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The effects of episodic predation by migratory shorebirds in Grays Harbor, Washington

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Abstract

Exclusion experiments were performed in Grays Harbor, Washington, in the springs of 1989 and 1990 to test the effect of predation by migratory Western Sandpipers [*Calidris mauri* (Cabanis)] on invertebrate abundance. Although over a million shorebirds pass through Grays Harbor each spring, experimental data showed no significant depression of prey abundance for any of the sandflat invertebrates. Unlike better studied stop-over areas, Grays Harbor is not characterized by rich prey densities. The surprising lack of effects on prey abundance likely arises because these sandpipers do not need to deposit large fat stores to fuel their migration to their next stop-over area, the Fraser River delta in British Columbia, or the Copper River Delta in south-central Alaska. The effects of episodic predation by shorebirds appears to differ at different stop-over areas.

Key words: Corophium; Migration; Predation; Shorebird; Soft-sediment; Spionid polychaete

1. Introduction

Many shorebirds (Suborder Charadrii) migrate between arctic breeding grounds and temperate zone or tropical wintering grounds along a series of traditional stop-over sites (Gill & Jorgensen, 1979; Morrison, 1984; Pienkowski & Evans, 1984; Myers et al., 1987; Morrison & Myers, 1989; Ens et al., 1990). For a week or more during a migratory period, a majority of the population of many migratory shorebirds may be found at a single stop-over site. For instance, over 90% of the western hemisphere population of Red Knots (*Calidris canutus*) may be found in Delaware Bay, USA, in late May (Harrington et al., 1988).

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At these stop-over sites, the migratory shorebirds must fatten sufficiently before continuing their migration to their next stop-over area. The high metabolic demands of powered flight require that shorebirds deposit fat mass equal to 50% or more of their lean body mass (McNeil & Cadieux, 1972; Castro & Myers, 1990). Given the energetic demands of migration, one would predict that the episodic predation by shorebirds on intertidal communities might result in significant depression of prey abundance. In this contribution, I describe experiments performed in the springs of 1989 and 1990 at a major stop-over area in Washington state, USA, to determine the impact of migratory shorebirds on infaunal prey abundance.

2. Study area and methods

Grays Harbor is one of two embayments on the outer coast of Washington (Fig. 1). The Harbor covers about 100 square miles of which half is exposed at mean low tide. Between mid-April and mid-May, Grays Harbor is a major stop-over area for Western Sandpipers, hosting over a million of these birds (Herman & Bulger, 1981).

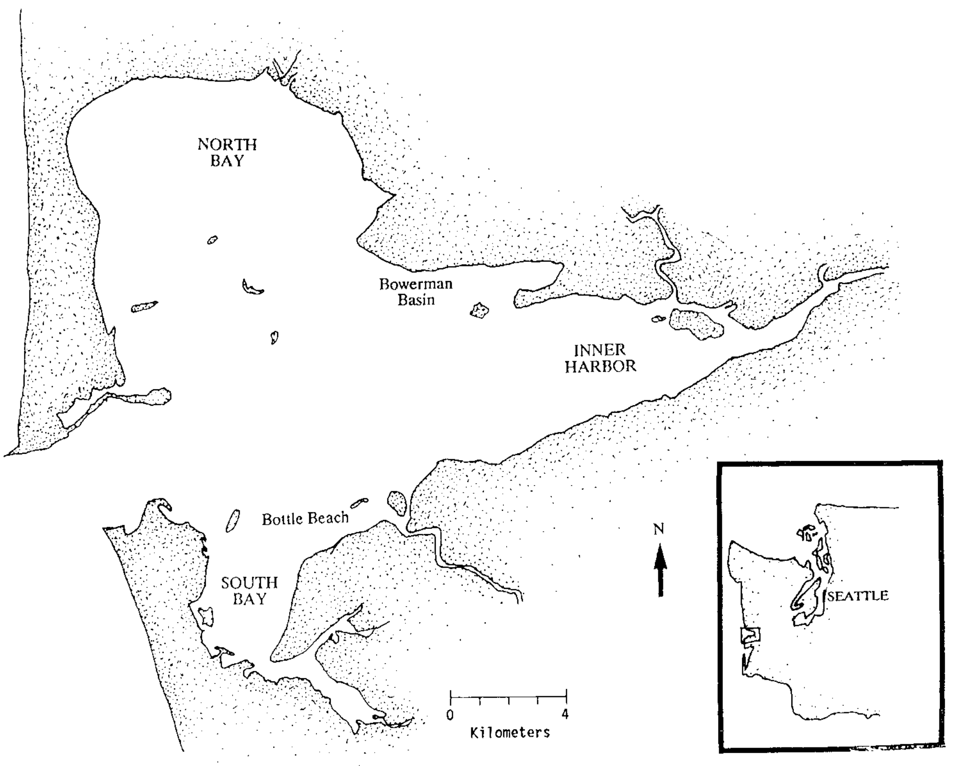


Fig. 1. Map of Grays Harbor, Washington, showing the primary study site, Bottle Beach, and the important roosting area, Bowerman Basin.

Smaller numbers of Dunlin [*Calidris alpina* (Linnaeus)] and Short-billed Dowitchers [*Limnodromus griseus* (Gmelin)] migrate through along with 36 other shorebird species in lower numbers (Herman & Bulger, 1981). Shorebirds pass through in fall migration as well but never build to the numbers seen during the spring.

The substratum of Grays Harbor varies from flocculent muds to coarse sand. Muddy habitats are dominated by the amphipod crustacean, *Corophium salmonis* Stimpson and capitellid polychaetes. Sandier habitats are dominated by *Corophium spinicorne* Stimpson, the tanaid crustacean, *Leptochelia dubia* (Krøyer), and many species of polychaetes.

Herman & Bulger (1981) identified major aggregation areas for shorebirds in Grays Harbor during the spring migration. Largest numbers occurred in Bowerman Basin with the second largest numbers occurring at Bottle Beach, my study site. Bowerman Basin is located in the extreme upper intertidal zone and provides a high-tide roosting area. Most birds leave Bowerman Basin to forage elsewhere as other sites in Grays Harbor are exposed by the falling tide (Wilson, 1993). Bottle Beach is only 8 km from Bowerman Basin and I contend that the Bottle Beach area is the most important foraging site for sandpipers in Grays Harbor.

To census shorebirds at Bottle Beach, I walked along a marked km of shoreline near high tide and photographed all aggregations of roosting shorebirds with a series of overlapping transparencies taken with a 300-mm lens. Shorebirds were counted by projecting the transparencies with a slide projector, taking care to avoid doubly counting the birds in consecutive slides. This method probably underestimates the total number of shorebirds that foraged at Bottle Beach because many of the foraging birds roosted elsewhere, primarily at Bowerman Basin and in adjacent agricultural fields (Wilson, 1993). However, the data do show the pattern of arrival and departure of the shorebirds from the Grays Harbor region.

To determine the impact of shorebird predation on the fauna at Bottle Beach, I performed a series of exclusion experiments in 1989 and 1990. Three sites were chosen at Bottle Beach. Site I was located at the + 1.8 m tidal mark. Site II was at the + 0.8 m tidal level and Site III was at the 0.0 tide level. Shorebirds were seen foraging at each site although no data on relative use of each site were collected. At each site, exclusion devices (hereafter, termed ceilings) were made by driving four wooden stakes into the sediment in a 60×80 cm rectangular array with each stake protruding 12 cm above the surface of the sediment. A piece of chicken wire (25 mm mesh), 60×80 cm, was stapled at each corner to the four stakes. Eight exclosures were emplaced at each site in 1989 and five exclosures per site were used in 1990. The ceilings were put in place in mid-April in both years (15 April 1989 and 12 April 1990). At those times, a core sample (10 cm in diameter) was taken to a depth of 10 cm adjacent to each exclosure to establish initial prey densities. In mid-May (15 May 1989 and 16 May 16 1990), after the majority of the shorebirds had departed, paired cores were taken from within the exclosure and from the unmanipulated area less than 1 m distant. If shorebirds were removing significant numbers of prey, then one should see a decline in control areas between April and May but no such decline in experimental areas from which the shorebirds were excluded.

The ceilings, using the same design as Wilson (1989, 1991a), effectively excluded shorebirds. I never saw a shorebird go underneath one of the ceilings although birds foraged within 10 cm of the exclosures. The ceilings doubtless altered the hydrodynamics of the water passing across the flat in the vicinity of each exclosure. Such alterations of flow could have artifactual effects on invertebrates living within the sediment which could confound interpretation of the data (Hulberg & Oliver, 1980). As a test for such artifacts, the same experiment described above was conducted between 22 May and 25 June 1990 when shorebirds are absent from the flats. By sampling at the beginning of the experiment and 5 weeks later, sampling both underneath the ceilings and in adjacent control areas, differences in invertebrate abundance could be examined. Because there were no shorebirds present, any significant difference in invertebrate abundance at the conclusion of the experiment would have to be attributed to hydrodynamic artifact caused by the ceilings. I adopted this same control procedure in the Bay of Fundy (Wilson, 1989, 1991a) and could detect no hydrodynamic effects of the ceilings on prey abundance. In late May, large amounts of drift algae, primarily the green alga *Ulva* sp., accumulated in the lower portions of Bottle Beach and badly fouled the shorebird exclosures at Sites II and III, causing the sediment within the cages to become anoxic. These control experiments were abandoned.

All sediment samples were sieved through a 500-μm screen. The residue and animals retained on the sieve were preserved in 10% formalin in seawater. The samples were sorted under a stereomicroscope at 12 × magnification.

3. Results

In 1989, Short-billed Dowitchers peaked at an earlier date than Western Sandpipers (Fig. 2). Peak abundance was maintained for only a short time, suggesting that most migrants spend only a few days at Grays Harbor. These patterns were not as clear in the 1990 data (Fig. 2). The period between 23 April and 29 April 1990, when the peak abundance is normally expected (Herman & Bulger, 1981), was quite stormy. These weather conditions undoubtedly forced many of the birds to find a more protected high-tide roosting site than the upper intertidal zone of Bottle Beach. Neither dowitchers nor Western Sandpipers attained the densities in the photographic censuses seen in 1989. I believe this difference is explained by weather conditions rather than any real difference in the number of birds present in the 2 yr.

Observations of foraging shorebirds and data from the literature (Smith & Mudd, 1976) indicated that the major prey taken by the shorebirds at Bottle Beach were the amphipod, *Corophium spinicorne*, the polychaetes, *Pseudopolydora kempi* (Southern) and *Notomastus tenuis*, and the larvae of a chironomid insect. Detailed analyses of these four species from the exclusion experiments will be presented.

The control experiments to test for unwanted artifacts of the bird exclusion ceilings demonstrated that the cages induced minimal changes in prey abundance at Site I (the experiments at Sites II and III were aborted because of fouling by drift algae). I compared the abundances of each of the 11 species found in samples on June 25, 1990, between unmanipulated control areas and bird exclusion areas. For 10 of the species, Student's t-tests indicated no significant difference between the two treatments,

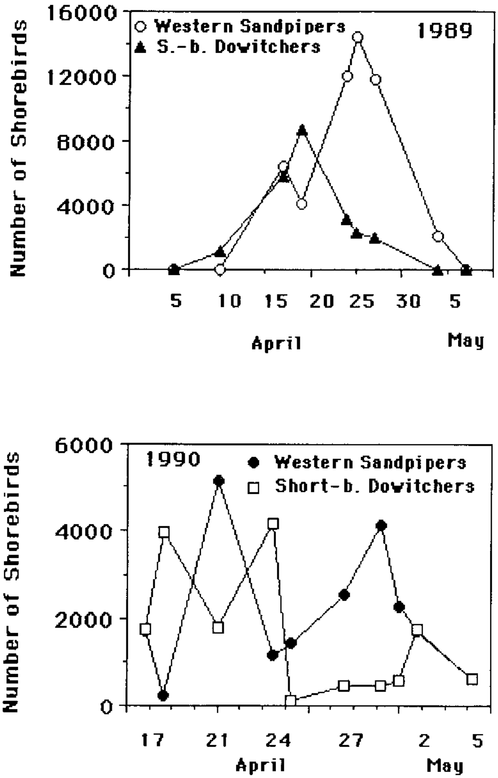


Fig. 2. The abundance of Western Sandpipers and Short-billed Dowitchers along a 1-km transect in 1989 and 1990.

indicating that the presence of the cages was not affecting invertebrate abundance. The eleventh species, the polychaete *Pygospio elegans*, was more abundant under exclusion ceilings (11.0 versus 5.0 (mean worms per 10-cm diameter core), $p = 0.048$).

The four major prey species exhibited strong variation in abundance among sites and between years (Figs. 3 and 4). Despite the variability, convincing evidence for an effect of shorebird predation on prey abundance was lacking. The polychaete *Pseudopolydora* (Fig. 3) in 1989 showed a significant increase in the Control treatment at Site I but no increase in the Experimental treatment, a result not explicable by the exclusion of shorebird predation. No differences among means were noted for Sites II and III. In 1990, there were no differences among the three means at any of the three sites. The polychaete *Notomastus tenuis* (Fig. 3) showed a significant drop from April to May, 1989, irrespective of shorebird exclusion, at Site I. No differences between means were evident at Sites II and III. In 1990, there were no significant differences among means at any of the three sites. There is therefore no experimental evidence that either of these two species of polychaetes suffer significant mortality from predation by migratory shorebirds.

Fig. 4 shows the experimental data for two species of arthropod prey species. For

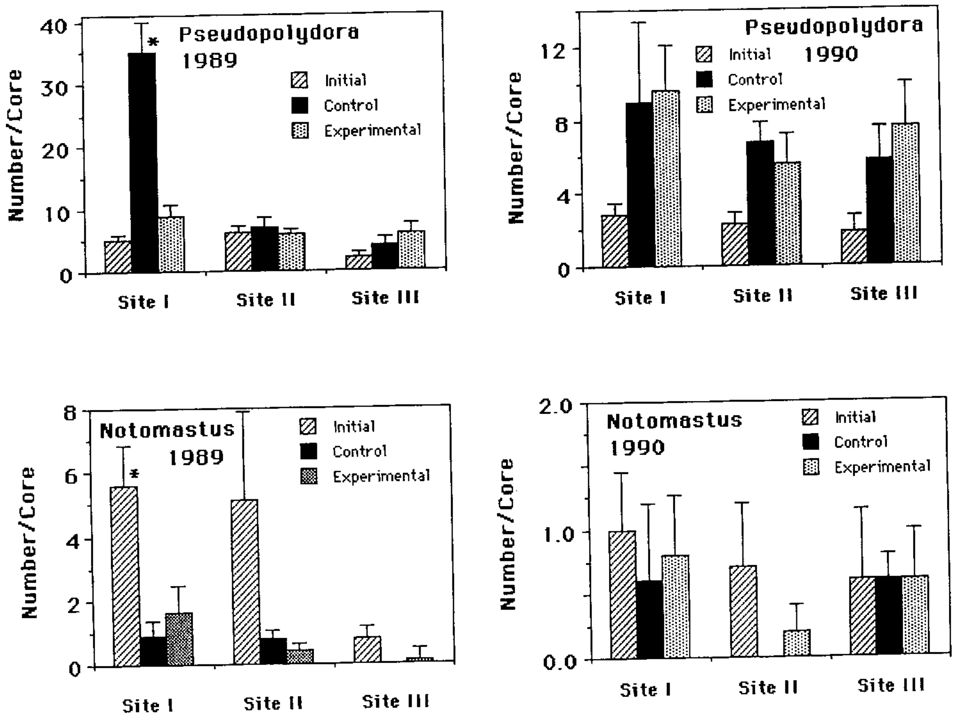


Fig. 3. Results of shorebird exclusion experiments for the polychaetes *Pseudopolydora kempi* and *Notomastus tenuis*. Initial refers to samples taken in mid-April before the shorebirds arrived. Control refers to samples taken in mid-May from unmanipulated areas. Experimental refers to samples taken from beneath shorebird exclusion ceilings in mid-May. Error bars are 1 SE. Means with an asterisk are significantly different from means without an asterisk (Scheffé tests, $p < 0.05$).

the amphipod crustacean, *Corophium spinicorne*, in 1989 at Site I, a significant increase in abundance was noted between April and May, independent of shorebird exclusion. At Sites II and III, abundance increased in the Experimental treatment relative to the other two treatments. However, there was no difference between the Initial and Control treatments, suggesting that *Corophium* were immigrating underneath the ceilings. In 1990, *Corophium* showed no difference among the three treatments at Sites I and III. At Site II, there was a significant rise in abundance from the Initial treatment in both of the May treatments, indicating that the population increase was not affected by exposure to shorebird predation. For the chironomid insect larvae at Site I in 1989 (Fig. 4), the results show the trend expected if shorebirds had a significant effect on chironomid abundance, a decrease in the Control treatment but not the Experimental treatment relative to the Initial treatment. However, even with each treatment replicated eight times, the variance was so high that none of these means is significantly different from the others. No significant differences were found at Site II. At Site III, there was a significant drop in abundance between the Initial treatment and the Control treatment; there was no significant difference between the Experimental treatment and either of the two other treatments. In 1990, chironomid larvae at Sites I and III showed

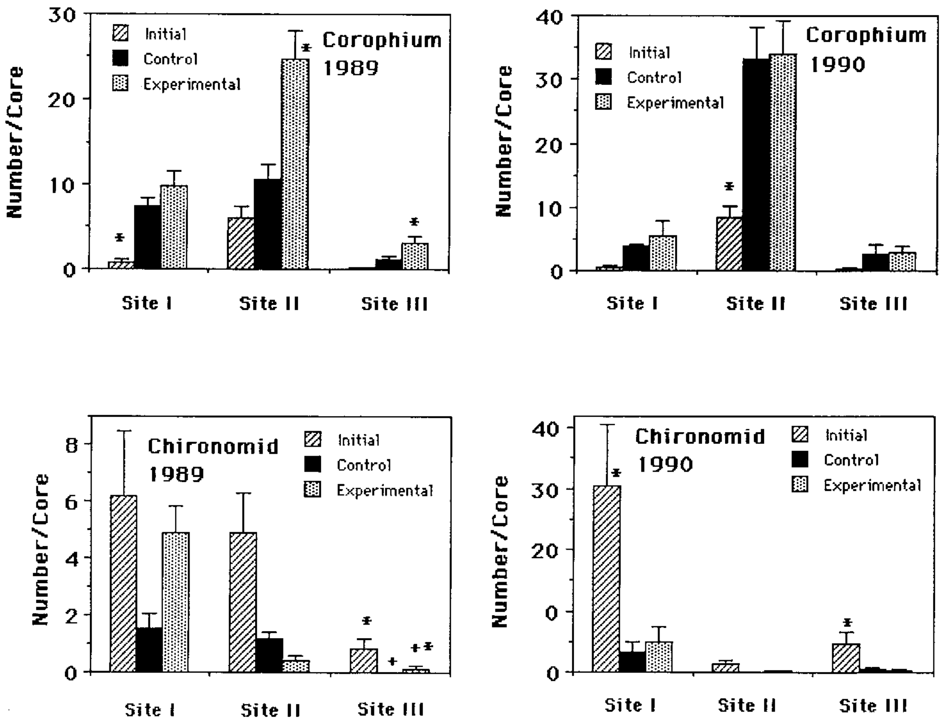
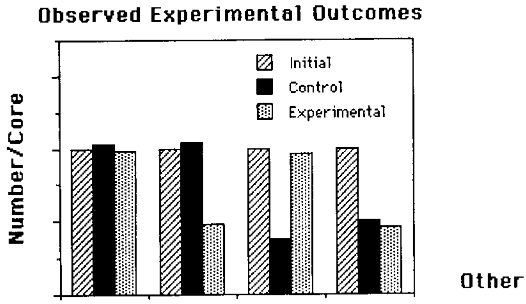


Fig. 4. Results of shorebird exclusion experiments on the crustacean *Corophium spinicorne* and chironomid larvae. Initial refers to samples taken in mid-April before the shorebirds arrived. Control refers to samples taken in mid-May from unmanipulated areas. Experimental refers to samples taken from beneath shorebird exclusion ceilings in mid-May. Error bars are 1 SE. Means with an asterisk or plus-sign are significantly different from means without those symbols (Scheffé tests, $p < 0.05$).

a significant drop in both Control and Experimental means compared to the Initial mean. No differences were seen among the means for Site II. As with the two polychaete prey above, the experiments in both 1989 and 1990 fail to show that shorebirds have a significant impact on the abundance of either of these two arthropod prey species.

It is possible that other prey species are important components of shorebird diets at Grays Harbor, even though I rarely observed their capture. To allow for this possibility, I analyzed the changes in abundance of all species at each site; all live in the top 5 cm of sediment and should be available to foraging shorebirds. A summary of these data is presented in Fig. 5. I tabulated the possible outcomes of the experiments using the Initial, Control and Experimental means. One possible outcome, depicted in the first trio of histograms in the figure, obtains when the prey population fails to show any significant change over the course of the experiment, regardless of the presence of shorebird predation. This result was the most common outcome, occurring in 56% of the species/site combinations in 1989 and 88% of the outcomes in 1990. The second set of histograms in Fig. 5 describes an experimental artifact; abundance declines



1989	26	5	1	5	9
1990	38	0	0	2	3

Fig. 5. Summary of experimental outcomes for all species at the three sites. See Figs. 3 or 4 for explanation of Initial, Control and Experimental.

underneath the ceilings (Experimental) while not changing in the unmanipulated area (Initial and Control). This outcome occurred in 11% of the cases in 1989 and none in 1990. The third trio of histograms defines strong evidence for a depressing effect of shorebirds on the prey. A decline from April to May in the control treatments (Initial and Control, respectively) is not accompanied by a decline in the shorebird exclusion areas (Experimental). However, this result occurred only once in 1989 and never in 1990. The fourth set of three histograms in Fig. 5 describes the situation where a prey population declines in both control and experimental areas (i.e. irrespective of shorebird predation). This outcome occurred five times in 1989 and twice in 1990. Other possible permutations of relative magnitudes of treatment means, none of which supports the predation hypothesis, were found in 20 and 6% of the cases in 1989 and 1990, respectively.

4. Discussion

Avian ecologists have used two approaches to determine the impact of shorebirds on their infaunal prey. The observational approach involves determining the abundance of prey before and after shorebird arrival and departure, respectively (see Baird et al., 1985, for review). Observations of the number of prey captured per unit time per bird may be extrapolated to estimate population-wide predation rates. The experimental approach, used in this study, involves the exclusion of shorebirds from experimental areas with the simultaneous sampling of unmanipulated, control areas where the shorebirds can feed freely (e.g. Kent & Day, 1983; Quammen, 1984; Raffaelli and Milne, 1987).

Few studies testing the impact of migratory shorebirds on infaunal prey abundance have been conducted (Wilson, 1991b). Schneider and Harrington (1981) found that prey densities declined during the fall migration of shorebirds at a small stop-over site in Massachusetts, USA. Botton (1984) was unable to demonstrate any effect of shorebirds and gulls on infaunal abundance in Delaware Bay. Wilson (1989) showed that migratory shorebirds in the Bay of Fundy had a complex effect on their major prey, the amphipod *Corophium volutator*. Strong size-selective predation on large *Corophium* ameliorated competition between adult and juvenile *Corophium*, resulting in increased prey abundance (but decreased adult abundance) in the presence of shorebird predation. In this study (Figs. 3, 4 and 5), no evidence of migratory shorebirds at Grays Harbor could be documented.

The lack of a detectable reduction in prey abundance at Grays Harbor is surprising in light of the relatively low prey densities. Infaunal densities during the spring are about 10000 animals/m^2. These densities are significantly less than those found in upper Bay of Fundy where the major prey, the amphipod *Corophium volutator*, reaches densities of 100000/m^2. The lack of predatory impact is even more surprising given that over a million shorebirds use Grays Harbor in spring, roughly the number of shorebirds using the upper Bay of Fundy in the fall (Hicklin, 1987). Furthermore, the available foraging area in Grays Harbor is less than that for migratory shorebirds in the upper Bay of Fundy.

Why then do shorebirds in the Bay of Fundy significantly reduce the abundance of their prey while similar numbers of shorebirds in Grays Harbor, feeding on less expansive, intertidal flats which have only one-tenth of the prey density of the Bay of Fundy have no demonstrable effect on prey abundance? One can surmise that the distance to the next stop-over area may be critical. In the upper Bay of Fundy, the most common migratory shorebird is the Semipalmated Sandpiper (*Calidris pusilla*) which engages in a transoceanic flight from the Bay of Fundy to their wintering grounds in Suriname (Harrington & Morrison, 1979), a flight of 2400 km requiring 48–60 h of sustained flight (Myers et al., 1987). Such a flight requires that these birds store a large quantity of fat to fuel this non-stop flight. Western Sandpipers leave Grays Harbor with some birds stopping at the Fraser River delta in British Columbia (Butler et al., 1987; Butler & Kaiser, 1988) and virtually all Western Sandpipers stopping at the Copper River Delta in south-central Alaska (Isleib, 1979). The lengths of these flights (200 km to the Fraser River, 900 km to the Copper River Delta) would require less fuel to successfully complete the journey and hence birds feeding at Grays Harbor may not have to feed at such a high rate as congeneric birds in the Bay of Fundy. It is likely that most Western Sandpipers spend only a few days in Grays Harbor. The results from this study and from prior studies (cited above) indicate that the episodic predation of migratory shorebirds has variable effects on prey abundance at different stop-over areas.

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