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Small Tidal Channels Improve Foraging Opportunities for Calidris Shorebirds

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RESEARCH ARTICLE

Small tidal channels improve foraging opportunities for *Calidris* shorebirds

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ABSTRACT

Estuarine intertidal habitats are heterogeneous, therefore migratory shorebirds are expected to forage in microhabitats where they can maximize their energy intake. Identifying proximate factors that migratory shorebirds use to accept or reject a particular habitat patch will help land managers make conservation and restoration decisions that provide the greatest benefits to shorebird populations during migration, a period of intense energy usage. We examined whether small semipermanent tidal channels were preferentially used by foraging Western Sandpipers (*Calidris mauri*) and Dunlins (*C. alpina*) during a spring migratory stopover in Bandon Marsh, an Oregon, USA, estuary. Further, we tested alternative hypotheses about how channels might be beneficial to shorebirds by examining infauna abundance, composition, and depth alongside channels compared with that in open mudflats. The densities of Western Sandpipers and Dunlins were at least 4 times higher along channels than in open mudflat habitats. Infauna along channels were twice as abundant as those in the surrounding mudflats, and infauna were generally found closer to the surface. Furthermore, sediment alongside channels required less than half the force to probe, probably increasing shorebirds' overall access to prey. We conclude that shorebirds selected microhabitats near channels because of the greater food abundance and availability. Additional evidence suggested that another microhabitat, patches of red algae (*Gracilaria* sp.), may also have conferred advantages on foraging shorebirds. Channels may be a valuable microhabitat to consider when selecting conservation areas for shorebirds, and maintaining channels (e.g., through maintaining natural hydrology and sedimentation patterns) should be considered in management practices.

Keywords: Western Sandpiper, Dunlin, channel, estuary, benthic infauna, microhabitat

Los pequeños canales de marea mejoran la búsqueda de alimento en los correlimos *Calidris*

Los hábitats estuarinos intermareales son heterogéneos, y por tanto, se espera que las aves playeras migratorias se alimenten en microhábitats donde puedan maximizar su consumo de energía. La identificación de factores próximos utilizados en la aceptación o rechazo de parches particulares de un hábitat por correlimos migratorios, ayudaría a los gestores del territorio a tomar decisiones de conservación y restauración, que provean los mayores beneficios para las poblaciones de correlimos durante este período de intenso consumo de energía. Examinamos si los pequeños canales intermareales y semipermanentes son utilizados con cierta preferencia para el forrajeo de *Calidris mauri* y *C. alpina*, durante escalas migratorias de primavera en Bandon Marsh, un estuario en Oregon. Además, probamos hipótesis alternativas sobre cuan beneficiosos son los canales para los correlimos al muestrear la abundancia, composición y profundidad de infauna a lo largo de canales versus lodazales abiertos. Las densidades de *Calidris mauri* y *C. alpina* fueron al menos cuatro veces mayor a lo largo de los canales que en los hábitats abiertos y planos. La infauna a lo largo de los canales fue dos veces mas abundante que en los lodazales circundantes, y generalmente se encontró mas infauna cerca de la superficie. Además, se requirió menos de la mitad de la fuerza para sondear en los sedimentos junto a los canales, probablemente aumentando el acceso general a las presas de los correlimos. Concluimos que los correlimos seleccionaron microhábitats cercanos a los canales debido a la mayor abundancia y disponibilidad de alimentos. Evidencia adicional sugiere que otro microhábitat, los parches de algas rojas (*Gracilaria* sp.), confieren ventajas a los correlimos mientras forrajean. Los canales son microhábitats valiosos al considerarse la selección de áreas de conservación para correlimos, además el mantenimiento de canales (por ejemplo, permitiendo los patrones de sedimentación y la hidrología natural) deben tenerse en cuenta en las prácticas de gestión ambiental.

Palabras clave: Calidris mauri, *Calidris alpina*, canal, estuario, infauna béntica, microhábitat

INTRODUCTION

Microhabitat selection by foraging animals can have direct impacts on food intake rates and, therefore, fitness. Estuarine intertidal microhabitats are nonuniform and both abiotic and biotic factors may serve as predictors of whether predators will use a given habitat patch (Colwell and Landrum 1993, Yates et al. 1993, Warnock and Takekawa 1995, Beauchamp and Ruxston 2008, Finn et al. 2008, Beauchamp 2009). Microhabitat characteristics such as sediment size, elevation, salinity, and hydrodynamics can directly alter the prey community (Lenihan and Micheli 2001) as well as the availability of prey (Neira et al. 2006). These features may therefore be useful as indicators of potential foraging opportunities for estuarine predators.

Migrating shorebirds, including several at-risk species, forage at estuarine stopover sites during their migration (Warnock and Bishop 1998, Warnock et al. 2004). Migration is a critical period for birds. Migration itself is energetically demanding, and energy needs are heightened by the need to prepare for or recover from breeding (Alerstam and Hedenström 1998). For migratory birds, most mortality occurs outside the breeding season, therefore survival during migration is likely to be a strong driver of population dynamics (Colwell 2010).

The Western Sandpiper (*Calidris mauri*) and the Dunlin (*C. alpina*) use estuaries in the Pacific Northwest as stopover sites during their migrations (Merrifield 1998, Page et al. 1999). Both of these populations are designated as being of "high concern" by the U.S. Shorebird Conservation plan (Brown et al. 2000, U.S. Shorebird Conservation Plan 2004). More recent estimates suggest that Western Sandpiper populations are declining while Dunlin populations using the Pacific Flyway (*C. alpine pacifica*) are stable (Andres et al. 2012). Managers are most likely to control and modify shorebird habitat at small spatial scales due to economic and logistical constraints, therefore detailed information on the microhabitat requirements of shorebirds is needed so that land managers can make conservation and restoration decisions with greatest benefits to threatened shorebird populations. Herein, we investigate how a common microhabitat feature, small tidal channels in mudflats, influences foraging shorebirds. These channels are generally formed through hydrodynamic forces; however, human activities may alter natural hydrology indirectly through the placement or removal of dikes and levees or through sedimentation (erosion from development, direct infill, etc.; Perillo and Iribarne 2003, Hood 2004), or directly by digging channels.

In estuaries, shorebirds forage primarily on benthic infauna, including polychaete worms and amphipods (Wilson 1994, Warnock and Gill 1996). 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 their prey may be found closer to the surface after the tide has just ebbed when water content in the sediment is still high and the infauna are at lower risk of desiccation. Alternatively, the sediment may be easier to probe when it is still relatively waterlogged. Kuwae et al.'s (2010) observation that Dunlins 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 create similar physical conditions to the tidal edge and may offer similar advantages for foraging shorebirds. Channels and other similar water features have been found to be weakly positively associated with Western Sandpiper and Dunlin presence or density in several studies in Western Europe and the west coast of the United States (Warnock and Takekawa 1995, Danufsky and Colwell 2003, Ravenscroft and Beardall 2003). Lourenco et al. (2005) more thoroughly investigated shorebird associations with tidal channels for wintering shorebird populations in Portugal and showed that shorebirds, including Dunlins, foraged more often near channels. The authors attributed this finding to the greater abundance of prey they found in the sediment near the channels. Therefore, channels may confer another advantage—increased prey density—beyond that conferred by the tidal edge of the greater mudflat. However, this pattern has not been examined at other stopover sites or for other shorebird species. Furthermore, differences between channels and open flats in prey abundance, depth, and accessibility (sediment softness) have not been evaluated together to understand their relative importance. In earlier research in 2 Oregon estuaries, we observed that sandpipers foraged with higher frequency along channels and tidal edges compared with open flats (Miller 2012); here, we quantify this pattern and its underlying factors.

Our first objective was to determine whether shorebirds preferentially fed near tidal channels and tidal edges in Bandon Marsh National Wildlife Refuge, a primary stopover site in Oregon. By surveying foraging shorebirds at sites adjacent to and distant from channels at different times of the tidal cycle, we tested 2 hypotheses: (H1) that a greater proportion of *Calidris* shorebirds forage along the edges of channels and that birds probe more deeply into the sediment along the edges of channels, and (H2) that a greater proportion of *Calidris* shorebirds forage along channels later in the cycle of tidal exposure when the surface of the open flats may be more dried out and therefore have less accessible prey.

Our second objective was to determine which characteristics differentiated the quality of foraging along channels. We tested 3 nonexclusive hypotheses about how channels might improve foraging efficiency for

Calidris shorebirds. We 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) sediment is softer and easier to probe throughout tidal exposure.

METHODS

Research Site

We worked in Bandon Marsh National Wildlife Refuge in the Coquille River Estuary in Bandon, Oregon, USA. Bandon Marsh hosts one of the highest densities of migratory shorebirds in Oregon (Miller 2012). The site includes approximately 0.5 km^2 of mudflat surrounded by low and high marsh zones. Several larger channels (1–3 m wide and 0.25–1 m deep) and many smaller channels ($<$1 m wide, $<$0.25 m deep) meander through the site. Most channels persist from year to year, although exact channel courses may alter when hydrodynamics or sedimentation patterns change (e.g., during a major storm).

Shorebird Surveys

We surveyed shorebirds from April 25, 2012, to May 1, 2012; based on scans of the area on earlier and later dates, this time period represented the peak of migration when the majority of shorebirds passed through. Surveys focused on Western Sandpipers and Dunlins as these 2 species were the most common ($>$95% of all shorebirds). Surveys were conducted daily between mid-ebb and mid-flow tides. One observer scanned the entire northwest region of Bandon Marsh when the tide was at 0.91 m, just as the mudflats were beginning to be exposed, and 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 to 75 min. The observer was stationed in locations with sufficient elevation and proximity to consistently detect all shorebirds in the area. For each scan we recorded the number of individual shorebirds, the number of flocks of shorebirds, species, distance from channel edge (0–5 m, $>$5 m), and behavior (foraging, roosting, etc.). Our goal was to compare the microhabitat next to channels with that of open flats; however, we observed that parts of the open flat were covered in various algae, which might also have affected infaunal availability and/or desiccation risk. Therefore, we also recorded the microhabitat as flats (open flats; total area of 38,089 m^2), sandy beach (sandy flats along the Coquille River beach; 29,460 m^2), red algae (sandy mudflat of which $>$50% was covered with *Gracilaria* sp., a branching red algae; 3,475 m^2), green algae (sandy mudflat of which $>$50% was covered with dense green algal mat; 9,744 m^2), or channel (within 1 m of a channel or exposed channel bed; 8,790 m^2).

We conducted focal observations during the same dates to assess individual foraging behaviors and allocation of time to different behaviors along channels and in open mudflats. No focal observations of individuals were conducted in the red algae because the algae obstructed our view of shorebirds' bills. We selected shorebird flocks opportunistically, and then selected an individual bird within the flock haphazardly. Observations lasted $\sim$1 min unless the bird was lost from view. We recorded the number of pecks and probes into a handheld digital voice recorder. We also recorded the percentage of time spent foraging or performing 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 within 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 5 m away from the channel to determine differences in prey abundance. The distance of 5 m was selected following the finding of Lourenco et al. (2005) that differences in the infaunal community could be detected at this distance, yet 5 m was close enough to minimize physical differences other than the presence of the channel itself. These 5 m distant samples (hereafter, nonchannel locations) were all in either open flat or green algae habitats (none were in the red algae). To determine differences in prey depth, each core was split by depth strata: surface–0.5 cm, 0.5–1.5 cm, and 1.5–3.0 cm. The maximum length of a Western Sandpiper bill is 3 cm but most are shorter (Wilson 1994), and while Dunlin bill length can exceed 3 cm they do not probe deeper than 3.5 cm (Mouritsen and Jensen 1992). To determine whether tide level affected the depth of infaunal organisms differently at channel and nonchannel sites, samples were collected at ebb tide (0.61 m) and at low tide (0 m). In total, there were 8 replicates for each combination in this $3 \times 2 \times 2$ design (total $n = 96$). Infauna samples were later sieved at 500 μm, preserved in formalin, and transferred to ethanol. Individual infauna were counted and identified to major taxonomic group. Larger infauna ($>$2 mm for amphipods, $>$5 mm for polychaetes) were also counted separately. 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.

Additional infauna samples ($n = 5$) were taken in areas covered in red algae (*Gracilaria* sp.) because shorebirds were often found in this habitat. However, the red algae was all found in one small area of the marsh, whereas channels were well-distributed throughout. Given the limited spatial coverage, we are cautious in extrapolating results from this sampling. All sites in the red algae habitat were at least 5 m from a channel. None of the paired channel and nonchannel sites were in the red algae habitat.

Statistical Analysis

We tested differences in the relative density of shorebirds among habitats using ANOVA and Tukey Kramer post-hoc tests. We used a percentage for comparisons rather than raw counts because there was high variability among days in the numbers of birds observed. The percentage of the total number of shorebirds seen in one day in a given habitat was divided by the area of that habitat to give relative density of individuals. Data were log-transformed to meet normality assumptions. Logistic regression was used to evaluate whether the number of shorebirds foraging in channels versus all other habitat types changed with tidal height. For focal observations, individual birds were treated as the sample units and a *t*-test was used to test the difference in percentage of probes (the number of probes divided by the total number of pecks and probes) between channels and open mudflats.

Differences in abundance of infauna in relation to sediment depth, distance from a channel, and difference in tide height were tested using ANOVA. Infauna numbers were adjusted to number per 0.5-cm depth for statistical tests because depth stratifications differed in total volume. First- and second-order interactions were considered and nonsignificant interaction terms were removed. Both total infauna abundance and abundance of *Corophium* amphipods were tested. ANOVA was also used to test the amount of force required to probe into sediments in relation to distance from channel and tide height. All analysis was performed in R (version 2.8.1; R Development Core Team 2008).

RESULTS

Shorebirds

Western Sandpipers and Dunlins were both commonly observed on a daily basis during our study, although total numbers varied considerably among days. We observed an average of 3,480 Western Sandpipers per day (SD = 3,257; range: 358–9,452), and an average of 785 Dunlins per day (SD = 1,628; range: 20–4,459).

Our first hypothesis predicted that shorebirds would be more abundant and forage more efficiently along channels. We found that, relative to total area of the habitat, the highest proportions of Western Sandpipers and Dunlins foraged in a small section of Bandon Marsh covered with red algae (*Gracilaria* sp.), followed by channel beds (Figure 1). Many fewer individuals of both species were observed foraging in the green algae, open flat, and sandy beach habitats. The differences among habitats were significant for both numbers of Western Sandpipers ($F_{4,30} = 17.6$, $P < 0.001$) and numbers of Dunlins ($F_{4,30} = 10.6$, $P < 0.001$). Habitat use patterns were very similar when looking at the number of flocks rather than at individuals.

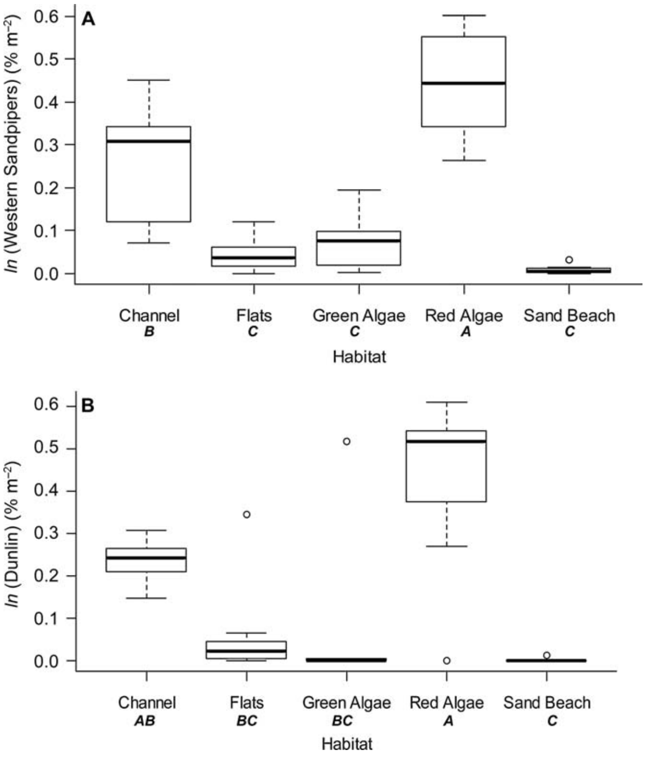

FIGURE 1. Relative density (percent per m^2; log-transformed + 1) of (**A**) Western Sandpipers and (**B**) Dunlins by habitat type. Letters indicate habitat types that differed significantly based on post-hoc tests. There were 7 observation dates. The boxplots illustrate the median lines, first and third quartile boxes, and minimum and maximum values, with outliers excluded and shown as circles.

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 (red algae excluded from ‘other’ habitats; Figure 2; $t = 4.1$, df = 31, $P < 0.001$). Dunlins were not observed during focal observations frequently enough to make this comparison.

Our second hypothesis predicted that greater proportions of shorebirds would use channels the longer the intertidal area had been exposed. Instead, higher proportions of Western Sandpipers were observed along channels shortly after the tide ebbed than after the flats had been exposed for longer periods (logistic regression estimate = -0.16 ± 0.01 SE, $z = -20.1$, $n = 33$, $P < 0.001$). Somewhat higher proportions of Dunlins foraged along channels after

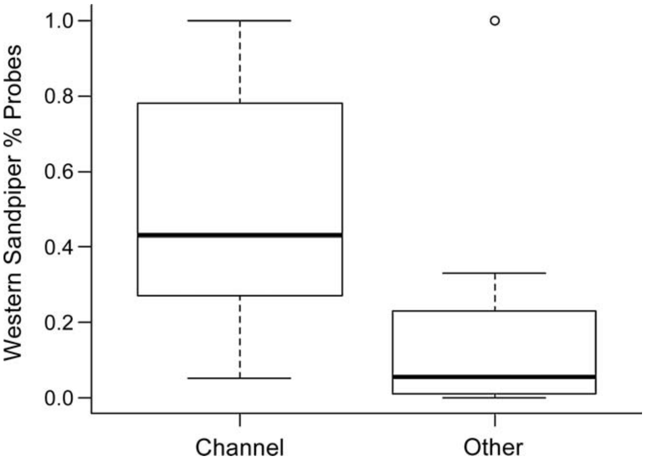

FIGURE 2. Proportion of Western Sandpiper foraging actions that were probes (as opposed to pecks at the surface) along channels ($n=13$) or in other habitats ($n=44$; includes open flat, sandy beach, and green algae habitat, but observations from red algae habitat were excluded). The boxplots illustrate the median lines, first and third quartile boxes, and minimum and maximum values, with outliers excluded and shown as circles.

longer periods of exposure (logistic regression estimate = 0.05 ± 0.02 SE, $z=3.1$, $n=33$, $P=0.002$). For both species, these effects were weak, although significant.

Infauna

Our third hypothesis predicted that infauna would be more abundant near channels, and our fourth predicted that more infauna would be found near the surface alongside channels. Infauna abundance was over twice as high immediately adjacent to the channel as it was in other habitats 5 m away from the channel (Table 1 and Figure 3A). This was true regardless of tidal height. Most infauna were found in the top 0.5 cm of the sediment in all samples regardless of tide height or whether the samples were from channel or other habitats (Table 1 and Figure 3A). Nonetheless, there was a greater proportion of total infauna in the top 0.5 cm at channel versus nonchannel sites, explaining the significance of the interaction between depth and distance to channel. Additionally, the proportion of infauna in larger size classes was higher next to a channel (Table 2).

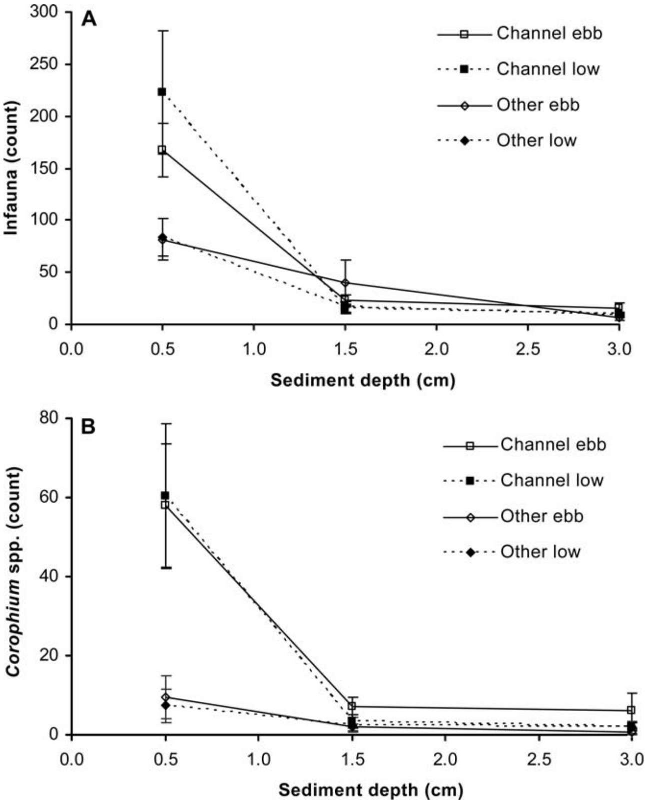

FIGURE 3. Abundance (mean ± SE) of (**A**) all infauna and (**B**) corophiid amphipods in relation to depth in the sediment and ebb versus low tide for channel habitat and other habitats. Other habitats include open flat, sandy beach, and green algae (none from red algae).

Corophiid amphipods dominated infauna samples (Table 2), and showed the same patterns with depth and distance to channel as overall infauna abundance (Table 1); they were more abundant in the top 0.5 cm (Figure 3B) and more abundant next to channels, but not affected by tidal height. Most infauna species were more abundant in channel samples, although the opposite pattern was observed for oligochaetes (Table 2).

TABLE 1. Results of multifactor ANOVA of infauna abundance in relation to depth in the sediment (0.0–0.5 cm, 0.5–1.5 cm, 1.5–3.0 cm), distance from a channel (0 m, 5 m), and tide (ebb, low). Nonsignificant interaction terms were removed. There were 8 site replicates for each combination of the above treatments, giving a total sample size of 96.

	All infauna		Large infauna		*Corophium* spp.	
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	0.01**	27.2	<0.001**	23.7	<0.001**
Tide	0.0	0.96	0.2	0.63	0.3	0.58
Depth* Distance to channel	5.7	0.02*	12.9	<0.001**	13.1	<0.001**

* denotes significance at $\alpha = 0.05$; ** denotes significance with Bonferroni correction for multiple comparisons.

TABLE 2. Total abundance of infauna (mean ± SD) in paired channel and nonchannel sites, and in red algae (*Gracilaria* sp.) habitat. Samples taken at both ebb and low tides are included (8 locations for channel and nonchannel, 5 locations in red algae). Large infauna includes amphipods >2 mm and polychaetes >5 mm.

	Channel ($n = 16$)	Nonchannel ($n = 16$)	Red algae ($n = 10$)
Bivalves	7.1 ± 7.3	2.5 ± 2.4	4.1 ± 2.9
Polychaetes	4.9 ± 5.9	4.5 ± 3.5	8.3 ± 5.3
Polychaetes ≤ 5 mm	3.0 ± 4.1	2.6 ± 2.9	2.7 ± 4.2
Polychaetes >5 mm	1.9 ± 2.3	1.9 ± 1.4	5.6 ± 3.7
Oligochaetes	38.9 ± 28.7	67.4 ± 51.7	40.1 ± 14.4
Corophid amphipods	68.5 ± 57.9	11.9 ± 19.2	31.4 ± 24.1
Corophid amphipods ≤ 2 mm	44.0 ± 39.0	8.5 ± 13.1	22.3 ± 16.9
Corophid amphipods >2 mm	24.5 ± 19.8	3.4 ± 6.3	9.1 ± 8.3
Gammarid amphipods	7.9 ± 20.1	0.1 ± 0.3	6.1 ± 4.9
Gammarid amphipods ≤ 2 mm	5.7 ± 14.3	0.1 ± 0.3	0.1 ± 0.3
Gammarid amphipods >2 mm	2.3 ± 6.8	0.0 ± 0.0	6.0 ± 4.6
Cumaceans	3.6 ± 3.7	0.8 ± 1.5	0.7 ± 0.8
Copepods	89.9 ± 98.3	28.9 ± 31.0	19.0 ± 15.2
Total infauna	227.4 ± 134.4	118.2 ± 52.0	120.6 ± 36.4
Large infauna (%)	11.6% ± 4.8%	4.8% ± 3.6%	16.9% ± 7.5%

Total infauna abundance in the red algae was, on average, comparable to the other nonchannel sites and less than in channel sites (Table 2 and Figure 4A). There were greater numbers of large infauna in the red algae than in other nonchannel samples, but still fewer than numbers found in channel samples (Table 2). However, the proportion of infauna from large size classes was higher in samples from the red algae than in either the channel or nonchannel (open flat) site samples.

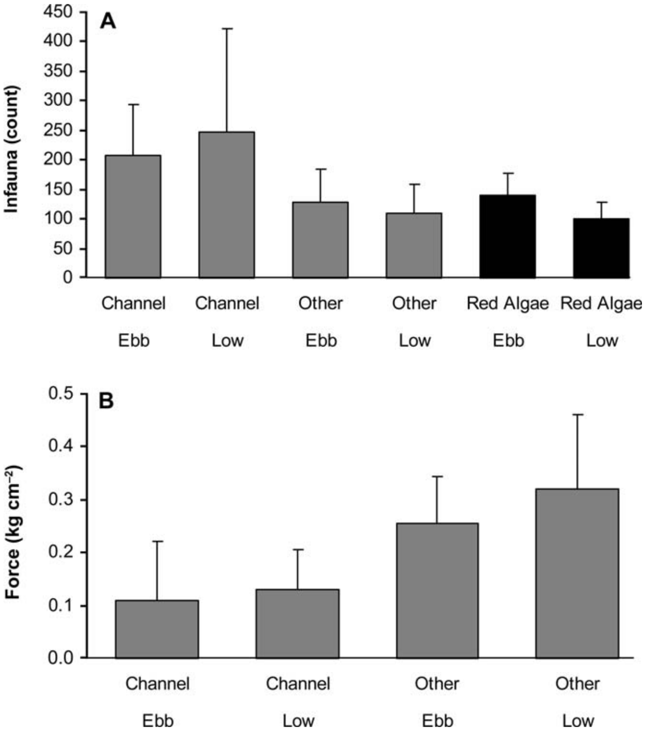

FIGURE 4. Abundance (mean ± SE) of infauna in all sediment depths combined (**A**), and Force (mean ± SE) required to probe into the sediment (**B**). Channel and other habitats were from paired samples taken 5 m apart; random samples were collected separately for the red algae microhabitat. Other habitats include open flat, sandy beach, and green algae (none from red algae).

Sediment Penetrability

Our fifth and final hypothesis predicted that less force would be needed to probe sediment near channels than farther from channels. Our measurements showed that less than half of the force was needed to probe in sediment alongside channels compared with sediment at sites 5 m away from channels (Figure 4B). A multifactor ANOVA showed a significant effect of distance from a channel on probe force ($F = 24.8$, $P < 0.001$), but no statistically significant difference in probe force with tide height ($F = 1.6$, $P = 0.21$). The interaction term was not significant and was removed from the model.

DISCUSSION

Western Sandpipers and Dunlins both foraged in greater proportions, relative to area, along small tidal channels than in open mudflats in Bandon Marsh as we had predicted (Hypothesis 1), although the greatest proportion per area foraged in the red algal microhabitat. Our previous research in Oregon provided similar evidence that shorebirds preferentially use channels: During the autumn migration we found that sandpipers foraged more frequently along channels than in open mudflats in Bandon Marsh and in Tillamook Bay (Miller 2012). Several other studies of Western Sandpiper habitat use on the west coast of North America have also suggested a positive association with channels (Warnock and Takekawa 1995, Danufsky and Colwell 2003), although the value of channels over open flats was not statistically validated in previous studies. Lourenco et al. (2005) found that Dunlins wintering in a Portuguese estuary were more likely to forage along channels, and Ravenscroft and Beardall (2003) found a similar but nonsignificant 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 channels in Humboldt Bay, although they made observations over a broader spatial scale. Taken together, this literature suggests that channels are commonly used by both Western Sandpipers and Dunlins. Lourenco et al. (2005) evaluated the total abundance of prey alongside channels, but did not consider how the depth of prey or availability of prey was influenced by the channel. None of these other studies gathered data on why shorebirds may have selected microhabitat near channels.

In our study area, infauna were about twice as abundant next to channels as they were in open flats. This pattern was true for corophiid and gammarid amphipods, bivalves, copepods, and cumaceans. Oligochaetes were the only taxon to exhibit greater abundance farther from the channel. Channel and nonchannel samples became accessible to shorebirds at nearly the same time, so infaunal abundance is not likely to be the result of a difference in exploitation time. 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 infauna may regularly be more abundant alongside channels. If this is the case, channels are likely to be advantageous to shorebirds across regions.

Most infauna (>90%) were found in the top 0.5 cm of sediment regardless of location. The proportion of total infauna in this top layer was greatest alongside channels. However, the depth stratification of infauna did not change with tidal height. Taken together with total infauna abundance, these patterns indicate that more shorebirds forage along channels than in open flats primarily because prey is more abundant (Hypothesis 3). The higher percentage of infauna near the surface along channels, and hence greater availability to foraging shorebirds, is likely a secondary advantage (Hypothesis 4).

In addition to increased abundance of infauna, channels may have attracted foraging shorebirds because the sediment required less force to probe as measured with a penetrometer. Furthermore, focal observations showed that Western Sandpipers used more probing behaviors next to channels than in open flats. In previous studies, Dunlins were shown to probe more when sediment was waterlogged (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. We were not able to consistently determine whether a peck or a probe was successful, but we did often see large polychaete worms captured when a shorebird was probing, and never saw such large infauna caught 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 more deeply into the sediment. We therefore expected channels to be particularly important to shorebirds later in the tidal cycle if the sediment near channels retained moisture, allowing prey to remain nearer to the top of the sediment than in the open flats. We did not detect differences in infaunal abundance or depth between ebb and low tides, however. Our sampling approach may not have effectively detected these differences because infauna near the surface may have always burrowed more deeply due to the activity we created when sampling. The hypothesis that shorebirds would preferentially forage along channels during low tide (H2) was not supported either; shorebirds appeared to use channels approximately equally throughout the tidal cycle, perhaps because infauna tended to be in the top-most substrate regardless of the time in the tidal cycle. Given that the total abundance of infauna 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.

Our research was conducted at a generally cool and rainy location. On most survey days there was some rain, and we observed a noticeable slick of water over the mudflats on these days even close to low tide. Nonetheless, sediment water content was still much lower on the mudflats than in channel beds. We would therefore predict that in drier locations, for example more southerly locations, the timing of the tide may have a greater impact on the depth at which infauna would be encountered. 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 tidal cycle.

The relatively small patches of red algae in the mudflats attracted even greater densities of shorebirds than did channels. Our study area and design were not selected to test the value of algal habitats in particular, and all red algae was limited to one section of the observation area; however, the high density of foraging shorebirds in this area suggests that additional microhabitat features may be valuable to shorebirds by increasing prey availability. Infaunal abundance in the red algae patches was not any greater than in other areas of the open flats. However, when collecting infauna samples we did observe that some large invertebrates were inhabiting the algae itself. We took cores of the substrata to measure infauna abundance and these cores likely did not effectively capture the infauna residing on and among the algae. Furthermore, whether more abundant or not, it may be easier for Western Sandpipers and Dunlins to capture invertebrates in this branching algae compared with probing in the sediment. Additionally, we noted that the red algae patches retained small puddles of water. Although the sediment was not softer than that along channels, it was softer than the sediments of the open flats. Also, if the retained water led to increased invertebrate activity, this could assist foraging shorebirds. Finally, shorebirds were well camouflaged when in the red algae so this environment could potentially reduce their predation risk.

In conclusion, we demonstrated that Western Sandpipers and Dunlins preferentially foraged along channels compared with open mudflats in Bandon Marsh. We also demonstrated 3 reasons why channels may be advantageous to shorebirds: Infauna are more abundant, including an important prey item (*Corophium* spp.); infauna are more likely to be near the surface; and the sediment is easier to probe. Additionally, we found initial evidence that mudflat habitat covered with red algae was highly preferred by foraging shorebirds, even compared with channels. Further research could help determine whether this red algae offers greater access to prey, cover from predators, or other advantages to migratory shorebirds.

Microhabitats in an estuary can in some cases be improved or protected by land managers. Although many channels are formed dynamically by tides, this process can also be influenced by management either directly through restoration (e.g., by removing barriers to natural hydrodynamic cycles such as dikes and levees) or indirectly by controlling sediment or freshwater runoff. Our findings can therefore be used to help improve stopover site quality as well as to assist selection of the highest quality conservation areas for at-risk shorebird species.

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