estuaries also host thousands of migratory shorebirds (Drut and Buchanan 2000).

In Oregon estuaries, there has been minimal research on migratory shorebirds. Shorebird abundance and diversity were measured during peak migration periods at most major estuaries by PRBO Conservation Science from 1990-1995 (Page et al. 1999) to identify major stop-over sites for the U.S. Shorebird Conservation Plan. Counts have also been conducted in a few estuaries by wildlife management agencies (e.g., Merrifield 1998 and other unpublished reports). Recently Lamberson et al. (2011) conducted shorebird surveys in Yaquina Bay and related total shorebird abundance to season and habitat types. However, detailed studies of shorebirds, their prey, and specific habitat associations are generally lacking.

My over-arching goal in this research is to identify features that predict shorebird abundance in Oregon estuaries. Conservation and management cannot proceed without baseline information and I intend to elucidate patterns that can be used to guide conservation priorities on both estuary and coast-wide scales. In Chapter 1, I analyze shorebird site selection among estuaries in relation to site quality characteristics. In Chapter 2, I examine prey abundance and other habitat features related to site quality within estuaries, in particular looking at the numerical response of shorebirds to abundance of infauna and biofilm. In Chapter 3, I focus specifically on whether Calidrid shorebirds forage preferentially around channels and test alternative hypotheses for why this may be the case.

Chapter 1. Shorebird site quality and selection among Pacific Northwest Estuaries

INTRODUCTION

Neartic breeding shorebirds stop over at estuaries and other wetlands during their long north and southbound migrations. The number and duration of stops that a bird makes, and where it makes them, are complex decisions that integrate basic life-history trade-offs (generally, balancing energy gain with timing constraints and predation risk; Hedenström and Alerstam 1997) and demographics (e.g., differential migration based on age or sex), with current weather conditions and knowledge of future opportunities (Hedenström and Alerstam 1997, Alerstam and Hedenström 1998, Farmer and Wiens 1998, Houston 1998). The quality of sites used for stop-over is an important component of these decisions.

Given the energetic demands of migration and the need to prepare for or replenish after the breeding season, the availability of prey is expected to be one of the most important factors influencing site quality and selection (e.g. Evans 1976). Models of shorebird migration support the view that food acquisition rates determine migration strategies (Farmer and Wiens 1998). Threats from predation can also influence migration patterns (Lank et al. 2003) and so predation risk, including number of predators as well as safe roosting sites, should be considered an integral part of site quality. Absence of other threats, such as human activity, pollution, or other elements of development can also affect the quality of a stop-over site. Social potential to

interact with congeners could also be considered an element of stop-over site quality, but this depends on other birds' behavior as well as the capacity of the site to hold a large number of birds.

Shorebirds make selections about where to feed at very broad scales (selecting a particular estuary) and fine scales (micro-habitat selection). Site selection has been studied most often within large estuaries examining the use of different sites within large estuary complexes. Site selection at this scale has been most often associated with abundance of infauna (e.g. Goss-Custard 1970, Yates et al 1993, Botton et al. 1994, Finn et al. 2008) or habitat type (e.g. Ramer et al. 1991, Warnock and Takekawa 1995, Burger et al. 1996). Site selection among estuaries over larger scales is much less studied, but similar factors are expected to impact site selection (e.g. Evans 1976). Hill et al. (1993) compared shorebird communities and habitat characteristics of over 100 British estuaries and found that community composition differed among estuaries in relation to the size of the estuary, the latitude, sediment composition, tidal exchange and salinity, and nutrient concentrations.

The site quality of migratory shorebird stopover sites, and how this relates to site selection, is not well researched or understood for the west coast of North America (Warnock et al. 2004). The most used estuaries have been identified, in terms of the total number and diversity of shorebirds (Warnock and Bishop 1998, Page et al. 1999, Warnock et al. 2004). Habitat use has been investigated within a few of the Pacific Northwest (PNW) estuaries. In Yaquina Bay, Oregon, shorebirds use sandflats more

frequently than mudflat or seagrass habitats (Lamberson et al. 2011). Shorebirds in Willapa Bay, Washington were more abundant in mudflats than in patches of invasive *Spartina* (Patten and O'Casey 2007). In Humboldt Bay, California shorebird community composition depended on sediment size, the time in the tide cycle, and the presence of standing water or channels (Danufsky and Colwell 2003). Sediment size and prey density were also found to be important predictors of shorebird distribution on smaller spatial scales in Northern California (Colwell and Landrum 1993).

The largest estuaries of the Pacific Northwest, and more generally of the west coast, are known to support the greatest abundance and diversity of shorebird species (Page et al. 1999, Drut and Buchanan 2000). However, smaller estuaries of the PNW are also used by thousands of shorebirds during migrations (Drut and Buchanan 2000). It has not been established whether these estuaries differ in terms of quality. Large estuaries may be the most used simply because of their size; that is, they may attract the same density of birds as smaller estuaries, but hold more in total because they are simply large. Alternatively these estuaries may differ in quality. Larger estuaries may have different physical characteristics (e.g. hydrography, productivity) that alter the amount and availability of prey, or provide more opportunity for local movement to exploit patchy prey. Larger estuaries may also be important for social interactions for shorebirds, particularly if they stage for migration. If larger estuaries differ in any of these aspects of site quality, then the density, not just the total number, of shorebirds should increase with estuary size.

I examined relationships between shorebird density and estuary characteristics that I expected would relate to site selection in small and large estuaries of the PNW. Specifically, I expected that (1) shorebird abundance would increase with estuary size, but density would not; (2) shorebird density would increase with density of food resources (i.e., infauna or biofilm); (3) shorebird density would increase with the amount of intertidal and marsh habitat; and that (4) shorebird density would be positively related to the amount of potential roosting habitat in the surrounding watershed but negatively related to development.

METHODS

I compared shorebird abundance and density among estuaries in relation to measures of food supply and habitat characteristics using existing published and unpublished data (Table 1.1). I included all Oregon estuaries in my analysis. I also included Humboldt Bay, CA and Willapa Bay, WA as these are relatively large and well studied estuaries that lie just to the south and north of Oregon, respectively. I collectively refer to all of these as PNW estuaries.

Table 1.1. Data used in analysis and sources. X indicates that the particular data type was available for that estuary. San Francisco Bay was not included in analysis, but shorebird and infauna density were included as a comparison point. RE=river estuary.

Estuary	Birds ^a	Area ^b	Chl A ^b	Infauna ^c	Estuary habitats ^{d, e}	Land Use ^b
Willapa Bay	x	x		x	x	x
Columbia RE	x	x			x	x
Necanicum RE	x	x			x	x
Nehalem Bay	x	x			x	x
Tillamook Bay	x	x	x	x	x	x
Netarts Bay	x	x				x
Sand Lake	x	x				x
Nestucca Bay	x	x	x		x	x
Siletz Bay	x	x			x	x
Yaquina Bay	x	x	x		x	x
Alsea Bay	x	x	x		x	x
Siuslaw RE	x	x			x	x
Coos Bay	x	x	x		x	x
Coquille RE	x	x		x	x	x
Humboldt Bay	x	x		x	x	x
San Francisco Bay	x			x		

^a PRBO Conservation Science unpublished data; Colwell (1994); Buchanan and Everson (1997); Stenzel et al. (2002)

^b Lee and Brown (2009)

^c Ferraro and Cole (2007), Mathot et al. (2007), Ferraro and Cole (2012), this study (Ch 1)

^d Oregon Estuary Plan

^e Estuary habitats include bare intertidal flats, marsh, aquatic beds (eelgrass or macroalgae), shore, or subtidal

Data on shorebird abundance and composition were collected through a multi-group effort coordinated by PRBO Conservation Science from 1988-1995. The primary goal of that project was to provide data to the Western Hemisphere Shorebird Reserve Network to help determine the relative importance of sites based on the number and species of shorebirds that use them. Counts were conducted by teams of trained volunteer observers at each estuary during the peak of spring and fall migration. Teams coordinated so as not to double-count any birds. Counts at all estuaries were made

within one week for spring and within two weeks in fall. Only a single count was taken during each season of each year at a given site; therefore the reliability of the counts within a year could not be assessed. However, counts were repeated during each season once a year for 1-5 years. The Columbia River Estuary and Willapa Bay were counted aerially with ground counts used to confirm species composition. For more detailed description of methodology as well as a summary of species abundance and diversity from the west coast see Page et al. (1999). No previous analyses of these data had been conducted to test for relationships between site factors and the abundance or diversity of shorebirds. Unpublished data from Oregon estuaries were provided by PRBO Conservation Science, while data from Willapa Bay, Humboldt Bay, and San Francisco Bay had been previously published (Colwell 1994, Buchanan and Everson 1997, Stenzel et al. 2002).

The percent of estuary area that was intertidal flats, aquatic beds, marsh, shore or subtidal was determined using GIS layers digitized from the Oregon estuary plan book (Cortwright and Bailey 1987; GIS layers retrieved from www.inforain.org/mapsatwrok/oregonestuary/). Infauna data were available for a select number of estuaries from my research (see chapter 2) and from published literature (Table 1.1). Chlorophyll a measurements (median dry season water samples, used as an indicator of general estuary productivity), and total estuary area were collected by EPA as part of a study of PNW estuaries (Lee and Brown 2009). Land-use in the surrounding watershed was also calculated by the EPA (Lee and Brown 2009), based

on the National Land Cover Database (www.mrlc.gov). I grouped NLCD categories yielding percent developed land (areas with >25% impervious surface; NLCD classes 21-23), and percent agriculture and grassland per estuary (NLCD classes 71,81 & 82; grassland was generally >80% of this category). Data on land-use were available for both 1992 and 2001. I used the 2001 dataset for my analyses; although this earlier date overlaps more closely with the shorebird counts, improvements in measurements existed in the 2001 dataset. Correlation plots between the two years for each land class showed that estimates from these two years were closely correlated.

Six shorebird species were selected to test relationships between bird density and habitat or prey characteristics: Western Sandpipers *Calidris mauri*, Dunlin *C. alpina pacifica*, Least Sandpipers *C. minutilla*, Dowitchers *Limnodromus* spp., Black-bellied Plovers *Pluvialis squatarola*, and Semi-palmated Plovers *Charadrius semipalmatus*.

These represent the most abundant and ubiquitous species in PNW Estuaries.

Sanderlings *C. alba* were also abundant and ubiquitous but were not included in this analysis because they forage more often along the ocean front than in the interior of estuaries (Macwhirter et al. 2002). Visual examination of correlation plots showed that average abundance of a species was highly correlated to median abundance, so only mean abundances were used in all analysis. Density of shorebirds (mean number/km²) was calculated for total estuarine area and for each habitat type.

Shorebird density as well as habitat and food characteristics were log-transformed before analysis in order to fit normal distributions. Scatterplots were

examined in advance of statistical testing to determine whether quadratic terms should be tested as well as linear terms. Regression models were fit comparing each of the six shorebird species to total estuary area, estuary habitat types (as a proportion) and land-use in the surrounding watershed (also as a proportion) for spring and fall. AIC values were also calculated for model comparison. Information on infauna abundance was available for only a few estuaries; for some, infauna abundance was partitioned by habitat type. I therefore used a spearman rank correlation to evaluate correlations between shorebird density and infauna abundance. The alpha value was set at $\alpha = 0.05$. All analysis was performed in R (v. 2.8.1; R Development Core Team 2008).

RESULTS

Shorebird abundance and species composition

The density of shorebirds was highly variable among estuaries, and within estuaries (Table 1.2). Willapa Bay and Humboldt Bay held the highest densities in the spring followed by the Columbia River Estuary. Humboldt Bay and the Coquille River Estuary, which contains Bandon Marsh, had the highest densities in the fall followed by the Siletz River Estuary and Coos Bay.

Western Sandpipers were the most abundant shorebird in both spring and fall, followed by Dunlin, Least Sandpipers, and Marbled Godwits *Limosa fedoa* in the spring and Least Sandpipers, Marbled Godwits, and Sanderlings in fall (Figure 1.1). In winter, Dunlin were most abundant followed by Western Sandpipers, Least Sandpipers,

Marbled Godwits, Black-bellied Plovers and Sanderlings. Other species with relatively high densities in most seasons were Black-bellied Plovers, Semipalmated Plovers, Willets *Tringa semipalmata* and American Avocets *Recurvirostra americana*. Although Marbled Godwits, Willets and American Avocets were relatively common overall, they were limited in distribution to primarily Humboldt Bay and Willapa Bay.

Figure 1.1. Composition of shorebird communities in PNW estuaries, 1990-1995 (PRBO Conservation Science unpublished data; Page et al. 1999). Mean percent abundance of each species ($\pm$ SD).

Table 1.2. Density of shorebirds ($\pm$ SD) in each PNW estuary for spring and fall 1990-1995. Estuaries are listed from north to south. Sample size indicates the number of years counts were conducted for that season and estuary. RE=river estuary.

Estuary	Lat (N)	Area (km ²)	SPRING			FALL		
			n	Median	Mean $\pm$ SD	n	Median	Mean $\pm$ SD
Willapa Bay	46.37	389.7	3	279	272 $\pm$ 26	1	26	26 na
Columbia RE	46.26	411.5	5	137	145 $\pm$ 87	4	14	13 $\pm$ 8
Necanicum RE	46.01	1.6	3	21	44 $\pm$ 58	4	21	25 $\pm$ 30
Nehalem Bay	45.66	10.4	3	12	9 $\pm$ 6	2	59	59 $\pm$ 81
Tillamook Bay	45.51	37.0	3	11	35 $\pm$ 48	2	75	75 $\pm$ 38
Netarts Bay	45.40	10.4	3	11	10 $\pm$ 9	3	6	157 $\pm$ 264
Sand Lake	45.28	4.3	2	10	10 $\pm$ 4	5	7	31 $\pm$ 40
Nestucca Bay	45.18	4.7	4	56	53 $\pm$ 13	4	68	62 $\pm$ 37
Siletz Bay	44.90	7.5	5	5	7 $\pm$ 6	6	112	125 $\pm$ 60
Yaquina Bay	44.62	19.0	5	58	68 $\pm$ 18	6	39	33 $\pm$ 24
Alsea Bay	44.42	12.5	4	23	25 $\pm$ 21	5	48	61 $\pm$ 39
Siuslaw RE	44.02	15.6	5	34	72 $\pm$ 65	5	26	31 $\pm$ 15
Coos Bay	43.43	54.2	5	43	43 $\pm$ 26	6	101	85 $\pm$ 50
Coquille RE	43.12	5.1	5	63	91 $\pm$ 58	6	281	485 $\pm$ 503
Humboldt Bay	40.75	71.4	3	289	581 $\pm$ 511	3	379	385 $\pm$ 122

Shorebird density in relation to estuary size, estuary habitats, and watershed land-use

Shorebird density in spring was best explained by the total size of the estuary when examining all PNW estuaries (Table 1.3). Shorebird density increased with estuary size for all shorebirds combined, as well as for Western Sandpipers, Dunlin, and Dowitchers. There was a marginally insignificant relationship between estuary size and density of Black-bellied Plovers. These positive relationships between shorebird density and estuary size in spring indicate that large estuaries attract somewhat more birds per unit of area than smaller estuaries. Relationships between shorebird density and estuary area could not be detected when the largest two estuaries were excluded (when looking at Oregon estuaries alone).

Table 1.3. Shorebird abundance in relation to total estuary area, estuary habitat composition (%Flats, %Marsh, or %Flats+%Marsh), or watershed land use (%Development, %Grassland & Agriculture, or %Development + %Grassland & Agriculture). Linear regression model results. Comparisons were made for all PNW estuaries and for only Oregon estuaries since habitat data was not available for either Willapa Bay or Humboldt Bay. Model in bold has the lowest AIC value.

		Spring						Fall									
		Oregon Estuaries			PNW Estuaries			Oregon Estuaries			PNW Estuaries						
		F	r ²	p	AIC	F	r ²	p	AIC	F	r ²	p	AIC	F	r ²	p	AIC
All Shorebirds	Density ~ Estuary/Area	2.2	0.09	0.17	38.1	7.3	0.31	0.02	47.5	1.2	0.02	0.30	38.1	0.6	-0.03	0.44	46.76
	Density ~ %Flats	1.1	0.00	0.33	39.3					0.1	-0.09	0.82	39.4				
	Density ~ %Marsh	0.4	-0.05	0.52	39.9					0.1	-0.08	0.75	39.3				
	Density ~ %Flats+%Marsh	1.3	0.05	0.31	39.4					0.1	-0.19	0.95	41.3				
	Density ~ %Devel	1.0	0.00	0.34	39.3	0.2	-0.06	0.67	53.9	3.7	0.19	0.08	35.7	1.4	0.03	0.26	45.97
	Density ~ %GrassAg	2.7	0.12	0.13	37.6	6.4	0.28	0.03	48.1	0.4	-0.06	0.57	39.0	4.1	0.18	0.06	43.36
	Density ~ %Devel+%GrassAg	1.7	0.11	0.23	38.6	3.0	0.22	0.09	50.1	2.2	0.17	0.16	36.7	3.9	0.29	0.05	42.02
Western Sandpiper	Density ~ Estuary/Area	2.4	-0.04	0.45	42.5	7.0	0.30	0.02	52.1	0.0	-0.09	0.90	47.5	0.0	-0.08	0.90	54.5
	Density ~ %Flats	0.5	-0.04	0.47	46.5					3.4	0.16	0.09	44.0				
	Density ~ %Marsh	2.1	0.09	0.17	44.8					0.7	-0.03	0.43	46.7				
	Density ~ %Flats+%Marsh	2.6	0.21	0.13	43.7					1.6	0.08	0.26	46.0				
	Density ~ %Devel	1.3	0.02	0.28	45.7	0.4	-0.04	0.53	58.1	5.3	0.26	0.04	42.4	3.3	0.14	0.09	51.2
	Density ~ %GrassAg	0.7	-0.03	0.42	46.3	3.1	0.13	0.10	55.3	5.0	0.25	0.05	42.7	9.1	0.37	0.01	46.6
	Density ~ %Devel+%GrassAg	0.9	-0.02	0.44	47.0	1.6	0.07	0.25	57.1	11.9	0.64	0.00	33.7	15.3	0.67	<0.001	37.5
Dunlin	Density ~ Estuary/Area	7.3	0.34	0.02	40.9	15.1	0.50	0.00	51.1	na				na			
	Density ~ %Flats	0.1	-0.08	0.76	47.3												
	Density ~ %Marsh	4.5	0.22	0.06	43.0												
	Density ~ %Flats+%Marsh	3.5	0.30	0.07	42.5												
	Density ~ %Devel	1.7	0.05	0.22	45.6	0.3	-0.05	0.57	62.3								
	Density ~ %GrassAg	3.8	0.19	0.08	43.6	6.9	0.30	0.02	56.3								
	Density ~ %Devel+%GrassAg	2.8	0.23	0.11	43.8	3.3	0.24	0.07	58.2								
Least Sandpiper	Density ~ Estuary/Area	0.1	-0.08	0.76	46.2	0.0	-0.07	0.86	55.2	0.0	-0.09	0.97	47.5	0.0	-0.07	0.87	54.5
	Density ~ %Flats	1.9	0.07	0.20	44.3					0.8	-0.02	0.40	46.9				
	Density ~ %Marsh	2.3	0.10	0.16	43.9					0.7	-0.03	0.44	47.1				
	Density ~ %Flats+%Marsh	1.5	0.07	0.28	45.0					0.5	-0.10	0.64	48.6				
	Density ~ %Devel	1.8	0.06	0.20	44.4	0.6	-0.03	0.44	54.5	5.6	0.28	0.04	42.4	3.0	0.12	0.11	51.4
	Density ~ %GrassAg	1.5	0.04	0.25	44.7	6.6	0.29	0.02	49.1	3.9	0.20	0.07	43.8	6.4	0.28	0.03	48.5
	Density ~ %Devel+%GrassAg	2.0	0.15	0.18	43.9	4.6	0.34	0.03	48.7	10.1	0.60	0.00	35.5	9.2	0.54	0.00	42.5

		Spring						Fall					
		Oregon Estuaries			PNW Estuaries			Oregon Estuaries			PNW Estuaries		
		F	r ²	p	AIC	F	r ²	p	AIC	F	r ²	p	AIC
Dowitcher Sp.	Density ~ EstuaryArea	0.1	-0.08	0.72	34.9	2.3	0.08	0.15	48.1	0.0	-0.09	0.91	33.3
	Density ~ %Flats	2.6	0.11	0.14	32.4					1.6	0.05	0.23	31.6
	Density ~ %Marsh	0.1	-0.10	0.83	35.0					0.0	-0.09	0.99	33.3
	Density ~ %Flats+%Marsh	1.3	0.05	0.32	34.1					0.9	-0.02	0.42	33.1
	Density ~ %Devel	1.4	0.04	0.26	33.5	1.8	0.06	0.20	48.5	2.5	0.11	0.14	30.7
	Density ~ %GrassAg	0.3	-0.06	0.59	34.7	1.4	0.02	0.27	49.0	9.0	0.40	0.01	25.6
	Density ~ %Devel+%GrassAg	0.9	-0.01	0.43	34.9	2.1	0.13	0.17	48.1	11.6	0.64	0.002	19.7
Black-bellied Plover	Density ~ EstuaryArea	0.5	-0.04	0.51	6.7	4.3	0.19	0.06	16.8	0.0	-0.09	0.93	32.2
	Density ~ %Flats	3.4	0.17	0.09	3.7					1.3	0.03	0.27	30.8
	Density ~ %Marsh	0.0	-0.09	0.96	7.2					0.1	-0.10	0.73	32.1
	Density ~ %Flats+%Marsh	2.1	0.15	0.17	4.7					0.6	-0.08	0.56	32.7
	Density ~ %Devel	1.0	0.00	0.35	6.1	0.7	-0.02	0.41	20.3	2.2	0.09	0.166	29.9
	Density ~ %GrassAg	1.2	0.01	0.30	5.9	6.2	0.27	0.03	15.3	2.8	0.13	0.12	29.3
	Density ~ %Devel+%GrassAg	1.2	0.03	0.34	6.4	4.4	0.33	0.04	14.9	3.4	0.29	0.07	27.4
Semipalmated Plover	Density ~ EstuaryArea	8.4	-0.07	0.66	8.4	1.1	0.01	0.31	21.5	2.9	0.14	0.12	24.4
	Density ~ %Flats	1.7	0.05	0.22	6.8					0.2	-0.09	0.69	27.3
	Density ~ %Marsh	0.0	-0.09	0.91	8.6					0.2	-0.07	0.65	27.2
	Density ~ %Flats+%Marsh	1.1	0.01	0.38	8.2					0.1	-0.17	0.88	29.2
	Density ~ %Devel	0.9	-0.01	0.37	7.7	0.1	-0.07	0.72	22.6	0.1	-0.08	0.77	27.4
	Density ~ %GrassAg	0.6	-0.03	0.46	8.0	11.7	0.43	0.01	13.1	2.2	0.17	0.09	25.2
	Density ~ %Devel+%GrassAg	0.8	-0.04	0.48	8.7	13.8	0.44	0.01	13.8	1.0	0.00	0.40	27.1
										0.3	-0.06	0.62	41.3
										0.8	-0.01	0.38	40.7
										12.6	0.45	0.004	31.4
										9.8	0.56	0.003	29.1
										2.3	0.08	0.16	28.7
										0.4	-0.05	0.55	30.7
										4.5	0.20	0.05	26.7
										2.2	0.14	0.16	28.5

Patterns in the fall differed, and some of the highest densities were observed in some of the smaller estuaries (Table 1.2). Shorebird density did not show a significant relationship to estuary size for any species (Table 1.3). Overall, shorebird density was thus independent of estuary size in the fall.

Total shorebird abundance was, as expected, highly correlated with total estuary size in spring ($F_{1,13} = 75.9$, $r^2 = 0.84$, $p < 0.001$) and fall ($F_{1,13} = 25.6$, $r^2 = 0.64$, $p < 0.001$), although the fit of the model was stronger in spring.

Estuary habitats were not good predictors of shorebird density in either season (Table 1.3). The proportion of flats or marsh provided the best model for a few species in the spring; however, in these cases none of the models for spring were statistically significant. Estuary habitats were not the best model for any species in the fall.

Land uses in the surrounding watershed were better predictors of shorebird abundance than habitats within the estuaries (Table 1.3). In the fall, when including all PNW estuaries, shorebird density was best described by models including both %Development and %Grassland/Agriculture. This was true for all species except Semipalmated Plovers, which were better described by the %Grassland/Agriculture alone. Development was negatively related to shorebird density while Grassland/Agriculture was positively related to shorebird density. Models of %Grassland/Agriculture alone also were significantly related to shorebird density in the fall for each individual species.

In the spring, total area was a better predictor than land use or habitat type for the two most abundant species, Western Sandpiper and Dunlin. However, for the less abundant but ubiquitous species - Least Sandpiper, Dowitcher, Black-bellied Plover and Semipalmated Plover - land uses were generally the better predictors of densities (Table 1.3).

Shorebird density in relation to food availability

Infauna abundance was relatively higher in San Francisco Bay, Humboldt Bay and Bandon Marsh (part of the Coquille River Estuary) than in Tillamook Bay or Willapa Bay (Table 1.4). Shorebird density varied with season but was low in Tillamook for spring and fall and low in Willapa in the fall. Shorebird density was significantly related to infauna abundance in the fall based on rank order correlation ($r = 0.9$, $p = 0.05$), but not in the spring ($r = -0.2$, $p > 0.05$). This suggests that food density may be most important for determining distribution in the fall, but more data on infauna would be helpful to make this assessment more rigorous.

Table 1.4. Infauna and shorebird density for PNW Estuaries. Infauna is calculated as density per 0.01m². Cores were of differing depths, but ~90% of infauna live in the top 3 cm so this difference should introduce only a small bias. Actual core depth given with source.

Estuary	Infauna/ 0.01m ²	Shorebird Density			
		Spring	SD	Fall	SD
Willapa Bay	12-308 ^a	272	± 26	26	na
Tillamook Bay	17-544 ^b , 442 ^c	35	± 48	75	± 38
Bandon Marsh (Coquille RE)	1520 ^c	91	± 58	485	± 503
Humboldt Bay	722 ^d	581	± 511	385	± 122
San Francisco Bay	1520 ^d	174	na	89	na

^a Ferraro and Cole (2007), core depth=5cm

^b Ferraro and Cole (2012), core depth=5cm

^c This study (Ch.1), core depth=3cm

^d Mathot et al. (2007), core depth=4cm

DISCUSSION

In the fall, small and large estuaries were equally likely to support high densities of shorebirds. Hence, small estuaries may be equally valuable to migratory shorebirds on a unit area basis during this time period. The positive correlation between shorebird density and estuary area in spring for the most abundant species, Western Sandpiper and Dunlin, suggests that large estuaries confer some advantages during this season. These two species are known to gather in large flocks in the spring that may serve as protection from predation or may be corollary to synchronization of breeding (O'Reilly and Wingfield 199). Migration theory predicts that shorebirds are trading off time constraints with energetic demands (Hedenström and Ålerstam 1997). Timing is a greater constraint in spring, when shorebirds must arrive in time for the narrow arctic breeding season, whereas in fall shorebirds likely prioritize energy gain. Flock size may

supersede other aspects of site quality in determining where shorebirds spend time during their northbound migration, whereas in the fall site quality, including infauna abundance and roosting habitat, may be more important. Alternatively, the importance of large estuaries may not have been detected in the fall data because the migration is more dispersed. The surveys were conducted only on a single day per year and thus reflect a daily usage rather than total seasonal usage.

For most species, neither of the habitat variables that I used performed better than total estuary area. Because shorebirds generally forage on intertidal flats, I expected that the proportion of intertidal flats would be a strong predictor of shorebird density. Surprisingly, this was not the case for any of the six species.

Although shorebirds typically feed in open intertidal flats, they can also feed in marshes and grasslands during high tides (Rogers 2003), so presence of marsh may allow these birds to feed throughout the day rather than being limited to low tide. However, shorebird density was not correlated with the proportion of marsh habitat within Oregon estuaries. Nonetheless, shorebird density increased with the amount of Grassland/Agriculture in the surrounding watershed. Shorebirds are known to roost, as well as to feed, in grasslands or agricultural fields. Given the limited extent of marsh in Oregon estuaries relative to other regions, usable roost habitat in the surrounding watershed may be of particular importance.

Development was low in all of the watersheds examined (<15%) but still contributed to the best predictor models for most of the species. In many PNW coastal

watersheds, high intensity development is found immediately adjacent to estuaries while interior portions of the watersheds are forested or have lower intensity development. Development on a watershed level could affect shorebirds through runoff that includes increased sediment, nutrient or pollutant inputs that alter estuarine ecosystems. Development immediately adjacent to estuaries is likely to have an even stronger impact on migratory birds. Development is effectively habitat loss for shorebirds as it often replaces marsh habitat. Human activity may also cause shorebirds to avoid an area or forage less efficiently (Botto et al. 2008). Trulio and Sokale (2008) found that trails with high use did not impact nearby waterbirds; however, higher intensity development may have a stronger influence, as might people going into an estuary (e.g. clamming) as compared to staying on a trail on the outskirts. Furthermore, development and human activity may increase the presence of other animals that could deter shorebirds (pet dogs, gulls) or provide structures such as power poles that can be used by predators. Future research into the impact of development could consider development more locally and focus on specific ways in which development may negatively impact migratory shorebirds.

My analyses showed that food density may also influence shorebird site selection. Infauna were more abundant in the two southernmost estuaries I included in this analysis, Coquille River Estuary/Bandon Marsh and Humboldt Bay. These sites also held relatively high densities of shorebirds in the fall, whereas in Willapa and Tillamook Bays, both shorebirds and infauna were found at relatively low densities in the fall. In

spring, however, Willapa Bay had very high densities of shorebirds. Although the sample sizes are too small for rigorous analysis or for comparison with other predictor variables, the data available suggest infauna abundance may be an important predictor of shorebird density in the fall.

Shorebird counts were conducted only once per year in each season. Shorebirds arrive in PNW estuaries in waves and therefore there may be a great deal of day to day variability in shorebird abundance (see Ch. 2). I used average abundance over several years of counts (>3 for most estuaries) which should reduce some of the variability, nonetheless there may have been bias introduced to this analysis if counts happened to occur on days of unusually high or low shorebird abundance.

There are a number of aspects of site quality that I was not able to investigate including predation risk, the availability of biofilm, more detailed aspects of infauna abundance and availability such as size of the prey, other species that interact with sandpipers such as gulls, and water quality measures and pollutants. To more thoroughly address how site qualities relate to shorebird site selection, these potential influences should be evaluated.

Site selection by shorebirds is likely to depend on several factors external to an estuary's qualities. Shorebirds may weigh the choice to stop versus future stop-over opportunities, and in the spring they may weigh the choice to stay at a high quality site versus the push to move up to their breeding grounds. Social and demographic patterns are further involved because of differential migration. Male Western Sandpipers, which

have shorter bills than females, are known to winter further north than females because infauna are not as deep in the sediment (Nebel et al. 2002, Mathot et al. 2007); therefore physiological differences among birds may influence site choice. Similarly, weather fronts may influence whether or not shorebirds use a site in a given year. Migrating shorebirds use atmospheric fronts and wind to help assist their migration; flying with wind in their favor can dramatically reduce energetic costs (Alerstam and Hedenström 1998). Storms or other unusual wind patterns can blow birds off their migratory course. Shorebirds might stay at lower quality sites or skip higher quality sites to select the best weather fronts for migration. The interaction of all these external factors on site selection can obscure patterns of how estuary quality relates to shorebird site selection. Nonetheless, I identified several aspects of site quality - surrounding land use and prey density - that appear to influence shorebird site selection, particularly in the fall.

Conclusions

The density of migratory shorebirds in PNW estuaries during spring migration was positively associated with the size of an estuary, but in the fall aspects of site quality appeared to be more important. Hence, estuary size should be one of the factors, but not the only factor, used to prioritize estuaries for management. Landscape composition relating to available roost habitat was apparently important in site selection in both seasons but especially in fall. Food resources also appeared to be important factors

influencing site selection although data were too limited to make this a robust conclusion. Given the importance of stop-over grounds for successful migration and population viability of shorebirds, preservation and restoration of key estuaries and marshes is of utmost importance. In restoration or protection of shorebird habitat, managers should take into account factors that can improve site quality for migratory shorebirds.

Chapter 2. Shorebird numerical responses to prey distribution within Oregon estuaries

INTRODUCTION

Migratory shorebirds depend on stop-over sites along their migration routes to rest and replenish energy reserves. Shorebirds are known to forage extensively on benthic infauna (reviewed in Evans and Dugan 1984), and recently they have been shown to also feed on biofilm (Kuwaie et al. 2008). Abundance of these food resources is likely to be critical to short and long term survival given the energetic demands of migration as well as the need to prepare for or recover from breeding (Evans 1976, Piersma 2002). Shorebirds are therefore predicted to show numerical and functional responses to changes in their food resources (Holling 1959).

Positive numerical responses to their infauna prey have been observed among regions within estuaries (Goss-Custard 1970, Yates et al. 1993, Finn et al. 2008, Rose and Nol 2010). However, this relationship has been less apparent at finer scales (tens of meters; e.g. Goss-Custard 1970, Evans and Dugan 1984, but see Colwell and Landrum 1993 for an exception). The relationship between shorebird and prey density shows high variability; counterexamples of a failure of shorebirds to use areas with high prey density are not uncommon (Goss-Custard 1970, Botton et al. 1994). In addition to responding numerically to prey, predators may change their behaviors; a pattern known as a functional response (Holling 1959). Functional responses of shorebird feeding rates

to prey density have been best described as Type II functional responses (Goss-Custard et al. 1996, Beauchamp 2009). Similarly numeric responses may be non-linear.

Availability of prey may be as important to foraging shorebirds as abundance of prey. Theory predicts that predators will make a trade-off between prey abundance and the costs of foraging in order to optimize their energy intake (Stephens and Krebs 1986). Microhabitat characteristics can affect accessibility of prey and therefore the energy required for capture. Shorebirds have been shown experimentally to capture more prey in finer sediments, suggesting that larger sediments interfere with detection or capture (Myers et al. 1980, Quammen 1982). Additionally, in wetter sediments shorebirds probe more deeply in the sand (Myers et al. 1980, Kuwae et al. 2010).

In Oregon estuaries, relationships between shorebirds and their prey have not been investigated on any scale and therefore the type and scale of numerical response is unknown. Important food resources have also never been identified locally. Relationships between shorebirds and their food resources in Oregon may differ from other regions because most estuaries are small and attract relatively small numbers of shorebirds, and because these are primarily stop-over sites as opposed to wintering sites. Furthermore, Pacific Northwest estuaries differ abiotically from many of the regions where investigations have occurred in that they have high freshwater input in winter, intense coastal upwelling in the spring and summer (Lee and Brown 2009), and less contiguous marsh habitat. These differences may influence either the benthic infauna community or the abundance of biofilm.

I investigated the relationship between shorebird abundance and food abundance within two Oregon estuaries in order to establish baseline information about the types of food resources available and the relationship to shorebird abundance. I also examined habitat features that may co-vary with prey abundance or may independently affect prey availability. I predicted that (1) shorebirds would forage non-randomly in estuaries because they are selecting for prey or micro-habitats, (2) shorebirds would forage more often in areas with moderate to high density infauna, and (3) shorebirds would forage more often in areas with moderate to high density of biofilm. In addition, I investigated habitat types that would be likely covariates of food resource abundance.

By looking at how shorebirds distribute themselves within estuaries in Oregon, I hope to determine what habitat and prey features they are targeting. Patterns within estuaries may then serve as predictors about larger scale site selection. Furthermore, identifying needed habitat features and prey will provide useful information to wildlife managers in Oregon who are seeking ways to improve the quality as well as quantity of foraging grounds for at-risk migratory shorebird populations.

METHODS

In order to investigate whether habitat features or food abundance influenced shorebird distribution within estuaries, I sampled line transects in one large and one small estuary on the Oregon coast. Birds were surveyed along these transects during the fall migration period, and habitat features and food abundance were quantified.

Figure 2.1. Maps of Tillamook Bay, OR and Bandon Marsh, OR. Lines in red represent survey transects.

Sites

Shorebird studies were conducted at Bandon Marsh National Wildlife Refuge near Bandon, OR and Tillamook Bay near Tillamook, OR. Bandon Marsh is part of the larger Coquille River Estuary, a river-dominated drowned river mouth estuary (43.123° N; Lee

and Brown 2009). The intertidal zone ($\sim 0.5 \text{ km}^2$) consists of sand and mudflats within a matrix of low marsh that is located 1.75 km from the mouth of the larger estuary.

Tillamook Bay is a tide-dominated drowned river mouth estuary (45.513° N ; Lee et al. 2009). It is one of the largest Oregon estuaries. The intertidal zones (25.6 km^2) include flats ranging from coarse sand to very fine silts. Some flats are bare while others include seagrass and macro-algae beds.

Shorebird, prey, and habitat surveys were conducted from line transects (Figure 2.1). In Bandon Marsh, four line transects (range = 300-700 m in length) had been previously established by refuge staff and roughly followed the edge of the major mudflats. All mudflats had fairly similar elevation based on their flooding within ~ 30 minutes as the tide came in. In Tillamook, survey transects were randomly located within four regions of the bay with good access points (northeast, NE ($n = 1$ transect; 200 m in length); southeast, SE ($n = 2$; 200-400 m); southwest, SW ($n = 2$; 200-400 m); and west, W ($n = 3$; 200-400 m)). All eight Tillamook transects paralleled the shoreline. In areas with relatively stable sediment, both the location along the shoreline and distance from shore were randomly selected ($n = 5$ transects); in areas with unstable sediment the location along the shoreline was randomly selected but the transect line was placed along the shore ($n = 3$ transects). In Tillamook Bay, the survey area boundary for each transect was separated by $>100 \text{ m}$ from neighboring survey area boundaries. Based on inundation time, the SW region was relatively high elevation while the NE region was low and the SW and W region were intermediate. While tidal

elevation was variable among regions, it tended to be similar within regions based on the observation that when the tide came in it would cover a whole region very quickly.

Shorebird surveys

Shorebirds were surveyed every 7-10 days during the fall migration period from the end of July to mid-September 2011. All surveys were started before noon. Six surveys were completed in Tillamook and nine in Bandon. On each survey date, I or another trained observer (1 observer per estuary) walked all of the transects at a given site during one low tide period. For all shorebirds within 200 m of the transect line, the size of the flock, species, and behavior (foraging, resting, flying) were recorded. We used 10x power binoculars to identify and count birds and a laser range-finder to verify distances. The specific location of the bird/flock was recorded (based on distance from and location along the transect) and later mapped. Additionally, the general habitat type of the bird or flock's location was recorded (mudflat, sandflat, seagrass bed, macroalgal bed, low marsh or channel bed), including whether the bird was adjacent to the tidal edge. We surveyed ahead with sufficient frequency to note locations of birds before they could be disturbed. Given that a smaller proportion of Tillamook estuary was covered by these transects, and that transects were relatively close to the shoreline, I also scanned larger expanses of intertidal area with a spotting scope to qualitatively determine whether the density of shorebirds along each transect was similar to that in the greater area of the bay. In all cases, the density was similarly low in the surrounding flats.

Food resources and habitat measures

Infauna and biofilm were sampled systematically along all survey transects midway through fall migration (Tillamook on 14 August 2011, Bandon on 18 August 2011). A 1m² quadrat was placed every 100m along each transect at a random distance 0-100 m from the transect. Infauna and biofilm samples were collected from within the quadrat. The percent cover of seagrasses and macro-algae was estimated visually and the approximate average size of sediment (coarse sand, fine sand, sand/mud, mud) was estimated visually when sieved on a 500 µm screen.

For infauna, three 4 cm diameter cores were collected haphazardly within each quadrat. Each core was split by depth: 0-3cm depth and 3-6cm depth samples. Three centimeters corresponds to the maximum bill length of western sandpipers, while 6 cm corresponds to the depth of larger billed shorebirds found in Oregon estuaries (e.g., *Dowitcher spp*). The upper sections of the three cores were combined as were the three lower sections. Samples were sieved on a 500 µm screen, and then preserved in 10% buffered formalin. After 1-10 days, samples were transferred to 70% ethanol. Infauna were sorted using a dissecting scope, identified to broad taxonomic groups, and enumerated. Because less than 10% of organisms were in the lower half of the samples and the majority of the birds observed had bills <3 cm, the analyses below were from the upper three cm of the cores only.

Biofilm abundance was estimated by measuring Chlorophyll a and ash-free dry mass of the surface sediment. The top 2mm of sediment were collected by placing an

inverted petri dish haphazardly within the quadrat (any macroflora were avoided). A flat spatula was inserted underneath and the contents were rinsed into a sample bottle. This was repeated three times within the quadrat and all of these sub-samples were combined into one sample bottle. Sample bottles were promptly wrapped in tinfoil or placed in an opaque bag to avoid light exposure. Samples were placed on ice and then frozen upon return to the lab. Sub-samples were later taken for biofilm estimates. Chlorophyll a was measured with a spectrometer and ash-free dry mass was measured using loss-on-ignition methods; both measurements followed standard procedures (APHA 1999).

Data Analysis and Statistics

In some cases, Western or Least sandpipers could not be distinguished so they were grouped for analysis (hereafter referred to as "Small Sandpipers"). Because transects differed in length between the estuaries, all data except for the raw number shorebirds/survey and species composition data are presented as densities.

The study was designed to compare shorebird abundance to prey and habitat features on a relatively broad within-estuary scale by comparing regions of the bay with different habitat types to one another, and also to look at finer scale associations by binning shorebird observations into 100 m x 100 m units. Because of the extremely low number of shorebird observations in Tillamook Bay, this finer scale analysis was not possible. Instead, comparisons were made using regions of the bay or individual

transects as the spatial unit. Groups of birds seen flying low to the ground (indicating very local travel) were included in analysis of associations with food resources for Tillamook only, because of the low sample size. I consider this valid because data were grouped by region but not finer spatial scales. Only shorebirds on the ground were included for Bandon.

Shorebird observations from Bandon Marsh were binned into 100 m² bins for subsequent analysis that related shorebird density to prey measures. Measurements of food abundance were made within 100 m on one side of the transect whereas shorebird observations were made to 200 m on either side of the transect. We used only the shorebird observations within the 100 m band for shorebird vs food comparisons. Binned shorebird observations, as well as prey measurements, were all tested for autocorrelation using an autocorrelation function in order to ensure independence of data points prior to proceeding with regression analyses.

Differences in food abundance between regions of the estuary were tested using one-way ANOVAs. Differences in infaunal community composition among regions of the estuary were evaluated with an NMDS ordination plot and Analysis of Similarity (ANOSIM). The abundance of birds in relation to food resources was modeled using negative binomial GLMs. The negative binomial was suitable because shorebird abundance is count data and because it was highly over-dispersed (many zero values and a few large values; the variance exceeded the mean). All analyses were conducted with program R using library MASS for GLMs and library vegan for NMDS.

RESULTS

Overall shorebird abundance and composition

Observations during the six surveys in Tillamook ranged from 7- 472 birds in 1-6 groups per survey (Figure 2.2a-b). Observations during the nine Bandon surveys ranged from 69-1,524 birds in 5-28 groups (Figure 2.2c-d). At Tillamook, 32% ($\pm 41\%$ SD) of all shorebirds were foraging; in Bandon 35% ($\pm 32\%$ SD) were foraging. The majority of the remaining birds were seen flying, or their behavior could not be determined.

Most shorebirds observed were Western or Least Sandpipers (Figure 2.2; Bandon: 90.3%, Tillamook: 99.6%). Not all observations of small Sandpipers were made to species level, but of those that were, 75% in Bandon and 100% in Tillamook were Western Sandpipers; the remaining were Least Sandpipers. Semipalmated Plovers were also observed regularly in Bandon (7.7%). Less than 2% of all observations were of other species including Black-bellied Plovers, Black Turnstones, Greater Yellowlegs, Dunlin, Dowitcher sp., and Red-necked Phalarope.

Figure 2.2. Number of shorebirds and number of flocks by species seen per survey in Tillamook Bay and Bandon Marsh, OR.

A.

B.

C.

D.

Patterns within Tillamook

The four regions of Tillamook Bay each had qualitatively distinct sediment and habitat characteristics. The NE region primarily had silty sediment and had an average of 15% cover of macroalgae. The SE region was dominated by large sand/cobble sediment and 20% cover of *Zostera marina* (with somewhat finer sediment in the seagrass beds). The SW region had extremely fine silt sediments. There was 50% cover of seagrasses, primarily *Zostera japonica*. The W region had sandy sediment, 12% cover of macroalgae, and 9% cover of *Z. marina* based on the sampled quadrats.

Relatively small numbers of shorebirds were seen in Tillamook, and most of those seen were flying. There were significant differences among regions of the bay in both the number of flocks (Kruskal-Wallis $\chi^2 = 12.67$, $df = 3$, $p = 0.005$) and the total number of sandpipers (Kruskal-Wallis $\chi^2 = 12.63$, $df = 3$, $p = 0.006$). Sandpipers were seen most frequently in the W region (Sandflats) and less frequently in the SE region (Cobbleflats; Figure 2.3). No shorebirds were observed in the NE or SW regions, the areas characterized by finer sediments.

Figure 2.3. Density of shorebird (A) groups and (B) individuals by region in Tillamook Bay, OR. Boxplots illustrate the median line, first and third quartile boxes and min and max value hinges.

A.

B.

Figure 2.4. Infauna abundance and biofilm indicators, ash-free dry mass (AFDM) and chlorophyll a (CHLA), by region in Tillamook Bay, OR. Boxplots illustrate the median line, first and third quartile boxes and min and max value hinges with outliers excluded and shown as circles.

A.

B.

C.

Infauna communities also varied with region, but abundance was not greatest in the regions with the most sandpipers (Figure 2.4). Total abundance did not differ significantly among regions (ANOVA: $F_{3,23} = 0.73$, $p = 0.55$). Certain taxonomic groups were higher in particular regions, but variability tended to be high (Table 2.1). Ordination indicated that the community of infauna in the West region was distinct from that in the other regions (Figure 2.5; stress = .18; ANOSIM W-NE: $R = 0.52$, $p = 0.003$; ANOSIM W-SE: $R = 0.37$, $p = 0.003$; ANOSIM W-SW: $R = 0.32$, $p = 0.2$). The west region had more bivalves and tanaids and fewer oligochaetes and cumaceans than the other three regions in Tillamook Bay.

Table 2.1. Infauna abundance (mean $\pm$ SD) in the four regions of Tillamook Bay, OR, from three 4 cm diameter x 3 cm deep cores. "Unknown" includes species that could not be identified either because they were rare or because they had been damaged.

Region:	NE		SE		SW		W	
<i>n</i>	3		5		5		8	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Bivalves	1	1	1	2	3	5	6	9
Polychaetes	1	1	3	3	73	54	11	8
Oligochaetes	151	147	66	90	51	47	24	61
Tanaids	0	0	0	0	2	5	28	41
Corophid amphipods	6	8	23	44	40	47	17	23
Cumaceans	16	6	11	20	37	40	4	10
Copepods	0	1	19	33	28	44	13	27
Unknown	11	5	5	4	41	85	9	10
TOTAL	147	161	128	109	273	238	111	69

Figure 2.5. Ordination of infauna samples based on community composition, labeled by region, for Tillamook Bay, OR.

Biofilm indicators differed by region. Ash-free Dry Mass was significantly lower in the West region, where the most shorebirds were seen, than in other regions (Figure 2.4b; ANOVA: $F_{3,22} = 26.6$, $p < 0.001$; Tukey-Kramer post-hoc tests for individual comparisons). Chlorophyll a was lowest in the SE (Figure 2.4c; ANOVA: $F_{3,22} = 10.3$, $p < 0.001$). The other regions did not differ from one another for either AFDM or Chl A.

Sandpiper abundance was also compared to food abundance by transect. At the scale of a transect, sandpiper abundance was negatively related to AFDM, although the estimated effect was small. Sandpiper abundance was not correlated with overall abundance of infauna or chlorophyll a (Table 2.2).

Table 2.2. Models of shorebird abundance in relation to infauna abundance and biofilm indicators, ash-free dry mass (AFDM) and chlorophyll a (CHLA) from surface sediment.

Negative Binomial GLMs:	Estimate	SE	z-value	p	AIC
Infauna	-0.02164	0.01266	-1.71	0.09	38.14
AFDM	-7.18E-05	1.94E-05	-3.693	0.0002	34.13
CHLA	-0.00022	0.000179	-1.226	0.22	45.38

Only five flocks of sandpipers were observed foraging during the surveys in Tillamook, and all of these flocks were along the transect located furthest from shore in the West region. All of these observations were also along channels or at the main edge of the tide.

Patterns within Bandon Marsh

Overall, many more shorebirds were seen in Bandon Marsh on all surveys, despite a smaller survey area. There was little variability within the survey region in terms of our *a priori* habitat characterizations; therefore, we did not group our observations by habitat or region as with Tillamook. Macroalgae and seagrasses covered less than 25% of all sampling quadrats. All sediment in Bandon was qualitatively similar in sediment composition, consisting of sandy-mud with many small wood particles. Despite the relative homogeneity of sediment grain along the transects, the habitat was not homogenous. Bandon Marsh has a large amount of marsh habitat in the inter-tidal matrix, including along the transects (whereas there is no marsh habitat in the Tillamook transects), as well as many small channels.

Shorebirds were observed on all of the transects, although there were relatively few observations on the northern transect, which was dominated by marsh habitat. Detection of shorebirds is more limited in the marsh environment; we observed only one shorebird in the low marsh. However, our focus was on foraging birds and marsh habitat is used primarily for roosting (Zharikov and Milton 2009). In general it appeared that more observations occurred farther from the shore, and at several of the mouths where the tide enters the mudflats.

Infauna were highly abundant but variable in Bandon Marsh. Corophid amphipods dominated the infauna community (Table 2.3). Ash-free dry mass was variable throughout Bandon Marsh ($76,186 \pm 20,702$; $n=18$); chlorophyll a was much

higher than in Tillamook samples and was highly variable among samples in Bandon Marsh ($38,821 \pm 28,382$, $n=18$).

Table 2.3. Infauna abundance (mean number of individuals $\pm$ SD) in Bandon Marsh, OR, from three 4cm diameter x 3 cm deep cores. "Unknown" includes species that could not be identified either because they were rare or because they had been damaged.

<i>n=16</i>	Mean	SD
Bivalves	12	18
Polychaetes	67	47
Oligochaetes	68	47
Tanaids	0	0
Corophid Amphipods	411	525
Cumaceans	26	58
Copepods	17	20
Unknown	56	91
TOTAL	658	580

Autocorrelation plots showed no indication of spatial autocorrelation for birds or for any of the food indicators, suggesting that bird and food abundances were independent at the 1 hectare scale. Shorebird abundance was not correlated with either infauna abundance or chlorophyll a, but did exhibit a very slight but positive relationship with AFDM (Table 2.4; Figure 2.6). This relationship is driven by the fact that the very largest flocks of shorebirds were observed in bins that also had high AFDM.

Table 2.4. Models of shorebird abundance in relation to infauna abundance and biofilm indicators, ash-free dry mass (AFDM) and chlorophyll a (CHLA) from surface sediment.

Negative Binomial GLMs:	Estimate	SE	z-value	p	AIC
Infauna	-0.00022	0.0018	-0.117	0.91	123.4
AFDM	8.66E-05	3.49E-05	2.48	0.013	122.1
CHLA	-3.28E-05	4.36E-05	-0.752	0.45	126.0

Figure 2.6. Infauna abundance and biofilm indicators, ash-free dry mass (AFDM) and chlorophyll a (CHLA), in relationship to shorebird abundance per hectare plot in Bandon Marsh, OR.

A.

B.

Although channels occupied only a small proportion of the total survey area, 41% of all flocks of sandpipers and 51% of the total numbers of shorebirds were observed in or immediately adjacent to channels. A higher percent of sandpipers were foraging when observed next to a channel (73%) than when observed in open mudflats (60%; Pearson's $X^2 = 50.296$, $df = 1$, $p < 0.001$).

DISCUSSION

In Tillamook Bay, shorebirds had a non-uniform distribution with most observations along a single transect in the Western region, supporting my first hypothesis that

shorebirds would have non-random distributions within estuaries. In Bandon Marsh shorebirds also appeared to have a non-random distribution; however, there was too much variability in shorebird locations among observation dates to identify specific targeted areas.

The hypothesis that shorebirds would be more abundant where there was moderate to high density of food within each estuary was not supported. Shorebirds in Tillamook were found primarily in a region with lower infauna abundance and lower measures of biofilm than the other regions. Analysis at the scale of individual transects also did not show any relationship between shorebirds and infauna or Chl A, and there was a negative relation to AFDM. It is unlikely that sandpipers actively avoided areas with high surface organic content; rather, shorebirds may have favored the region of lower AFDM for independent reasons. Shorebird distribution in Bandon Marsh, measured at a finer scale, also did not correlate to infauna abundance or Chl A. A positive relationship existed between shorebird abundance and AFDM. However, this relationship was quite weak and driven largely by several data-points: the three bins where the most birds were observed had high AFDM but there were many other locations with high AFDM where birds were not frequently observed. The fact that a negative relationship was detected in Tillamook but a positive relationship was detected in Bandon further suggests that this is not a consistent pattern and may be spurious.

In Bandon Marsh, we may not have seen a numerical response to infauna density in part because prey density was so high. Bandon Marsh samples contained an

average of 658 ($\pm$ 580, $n = 16$) invertebrates, whereas Tillamook had 165 ($\pm$ 150, $n = 21$) on average. The density of infauna at Tillamook was comparable to estimates made by other researchers at Tillamook and at Gray's Harbor and Willapa Bay (Ferraro and Cole 2011, 2012; see Chapter 1 for details). Therefore, the density of prey may be several times higher at Bandon Marsh than other Pacific Northwest Estuaries. Numerical responses are often non-linear. It is plausible that no numerical response to prey was observed in Bandon because infauna abundance was high enough to exceed the plateau of an asymptotic numerical response (Type II or Type III; Holling 1959).

I measured prey abundance as all infauna that did not pass through a 500 μm sieve; however, shorebirds may select for certain prey species either because of a difference in nutritional content or a difference in behavior that leads to easier capture and handling. The Western region of Tillamook Bay, where most shorebirds were observed, did differ from other regions in infauna community composition. It had greater relative abundances of bivalves and tanaids. It is plausible that these were preferable prey items, although there has been no specific research on sandpiper prey selection in this region. Infauna at Bandon Marsh was dominated by *Corophium sp* amphipods. *Corophium* are known to be the primary prey item for Semipalmated Sandpipers in the Bay of Fundy, Canada (Wilson 1990) as well as for small sandpipers in Northern California (Colwell 1993, Colwell and Landrum 1993). Alternatively to shorebirds selecting prey, certain prey may be more available because of their depth

relative to the depth a bird can probe, or because of some other difference such as their activity pattern. I did not measure availability *per se* in this study.

Sandpipers in Tillamook were found most often in the sand-flat region and never in the muddiest region. Lamberson et al. (2011) investigated shorebird distribution within Yaquina Bay, Oregon over one year. They found that shorebirds used sandflats more frequently than other habitat types overall, although mudflats were used more often than sandflats during the fall and spring migration periods. However, region within an estuary predicted abundance better, controlling for habitat types. Taken together with our results, it appears that shorebirds in Oregon forage primarily in open mud and sandflats, but also may select regions of estuaries independently of sediment grain. Sediment at Bandon Marsh was too uniform to make a comparison of habitats.

At both sites foraging sandpipers were frequently found along channels. Micro-habitat features such as the tidal edge, channels, or ponds have previously been found to be predictors of shorebird abundance (Colwell and Landrum 1993, Yates et al. 1993, Warnock and Takekawa 1995, Danufsky and Colwell 2003, Finn et al. 2008, Lamberson et al. 2011) either due to elevated prey abundance or availability. Because channels remain inundated for longer times during the tide cycle, the wetter sediments may increase prey abundance or availability. I investigate this pattern with more detailed observations in Chapter 3.

Factors other than food abundance and availability may be more important drivers of shorebird distribution in these estuaries. Shorebirds are often attacked by

falcons at estuaries. Dekker and Ydenberg (2004) demonstrated that Dunlin in British Columbia were killed more frequently when they foraged close to shore. Pomeroy (2006) found that Western Sandpipers in the same region trade-off proximity to shoreline versus infauna abundance in choosing foraging locations. Therefore, being further from shore, where predators may more easily hide, may be of significant importance, particularly when the density of other shorebirds is low. The transect where the most shorebirds were observed in Tillamook was the furthest from shore. The influence of predation may be particularly important in smaller estuaries where there is a greater edge effect. If shorebirds habitat use reflects avoidance of either predators or areas with human activity, these effects may limit how much of the estuary they are able to use and supersede the influence of local prey distribution. Future work in Oregon should investigate predation risk and human disturbance and how these impact shorebird distributions and abundance.

Proximity to marsh habitat and other potential roost sites may also be an important factor determining shorebird distribution within estuaries. Preferred roost sites are typically closer to large foraging areas (Zharikov and Milton 2009). Although Tillamook Bay is much larger than Bandon Marsh, both are small compared to the major West Coast estuaries. In smaller estuaries, flight costs to a specific roost site are minimized but should still be considered, particularly since marsh and grasslands were both factors I identified in Chapter 1 as being positively correlated with shorebird density among estuaries.

Spatial and temporal scales are important to consider when evaluating shorebird associations with prey and habitat. In comparing food abundance among estuaries in Chapter 1, I showed a general trend of increasing shorebird density with food density in the fall although the total number of sites was limited. The relationship to food resources may be stronger when comparing estuaries to one another rather than movement within an estuary. Mismatches in scales of measurement in this study could also explain the lack of correlation between shorebirds and food resources. Shorebirds were surveyed over several months and the survey area was large relative to the number of food resource samples. If infauna or biofilm were highly patchy, the samples we collected may not have adequately reflected the broader areas they represented. If this is the case, then a numerical response might be detected at a finer scale. I describe more detailed study of shorebird movements within estuaries in Chapter 3 in relation to channels and associated prey resources.

Chapter 3. Small tidal channels improve foraging opportunities for *Calidris* shorebirds

INTRODUCTION

Migration is energetically demanding, so many shorebird populations stop to rest and forage in the mudflats of estuaries. Estuarine inter-tidal microhabitats are non-uniform and both abiotic and biotic factors may serve as predictors of whether migratory shorebirds will use a given site. Microhabitat characteristics such as the sediment size, elevation, salinity, and hydrodynamics can directly alter the prey community (Lenihan and Micheli 2001) as well as the availability of prey to foraging birds and, therefore, indirectly relate to shorebird abundance. These features may therefore be useful as indicators of potential foraging opportunities for shorebirds.

At-risk populations of the Western Sandpiper *Calidris mauri* and the Dunlin *C. alpina pacifica* use estuaries in the Pacific Northwest as stop-over sites during their migrations. Wildlife managers and land managers are seeking ways to improve the quality as well as quantity of foraging grounds for these and other declining shorebird populations. In this chapter I investigate how a common microhabitat feature, small tidal channels in mudflats, influences foraging shorebirds.

Shorebirds often follow the main tidal edge as the tide ebbs and flows (Recher 1966, Colwell and Landrum 1993, Finn et al. 2008), possibly because the shorebirds' prey may be found closer to the surface after recent exposure when they are at lower risk of desiccation. Alternatively, the sediment may be easier to probe when it is still

relatively water logged. Kuwae et al.'s (2010) observation that Dunlin switched from probing in the sediment to pecking at the surface after a longer period of mudflat exposure is consistent with either hypothesis.

Channels in mudflats may offer similar advantages to foraging shorebirds, either in terms of the depth of their prey or the penetrability of the sediment, because they create similar physical conditions to the tidal edge. Channels and other similar water features have been found to be positively associated with Western Sandpiper or Dunlin presence or density in several studies in Western Europe or the west coast of the U.S. However, the effects were weak and/or statistically insignificant (Ravenscroft and Beardall 2003, Danufsky and Colwell 2003, Warnock and Takekawa 1995). One study more thoroughly investigated shorebird associations with tidal channels. Lourenco et al. (2005) examined wintering shorebird populations in Portugal and showed that shorebirds, including Dunlin, foraged more often near channels. They attributed this to the greater abundance of prey found in the sediment near the channels. Therefore, channels may confer another advantage – prey density – beyond that conferred by the tidal edge. However, this pattern has not been examined at other stop-over sites or for other shorebird species. Furthermore, the differences along channels in prey abundance, depth and accessibility (in terms of how soft sediment is) have not been evaluated together to understand their relative importance.

The first objective of my research was to determine whether shorebirds preferentially fed near tidal channels and tidal edge in Bandon Marsh National Wildlife

Refuge, a primary stop-over site in Oregon. By surveying foraging shorebirds at sites adjacent to and distant from channels at different times of the tide cycle, I tested two hypotheses: (H1) *Calidris* shorebirds forage more often and probe deeper in the sediment along the edges of channels, and (H2) *Calidris* shorebirds forage along channels more often later in the cycle of tidal exposure (at low and flow tides as compared to ebb tides).

My second objective was to determine what characteristics differentiate the quality of foraging along channels. I tested three non-exclusive hypotheses about channels that are consistent with improved foraging efficiency for *Calidris* shorebirds. I hypothesized that foraging would be improved along channels because (H3) infauna are more abundant, (H4) prey is closer to the surface throughout tidal exposure, and (H5) the sediment is softer and easier to probe throughout tidal exposure.

To test these hypotheses, I collected samples of prey at set distances from a channel during ebb and low tides and separated these samples by sediment depth. I also measured the force required to probe in the sediment at these locations. Herein, I evaluate the relative merit of these three hypotheses.

Methods

Research Site

Evaluation of the value of channel habitat to shorebirds was conducted at Bandon Marsh National Wildlife Refuge in Bandon, OR. Bandon Marsh hosts one of the highest

densities of migratory shorebirds in Oregon (PRBO unpublished data, chapter 1).

Bandon Marsh is located in the Coquille River Estuary and is on a side channel of the river. The site is approx 0.5 km² of mudflat surrounded by low and high marsh zones. Several major channels and many smaller channels meander through parts of the mudflats. Research focused on the NW corner of the marsh where several channels flow through the mudflat.

Shorebird Surveys

Shorebird surveys were conducted daily from 25 April to 1 May between mid-ebb and mid-flow tides. I scanned the entire NW region of Bandon Marsh when the tide was at 0.91 m, just after the majority of the mudflats became exposed, then again at 0.61 m, 0.30 m, 0 m, low tide (if lower than 0 m) and at the same tidal heights during tidal flow. The time between the scans ranged from 45-75 min apart. For each flock of shorebirds, I recorded the species, size of flock, distance from channel edge (0-5m, >5m), and behavior (foraging, roosting, etc.). I also recorded the microhabitat as either Flats (open flats; total of 38,089 m²), sandy beach (sandy flats along the Coquille River beach; 29,460 m²), Red Algae (sandy-mudflat covered >50% with *Gracilaria* sp; 3,475 m²), Green Algae (sandy-mudflat covered >50% with dense green algal mat; 9,744 m²), or channel (within 1 m of a channel or exposed channel bed; 8,790 m²).

I conducted focal observations during the same dates to assess individual foraging behaviors and allocation of time to different behaviors at channel and non-

channel sites. I selected shorebird flocks opportunistically, and then selected an individual bird within the flock haphazardly and blindly. Observations lasted ~1 min unless the bird was lost from the field of view. I recorded the number of pecks and probes into a handheld digital voice recorder. I also recorded the percentage of time spent foraging or in other behaviors (e.g., running or other movement, predator vigilance, preening).

Quantifying Quality of Channel Sites

The abundance and depth of infauna, as well as the penetrability of the sediment, were measured at sites along channels and away from channels at different tide heights. Eight sites were randomly selected along channels in the area of observation. At each site, a 4 cm diameter core of infauna was collected immediately adjacent to the channel (within 0.1 m of the channel water edge) and at 5 m distance away from the channel to determine differences in prey abundance. The distance of 5 m was selected following the findings of Lourenco et al. (2007) that infauna community differences could be detected at this distance, yet 5 m was close enough to minimize physical differences other than the presence of the channel itself. To determine differences in prey depth, each core was split by depth strata: surface-0.5 cm, 0.5-1.5 cm, and 1.5-3 cm (maximum length of a Western Sandpiper bill is 3 cm but most are shorter, Wilson 1994; Dunlin bill length can exceed 3 cm but Mouritsen and Jensen 1992 measured 3.5 cm as maximum probing depth). To understand how these factors interact with tidal height, samples

were collected at mid-ebb tide (2') and at low tide (0'). Infauna samples were later sieved at 500 μm , preserved in formalin and then transferred to ethanol. Individual infauna were enumerated and identified to major taxonomic group. Larger infauna were also counted separately (>2 mm for amphipods, >5 mm for polychaetes). One trained observer measured these organisms initially and then visually placed them into a size category. Sediment penetrability was measured adjacent to each core location and time with a soil penetrometer. Any seagrass or algal cover was noted.

Because shorebirds were often found in areas covered in red algae (*Gracilaria* sp.), additional infauna samples ($n = 5$) were taken in this habitat. All sites in the red algae habitat were at least 5 m from a channel. The paired channel and non-channel sites were not in the *Gracilaria*.

Analysis

Differences in the relative density of shorebird flocks and individuals were tested using ANOVA and Tukey Kramer post hoc tests. A percentage was used as opposed to raw counts because there was high variability among days in the numbers of birds observed. The percentage of all the birds or flocks seen in one day in a given habitat was divided by the area of that habitat to give relative density. Data were log transformed to meet normality assumptions. Logistic regression was used to evaluate whether the likelihood of foraging along a channel changed with tidal height. A *t*-test was used to test the

difference in percentage probes (the number of probes divided by the total number of pecks and probes) between channel and non-channel habitats.

Differences in infauna abundance in relation to sediment depth, distance from channel, and difference from tide height were tested using multi-factor ANOVA models. Because depth stratifications differed in total volume, infauna numbers were adjusted to number per 0.5 cm depth for statistical tests. First and second-order interactions were considered and non-significant interaction terms were removed. Both total infauna abundance and abundance of *Corophium* amphipods were tested. A multi-factor ANOVA was also used to test the difference in force required to probe in sediment. Further, paired one-tailed t-tests were used to compare differences between ebb and low tide. All analysis was performed in R (v. 2.8.1; R Development Core Team 2008).

RESULTS

Shorebirds

Western Sandpipers and Dunlin foraged most often, relative to total area, in the sections of Bandon Marsh covered with red algae (*Gracilaria* sp.), followed by channel beds (Figure 3.1). Many fewer of both species were observed foraging in the green algae, open flat or sandy beach habitats. The differences among habitats were significant for Western Sandpiper flocks ($F_{4,30} = 103.71$, $p < 0.001$), Western Sandpiper

individuals ($F_{4,30} = 17.62$, $p < 0.001$), Dunlin flocks ($F_{4,30} = 16.48$, $p < 0.001$), and Dunlin individuals ($F_{4,30} = 10.64$, $p < 0.001$).

Western Sandpipers foraged more along channels shortly after the intertidal areas had been exposed (ebbing tide) than after the flats had been exposed (flow tides; Figure 3.2a; $n = 33$, estimate = -0.16, SE = 0.008, $z = -20.06$, $p < 0.001$). Dunlin foraged somewhat more often along channels after longer periods of exposure (Figure 3.2b; $n = 33$, estimate = 0.047, SE = 0.015, $z = 3.097$, $p = 0.002$). For both species, these effects were weak, although significant.

Western Sandpipers probed the sediment (as opposed to pecking at the surface) a greater proportion of the time when feeding along channels than when feeding in other habitats (Figure 3.3; $t = 4.05$, $df = 31$, $p < 0.001$). Dunlin were not observed in focal observations frequently enough to make this comparison.

Figure 3.1. Relative density (percent per m²) of (a) Western Sandpiper flocks, (b) Western Sandpiper individuals, (c) Dunlin flocks, and (d) Dunlin individuals by habitat type. and log transformed. Letters indicate habitat types that differed significantly based on post-hoc tests. N=7 observation dates. Boxplot illustrates the median line, first and third quartile boxes and min and max value hinges with outliers excluded and shown as circles.

A.

B.

C.

D.

Figure 3.2. Proportion of (a) Western Sandpipers and (b) Dunlin foraging along channels in relation to tide height. Negative tide heights refer to ebb tides and positive height refer to flow tides. Lines show fitted logistic regression models.

A.

B

Figure 3.3. Proportion of Western Sandpiper foraging actions that were probes (as opposed to pecks at the surface) along channels or in other habitats (red algae habitat excluded). Boxplot illustrates the median line, first and third quartile boxes and min and max value hinges with outliers excluded and shown as circles.

Infauna

Total infauna abundance and large infauna abundance varied significantly with depth and distance from the channel, but not with tidal stage (Table 3.1). Most infauna were found in the top 0.5 cm of the sediment in all samples regardless of distance from channel or tide height (Figure 3.4a). Infauna abundance was over twice as high, on average, immediately adjacent to the channel as it was 5 m away from the channel. This was true regardless of tidal height. There was a greater proportion of total infauna in the top 0.5 cm at channel versus non-channel sites (Figure 3.4a), explaining the

significance of the depth*distance to channel interaction term. Additionally, the proportion of infauna that were in larger size classes was higher next to the channel (Table 3.2).

Corophiid amphipods dominated infauna samples (Table 3.2), and showed the same patterns as overall infauna abundance with relation to depth and distance from channel (Table 3.1); they were more abundant in the top 0.5cm (Figure 3.4b) and more abundant next to channels, but not affected by tidal height. Most infauna species were more abundant in channel samples, though the opposite pattern was observed for oligochaetes.

Total infauna abundance in the red algae was, on average, comparable to the other non-channel sites and much less than in channel sites (Table 3.2, Figure 3.5a). There were more large infauna in the *Gracilaria* than in other non-channel samples, but still less than that found in channel samples (Table 3.2). The proportion of infauna from large size classes was, however, higher than either the channel or non-channel (open flat) sites.

Table 3.1. Multi-factor ANOVA results of infauna abundance in relation to depth in the sediment (0-0.5 cm, 0.5-1.5 cm, 1-5-3 cm), distance from channel (0 m, 5 m), and tide (ebb, low). Non-significant interaction terms were removed. N = 9 sites with samples of each combination of the above treatments.

	All Infauna		Large Infauna		<i>Corophium</i> sp.	
Factor	F	p	F	p	F	p
Depth	117.7	<0.001	41.5	<0.001	50.6	<0.001
Distance to channel	6.9	0.010	27.2	<0.001	23.7	<0.001
Tide	0.0	0.964	0.2	0.631	0.3	0.578
Depth*Distance to channel	5.7	0.019	12.9	<0.001	13.1	<0.001

Figure 3.4. Average abundance of (A) all infauna and (B) Corophiid amphipods in relation to depth in the sediment, distance from channel and tide. Error bars represent 1 SE.

A.

B.

Table 3.2. Total abundance of infauna (mean $\pm$ SD) in paired Channel and Non-channel sites, and in *Gracilaria* habitat. Large infauna includes amphipods >2 mm and polychaetes >5 mm.

	Channel		Non-channel		Red Algae	
	<i>n</i> = 16		<i>n</i> = 16		<i>n</i> = 5	
	Mean	SD	Mean	SD	Mean	SD
Bivalves	7.2	$\pm$ 7.2	2.5	$\pm$ 2.4	3.4	$\pm$ 1.3
Polychaetes	5.4	$\pm$ 7.2	4.5	$\pm$ 3.5	6.0	$\pm$ 1.9
Oligochaetes	39.3	$\pm$ 28.7	67.4	$\pm$ 51.7	36.8	$\pm$ 9
Corophid Amphipods	68.6	$\pm$ 58	11.9	$\pm$ 19.2	26.8	$\pm$ 15.1
Gammarid Amphipods	7.9	$\pm$ 20.1	0.1	$\pm$ 0.3	5.6	$\pm$ 3.8
Cumaceans	3.7	$\pm$ 3.7	0.8	$\pm$ 1.5	0.6	$\pm$ 0.9
Copepods	89.9	$\pm$ 98.3	28.9	$\pm$ 31	15.8	$\pm$ 9.7
TOTAL INFAUNA	228.6	$\pm$ 134.1	118.2	$\pm$ 52	100.8	$\pm$ 26.6
% LARGE INFAUNA	11.7%	$\pm$ 6.8%	4.8%	$\pm$ 3.6%	16.0%	$\pm$ 3.5%

Sediment Penetrability

Less force was required to probe in sediment next to channels than away from channels (Figure 3.5b). A multi-factor ANOVA showed that this distance from channel was significant ($F = 24.82$, $p < 0.001$), but that there was no difference in force with tide height ($F = 1.60$, $p = 0.21$). The interaction term was not significant and was removed from the model. However, paired t-tests showed that non-channel sites required more force to probe at low than ebb tides ($t = -6.057$, $df = 19$, one-tailed $p < 0.001$) but channel sites did not differ between ebb and low tides ($t = -2.042$, $df = 9$, one-tailed $p = 0.36$).

Figure 3.5. Average (A) abundance of infauna for all depths combined and (B) force required to probe in the sediment. Channel and other habitats were from paired samples taken 5 m apart; random samples were collected separately for the red algae microhabitat. Error bars show 1 SD.

A.

B.

DISCUSSION

Western Sandpipers and Dunlin both foraged relatively more often along small tidal channels than in most other habitat types in Bandon Marsh as I had predicted (Hypothesis 1). Several previous studies of Western Sandpiper habitat use on the west coast of North America have suggested a positive association with channelization (Danufsky and Colwell 2003, Warnock and Takekawa 2005), although the first of these was not supported with statistical validation and the second could not clearly distinguish between the value of tidal sloughs and open mudflat. Lourenco et al. (2007) found that Dunlin wintering in a Portuguese estuary were more likely to forage along channels, and Ravenscroft and Beardall (2003) found a similar but non-significant pattern in estuaries in the United Kingdom, observing that variability in numbers was high. Danufsky and Colwell (2003) found no association between Dunlin presence or density and channelization in Humboldt Bay although they made observations over a broader spatial scale. Taken together, this literature suggests channels are commonly used by both Western Sandpipers and Dunlin, but detecting this trend can be difficult because of the frequent movement of flocks or because habitat selection occurs on a finer spatial scale.

Infauna were about twice as abundant next to channels compared to open flats. This pattern was true for corophiid and gammarid amphipods, bivalves, copepods and cumaceans. Oligochaetes were the only taxon to exhibit greater abundance further from the channel. Similarly, Lourenco et al. (2005) also showed greater abundances of bivalves, polychaetes, and a gastropod along channels in Portugal. These parallel results

in different parts of the world suggest that this is not just a local effect; channels are likely to be advantageous to shorebirds world-wide.

Most infauna (> 90%) were found in the top 0.5 cm of sediment regardless of the location. The proportion of total infauna in this top layer was greatest alongside channels. However, the depth stratification of infauna did not change with the tide height. Taken together with total infauna abundance, these patterns indicate that shorebirds forage along channels primarily because prey is abundant (Hypothesis 3). The decrease in prey depth next to channels is likely a secondary advantage (Hypothesis 4).

In addition to increased infauna abundance, channels may have attracted foraging shorebirds because the sediment required less force to probe as measured with the penetrometer. Furthermore, focal observations showed that Western Sandpipers used more probing behaviors next to channels than in open flats. In previous studies Dunlin were shown to probe more when sediment is water-logged (Mouritsen and Jensen 1992, Kuwae et al. 2010). Mouritsen and Jensen (1992) estimated with a simple model that Dunlin foraging success would increase up to 4-fold with increased ability to probe because of an increased probability of encounter with prey. I was not able to consistently determine whether a peck or probe was successful, but I did often see large polychaete worms captured when a shorebird was probing, but never saw such large infauna when the birds pecked.

Estuarine infauna are able to tolerate varying amounts of desiccation when the tide is out (Lenihan and Micheli 2001); however, they may also avoid desiccation by

burrowing deeper in the sediment. I therefore expected that channels might be particularly important to shorebirds later in the tide cycle because the sediment would retain moisture and the prey would be more likely to remain near the top of the sediment than in the open flats. I did not detect differences in infauna abundance or depth between ebb and low tides. My sampling approach may not have effectively detected these differences because infauna near the surface may have always burrowed deeper due to the activity we created when sampling. However, the hypothesis that shorebirds would forage more along channels during low tide (H2) was not supported either; shorebirds appeared to use channels approximately equally throughout the tide cycle, and infauna tended to be in the top-most substrate regardless of the time in the tide cycle. Given that total infauna abundance was so much higher along channels, it is likely that shorebirds were attracted to these locations at all times, and therefore would have showed no change in distribution even if the depth of infauna were changing somewhat.

This research was conducted at a generally cool and rainy location, which also may have affected infauna depth patterns. On most days of survey, there was some rain, and I observed a noticeable slick of water over the mudflats on these days even late in the tide cycle. There was only one continuously sunny day of observation, and on that day both Western Sandpipers and Dunlin used the channel in much greater proportions during flow tide (75%) than ebb (25%). This anecdotal observation suggests that in more southern locations the timing of the tide may have a greater impact on

infauna depth. Shorebird prey have been shown to be found deeper in the sediment at more southern or sunnier wintering locations (Mathot et al. 2007). Further investigation could determine whether depth stratification in these locations is affected by proximity to channels and how this affects shorebird movement during the tide cycle.

Although small tidal channels were generally used more than other habitats, the relatively small patches of *Gracilaria* in the mudflats attracted even greater densities of shorebirds. Infauna in the *Gracilaria* patches was not, surprisingly, any greater than in other areas of the open flats. Although total infauna abundance was not higher, I did observe when collecting the samples that a fair number of large invertebrates were inhabiting the algae itself. Although some *Gracilaria* was in each core we collected, we may not have effectively captured the infauna residing in it. Furthermore, whether more abundant or not, it may be easier for Western Sandpipers and Dunlin to capture invertebrates in this filamentous algae compared to probing in the sediment. Additionally, I noted that the *Gracilaria* patches retained small puddles of water. Although the sediment was not softer than along channels, it was softer than the open flats. Furthermore, if the retained water led to increased invertebrate activity, this could assist foraging shorebirds. Finally, I also noted that shorebirds were well camouflaged when in the *Gracilaria* so this environment could potentially reduce their predation risk.

Conclusions

In this research, I demonstrated that Western Sandpipers and Dunlin preferentially forage along channels in Bandon Marsh. This is the first such evidence for Western Sandpipers, and the first for the Dunlin subspecies *C. alpina pacifica*. Furthermore, I demonstrated why channels may be advantageous: infauna are more abundant, including an important prey item *Corophium sp.*; infauna are more likely to be near the surface, and the sediment is easier to probe. Based on the magnitude of variation, it appears that total infauna abundance and ease of probing are likely to be of primary importance while the difference in infauna depth stratification is secondary. Because channelization in an estuary can be influenced by management actions, either directly in restoration or indirectly in controlling sediment or freshwater run-off, these findings can be used to improve site quality in stop-over sites for these at-risk shorebird species.

Conclusions

My goal in this research was to identify environmental features or habitat characteristics that predict shorebird abundance in Oregon estuaries. Given the dependency of sensitive shorebird species on estuaries, increasing our knowledge about their habitat or prey needs can help wildlife managers increase both the amount and the quality of shorebird habitat.

On a large spatial-scale, comparing estuaries throughout the Pacific Northwest, I showed that shorebird density in the spring was best predicted by total size rather than the amount of any one habitat. For shorebirds heading into their breeding season, timing of migration and, potentially, related social interactions may be especially important. In contrast, in the fall some species were more strongly influenced by habitats rather than estuary size. Inter-tidal habitat was not a strong predictor of estuary use for stopping over, but marsh habitat was. A related finding was that the amount of grassland in the surrounding watershed was also a good predictor of shorebird abundance, suggesting the importance of roost sites as well as feeding grounds. Information on food resources was more limited but also suggested that productivity of an estuary and the amount of infauna may relate to the density of shorebirds using a site.

On a smaller-scale, looking at shorebird associations with habitat and prey within estuaries, I found that shorebird distribution was not clearly predicted by prey

abundance. In part I attribute this to challenges in matching the temporal and spatial scales of shorebird movement with patchy distribution of infauna prey. Nonetheless, the evidence I show suggests that other factors besides prey - including possibly avoidance of predators and human activity or the nearby landscape matrix as found on the larger spatial-scale - are critical in determining shorebird distribution.

When I focused on shorebird habitat use on an even finer scale, examining habitat use around channels, I found that channels were used preferentially by shorebirds, as were other habitats that remained somewhat wet after the tide had exited. Prey abundance was higher along channels, consistent with the hypothesis that shorebird foraging would be improved along channels. The sediment was also easier to probe. The ability to capture prey easily is likely to be as important as prey abundance in influencing these shorebirds' distribution.

Proactive steps are being taken in some locations to improve or expand shorebird stop-over locations. Knowledge about how migratory shorebirds select sites on the west coast has been generally limited and nearly absent in Oregon, so my findings can help direct future and more detailed research and inform management decisions.

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