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Sediment in Stomach Contents of Western Sandpipers and Dunlin Provide Evidence of Biofilm Feeding

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Abstract.—Western Sandpipers and Dunlin are capable of grazing biofilm. As there has been no assessment of this dietary constituent in stomach contents, the stomachs of 89 Western Sandpipers and 56 Dunlin collected during breeding migration through the Fraser River delta, British Columbia, Canada, were examined. Invertebrates, traditionally regarded as the principal prey, comprised a minor fraction of mean stomach volumes (Dunlin: <25%; Western Sandpiper <10%). Three phyla accounted for most of these invertebrates: molluscs, annelids and arthropods. In comparison, sediment (a mixture of sediment particles, broken and unbroken diatoms plus organic detritus) comprised the major component of stomach volumes (Dunlin: >40%; Western Sandpipers: >75%). Although the mean volume of sediment was significantly greater in Western Sandpipers than Dunlin, there was no effect of sex for either species. Stomach sediment volume appears a convenient index of biofilm intake and sediment loads indicative of biofilm grazing have been reported in stomach contents from other shorebird species. Re-examination of shorebird diets appears necessary given that conditions promoting biofilm are not necessarily conducive for invertebrate prey. *Received 6 October 2009, accepted 25 May 2010.*

Key Words.—biofilm, foraging behavior, natural diet, sediment, shorebirds, stomach contents.

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Shorebird populations are declining globally (Wetlands International 2006) and a comprehensive understanding of their natural diets appears a prerequisite to conservation efforts (Kuwae 2007). However, there are two contrasting views on the nature of shorebird foraging. On one hand is the original notion that shorebirds are opportunistic foragers whose diets are dictated by the relative availabilities of their macro-invertebrate prey (see Skagen and Oman 1996 for review; Davis and Smith 2001; Andrei *et al.* 2009). Alternatively, while the overall diet for a species may appear either plastic or opportunistic, recent studies reveal complexities that belie the assumed simplicity of the original notion. In particular, the diets of individuals tend to be more specialized than the population as a whole and related to differences in morphological attributes of feeding within subsets, or morphs, of the species (Elner and Seaman 2003; Stein *et al.* 2008). Intra-species variation in shorebird feeding behavior and diet related to morphology (Lauro and Nol 1995; Rubega 1996; Nebel *et al.* 2005) and sex (Puttick 1981; Summers *et al.* 1990; Zharikov and Skilleter 2002; Mathot and Elner 2004) have continued to be identified.

Biofilm grazing, a previously unknown foraging mode and dietary component, was postulated for Western Sandpipers (*Calidris mauri*) and Dunlin (*C. alpina*) based on functional morphology; in particular, the presence of papillae and keratinized spines on the tongues complimented by batteries of salivary glands and taste buds (Elner *et al.* 2005). The biofilm layer (0.1-2.0 mm) on the surface of intertidal flats, comprises a dense mixture of microbes and organic detritus in a mucilaginous matrix secreted by benthic bacteria and microphytobenthos bound up with sediment particles (Decho 1990). Subsequently, Kuwae *et al.* (2008), using evidence from video recordings, stable isotopes and photopigments from microphytobenthos in stomach contents, confirmed that migrating Western Sandpipers feed heavily on unfiltered biofilm during their stop-over

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on the Fraser River delta, British Columbia, Canada. Previously, biofilm was believed to be consumed only by rasping invertebrates and a few specialized fish (Decho 1990; Horn and Ojeda 1999) although faeces of Shelduck (*Tadorna tadorna*) suggest that they may feed on both blue-green algal mats in shallow water (Walmsley and Moser 1981) and diatom "thickets" on tidal mud flats (Meininger and Snoek 1992).

Given the mechanics of transporting biofilm up a bill, Elner *et al.* (2005) hypothesized that biofilm feeding may be more prevalent in Western Sandpipers than Dunlin due to their comparatively shorter bills. Also, Elner *et al.* (2005) hypothesized that within populations, shorter-billed individuals would be better able to feed on biofilm. In both Western Sandpipers and Dunlin, females have longer bills than males (Page and Fearis 1971; Meissner and Pilacka 2008), suggesting the possibility of sex-related differences in biofilm consumption within species. In Western Sandpiper, the dimorphism in bill size is known to be associated with differences in the use of surface (pecking) versus sub-surface (probing) foraging modes (Mathot and Elner 2004).

Here, we used microscopic techniques to analyze the stomach contents of Western Sandpipers and Dunlin in order to further assess biofilm feeding as well as possible species- and sex-related differences in diet.

METHODS

Western Sandpipers and Dunlin were obtained in the course of other studies (Kuwae *et al.* 2008). All birds were collected by shotgun under permit between April 22 and May 10, 2003 on Roberts Bank, an intertidal mudflat in the Fraser River estuary near Vancouver, British Columbia (49°05'N, 123°12'W) (Fig. 1) during northward migration. Totals of 32 female and 57 male Western Sandpipers and 21 female and 35 male Dunlin were sampled. Birds were anatomically sexed based on the presence of either ovaries or testes. Eight Western Sandpipers and four Dunlin had insufficiently developed reproductive organs to allow for unambiguous sex assignment and were excluded from the analyses. The majority of collections (115 out of 145) were carried out on rising tides (after a full foraging cycle) to ensure that birds had ample opportunity to feed.

Birds were placed in an insulated container filled with dry ice immediately after collection. On arrival at the laboratory, stomachs and intestines were extracted and stored in 80% ethanol. Vials were labelled with a three digit code in order to allow stomach contents to be scored blind to species and sex. Later, the contents were washed with 80% ethanol into a Petri dish marked with a 20 cell grid. After settling for approximately 15 minutes, invertebrates in stomach contents were identified to the lowest possible taxonomic level (Kozloff 1987) using a dissecting microscope at 40× magnification. Indicator fragments, recognizable indigestible body parts such as polychaetes jaws and bivalve umbones, were used to identify incomplete prey. All stomach content analyses were carried out by a single observer (DRL).

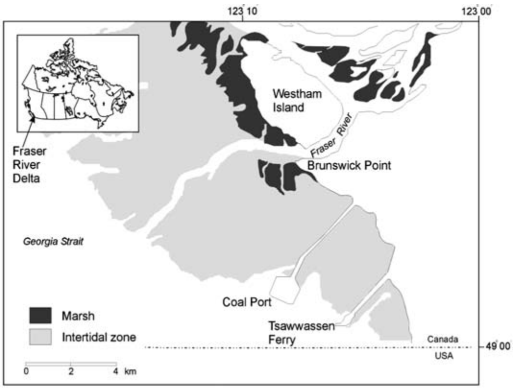

Figure 1. Roberts Bank, Fraser River Delta, British Columbia, Canada.

The volumetric contribution of contents were estimated using the points method (Swynnerton and Worthington 1940). The points method offers advantages over other methods for quantifying stomach contents (such as weighing prey items) as the technique is simple and not unduly influenced by either the presence of small organisms in small numbers or heavy bodied prey (Hynes 1950). Briefly, ten cells were randomly selected from the 20-cell grid on the Petri dish and each stomach content item type (from three general categories: invertebrates, sediment and "other" which included both macro-algae and plant material) was assigned points based on its contribution to the total volume. The sum of the volumetric contribution of each stomach content item was calculated for the ten cells and the estimate multiplied by two to obtain the volumetric contribution of each item for the entire stomach (i.e. 20 cells).

Statistical analyses

We used ANOVAs to test whether species- and sex-related differences were associated with differences in the prevalence of biofilm (using sediment as an index) and invertebrates in the diet. Sediment was used as an index of biofilm consumption for the following reasons. First, inspection of the samples at 200× magnification revealed that the sediment contained diatoms and organic detritus, two major components of biofilm (Decho 1990). Secondly, as the mucilaginous extra-polymeric secretions (EPS) of biofilm bind to sediment (de Brouwer *et al.* 2002), unfiltered grazing of biofilm necessarily involves the ingestion of sediment (Elner *et al.* 2005).

We also tested whether the relative volumetric contributions of different invertebrate phyla found in the

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stomach contents differed according to species and sex. To do this, we assessed the proportional representation of the three major phyla (molluscs: surface and below surface prey, annelids: surface and below-surface prey, and arthropods: surface prey) (Sutherland *et al.* 2000; Mathot 2005).

In all cases, non-significant interactions ($p > 0.05$) were removed from the models. Proportion data were ln (x+1) or arcsine square root transformed prior to analyses as appropriate, in order to normalize their distributions (Zar 1999). Data were visually inspected to confirm that they satisfied the assumption of homogeneity of variances. Values presented in the text are means ± 1 S.E.

Results

Invertebrate prey comprised a mean of 8.5 ± 0.7% and 24.4 ± 2.1% of stomach volumes for Western Sandpipers and Dunlin, respectively (Table 1). Three phyla accounted for most of these invertebrates; molluscs, made up of both gastropods and bivalves (Western Sandpipers: 0.3 ± 0.1%; Dunlin: 12.8 ± 2.2%), annelids (Western Sandpipers: 2.0 ± 0.2%; Dunlin 3.3 ± 0.3%) and arthropods (Western Sandpipers: 5.5 ± 0.6; Dunlin 4.6 ± 0.6%). Arthropods included: amphipods, cumaceans, ostracods, harpacticoid copepods, insects, tanaids, and unknown arthropods.

The composition of the invertebrate component of the diets differed between Dunlin and Western Sandpipers, as well as between males and females (see Table 2 and Fig. 2). The effect of sex on the percent contribution of molluscs to the animal component of diet varied according to species (sex × species: $F_{1,138} = 7.93$, $p = 0.006$). A greater proportion of the animal diet came from molluscs in Dunlin than in Western Sandpipers. Sex-related differences in mollusc consumption were only significant for Dunlin, with females consuming more molluscs than males. The effect of sex on the percent contribution of annelids to the animal component of diet also varied according to species (sex × species: $F_{1,138} = 5.74$, $p = 0.018$). Western Sandpipers consumed more annelids as compared against Dunlin, and again sex-related differences in annelid consumption were only significant for Dunlin, with females consuming significantly more annelids than males. There was no significant sex × species interaction on the relative contribution of arthropods to the diet ($p > 0.35$). However, the contribution of arthropods to the animal component of the diet did vary according to species ($F_{1,138} = 54.71$, $p < 0.0001$). Western Sandpipers had a significantly greater amount of arthropods among their invertebrate prey than did Dunlin.

For both shorebird species, the major component of their stomach contents was sediment, comprised of mineral particles, broken and unbroken diatoms plus organic detritus (Table 1; Fig. 3). There was no sig-

Table 2. ANOVA results for the relative contribution of molluscs, annelids and arthropods to the invertebrate component of the diets of Western Sandpipers and Dunlin. Note that the total sample size for these analyses is 142, because 3 of the 145 stomach contents analyzed contained no animal components.

	df	SS	F	p
Dependent variable: ln (proportion molluscs + 1)				
Species	1	2.51	129.66	<0.0001
Sex	1	0.19	10.07	0.002
Species × Sex	1	0.15	7.93	0.006
Error	138	2.67		
Dependent variable: ln (proportion annelids + 1)				
Species	1	0.20	9.06	0.003
Sex	1	0.04	1.91	0.17
Species × Sex	1	0.13	5.75	0.018
Error	138	3.06		
Dependent variable: ln (proportion arthropods + 1)				
Species	1	1.75	54.71	<0.0001
Sex	1	0.11	3.33	0.070
Error	139	4.44		

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Table 1. Mean volumetric contributions (% points ± S.E.) for the major categories of contents from the stomachs of Western Sandpiper and Dunlin sampled on Roberts Bank, Fraser River delta, during spring migration, April, May 2003.

			Volumetric contribution (mean ± S.E.)							
Species	Sex	N	Sediment	Invertebrate	*annelid*	*arthropod*	*mollusc*	*gastropod*	*bivalve*	Other±
WESA	M	57	75.7 ± 1.6	8.6 ± 0.9	1.6 ± 0.2	5.9 ± 0.9	0.3 ± 0.1	0 ± 0	0.3 ± 0.1	15.7 ± 1.5
	F	32	76.1 ± 2.8	8.5 ± 0.7	2.6 ± 0.4	4.9 ± 0.7	0.4 ± 0.1	0 ± 0	0.4 ± 0.1	15.4 ± 2.9
	Overall	89	75.9 ± 1.4	8.5 ± 0.7	2.0 ± 0.2	5.5 ± 0.6	0.3 ± 0.1	0 ± 0	0.3 ± 0.1	15.6 ± 1.4
DUNL	M	35	43.0 ± 3.2	20.0 ± 2.3	2.9 ± 0.3	5.2 ± 0.8	8.0 ± 2.1	0.2 ± 0.2	7.8 ± 2.0	37.1 ± 3.0
	F	21	39.8 ± 3.5	31.9 ± 3.8	4.0 ± 0.6	3.7 ± 0.8	20.9 ± 4.2	0 ± 0	20.9 ± 4.2	28.3 ± 4.8
	Overall	56	41.8 ± 2.4	24.4 ± 2.1	3.3 ± 0.3	4.6 ± 0.6	12.8 ± 2.2	0.1 ± 0.1	12.7 ± 2.2	33.8 ± 2.6

±'Other' diet items included fragments of macro-algae and seeds from plants.

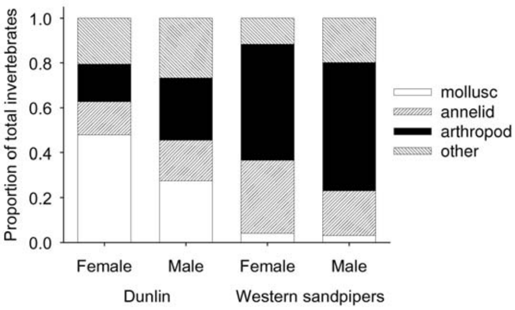

Figure 2. Contribution of molluscs, annelids, arthropods and 'others' to the invertebrate component of Dunlin and Western Sandpiper diets. 'Others' includes foraminiferans, nematodes and fragments of unidentified invertebrates.

nificant interaction between sex and species on the proportion of sediment in the stomach ($p > 0.40$). The volume of sediment in the stomach did vary according to species ($F_{1,\ 141} = 158.55$, $p > 0.0001$), but not sex ($F_{1,\ 141} = 0.06$, $p = 0.80$). Western Sandpipers had a significantly higher proportion of sediment in their stomachs than Dunlin.

DISCUSSION

The contents of the Western Sandpiper and Dunlin stomachs examined provided evidence in support of active grazing on unfiltered biofilm. Stomachs for both species were dominated by volumes of sediment that

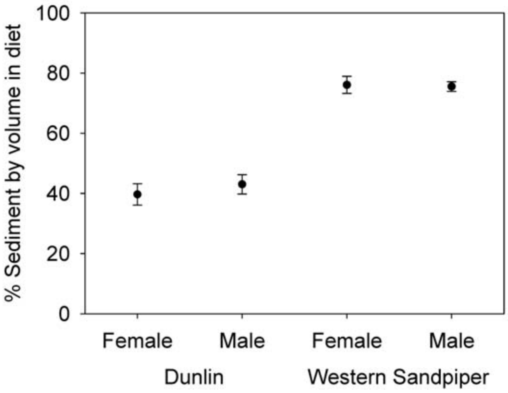

Figure 3. Proportion contribution of sediment to the total food as a function of sex and species. Sediment was used as an index of biofilm feeding (see Methods). Values presented are means ± 1 S.E. Note that raw proportions are presented in the figure.

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exceeded invertebrate remains by an average approaching 9:1 for Western Sandpipers and 2:1 for Dunlin. Enigmatically, most previous studies on the stomach contents of Western Sandpipers and Dunlin do not mention sediment content (Couch 1966; Holmes 1966; Baker 1977; Senner *et al.* 1989; Brennan *et al.* 1990; Skagen and Oman 1996; Lee *et al.* 1999), presumably because it was either absent or ignored as not being of nutritional significance. An exception is Bengston and Svensson (1968), where sediment was recorded in all 23 Dunlin stomachs examined, often to 70-80% by volume. The volumes of sediment found here are on par with Bengtson and Svensson (1968) and far exceed values that might be expected if the material was ingested coincidentally only while foraging on invertebrates, either because it was present on and around the prey or in the digestive tracts of the consumed prey (Hui and Beyer 1998). Rather, the most parsimonious explanation is that the sediment is taken-up in quantity while grazing biofilm. Further, not only does sediment appear a compelling indicator of biofilm feeding but without it, the invertebrate components alone would not account for the nutritional needs of the birds at a time when they are feeding voraciously to "re-fuel" en route to the breeding grounds (Clark and Butler 1999; Guglielmo and Williams 2003).

Kuwae *et al.* (2008) estimated that biofilm accounted for between 45–59% of the total diet by mass, or approximately 50% of the total daily energy requirement, of Western Sandpipers during migration. We found 75.7 ± 1.43% (range 32-95) by volume of the stomach contents were comprised of sediment for Western Sandpipers collected on spring migration at the same site. Although we did not estimate the proportion of diatoms in the sediment collected from stomach contents in this study, the estimated contribution of biofilm to the diet by Kuwae et al. (2008) and the percent contribution of sediment to the stomach contents found in this study are similar. Thus, sediment loads may complement stable isotope methodology by providing an alternative index for assessing biofilm intake.

Biofilm feeding was previously predicted for both Western Sandpipers and Dunlin based on their bill and tongue morphology (Elner *et al.* 2005). Also, given inter-specific differences in bill and tongue morphology, Elner *et al.* (2005) postulated that the extent of biofilm feeding would be greater for Western Sandpipers. Our results support this prediction, as we found that Western Sandpipers had significantly more sediment in their stomachs than Dunlin. Sex-related differences in bill morphology within species may be associated with differences in feeding mode (pecking versus probing) and diet (Elner and Seaman 2003). However, despite sex-related differences in bill morphology within species (Page and Fearis 1971; Meissner and Pilacka 2008), we did not find evidence for sex-related differences in the amount of sediment in the stomachs within either species.

We did observe sex-related differences in the macro-invertebrate components of diet that further indicate differentials between surface and sub-surface food types and feeding modes (Mathot and Elner 2004). In both species, males tended to have a higher consumption of arthropods (Fig. 2); prey which are more common on, as opposed to under, the surface (Sutherland *et al.* 2000). Concomitantly, males had a lower consumption of molluscs, made up mostly of bivalves, a characteristic infaunal prey type (Mathot 2005). In Curlews (*Numenius arquata*), males, which have shorter bills than females, also consume significantly more surface-living invertebrates (Berg 1993). These sex-related differences in diet were only statistically significant in Dunlin. However, given that sex-related differences in diet specializations can have population-level consequences, including differential susceptibility of subsets of the population to habitat loss or degradation (Durell 2000), further study is warranted.

Macro-invertebrate prey have long been considered the major dietary component of shorebirds (Sutherland *et al.* 2000). Our results on the macro-invertebrate constituents in the natural diets of Western Sandpipers and Dunlin are in general agreement with previous findings of annelids, arthropods

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and molluscs as the most prevalent invertebrates in the diet (Couch 1966; Bengston and Svensson 1968; Senner *et al.* 1989; Brennan *et al.* 1990; Lee *et al.* 1999). However, there is now compelling evidence that such a view of shorebird diets is too restrictive. More recently, meiofaunal invertebrates (<500 µm) have been shown to form part of the natural diet of Western Sandpipers (Sutherland *et al.* 2000) and now an even smaller component, biofilm, needs to be considered. Given the gross morphological, ecological and behavioral similarities between small shorebirds, Western Sandpipers and Dunlin appear unlikely to be the only shorebirds capable of biofilm grazing. Indeed, sediment loads reported in the digestive tracts of twelve other shorebird species, ranging from 3-60% of the total volume of stomach contents (Reeder 1951; Beyer *et al.* 1994; Hui and Beyer 1998) are suggestive of biofilm grazing. Therefore, given that conditions promoting intertidal biofilm attractive to shorebirds are not necessarily conducive for invertebrate prey, further studies, including high resolution stomach content analyses, are necessary to re-assess the purported natural diets for most other shorebird species.

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