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Intertidal biofilm distribution underpins differential tide-following behavior of two sandpiper species (*Calidris mauri* and *Calidris alpina*) during northward migration

Ariam Jiménez [a, b], Robert W. Elner [c], Corinna Favaro [a], Karen Rickards [a], Ronald C. Ydenberg [a, *]

[a] Centre for Wildlife Ecology, Biological Sciences, Simon Fraser University, 8888 University Drive, British Columbia V5A 1S6, Canada
[b] Universidad de la Habana, Facultad de Biología, 25 e J e I Vedado, Ciudad Habana, Cuba
[c] Environment Canada, Pacific Wildlife Research Centre, 5421 Robertson Road, Delta, British Columbia V4K 3N2, Canada

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ABSTRACT

The discovery that some shorebird species graze heavily on biofilm adds importance to elucidating coastal processes controlling biofilm, as well as impetus to better understand patterns of shorebird use of intertidal flats. Western sandpipers (*Calidris mauri*) and dunlin (*Calidris alpina*) stopover in the hundreds of thousands on the Fraser River estuary, British Columbia, Canada, during northward migration to breeding areas. Western sandpipers show greater modification of tongue and bill morphology for biofilm feeding than dunlin, and their diet includes more biofilm. Therefore, we hypothesized that these congeners differentially use the intertidal area. A tide following index (TFI) was used to describe their distributions in the upper intertidal during ebbing tides. Also, we assessed sediment grain size, biofilm (= microphytobenthic or MPB) biomass and invertebrate abundance. Foraging dunlin closely followed the ebbing tide line, exploiting the upper intertidal only as the tide retreated through this area. In contrast, western sandpipers were less prone to follow the tide, and spent more time in the upper intertidal. Microphytobenthic biomass and sediment water content were highest in the upper intertidal, indicating greater biofilm availability for shorebirds in the first 350 m from shore. Invertebrate density did not differ between sections of the upper intertidal. Overall, western sandpiper behaviour and distribution more closely matched MPB biofilm availability than invertebrate availability. Conservation of sandpipers should consider physical processes, such as tides and currents, which maintain the availability of biofilm, a critical food source during global migration.

1. Introduction

Physical processes over and within soft intertidal zones underlie complex spatial and temporal patterns in the distribution and abundance of biota (e.g. Sewell, 1996). For example, tidal cycles and wave action control intertidal flat hydrodynamics (Le Hir et al. 2000), which influence sediment grain size and penetrability (Jackson et al. 2005), thus structuring constituent epifaunal (above-sediment) and infaunal (within-sediment) invertebrate communities (Whitlatch, 1977). In turn, avian foraging on invertebrates is facilitated by the morphological adaptations of the particular bird species (Nebel et al. 2005). For long-billed shorebirds, the suitability of a foraging habitat is governed by the interaction between bill length and sediment penetrability; longer bills and softer sediments resulting in greater predation success on infaunal prey (Nebel et al. 2005). Conversely, for short-billed birds, foraging habitat is determined by the availability of epifaunal invertebrates (Nebel et al. 2005), which in turn is associated with sediment grain-size and high tidal exposure (Whitlatch, 1977). Thus, shorebird adaptations, morphological and behavioural, for feeding on invertebrates are linked to physical processes on mudflats.

Intertidal biofilm, a ubiquitous thin layer of adhering microorganisms, provides a further example of a biotic community driven by physical processes occurring on intertidal mudflats. Intertidal biofilm comprises a matrix-enclosed community of microphytobenthos (MPB), bacteria, and organic detritus (Kuwae, 2002)

* Corresponding author.
E-mail address: ydenberg@sfu.ca (R.C. Ydenberg).

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bound together and stuck to the sediment surface by copious amounts of extracellular polymeric substances (EPS) secreted by microorganisms living within the biofilm (Stal, 2003; Underwood and Paterson, 2003). As intertidal exposure time increases (Herlory et al. 2004; Hanlon et al. 2006), biofilm builds up as a result of vertical migration of motile diatoms positioning themselves in the photic zone (Mitbavkar and Anil, 2004; Underwood et al. 2005).

Western sandpipers (*Calidris mauri*) and dunlin (*Calidris alpina)* are able to graze on intertidal biofilm as well as peck and probe to exploit macro- and meio-faunal invertebrate prey (Elner et al. 2005; Mathot et al. 2010; Kuwae et al. 2012). Both shorebird species have been observed foraging close to the tide line during ebbing and rising tides (Brennan et al. 1985; Colwell and Landrum, 1993; Butler et al. 2002) and are reported to exhibit a moderate to high degree of overlap in invertebrate consumption (prey composition and size; Couch, 1966; Senner et al. 1989). However, despite similarities in foraging behaviour, their capacities differ due to differences in feeding morphology and bill length (Elner et al. 2005). In particular, the higher density and length of keratinized lateral spines on the western sandpiper's tongue as compared to dunlin are indicative of a greater reliance on biofilm (Elner et al. 2005).

Tides are one of the most important factors affecting the distribution of foraging shorebirds (Connors et al. 1981; Granadeiro et al. 2006). During high tide, intertidal flats are inundated and shorebirds are restricted to roosting sites or inland areas. However, as the tide recedes, intertidal habitats become increasingly available for foraging shorebirds, exposing both invertebrate prey and biofilm (Colwell and Landrum, 1993). Thus, the discovery that small-bodied sandpipers graze on biofilm (Kuwae et al. 2008) has opened a fresh dimension for understanding the physical and biotic factors responsible for shaping western sandpiper and dunlin foraging patterns.

Roberts Bank on the Fraser River Estuary, British Columbia, Canada, is an internationally important stopover and wintering area for shorebirds along the Pacific flyway, with over one million shorebirds estimated to use the area annually (Butler and Campbell, 1987). In particular, hundreds of thousands of western sandpipers arrive in late April to early May each year, en route from wintering areas along the coasts of Central and South America to their Arctic breeding grounds (Butler, 1994). Their numbers are supplemented by tens of thousands of dunlin that overwinter in the estuary as well as migrate through to their breeding grounds in Alaska (Butler and Campbell, 1987). We used the opportunity to examine how the distribution of western sandpipers and dunlin related to the availability of invertebrates and biofilm as the ebbing tide exposed the intertidal habitat. We hypothesized that the two species would segregate their foraging behaviours as the tide retreats based on their different aptitudes for biofilm grazing (Elner et al. 2005; Kuwae et al. 2012). We predicted that if biofilm feeding is more prevalent in western sandpipers, then as the tide ebbs, western sandpipers will (1) feed farther from the tide line than dunlin as biofilm abundance and accessibility increases in exposed sediments; (2) preferentially feed in the areas with highest fine sediment and water content as such conditions promote biofilm abundance, and (3) spend more time than dunlin feeding in the upper intertidal as this region has the highest biofilm abundance on Roberts Bank, as measured by MPB biomass. We measured the dispersion of western sandpipers and dunlin in the upper intertidal zone at Robert Banks, focusing on the behavior of individuals foraging on the intertidal area exposed by the ebbing tide. Also, we examined physical characteristics (sediment grain size and water content), and food abundance (MPB biofilm and invertebrates) within the upper intertidal zone at Robert Banks to determine their relation to shorebird foraging distribution.

2. Methods

2.1. Study site

Roberts Bank is an 8000 ha intertidal area forming part of the Fraser River estuary (49°03′ N, 123°09′ W; Fig. 1). The bank environment comprises a complex of riparian boundaries, intertidal marshes, mud and sand flats, eelgrass meadows, macroalgae and biofilms (Sutherland et al. 2013). Hundreds of thousands of mixed-species shorebirds, primarily western sandpipers and dunlin, use the estuary (Butler, 1994; Butler and Vermeer, 1994). Drever et al. (2014) assessed the population sizes and stopover times of western sandpiper and dunlin during their breeding migration through the estuary over the period 1991–2013.

Tides are semidiurnal with a range of 0.0–3.8 m (North American Datum). Sediments are clay and sand, with the proportion of sand increasing towards the low water mark (Eisma, 1998; Zharikov et al. 2009). An extensive dendritic channel system occupies the upper intertidal and extends down to the mid-intertidal. Also, Roberts Bank hosts a large coal and container port, as well as the Tsawwassen ferry terminal, both connected to the mainland by causeways. Our study site was located off Brunswick Point, a salt marsh promontory north of these causeways.

2.2. Shorebird distribution

We measured the dispersion of western sandpipers and dunlin across the intertidal area as the tide ebbed. A 500 m transect marked with 1 m poles at 50 m intervals was established, with two shorter (0.5 m) markers delineating a circle of 5 m radius around each pole, within which shorebirds were counted (Fig. 1). Flocks of sandpipers often roosted at high tide, but by the time the tide had fallen to the top of the transect 150 m from the high tide line all western sandpipers and dunlin were actively foraging.

Counts were conducted during the morning receding tide beginning between 0525 h and 0910 h, depending on the daily tide conditions and subject to sufficient light to allow shorebird identification. A count sequence began as the receding tide line reached the first marker at 150 m from the high tide line (tidal height 3.6 m), and terminated when it reached the final marker at 650 m from shore (tidal height 2.7 m). Counts were carried out using a 40× spotting scope from a vantage point on Brunswick Point, located 250 m from the centre of the transect. We made sweeps of the transect at 6 minute intervals, recording the location of the tide line with reference to the markers, and the numbers of western sandpipers and dunlin foraging within the 5 m radius circle of each marker. Only days with a minimum average of 25 birds per counts were considered. We completed count sequences on eight days during northward migration in 2008 (April 24 – May 6) and on four days in 2009 (April 26 – April 30). In all, 158 counts were made over the 12 days, for a mean of 13.2 counts per day.

We compared the intensity of tide line foraging for both western sandpipers and dunlin with a tide following index (TFI), defined as the proportion of birds of a given species foraging within 100 m of the ebbing tide edge. The TFI was calculated for each species (western sandpiper and dunlin) and count interval ($n = 158$) using the formula:

$$\mathrm{TFI}_i = \mathrm{Tide\ followers}_i / \mathrm{Total\ birds}_i,$$

where 'Tide followers' denotes the number of individuals of the species foraging within 100 m of the tide edge, and 'Total birds' is