

INVERTEBRATE SURVEYS ON THE MENDENHALL WETLANDS

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(Photographs of common invertebrate taxa are included in Armstrong et al. 2003)

Abstract

Macroinvertebrates were found at higher densities in intertidal sediments (without a covering layer of *Fucus*, barnacles, or mussels) than in *Fucus* beds (attached to mussels or pebbles or other hard surfaces) or mussel cobbles (clumps of mussels resting on substrate). However, avian feeding activity was not related to the amount of intertidal sediment area in spring. Spring 'hot spots' for avian feeding activity were not distinguished by a high density of macroinvertebrates or by high standing crops (density \times area) of total macroinvertebrates or of any major prey type, except for standing crop of snails in *Fucus* and cobbles. Other factors affecting avian use of particular sites include risk of predation, availability of resting areas, and social behavior. This survey is the only known semiquantitative assessment of invertebrates of sedimentary intertidal habitats in Southeast Alaska. However, our survey is necessarily a preliminary one, and we recommend a more complete survey, with a larger sample size and a wider distribution of samples.

Introduction.

The Mendenhall Wetland, located within the City and Borough of Juneau, is of ecological interest because of the seasonally dense wildlife (especially birds), the presence of nursery areas for fishes, and the relatively rapid changes in vegetation communities and zonation due to post-glacial uplift. This area is used intensively for recreational walking and for waterfowl hunting. Because of its urban location, it is also vulnerable to potential developments near the airport and the proposed second crossing of Gastineau Channel.

In conjunction with a survey of bird activity on the wetland (USFWS Coastal Programs project no. 701812G146; Armstrong et al. 2003), we conducted a preliminary survey of macroinvertebrates in key habitats on the wetland. Many of the birds on the wetland forage on invertebrates (see Appendices), and prey density is one factor that may help determine the distribution of birds in the area. However, very little is known about the diversity, distribution, and density of invertebrates in intertidal wetlands in Southeast Alaska (T. C. Shirley, pers. comm.) or even in Alaska at large (but see Powers et al. 2002 for the Copper River Delta). This report constitutes the first survey of macroinvertebrates on the wetland and, indeed, the only known semiquantitative survey of invertebrates of sedimentary intertidal habitats in Southeast Alaska.

We focused chiefly on the spring season, for practical reasons related to the funding cycle. However, we also include in this report some information from pilot surveys in the previous fall and winter. The primary objective of the study was to compare the diversity, distribution, and density of macroinvertebrates in areas known to support high vs. low concentrations of foraging birds in spring. A secondary objective was a comparison of spring surveys with those in fall and winter. Finally, we give several sources of information on diets of bird species found on the wetland, provide references about macroinvertebrates that are common on the wetland, and summarize some particularly interesting interactions of potential relevance to the wetland (see Appendices).

Methods

Spring surveys. We chose three ‘hotspots’ of bird activity (Mendenhall River mouth, Fish Creek mouth, and Neilson Creek mouth near Era helicopters) and three ‘coldspots’ of lower activity (NineMile Creek mouth, FiveMile Creek mouth, and the broad flats between Lemon Creek and Vanderbilt creek mouths), based on data on avian foraging activity from the 2002 spring migration period (Armstrong et al. 2003). In each area, we sampled the density of macroinvertebrates in up to three common habitats: sediments lacking overlying *Fucus* or mussel beds, *Fucus* beds (expanses of this alga, attached to pebbles, mussels, or other hard surfaces), and mussel cobbles (clumps of mussels) lying on the sediments. Field sampling was done during times of diurnal minus tides, 30 April – 2 May, 2003.

Sediments were sampled by pressing a 15-cm-diameter ring into the substrate about 6 cm (a depth considered to be adequate for detection of invertebrates available to most foraging shorebirds, Sherfy et al 2000), slipping a flat shovel blade under the ring, and lifting the sample from the matrix. These samples were then sieved (2-mm mesh) on location to extract the larger organisms; note that thin organisms of somewhat greater length probably slipped through the mesh (Crewe et al. 2001). The extracted organisms were identified and counted in the field; identifications were later confirmed or revised in the laboratory by Baldwin. *Fucus* beds and mussel cobbles were sampled by timed searches (4 min), in which Baldwin searched carefully under and among the *Fucus* fronds, and between and below the mussel cobbles, in an area approximately 1m². Amphipods were divided into size classes (> or < 1 cm). Each habitat in each area was normally sampled with five replicates separated at least by several meters (5 replicates/habitat X 3 habitats X 6 areas). For purposes of presenting overall results, we have pooled invertebrate taxa into types (large amphipods (mainly *Spinulogammarus* and *Eogammarus*) and small amphipods (mostly amphipods

and small *Eogammarus*), isopods (chiefly *Pentidotea* and *Gnorimosphaeroma*), clams (mostly *Macoma*), snails (mostly *Littorina* and *Tectura*), worms (mostly nereids, phyllodocids, nephtyids, and capitellids).

Data were analyzed by Anova (Model I, with Type III Sums of squares for unbalanced data), using XLStat 6.1.8 (by Addinsoft).

Fall and winter surveys. These pilot surveys were done in some of the same locations as the spring surveys, permitting seasonal comparisons. However, some locations sampled in these seasons were not selected for the spring comparisons (Salmon Creek mouth, Barge area on the Mendenhall River, Otter Pond/ JunkCar Slough near the gazebo on the airport dike trail) and some locations sampled in spring were not sampled in the other seasons (the three cold spots). All surveys were done at times of minus tides. Fall surveys were conducted 8-10 September and 23-24 September, 2002; winter surveys were conducted 18-20 February 2003.

Habitat availability. Potential prey abundance for invertebrate-eating wetland birds is a function of both the density of macroinvertebrates in each habitat and the amount of habitat available at a location. Therefore, when the surveys were complete, Willson estimated cover (absolute area and percent cover) of the three principal habitats in the locations used for the spring invertebrate surveys plus Salmon Creek mouth. Four parallel transects were paced from the edge of continuous vegetation (sedges or grasses) to the waterline at a low tide (14-17 July, 2003), recording the habitat type every 5 paces (or 7 paces on the larger locations). The borders of the location sampled for percent cover were arbitrarily set to include the central portion of the 'spots' of the bird surveys. Areas were estimated from aerial photographs provided by Richard Carstensen.

Comparison of two special locations in four seasons. Otter Pond and JunkCar Slough, located near the dike trail gazebo, were sampled in four seasons, because they provide interesting contrasts to our other sample sites. They are distinguished from the other locations sampled by a lower salinity (judging from the invertebrates found there), and they harbor populations of tube-dwelling corophiid amphipods (*Americorophium*), which are known to be of immense importance to migrating shorebirds on the east coast (see appendix 1). These sites are used seasonally by migrating yellowlegs, dowitchers, and small sandpipers, when not disturbed by errant dogs. Only sediments were sampled in these locations: in Otter Pond on the side nearest the trail, and in JunkCar Slough both near the top of the slough and near the lower end. Summer sampling was done on 18 July 2003.

Results

Percent cover of key habitats. The sampled portions of the spring hotspots and cold spots ranged in estimated size from 4 ha to 88 ha (Table 1). Hot and cold spots were not clearly distinguishable by the frequency distribution of cover types (Table 1), but it may be noteworthy that both 9Mile and Lemon creeks (cold spots) lacked mussel cobbles. The three hotspots ranked highest in area with mussel cobbles, but Era actually had very little absolute amount of area of this habitat. Two of the three hotspots ranked highest in the estimated percent cover and absolute area of *Fucus* beds (Table 1). Lemon Creek (a cold spot) was very similar to Era (a hot spot) in absolute area of *Fucus*, but the *Fucus* beds at Lemon Creek were much less dense, with very short fronds, so the potential cover for invertebrates was actually much less than at Era. The amount of sediment area did not distinguish hot and cold spots.

Spring surveys. Two-way ANOVAs (habitat X location; Table 2a) showed that densities of macroinvertebrates (totals, and each type separately) differed significantly among habitats and among locations. Interaction terms were all significant, and in general the significance reflected different patterns of density among categories not just differences in magnitude.

Post-hoc Tukey tests revealed the sources of significance (Table 2b). Total invertebrates were generally much more dense in sediments than in *Fucus* beds and mussel cobbles (Table 2b). Amphipods and isopods tended to be most common in mussel cobbles, clams in sediments, and snails on *Fucus*.

The large flat isopod *Pentidotea* was not distributed differently among habitats or locations, but the smaller, hump-backed *Gnorimosphaeroma* clearly favored cobble habitats and tended to be most dense at Mendenhall and 5Mile. Small amphipods were not distributed differently among habitats or locations, but large amphipods were densest in cobbles and secondarily on sediments.

The three hotspots of avian feeding activity (Mendenhall, Fish Ck, Era) were not distinguished by higher macroinvertebrate densities (Table 2b). The highest recorded invertebrate density occurred at 5Mile (a cold spot), and relatively low densities were recorded at Mendenhall and Era. (However, note that, despite a significant location effect in the anova, the Tukey test did not distinguish among locations.) Snail density was relatively high at the three hotspots plus one cold spot (5Mile). Amphipods were densest at Era (hot) and Lemon Ck (cold). Isopods were densest at Mendenhall (hot), followed by 5Mile (cold), and clams were most dense at 5Mile.

An index of the standing crop of invertebrates found at each location, suitable for ranking purposes, was obtained by multiplying the average density of the principal invertebrate types by the area of their principal habitat type(s) at each location (Table 3). Hotspots did not rank above coldspots for standing crop of worms or clams (or their sum) in sediments, or of amphipods in mussel cobbles. Isopods in mussel cobbles had the highest standing crop at Mendenhall and Fish Ck (hot), followed by 5Mile (cold) and Era (hot). The three hotspots ranked highest in standing crop of snails in *Fucus* and cobbles. The grand totals for the abundance index were not a good indication of hot or cold spots.

Fall surveys. Two-way anovas showed that the densities of most types of macroinvertebrates differed significantly among habitats, although total invertebrate density did not differ significantly (Table 4). Significant interaction terms reflected differences in pattern as much as differences in magnitude. *Fucus* beds and mussel cobbles commonly had higher densities of snails, amphipods, and isopods than sediments (Table 4a). Clam density was high in sediments, but worms were generally scarce.

Differences among locations were significant in all cases except isopods (Table 4a), although in some instances the posthoc Tukey test could not locate the source of the difference (Table 4b). Fish Creek ranked the highest for snails, the Barge area was highest in amphipod density, and Salmon Creek was highest for clams, isopods, and total invertebrates.

The isopod *Pentidotea* was not distributed differently among habitats or locations, but *Gnorimosphaeroma* was most dense in cobble habitats, and did not differ among locations. Large amphipods were most common in cobbles also, but the density of small ones did not differ by habitat. Both large and small amphipods were most dense in the Barge area.

Winter surveys. Two-way anovas showed that habitat differences and the interactions of habitat X location were significant for all groups except isopods, although the posthoc Tukey test detected a difference in isopod density between mussel cobbles and the other habitats (Table 5). Worms and clams were densest in sediments, and amphipods and snails in cobbles and *Fucus* (Table 5b).

Differences among locations were significant for clams, snails, amphipods, and total macroinvertebrates. Fish Creek ranked highest in snail density, but lowest in amphipod density. Clams and total invertebrates were most dense at Salmon Creek.

The isopod *Pentidotea* was uncommon in all habitats, with a tendency to be most dense in *Fucus* beds, but *Gnorimosphaeroma* was, as in other seasons, most dense in cobbles. Neither isopod was

distributed differently among locations. Large amphipods were distributed similarly among habitats and locations, but small ones were denser in cobbles and *Fucus* than in sediments, and tended to be more common in the Barge area.

Three-way anova (habitat x location x season), for two locations sampled in three seasons

The anova showed that habitat and location factors had significant effects on the density of macroinvertebrates, and the interaction term was also significant (Table 6). Season had a marginally significant effect. Post-hoc Tukey tests detected a difference in invertebrate density between Fall (104) and Spring (282), but Winter (199) was indistinguishable from the other seasons. The same test found significant differences between Sediments (377) and the other habitats: *Fucus* beds (109) and Mussel cobbles (155). Differences between locations were significant (Mendenhall 137, Fish Ck 261).

The breakdown of results by prey type is not presented in detail here. Mendenhall and Fish Creek were similar in the densities of worms, isopods, and clams, but Fish Ck had more snails and amphipods. Sediments contained more worms and clams, and fewer isopods and snails; the density of amphipods was not distinguishable by Tukey test. Seasonal differences were not detected by Tukey test for any prey type.

Four-season comparison of invertebrate density at Otter Pond and JunkCar Slough.

Two-way ANOVA (site x season) showed significant differences in total invertebrate density among the three sites considered, although the post-hoc Tukey test did not discriminate among sites (Table 7). The ANOVA also showed significant effects of season (not detected by Tukey test), and a significant interaction term. A post-hoc Tukey test found significantly greater density of amphipods (both *Eogammarus* and *Americorophium*) in Fall, although there was also a trend for higher densities of clams (Table 7). There were few differences among the three sites, except for a higher density of clams in Otter Pond, and possibly a lower density of amphipods (location effect significant in anova, but not detected by Tukey). These locations supported a lower density of macroinvertebrates, in general, than most of the other locations in the survey.

Discussion

Although clear differences emerged among habitats and locations in the densities of macroinvertebrates, there was no detectable association with hot or cold spots of avian foraging activity in spring. However, the three hotspots did have a higher index of snail abundance, as well as a higher summed index of snails, amphipods, and isopods. Snails, as well as crustaceans, are commonly recorded prey of a number of the birds that occur on the wetland (e.g., in the accounts in *The Birds of North America*, see Appendix 4), but these generalized accounts seldom indicate the genera or species of prey. Therefore, we cannot say that the snails we recorded on the wetland (mostly *Littorina* and *Tectura*) or the numerous isopods *Gnorimosphaeroma* wedged in among the mussels were actually sought as prey. Seasonal differences in macroinvertebrate density were evident but not consistent among locations or prey types.

Prey distribution is one factor that contributes to the spatial distribution of birds (Kelsey and Hassall 1989). The risk of predation is known or suspected to affect avian distributions in many cases (e.g., Dierschke 1998, Lima 1998). On the wetland, the principal predators of birds are probably other birds, including eagles, hawks, and owls; in one case, a researcher proposed that dunlins flocked over open ocean when their feeding areas were submerged in order to avoid predation by raptors (Dekker 1998). Good visibility in all directions is a primary defense against such predators (Dekker 1998), so proximity to trees may tend to be avoided. Social behavior (here in the form of flocks of migrants), which may have evolved in part because of predation risks, also influences distribution, in that birds accustomed to foraging in flocks typically exhibit a contagious distribution (i.e., the individuals are not distributed independently of each other). The availability and proximity of resting sites can also influence avian distributions; for example, in the Bay of Fundy, migrating shorebirds seldom use mudflats that lack roosting sites (Matthews et al. 1992).

Therefore it is not surprising that few correlations emerged between prey density or abundance and levels of avian foraging activity.

Limitations of the survey. This survey was obviously limited in scope and must be considered to be a preliminary one. We do not know what the birds on the wetland were actually eating, so it is not possible to determine which prey types are most important to monitor here. Shorebird diets are very flexible (Skagen and Oman 1996): for example, migrating dunlins foraged principally on *Macoma* clams at a site in Alaska (Senner et al. 1989), but in other places they foraged chiefly on corophiid amphipods, gastropods, and nereids (Mouritsen 1994), fly larvae (Dierschke 1998), or polychaetes and amphipods (Dierschke et al. 1999). Diets may differ between day and night (Mouritsen 1994). Invertebrate distributions are notoriously patchy, and five replicate samples spread over a portion of the survey locations can hardly hope to represent a complete picture of invertebrate distribution. By definition, estimates of standing crop do not account for rates of recruitment to prey populations nor for rates of prey depletion by predators – which is known to be important frequently in the case of shorebirds in wetlands (e.g., Schneider 1978, Murdoch et al. 1986, Peer et al. 1986, but see Sewell 1996). Subtleties of invertebrate distributions with respect to patterns of inundation, substrate grain (Kelsey and Hassall 1989), salinity, etc., were obviously neglected, as were prey activity patterns, including responses to predator activity (Backwell et al. 1998). We did not sample the water's edge, where ducks and some shorebirds commonly feed, although it seems likely that the birds are feeding on invertebrates that emerge from or retreat to the substrates as water levels change with the tides. We also did not sample the areas of scattered sedges where some small shorebirds and songbirds (larks, pipits, longspurs, sparrows) sometimes forage. Fish are another important prey for some birds on the wetland, but they were not the focus of this survey. A much more complete survey, with attention to subtle differences in habitat conditions, more replication, and finer temporal partitioning, is highly recommended.

Acknowledgments

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Table 1. Estimated size of selected sampling areas on the Mendenhall wetlands, percent cover and area of three key habitat types for macroinvertebrates. In most cases ‘Other’ was standing water in tide pools or moving water in sloughs, but for Salmon Creek it also included *Ulva*. The three hotspots for bird activity are underlined, as are their habitat coverages when they rank in the top three. Salmon Creek data are presented here but are not part of the formal comparison of hot and cold spots.

Location	Estimated area (ha)	No. of points	Percent cover (area in ha)			
			<i>Fucus</i>	Sediments	Mussel cobbles	Other
<u>Fish Ck</u>	20	408	<u>46% (9.2)</u>	24% (4.8)	<u>18% (3.6)</u>	12%
<u>Mendenhall R</u>	88	1011	11 (9.7)	<u>79 (69.5)</u>	<u>7 (6.2)</u>	3
<u>ERA Ck</u>	9	454	<u>66 (5.9)</u>	27 (2.4)	<u>4 (0.4)</u>	3
5Mile Ck	4	109	23 (0.9)	60 (2.4)	2 (0.1)	15
9Mile Ck	10	130	3 (0.3)	75 (7.5)	--	22
Lemon Ck	52	555	11 (5.7)	61 (31.7)	--	28
Salmon Ck	29	428	28 (8.1)	41 (11.9)	14 (4.1)	17

Table 2a. Summary of two-way ANOVA p-values (Habitat x Location) for density of macroinvertebrates in spring. # Post-hoc Tukey test did not distinguish among locations

Prey type	Habitat	Location	Interaction
Total invertebrates	<0.0001	<0.0001#	<0.0001
Worms	<0.0001	0.052#	0.015
Snails	<0.0001	<0.0001	<0.0001
Amphipods	<0.0001	<0.0001	<0.0001
Large	<0.0001	<0.0001	0.0001
Small	0.640	0.124	0.476
Isopods	<0.0001	<0.0001	<0.0001
<i>Pentidotea</i>	0.778	0.282	0.401
<i>Gnorimosphaeroma</i>	<0.0001	<0.0001	<0.0001
Clams	<0.0001	<0.0001	<0.0001

Table 2b. Post-hoc Tukey tests identifying sources of significance in the ANOVAs for macroinvertebrate densities (per m²) in spring.

Habitat (* indicates a significant difference between adjacent values; n.s. indicates not significant). Note that when the values are not in numerical order, the third column that indicates statistical significance refers to Sediments vs Mussel cobbles

Prey type	Mean values for each habitat					
	Sediment		<i>Fucus</i>		Mussel cobbles	
Total invertebrates	748	*	103	n.s.	171	
Worms	70	*	3.6	n.s.	0.6	*
Snails	7.3	*	91	*	46	*
Amphipods	17	n.s.	0.7	*	41	*
Large	15	n.s.	0	*	38	
Small	1.8	n.s.	0.7	n.s.	3.2	*
Isopods	3.7	n.s.	5.0	*	74	
<i>Pentidotea</i>	1.8	n.s.	2.1	n.s.	1.7	
<i>Gnorimosphaeroma</i>	15	n.s.	2.9	*	72	
Clams	647	*	0.8	n.s.	0.2	*

Location (Locations ranked in ascending order; locations with the same letter are indistinguishable by the Tukey test). Avian hotspots are underlined.

Total invertebrates

9Mile	<u>M'hall</u>	<u>ERA</u>	Lemon	<u>Fish</u>	5Mile
156a	219a	260a	317a	344a	805a

Worms

Lemon	<u>ERA</u>	9mile	5mile	<u>M'hall</u>	<u>Fish</u>
3.9a	15a	23a	26a	33a	55a

snails

Lemon	9mile	<u>ERA</u>	<u>M'hall</u>	5mile	<u>Fish</u>
2a	4a	45ab	45ab	72b	85b

Amphipods (Large)((Small))

9mile	<u>Fish</u>	<u>M'hall</u>	5mile	Lemon	<u>ERA</u>
0a	2.5a	12a	14a	18ab	49b
(0)a	(1.5)a	(11)a	(7.3)a	(18)ab	(49)b
((0))a	((0.9))a	((2.0))a	((6.3))a	((0))a	((0))a

Isopods (Gnorimosphaeroma)((Pentidotea))

9mile	Lemon	<u>ERA</u>	<u>Fish</u>	5mile	<u>M'hall</u>
0a	0a	12a	16a	23ab	64b
(0)a	(0)a	(6.3)a	(15)a	(21)ab	(63)b
((0))a	((0))a	((5.2))a	((1.3))a	((2.0))a	((1.4))b

Clams

<u>M'hall</u>	9mile	<u>ERA</u>	<u>Fish</u>	Lemon	5mile
59a	128ab	139ab	176ab	282ab	667b

Table 3. Indices of standing crops of macroinvertebrates at each location in spring. The three hotspots are underlined, and the associated index of standing crop is also underlined if it ranks in the top three. Values in table should be multiplied by 10^4 (the number of square meters/ha) to obtain actual estimate of standing crop.

Location	Worms	Clams	Sum (W+C)	Snails	Amphipods	Isopods	Sum (S+A+I)
<u>M'hall</u>	<u>2294</u>	<u>4101</u>	<u>6395</u>	<u>716</u>	<u>191</u>	<u>397</u>	<u>1304</u>
<u>Fish</u>	<u>264</u>	845	1109	<u>1088</u>	32	<u>58</u>	<u>1178</u>
<u>Era</u>	36	334	370	<u>284</u>	<u>309</u>	6	<u>599</u>
5Mile	62	1601	1663	72	14	23	109
Lemon	127	8939	9066	11	103	0	114
9Mile	173	960	1133	1	6	0	7

Table 4a. Summary of two-way ANOVA *p*-values (Habitat x Location) for density of macroinvertebrates in fall. # Post-hoc Tukey test did not distinguish among locations; see next tables.

Prey type	Habitat	Location	Interaction
Total invertebrates	0.250	0.001	0.045
Worms	0.008	0.022#	0.052
Snails	0.000	<0.0001	0.004
Amphipods	0.332	<0.0001	<0.007
Large	<0.0001	<0.0001	<0.0001
Small	0.105	0.004	0.010
Isopods	<0.0001	0.481	0.000
<i>Pentidotea</i>	0.895	0.533	0.715
<i>Gnorimosphaeroma</i>	<0.0001	0.586	0.0
Clams	0.002	0.000#	0.005

Table 4b. Posthoc Tukey tests identifying sources of significance in the ANOVAs for macroinvertebrate densities (per m²) in fall.

Habitat (* indicates a significant difference between adjacent values; n.s. indicates not significant). Note that when the values are not in numerical order, the third column that indicates statistical significance refers to Sediments vs Mussel cobbles.

Location (M'hall – Mendenhall river mouth; barge = barge at bend of Mendenhall river). (Locations ranked in ascending order; locations with the same letter are indistinguishable by the Tukey test)

Prey type	Mean values for each habitat					
	Sediment		<i>Fucus</i>		Mussel cobbles	
Total macroinvertebrates	154	n.s.	111	n.s.	149	n.s.
Worms	0.0	n.s.	0.3	*	1.3	
Snails	0.0	*	61	n.s.	40	*
Amphipods	15	n.s.	31	n.s.	30	
Large	0	n.s.	9.4	*	27	
Small	15	n.s.	21	n.s.	2.9	
Isopods	0.0	n.s.	18	*	75	
<i>Pentidotea</i>	0.0	n.s.	5.1	n.s.	0.6	
<i>Gnorimosphaeroma</i>	0.0	n.s.	13	*	74	
Clams	139	*	0.0	n.s.	2.8	*

Total invertebrates

M'hall	Barge	Fish	Salmon
71a	94a	134ab	233b

Worms

Salmon	Barge	M'hall	Fish
0.2a	0.3a	0.4a	1.3a

Snails

Barge	Salmon	M'hall	Fish
4.0a	29a	32a	88b

Amphipod (Large)((Small))

Fish	M'hall	Salmon	Barge
7.1a	16a	19a	61b
(4.1)a	(6.8)a	(8.1)a	(32)b
((2.9))a	((8.7))ab	((11))ab	((29))b

Isopods (Pentidotea)((Gnorimosphaeroma))

M'hall	Barge	Fish	Salmon
19a	25a	34a	54a
(0.4)a	(0.1)a	(6.1)a	(2.1)a
((19))a	((25))a	((28))a	((52))a

Clams

Barge	Fish	M'hall	Salmon
3.7a	3.9a	4.2a	132a

Table 5a. Summary of two-way ANOVA *p*-values (Habitat x Location) for density of macroinvertebrates in winter. # Post-hoc Tukey test did not distinguish among locations.

Prey type	Habitat	Location	Interaction
Total invertebrates	<0.0001	<0.0001	<0.0001
Worms	<0.0001	<0.0001#	<0.0001
Snails	<0.0001	<0.0001	<0.0001
Amphipods	0.002	<0.0001	0.001
Large	0.274	0.372	0.421
Small	0.002	<0.0001	0.001
Isopods	0.142	0.893	0.924
<i>Pentidotea</i>	0.018	0.576	0.211
<i>Gnorimosphaeroma</i>	0.115	0.849	0.921
Clams	<0.0001	<0.0001	<0.0001

Table 5b. Post-hoc Tukey tests identifying sources of significance in the ANOVAs for macroinvertebrates in winter.

Habitat (* indicates a significant difference between adjacent values; n.s. indicates not significant). Note that when the values are not in numerical order, the third column that indicates statistical significance refers to Sediments vs Mussel cobbles.

Location (Locations ranked in ascending order; locations with the same letter are indistinguishable by the Tukey test)

Prey type	Mean values for each habitat					
	Sediments		<i>Fucus</i> beds		Mussel cobbles	
Total macroinvertebrates	543	*	65	*	125	*
Worms	61	*	0.0	n.s.	2.0	*
Snails	0.0	*	44	n.s.	39	*
Amphipods	0.0	*	14	n.s.	16	
Large	0.0	n.s.	1.1	n.s.	1.1	
Small	0.0	*	13	n.s.	15	
Isopods	0.0	n.s.	6.3	*	64	
<i>Pentidotea</i>	0.0	*	2.8	n.s.	1.4	n.s.
<i>Gnorimosphaeroma</i>	0.0	n.s.	3.5	*	62	
Clams	8.8	*	0.0	ns	0.1	*

Total invertebrates

Barge	M'hall	Fish	Salmon
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49a	110a	302a	664a
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Worms

Salmon	Barge	Fish	M'hall
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0.2a	0.7a	1.0a	1.6a
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Snails

Barge	M'hall	Salmon	Fish
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1.8a	22a	25a	67b
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Amphipods (Large)((Small))

Fish	M'hall	Salmon	Barge
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3.6a	8.9ab	9.9ab	16b
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(1.3)a	(0.2)a	(0.7)a	(0.7)a
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((2.3))a	((8.7))ab	((9.2))ab	((16))b
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Isopods (Pentidotea)((Gnorimosphaeroma))

Salmon	Fish	M'hall	Barge
--------	------	--------	-------

7.9a	19a	23a	27a
------	-----	-----	-----

(3.4)a	(2.0)a	(0.7)a	(0.4)a
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((4.5))a	((17))a	((23))a	((26))a
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Clams

Barge	M'hall	Fish	Salmon
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0.1a	0.7a	2.8a	11b
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Table 6. Three-way comparisons (habitat X location X season) for two locations sampled in three seasons.

Prey type	Habitat	Location	Season	Interaction
Total invertebrates	p < 0.0001	p < 0.0001	p = 0.055	p < 0.0001
Worms	p < 0.0001	p < 0.001	p < 0.398	p < 0.0001
Snails	p < 0.0001	p < 0.0001	p = 0.002	p < 0.0001
Amphipods	p = 0.061	p = 0.016	p = 0.582	p = 0.107
Isopods	p < 0.0001	p = 0.089	p = 0.097	p = 0.026
Clams	p < 0.0001	p < 0.0001	p = 0.453	p < 0.0001

Table 7. Four-season comparison of JunkCar Slough and Otter Pond.
Anova results:

Prey type	Site	Season	Interaction
Total invertebrates	p = 0.03	p < 0.0001	p = 0.017
All amphipods	p = 0.001	p < 0.0001	p < 0.0001
<i>Eogammarus</i>	p = 0.174	p < 0.0001	p = 0.023
<i>Americorophium</i>	p < 0.0001	p < 0.0001	p < 0.0001
worms	p = 0.871	p = 0.032	p = 0.013
clams	p = 0.001	p = 0.040	p < 0.0001

Table 7. (continued) Tukey tests on differences in seasonal densities:

Prey type	Comparison (density)			
Total invertebrates	Spring = Winter = Summer = Fall			
	8a	11a	12a	40a
All amphipods	Spring = Winter = Summer < Fall			
	1.2a	2.7a	5.9a	27b
<i>Eogammarus</i>	Spring = Winter = Summer < Fall			
	0.7a	2.0a	2.9a	16b
<i>Americorophium</i>	Spring = Winter = Summer < Fall			
	0.5a	0.7a	3.0a	11b
worms	Spring <or= Winter = Fall = Summer			
	0.6a	1.2 ab	1.7 ab	3.1 ab
clams	Summer <or= Spring = Winter = Fall			
	2.5a	5.6ab	7.2ab	11b

Appendix 1.

A summary of corophiid amphipod ecology, with special reference to shorebird predation, plus a partial list of references

We include this summary of corophiid amphipod ecology because these amphipods were common in certain sloughs on the Mendenhall wetland that were less saline than most other locations. Most of the available literature used the genus name *Corophium*, which may still apply to the species reported in the references. However, all the corophiid amphipods identified from the wetland samples are now classified in the genus *Americorophium* (Bousfield and Hoover 1995).

Many corophiid amphipods build double-ended, U-shaped tubes of “silk”, sediment, and debris, up to about 5 cm deep (Dixon and Moore 1997, Meadows and Reid 1966, Ulrich et al. 1955). They feed on diatoms, microalgae, and surface detritus (Smith et al. 1996, Omori and Tanaka 1998, Hawkins 1985), mostly particles 4-63 μm (Möller and Rosenberg 1982). They feed by sweeping the area surrounding the tube opening with antennae (Omori and Tanaka 1998), and they can eat 2000-3700 diatoms/day (Smith et al. 1996)

They generally occur on muddy substrates (Meadows 1964, Hicklin et al. 1980, Möller and Rosenberg 1982), sometimes are very high densities (over 120,000/m²; Möller and Rosenberg 1982, Birklund 1977, Cunha et al. 2000c). They are an important link in the carbon flux on mudflats (Hawkins 1985) and can also increase mineralization and removal of nitrogen from the system (Pelegri and Blackburn 1994). *Corophium* populations produce bioturbation—increasing suspension of sediments (de Deckere et al. 2000), which may affect establishment of pioneer vegetation (Hughes and Gerdol 1997) and increase the uptake of contaminants by filter-feeders in polluted waters (Ciarelli et al. 1999). Sediments are more easily eroded where *Corophium* is present (de Deckere et al 2000), because sediment cohesion decreases with removal of polysaccharides produced by diatoms (Daborn et al. 1993).

The life history of *Corophium* varies not only with the species, but also with location and season. The sex ratio of several species strongly favors females (Schneider et al. 1994, McCurdy et al. 2000, Peer et al. 1986, Rajagopal et al. 1999), and some are parthenogenetic (Moore 1981). Brood size and body size often vary seasonally (Fish and Mills 1979, Musko et al. 1998, Forbes et al. 1996, Hilton et al. 2002) and may also vary with the risk of bird predation (Hilton et al. 2002). The number of generations per year varies from one to four, depending on location (including temperature; Gratto et al. 1983, Fish and Mills 1979, Möller and Rosenberg 1982, Wilson and Parker 1996, Peer et al. 1986). Even within the Bay of Fundy, there are differences among populations in their DNA (Wilson et al. 1997), suggesting that many of the life-history differences may have a genetic basis.

Corophium are sensitive to many environmental contaminants—heavy metals, dioxins, organic pollutants (Bat et al. 1998, Kater et al. 2000, Conradi and Depledge 1998, 1999, Arvai et al. 2002, Hyne and Everett 1998) and contaminants accumulated by *Corophium* are passed on to higher trophic levels (Vermeer 1992).

Corophium serve as intermediate hosts in a number of parasite life cycles for which birds are the definitive host. Trematodes are capable of causing heavy mortality of *Corophium* (Mouritsen and Jensen 1997, Mouritsen et al. 1997, 1998, Meissner and Bick 1997, Jensen et al. 1998, but see Meissner and Schaarschmidt 2000), an effect influenced by both temperature and snail density (snails are the first intermediate hosts). Both trematode and nematode parasites can alter the behavior of infected *Corophium* in ways that increase susceptibility to bird predation (and hence the rate of transmission of the parasite; Mouritsen and Jensen 1997, McCurdy et al. 1999, 2000). Infected *Corophium* increase activity at the substrate surface as the parasite approaches the transmission stage, in some cases especially in daytime when visually searching sandpipers are most active (op. cit., Manseau and Ferron 1991)(although they also forage at night, McCurdy et al. 1997, Mouritsen 1994). Parasites can influence the optimal life history of both male

and female *Corophium* (McCurdy et al. 2000, 2001).

The distribution and abundance of other intertidal organisms, including bivalves, snails, lugworms, and *Nereis*, can affect the distribution and abundance of *Corophium* (Flach 1992, Flach and de Bruin 1993, Meziane and Retiere 2001, Hamilton et al. 2003). Abiotic factors influencing distribution of *Corophium* include salinity (McLusky 1968) and ice scour (Hicklin et al. 1980). Human activity (blood-worm harvest) disturbs sediments and decreases *Corophium* density (Shepherd and Boates 1999). Reproduction and fecundity are affected by contaminants (Conradi and Depledge 1998, 1999), temperature and salinity (Cunha et al. 2000a,b, Moore 1981, McLusky 1968) of the environment.

The energy content of *Corophium* is about 15 J/mgdw, or 19.3 J/mg ashfree dw, for those >4.5mm in length, and 17.2 J/mgdw, or 21.3 J/mg ashfree dw, for those < 4.5mm (*C. volutator*, Boates and Smith 1979). Another estimate reports 12.7 J/mgdw or 18.2 J/mg ashfree dw, and a lipid content of 5.8% (Dobrzycka and Szaniawska 1995).

Corophium has many predators, including snails (Moore 1981), nemertines (Kruse and Buhs 2000), fish (Boates and Smith 1989; sturgeon, McCabe et al. 1993; tomcod, Peer et al. 1986; gobies, Swenson and McCray 1996), as well as many birds. For instance, redshanks (*Tringa totanus*) in the UK usually prefer to feed on *Corophium* (>4mm in size) but take more worms and molluscs as amphipod density (and temperature) declines (Goss-Custard 1977a,b). Redshanks tend to avoid areas previously used by other individuals, which increases prey intake significantly (Yates et al. 2000), and when redshank numbers are high, more birds are found in less preferred foraging sites (Goss-Custard 1977b).

The best documented story of *Corophium* and its predators comes from the Bay of Fundy. Semipalmated plovers, semipalmated sandpipers, short-billed dowitchers, and least sandpipers all feed primarily (86% by volume) on *Corophium volutator* during fall migration, a 6-8 week period (Hicklin and Smith 1979, Peer et al. 1986). *Corophium* is a preferred prey of semipalmated sandpipers even when polychaetes are abundant (Hicklin and Smith 1984), and the sandpipers can double their weight during a foraging stop in the Bay of Fundy (Hicklin 1987). Above a minimum density of *Corophium*, semipalmated sandpiper density remains similar over a range of prey densities, and intake rate is probably determined more by rate of digestion than by prey abundance (Wilson 1990). Individual birds may consume 10,000 *Corophium* per tide cycle; the prey must exceed 4mm in length for the birds to stay in positive energy balance (McCurdy et al. 1997). Shorebird predation decreases the amphipod population (Murdoch et al. 1986), depleting especially males and large individuals (Peer et al. 1986). Sediment cohesion increases after arrival of sandpipers, because they eat the amphipods that consume sediment-binding diatoms (Daborn et al. 1993). Surface crawling activity of *Corophium* (e.g., mate-searching) is much reduced during the time when sandpipers are present, in part because the predators remove crawling individuals but more because crawling behavior is less (Boates and Smith 1989, Boates et al. 1995). The possibility that sandpiper predation might select for two generations of *Corophium* per year on certain heavily used mudflats has been debated (Matthews et al. 1992, Wilson and Parker 1996). On mudflats used by shorebirds, first brood sizes of the season are larger than on unused mudflats, and females of the second annual generation mature at smaller sizes, with smaller broods; this is not a phenotypically plastic response, but apparently an evolved difference among local populations (Hilton et al. 2002; see also Wilson et al. 1997 re DNA differentiation of local populations in this area).

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Appendix 2.

Selected ecological interactions of potential relevance to the local wetland system: siphon-nipping of *Macoma balthica* and amphipod grazing of algae.

Macoma balthica (Tellinidae). This small bivalve is an important prey for many predators, including birds (Hiddink et al 2002). On the Copper River Delta, densities reached over 4000/m² (Powers et al. 2002). These clams migrate, pelagically and usually at night, within the intertidal and subtidal zones, partly as a function of age; migration is inherently dangerous, perhaps partly as a result of predation (Hiddink and Wolff 2002, Hiddink et al. 2002). *Macoma* feeds on substrate deposits, using its siphon, and on suspended particles that are inhaled via the siphon. Flatfish exert important influences on *Macoma*, by grazing on their siphons (de Goeij et al. 2001, Skilleter and Peterson 1994, Peterson and Skilleter 1994). They are able to regenerate their siphons, but regeneration it is affected by body condition (de Goeij et al. 2001) and can be faster at lower densities, suggesting resource limitation (Skilleter and Peterson 1994). The presence of a competing suspension-feeder increased deposit-feeding by *Macoma* and thus increased the risk of siphon-cropping by fish (Skilleter and Peterson 1994). Siphon-cropping causes *Macoma* to bury itself less deeply in the sediments, thus increasing the risk of predation by birds (de Goeij et al. 2001). Burial depth also affects feeding rates of *Macoma* itself: shallow burial generally allows higher food intake and more rapid growth (De Goeij and Luttikhuisen 1998, de Goeij and Honkoop 2002). Rapid growth would allow small *Macomas* to outgrow the risk of predation by small epibenthic predators (Hiddink et al. 2002), as well as increase fecundity. Poorly nourished *Macoma* apparently are more likely to crawl on the substrate surface (Mouritsen 1997), which would enhance their risk of predation.

Amphipod grazing. Amphipods are important grazers on algae and plant debris, and growth efficiency can vary significantly with the type of algae in the diet (Levings 1980). The debris of *Carex lyngbyei* yielded a lower growth efficiency than various algae that were tested (op. cit.). *Ampithoe longimana* grazes preferentially on young tissues of the brown alga *Dictyota ciliolata*; young tissues contain fewer defensive chemicals than older tissues (Cronin and Hay 1996a). Some of the defensive chemicals are aimed rather specifically at amphipods (Schnitzler et al. 2001). Some amphipods, including *A. longimana*, can compensate for low quality diet by eating more (Cruz-Rivera and Hay 2000, 2001b). However, the ability to use the chemically defended alga efficiently obtains only for populations that co-occur with *D. ciliolata* (Sotka and Hay 2002). Grazing by amphipods can induce chemical defences in algae, making the algae less susceptible to future grazing (Cronin and Hay 1996c). Abiotic stresses can reduce production of defensive compounds and increase susceptibility to grazing (Cronin and Hay 1996b). Grazing by herbivorous amphipods is capable of altering the algal community; predation on the amphipods by fish reduces this effect (Duffy and Hay 2000).

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Appendix 3.

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Appendix 4.

Diet information extracted from **The Birds of North America**. Numbers in brackets refer to the issue number in that series, but the specific citation is not presented here. *Data are presented specifically for northwestern North American areas, if available.

species	foraging	general diet	winter	spring	summer	fall
Northwestern crow [407]	surface, under surface or stones	*clams, whelks, crabs, sand dollars, urchins, eggs and chicks, fruits, carrion				
Horned grebe [505]	<6m	aq. arthropods in summer; fish and crust. in winter, (more benthic)	fish; crustaceans (esp. amphipods and crayfish), polychaetes			
Bufflehead [67]	diving, <3m	in FW, insects; in SW, occ. fish; crustaceans and molluscs	shrimp, crabs, amphipods, isopods, snails, clams; seeds of pondweed, bulrush	some seeds, herring eggs	*caddisflies, possibly amphipods	seeds of pondweeds, bulrush, amphipods
Common goldeneye [170]	diving, usu. <4m; also mussel beds, rocky shores, mudflats	crust., insects, molluscs, some seeds, fish.	salmon eggs, flesh, sculpin, caddisfly, molluscs, crust.	*FW: insects esp Tricoptera, crustacea, fish, elsewhere also plants; SW: also snails	insects: d'flies, caddisflies	
Barrows goldeneye [548]	diving <4m, rocky shoreline, mussel beds	aq. inverts and fish eggs, some seeds, tubers	*FW: fish, insects, tubers; SW snails, bivalves, crustacea		*FW: insects of several taxa, amphipods, seeds	
Surf scoter [363]	diving, usu <5m	*blue mussels, clams (incl. Macoma), snails, barnacles; smaller items than WWscoter	clams, mussels, other molluscs, barnacles,	*mussels, other molluscs, herring eggs, plants		*mussels, moon snail
White-winged scoter [274]	diving, usu <5m, occ. 20m	SW: molluscs esp. bivalves, crust. occ. fish; FW: crust., insects.	*bivalves, snails, barnacles, crabs	*bivalves, barnacles, snails	FW: amphipods, some insects	*barnacles, bivalves, snails
Lesser scaup [338]	diving					
Greater scaup [650]	diving <7m	bivalves, snails, crust., insects, seeds and veg.	*veg, snails, worms, bivalves	*herring eggs	insects, crust. (amphipods, shrimps), worms, molluscs (bivalves, snails), veg, dead fish, *salmon eggs	
Ring-necked duck [329]	shallow diving, tip-ups	wetland seeds and tubers, aq. inverts	FW: veg, snails, clams, insects, tubers		FW: seeds and veg, insects, snails and clams, leeches	seeds, buds, insects
Red-breasted merganser [443]	surface and diving <9m; some coop foraging	small fish (<15cm), also worms, insects, amphibs	*sculpin, herring and eggs; salmon eggs (sticklebacks and other small fish, shrimp elsewhere)		small fish, fish eggs, seeds	
Common merganser [442]	diving esp. <4m; some coop foraging	small fish (usu.<40cm); also insects, molluscs, crust., worms, frogs, small mamm and birds	fish esp trout, shad		*FW: fish esp sculpin, chub, lake shiner, squawfish, crayfish; SW: fish esp sculpin	
Hooded merganser [98]	diving	aq. insects, fish, crust. (esp. crayfish), frogs, seeds and buds	fish, crayfish, insects			
Long-tailed duck [651]	SW: diving FW: surface and tip-ups also		SW: crust (amphipods, mysids, isopods), bivalves, snails, fish, fish eggs. FW: amphipods, fish, molluscs, oligochaetes		*insects esp. caddisfly, midges, plecoptera), oligochaetes, cladocerans, elsewhere crust. (amphipods, fairy shrimp), fish eggs, veg.	
Northern shoveler [217]	open water, mud; filtering	small nektonic inverts, seeds	nektonic inverts, seeds.		cladocerans; also seeds, midge larvae, corixids	
American wigeon [401]	esp. grazing	veg, some inverts	*veg, incl. seeds	veg., incl seeds	more seeds and fruits; more insects (females eat molluscs and crust. too)	

species	foraging	general diet	winter	spring	summer	fall
Green-winged teal [193]	shallows and mudflats, dabbling	seeds and inverts	seeds, veg, midges			*seeds (esp. Carex), some bivalves
Northern pintail [163]	dabbling, land surfaces	grains and seeds, pond weeds, insects, crust., snails	FW: seeds and veg.		*FW: midge larvae, other diptera, caddisfly, snails, clams, tubers, seeds elsewhere also crust., earthworms	veg and seeds, clams
Mallard [658]	shallows, fields; filtering, dabbling and tip-ups,	highly variable	*mostly veg and seeds, also inverts; similar elsewhere		snails, insects, crust., annelids, more animal food esp for females, seeds, veg	*mostly veg. and seeds; elsewhere insects too
Marbled murrelet [276]	dive and fly underwater	small fish, euphausiids, amphipods	*euphausiids, gammarid amphipods, mysids, capelin, smelt, herring	see winter	*sand lance, n. anchovy, herring, capelin, smelt, seaperch; sometimes euphausiids	
Bonapartes gull [634]	diving, dipping, surface, walking on land; highly diverse	small fish, euphausiids, amphipods, insects, highly variable	insects, marine worms, crust, snails, small fish, berries	*euphausiids, amphipods, fish, herring spawn, tidal and intertidal org.	insects	*amphipods, fish;
Herring gull [124]	highly variable	highly variable: inverts, fish, insects, birds and eggs, carrion, garbage				
Glaucous-winged gull[59]	highly variable	*highly variable: molluscs, urchins, barnacles, small fish, snails, squid, carrion				
Mew gull [687]	omnivorous, many habitats, many methods	highly variable, incl. fruit	*crust., Ulva, amphipods	*pellets with sm birds and fish		
Thayer's gull [699]	opportunistic, mostly marine, surface	mainly fish; also bird eggs and chicks , misc inverts, berries				
Arctic tern [707]	open water; plunge-dive, dipping, surface	small fish, crust., insects		*chicks: sm fish, euphausiids, amphipods		
American/Pacific golden plovers [201-202]	low plant cover: run-stop-run	inverts: terrestrial, also FW, SW; some seeds, fruit, lvs; small verts	insects, crust., snails	also fruits	insects(beetles, flies), worms	also fruits
Black-bellied plover [186]	marine mud, sand; tundra, run-stop-run	insects, polychaetes, bivalves, crust.	*polychaetes, lugworms; elsewhere earthworms, large insects, anemones, bloodworms, snails, bivalves		insects (many orders), berries	berries
Whimbrel [219]	tundra, mud flats, salt marshes, sandy and rocky beaches, lawns peck or probe	marine inverts, insects, berries	crabs and other crust., polychaetes, sipuncs and cucumbers, molluscs, fish		berries, later insects, some flowers	berries, crabs, other crust, worms, crayfish, insects
Hudsonian godwit [629]	mudflats, shallows; probe or peck	marine inverts, insects, berries, tubers	polychaetes, crabs, bivalves		insects (several families), berries	tubers, seeds
Short-billed dowitcher [564]	wet meadows, tide flats; probe or glean	polychaetes, molluscs, crust., insects, seeds		insects esp diptera, snails, beetles, seeds.	Diptera, also snails, beetles, seeds, worms, spiders, insects	also tubers
Long-billed dowitcher [493]	shallows, esp mud, wet meadows; probing	assorted inverts, insects, seeds	polychaetes, Corophium, oligochaetes, bivalves, cumacea, polydorids	insects, also seeds; misc. inverts	*FW: insects, esp. midges, worms, crust.; SW polychaetes, bivalves, amphipods	insects, also seeds; misc inverts
Ruddy turnstone[537]	variety of intertidal habitats; probe, peck, chase, turnstones	various insects, carrion, molluscs, anemones, starfish, earthworms, polychaetes, barnacles, crabs, eggs	crust. (barnacles, amphipods, copepods, decapods), polychaetes, molluscs, insects	see winter	first crust. and molluscs and carrion, then seeds, insects (esp. midges) and spiders	see winter

species	foraging	general diet	winter	spring	summer	fall
Black turnstone [585]	wet meadows, tide flats, rocky or sandy shores; turnstones, peck, chisel, roll algae, chase, probe	marine inverts, insects, eggs	various marine inverts	*barnacles, herring eggs, snails, mussels, limpets, amphipods,	*insects of several families, seeds, bivalves (Macoma), spiders, salmon carcasses, berries, eggs	
Common snipe [417]	probe	larval insects, crust., earthworms, molluscs, small verts, seeds			insects	
Lesser yellowlegs [427]	shallows; mudflats, beaches, lawns; peck, sidesweep	small inverts of many types	insects, snails	insects, crust., snails, polychaetes	insects	many insect types, snails, crust
Greater yellowlegs [355]	shallows, intertidal, low veg; peck, sidesweep, chase. 'p'low'	small inverts, insects, small fish, frogs; occ seeds, berries	insects, clams, snails, crayfish, small fish		*snails, stickleback, flies, frogs, beetles	*sculpin, salmon eggs, berries, insects
Solitary sandpiper [156]	pond edges, marsh ditches; peck, stir	insects, small crust., molluscs, frogs, fish, worms	terrest. and aq. inverts, fish			
Red knot [563]	intertidal sand flats, eroding banks; peck or probe	inverts, esp. bivalves, snails, crust. (amphipods), polychaetes; terrest inverts	mussels	horseshoe crab eggs	first veg, then insects	mussel spat, amphipods, snails, bivalves, polychaetes
Dunlin [203]	pond edges, wet marsh, mudflats; probe or peck	various inverts, occ. fish, veg	*tubicolous and algal amphipods, polychaetes, bivalves, snails, seeds, annelids	similar to winter	*insects esp. midges; beetles	*Macoma, Mytilus, amphipods
Least sandpiper [115]	mud near water (nonbreeding) or land, peck or probe	benthic inverts (sm. amphipods incl Corophium, snails); flies	*sm. amphipods incl Corophium, isopods, marine worms	horseshoe crab eggs	esp. dipterans; amphipods	Corophium, worms, midges and many other insects, seeds
Semipalmated sandpiper [6]	mud/silt, marsh edges, shallows; peck or probe	benthic inverts (sm. arthropods, molluscs, annelids), some terrest. inverts	crust.	FW: sm. crust. and insects	*insects of several taxa, esp midges and tipulids, spiders, beetles.	amphipods (Corophium); several sm. crust. and insects., bivalves, snails, polychaetes, shrimp, copepods, ostracods
Western sandpiper [90]	wet mud, shallow, sandflats, pond edges; peck or probe	FW benthic inverts, also insects; SW benthic inverts (esp. arthrop), polychaetes, bivalves	amphipods, bivalves, polychaetes, snails, ostracods	see fall	insects, esp diptera; beetles, spiders	*Migration (not clear if fall or spring: Corophium and copepods, bivalves incl. Macoma, Mytilus, dipterans
Surfbird [266]	rocky intertidal; tundra; chase, pull, peck		bivalves, snails, crabs, mussels, barnacles, algae, herring eggs	*barnacles, Mytilus, herring eggs, snails	*insects (beetles and flies)	

Appendix 5.

Systematic listing of the invertebrate taxa identified during this study. The most common taxa in spring (>10% of specimens) are marked **; those > 1% of taxa are marked *. Together, the starred taxa comprised 95% of the specimens.

Phylum	Class	Order	Family	Genus & Species
Platyhelminthes	Polycladia*	??	??	??
Annelida	Oligochaeta*	Haplotaxida	Enchytraeidae	??
Nemertea	Enopla	Hoplonemertea	Amphiporidae	Amphiporus formidibilis Griffin, 1898
Nemertea	Enopla	Hoplonemertea	Emplectonematidae	Emplectonema gracile (Johnston, 1837)
Annelida	Polychaeta	Capitellida	Capitellidae	Notomastus sp.
Annelida	Polychaeta	Phyllodocida	Phyllodocidae	Eteone sp.
Annelida	Polychaeta	Phyllodocida	Nephtyidae	Nephtys sp.
Annelida	Polychaeta	Phyllodocida	Nereididae	Neanthes brandtii (Malmgren, 1866)
Annelida	Polychaeta	Phyllodocida	Nereididae	Nereis vexillosa Grube, 1851
Molluska	Bivalvia	Myoida	Myidae	Mya arenaria Linnaeus, 1758
Molluska	Bivalvia	Veneroida	Tellinidae	Macoma balthica* (Linnaeus, 1758)
Molluska	Bivalvia	Veneroida	Tellinidae	Macoma inquinata (Deshayes, 1855)
Molluska	Bivalvia	Veneroida	Tellinidae	Macoma nasuta (Conrad, 1837)
Molluska	Bivalvia	Veneroida	Cardiidae	Clinocardium nuttallii (Conrad, 1837)
Molluska	Bivalvia	Veneroida	Veneridae	Saxidomus giganteus (Deshayes, 1839)
Molluska	Gastropoda	Pelto-gastropoda	Lottidae	Tectura scutum** (Rathke, 1833)
Molluska	Gastropoda	Pelto-gastropoda	Lottidae	Tectura persona** (Rathke, 1833)
Molluska	Gastropoda	Pelto-gastropoda	Lottidae	Lottia strigatella (Carpenter, 1864)
Molluska	Gastropoda	Mesogastropoda	Lacunidae	Lacuna variegata Carpenter, 1864
Molluska	Gastropoda	Mesogastropoda	Littorinidae	Littorina sitkana** Philippi, 1845
Molluska	Gastropoda	Mesogastropoda	Littorinidae	Littorina scutalata Gould, 1849
Molluska	Gastropoda	Pyramidellacea	Pyramidellidae	Odostomia sp.
Molluska	Gastropoda	Nudibranchia	Onchidorididae	Onchidoris bilamellata (Linnaeus, 1767)
Arthropoda (Uniramida)	Hexapoda	Coleoptera	Staphylinidae	Liparocephalis cordicollis LeConte, 1880
Arthropoda (Uniramida)	Hexapoda	Coleoptera	Staphylinidae	Diaulota densissima Casey, 1893
Arthropoda (Uniramida)	Hexapoda	Diptera	Chironomidae	??
Arthropoda (Uniramida)	Hexapoda	Diptera	??	??
Arthropoda (Chelicerata)	Arachnida	Pseudoscorpionida	Neobisiidae	Halobisium occidentale (Beier, 1931)
Arthropoda (Chelicerata)	Arachnida	Acarida	Bdellidae	Neomolgus littoralis (?)
Arthropoda (Chelicerata)	Arachnida	Araneae	Linyphiidae(?)	??
Arthropoda (Crustacea)	Malacostraca	Isopoda	Sphaeromatidae	Gnorimosphaeroma oregonense** (Dana, 1854)
Arthropoda (Crustacea)	Malacostraca	Isopoda	Sphaeromatidae	Gnorimosphaeroma insulare (Van Name, 1940)
Arthropoda (Crustacea)	Malacostraca	Isopoda	Idoteidae	Pentidotea wosnessenskii* (Brandt, 1851)
Arthropoda (Crustacea)	Malacostraca	Amphipoda	Pontogeneiidae	Pontogeneneia sp.
Arthropoda (Crustacea)	Malacostraca	Amphipoda	Anisogammaridae	Eogammarus oclairi Bousfield, 1979
Arthropoda (Crustacea)	Malacostraca	Amphipoda	Anisogammaridae	Eogammarus confervicolus* (Stimpson, 1856)
Arthropoda (Crustacea)	Malacostraca	Amphipoda	Anisogammaridae	Spinulogammarus subcarinatus (Bate, 1862)
Arthropoda (Crustacea)	Malacostraca	Amphipoda	Ampithoidae	Perampithoe spp.
Arthropoda (Crustacea)	Malacostraca	Amphipoda	Melitidae	Maera cf. <i>danae</i> Stimpson, 1853
Arthropoda (Crustacea)	Malacostraca	Amphipoda	Atylidae	Atylus collingi (Gurjanova, 1938)
Arthropoda (Crustacea)	Malacostraca	Amphipoda	Corophiidae	Americorophium brevis (Shoemaker, 1949)
Arthropoda (Crustacea)	Malacostraca	Amphipoda	Corophiidae	Americorophium spinicorne (Stimpson, 1857)
Arthropoda (Crustacea)	Malacostraca	Amphipoda	Corophiidae	Americorophium salmonis (Stimpson, 1857)
Arthropoda (Crustacea)	Malacostraca	Decapoda	Paguridae	Pagurus hirsutiusculus (Dana, 1851)

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