

# Detection of the impact of predation by migratory shorebirds: an experimental test in the Fraser River estuary, British Columbia (Canada)

Mary A. Sewell\*

Dept of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada V5A 1S6  
and

Environment Canada, Pacific Wildlife Research Centre, RR1 5421 Robertson Road, Delta, British Columbia, Canada V4K 3N2

**ABSTRACT:** Exclosure experiments are commonly used in marine soft sediments to examine changes in invertebrate density caused by shorebird predation. However, many of these exclosure experiments do not incorporate the spatial variability of the invertebrate prey in their design and/or analysis. This paper uses a short-term exclosure experiment and random sampling (Before/After predation) to assess reductions in invertebrate densities by western sandpiper *Calidris mauri* on the Fraser River estuary, British Columbia, Canada. During the spring >1 million western sandpiper stop over at the Fraser River estuary on their northward migration to breeding grounds in Alaska. Exclosure experiments and Before/After sampling were conducted at 3 sites on the Fraser River estuary that differed in their sediment characteristics and in their use for feeding by western sandpiper. An examination of cage effects showed that there were no alterations to sediment composition caused by the exclosure cage. However, there were changes in invertebrate numbers in the exclosure cage irrespective of shorebird predation. In particular, mobile invertebrates, such as gastropods and crustaceans, migrated into or out of the exclosure cages during the experiment. Overall, there was little evidence for reduction in invertebrate numbers caused by western sandpiper predation. In the exclosure experiment a significant decline was observed in the phyllodocid polychaete *Eteone* spp., but at a site with little evidence of shorebird predation. Before/After sampling showed some declines in invertebrate numbers, but this could reflect patchiness in invertebrate distributions rather than the direct action of predation. The use of statistical designs for detecting environmental impacts (e.g. BACI) is suggested for future studies of shorebird predation as they allow for the spatial and temporal variability of the invertebrate prey to be considered concomitant with the impact of the shorebird predator. General problems of sampling with sediment cores, high sample variance, and the reduced power of experimental tests need to be considered in future research on the interactions of shorebird predators and their marine invertebrate prey.

**KEY WORDS:** Shorebird predation · Western sandpiper · *Calidris mauri* · Soft sediments · Exclosure experiment

## INTRODUCTION

Exclosure experiments have been widely used to study the impact of predation by migratory shorebirds at both overwintering sites and stopover areas (reviewed by Baird et al. 1985, Piersma 1987, Székely & Bamberger 1992, Ólafsson et al. 1994). However, con-

sidering the *a priori* assumption that shorebirds remove a high proportion of the benthic productivity from intertidal areas (review of Baird et al. 1985: 6 to 44 % of prey production), there are few exclosure studies that have detected a significant reduction in invertebrate numbers by shorebirds. Only 5 studies have shown statistical differences in invertebrate numbers inside and outside exclosure cages after the period of shorebird predation, and often for only a subset of invertebrate species, or at restricted study sites (Schneider 1978, Schneider & Harrington 1981, Kent &

\*Present address: Harbor Branch Oceanographic Institution, 5600 U.S. 1 North, Fort Pierce, Florida 34946, USA.  
E-mail: sewell@hboi.edu

Day 1983, Quammen 1984, Mercier & McNeil 1994). In contrast, numerous studies have shown no reduction in invertebrate numbers in areas exposed to shorebird predation (Goss-Custard 1977, Reise 1978, Duffy et al. 1981, Botton 1984, Raffaelli & Milne 1987, Wilson 1989, 1991a, 1994b, Kalejta 1993).

For a clear demonstration of the importance of shorebird predation on infaunal marine invertebrates, experimenters need to consider the importance of experimental design (Hall et al. 1990b), cage effects (Virnstein 1978, Peterson 1979, Hulberg & Oliver 1980), the spatial layout of the treatments (Hurlbert 1984), and features of invertebrate populations such as spatial and temporal distribution patterns. However, some of the enclosure experiments conducted to date have been pseudoreplicated (Reise 1978, Schneider 1978, Duffy et al. 1981, Schneider & Harrington 1981), unreplicated for a particular tidal level or sediment type (Botton 1984, Mercier & McNeil 1994), have had cages and predation areas separated by large distances (Kent & Day 1983) or have inappropriately pooled samples for statistical analyses (Goss-Custard 1977, Wilson 1989, 1991a, 1994b, Mercier & McNeil 1994). These studies, therefore, did not consider or confounded the spatial variability of invertebrate numbers with the effect of the shorebird predator. The conclusions from these studies should be carefully reconsidered in light of problems with their experimental design and/or statistical analyses.

In this paper I describe a shorebird enclosure experiment conducted on the Fraser River estuary, British Columbia, Canada, during the northward migration of the western sandpiper *Calidris mauri*. Replicate enclosure cages, with adjacent areas open to predation, were placed at 3 study sites that differed in their sediment characteristics (see Table 1) and in their use for feeding by shorebirds. Additional random sampling was conducted at the same study sites, before and after predation, to examine spatial variability in invertebrate distributions and the potential for detection of a predator effect without an exclusion device. This multifaceted approach, together with knowledge of the prey consumed by western sandpiper (K. Vermeer & R. W. Elner unpubl. data), allowed a detailed examination of the effects of western sandpiper predation on the densities of their invertebrate prey.

#### Western sandpiper *Calidris mauri*

The western sandpiper is one of the commonest shorebirds of the western hemisphere, migrating in large flocks along the Pacific coast of North America to breeding grounds in the western subarctic of Alaska and eastern Siberia during the spring (Wilson 1994a).

Overwintering occurs in coastal areas of the Pacific, from California to Peru, and the Atlantic, from the southeastern United States to Surinam (Wilson 1994a). The primary migration route to the breeding grounds is along the Pacific coast of North America (O'Reilly & Wingfield 1995), with stopover areas including San Francisco Bay (California), Grays Harbor (Washington), the Fraser River estuary (British Columbia), Chesterman Beach and Tofino mudflats (British Columbia), the Stikine River Delta (Alaska), and the Copper River Delta (Alaska) (Iverson et al. 1996). At the Fraser River estuary the northward migration is characterized by a peak in numbers in the period from mid-April to late May (Butler et al. 1987), with maximum numbers in 1992 occurring in the week of 26 to 29 April when >500 000 shorebirds were present (Butler 1994). The greatest overall densities of western sandpiper were found on Roberts Bank, West Boundary Bay, and Sea Island (Butler 1994; for locations see Fig. 1). In contrast, the southward migration is spread over a longer time period (late June to early October; Butler et al. 1987), because of sex- and age-segregated movements by adult and juvenile shorebirds (Butler et al. 1987).

At stopover sites and at the wintering grounds, the main foods consumed by western sandpiper are marine benthic invertebrates such as arthropods, polychaete annelids and bivalve molluscs (Wilson 1994a). Preliminary studies in the Fraser River estuary have shown that molluscs (*Macoma balthica*, *Batillaria zonalis*), polychaetes (*Nereis* spp.) and crustaceans (amphipod: *Corophium* spp.; cumacean: *Leucon subnasica*; tanaid: *Sinelobus stanfordi*; podocopid ostracods) are present in the diet of western sandpiper (Vermeer & Elner unpubl. data; see Table 2).

#### METHODS

Experimental work was carried out in spring (April to May) 1994 on the Fraser River estuary, near Vancouver, British Columbia, Canada (Fig. 1), during the northward migration of the western sandpiper. Research was conducted at this time as the largest migrant population of shorebirds was present on the estuary during a discrete time period. Consequently, enclosure cages were present on the mudflat for only 1 mo, reducing the potential for long-term cage effects and the seasonal recruitment of marine invertebrates.

The 3 study sites were known feeding areas for western sandpipers (Butler 1994), differed in their sediment characteristics (Table 1), and had previously been used in studies of invertebrate distributions (Elner unpubl. data). Two sites were on Roberts Bank (Westham Island and Brunswick Point), and a single site was in

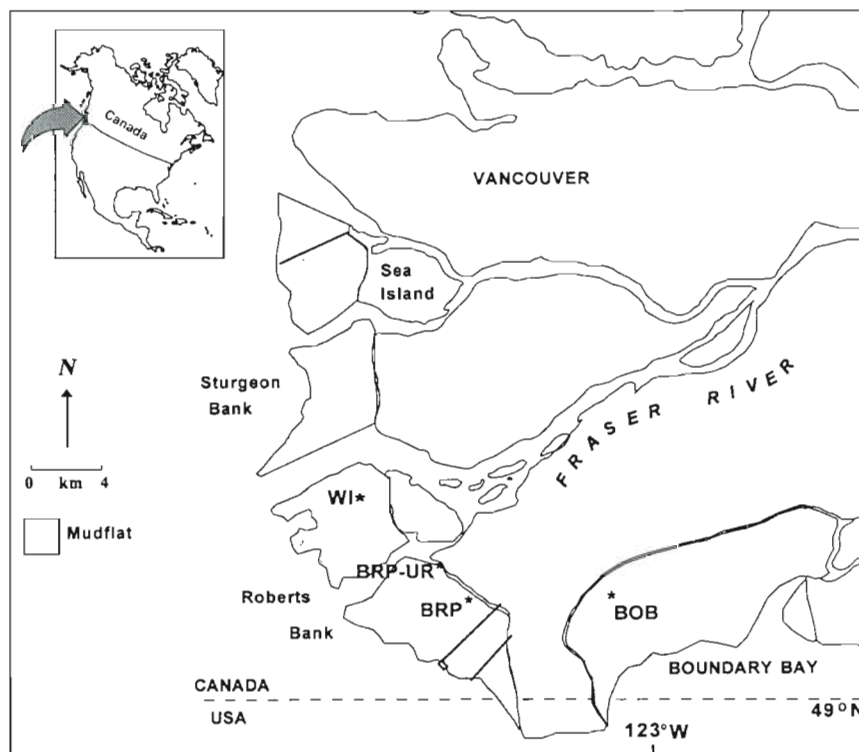


Fig. 1 Fraser River estuary, British Columbia, Canada, showing locations of enclosure experiments at Boundary Bay (BOB), Brunswick Point (BRP) and Westham Island (WI), and random sampling at Brunswick Point-Upper Roost (BRP-UR)

the western part of Boundary Bay (Fig. 1). All locations were in the upper intertidal zone (Table 1).

At each site, 2 studies were conducted to test for an impact of western sandpiper predation on the invertebrate populations. The first was an enclosure experiment that prevented birds from foraging on small areas of mudflat; the second was a comparison of invertebrate numbers before and after the western sandpiper northward migration in an area adjacent to the enclosures.

**Enclosure experiment.** The enclosure design was modeled on that used by Wilson (1994b) in an experiment testing for an impact of predation by western sandpiper in Grays Harbor, Washington, USA. Each enclosure was constructed from 4 wooden stakes

(0.6 m length) driven into the sediment in a  $0.8 \times 0.6$  m rectangular array until the top of the stake was 12 cm above the sediment surface. After sampling (see below) a roof of chicken wire (25 mm mesh) was stapled onto the top of the stakes. The height of the cage excluded western sandpiper (Wilson 1994b, author's pers. obs.); the open sides of the cage allowed predators other than shorebirds (e.g. crabs, fish) to enter the enclosure.

The enclosure cages (Cage = Predation-) and unmarked open areas (Open = Predation+) were arranged in a systematic design that ran parallel to the shoreline at the same tidal elevation. Five enclosure cages were spaced 5 m apart, as in Wilson (1994b),

Table 1. Characteristics of the 3 study sites used for enclosure experiments. Position: position of the enclosure cages. Tidal elevation: distance above Canadian chart datum (= the plane of lowest normal tides). Sediment type based on samples ( $N = 5$ ) taken at time of cage construction (Before,  $S^B$ ; Fig. 2). Methods for determining sediment penetrability are described in the text

Location	Position	Tidal elevation	Sediment type (median $\phi$ )	Mean % sand <sup>a</sup>	Sediment penetrability mean $\pm$ SD (cm)
Boundary Bay	49° 03' 04" N, 123° 01' 18" W	+3.2 m	2.73	99.4	8.39 $\pm$ 4.10
Brunswick Point	49° 03' 07" N, 123° 08' 31" W	+2.6 m	>4.0	46.5	13.42 $\pm$ 1.00
Westham Island	49° 05' 40" N, 123° 12' 41" W	+1.8 m	3.15	69.7	8.81 $\pm$ 1.34

<sup>a</sup>The remaining percentage is silt. Rare pieces of shell were retained in the gravel portion at samples from all sites



with the 12 open areas interspersed systematically around them (Fig. 2A). A similar arrangement of Predation–/Predation+ treatments was used by Hurlbert & Chang (1983), with the rationale that if the birds avoid the enclosure cages, randomly varying the distance between the enclosures would lead to increased variability among open areas in their use by birds (Hurlbert 1984). Open areas (Predation+) were 3 m shoreward or seaward from the centre of the enclosure cage (Predation–), spaced 5 m apart in a horizontal pattern offset by 2.5 m from the enclosure cages (Fig. 2A).

Enclosure cages were positioned on the mudflat in the period of low tides (11 to 15 April 1994) prior to the arrival of western sandpiper on the Fraser River estuary. Once the stakes were in the sediment, three 10 cm diameter by 10 cm deep cores were taken at 3 of the 4 corners of the cage as determined by a coin toss (UL/UR/LR or UR/LR/LL; Fig. 2B) to provide a Before sample for the enclosure cage. These cores were taken immediately outside the enclosure cage to avoid disturbance to the central part of the cage which would be used in the After sampling. The initial sediment sample was taken approximately 5 cm into the cage at the remaining corner ( $S^B$ ; Fig. 2B) as described below. Plant material, such as *Zostera* or filamentous algae, that was caught in the mesh of the

enclosure cages was removed during regular visits to each study site.

After western sandpipers had migrated north of the Fraser River estuary, the experiment was completed by sampling three 10 cm diameter (10 cm deep) invertebrate cores and a single sediment core ( $S^A$ ) within each enclosure cage as shown in Fig. 2B. The Open areas, available for feeding by western sandpiper, were sampled for invertebrates in the same manner using a  $0.8 \times 0.6$  m rectangular quadrat to define the position of the cores. Sampling was completed during the low tide period of 25 to 27 May 1994.

All invertebrate samples were frozen immediately after returning to the laboratory. Defrosted sediments were later sieved through a 500  $\mu$ m mesh screen to remove the macrofauna, and the invertebrates preserved in 85% ethanol. Invertebrates were sorted to the species level, where possible, using reference collections from a previous study (Elner unpubl. data).

**Bird feeding around enclosures:** Evidence for shorebird predation in the region of the enclosure experiment was collected throughout the period of western sandpiper migration (19 April to 12 May 1994). A rectangular grid ( $29 \times 6$  m) was placed around the enclosure cages, including the unmarked Open areas, and marked with pieces of bamboo stake that protruded 5 cm from the sediment surface (Fig. 2A). Visits were made to each enclosure area every 2 d at low tide and counts made of the number of shorebird faeces in the  $29 \times 6$  m rectangle. The same route was used from the shore to the enclosure cage to minimize the effects of human footprints on shorebird feeding. Tests showed that faeces were removed on subsequent high tides at all locations (author's unpubl. data), so counts made on a survey were evidence for presence of shorebirds in the enclosure area on that low tide period. Larger faeces produced by birds such as gulls and herons were excluded from the counts.

Observations on western sandpiper feeding and the presence of faeces showed that birds did not avoid the enclosures but fed adjacent to and between the cages (R. Butler, M. Lemon, and author's pers. obs.).

**Sediment analyses:** Sediment samples were collected at each study site using cores constructed from 30 cc disposable syringes (17.4 mm diameter, 105 mm length). Cores were taken from the inside corner of the cage at the beginning of the experiment ( $S^B$ ) and from the centre of the cage at the end of the experiment ( $S^A$ ; Fig. 2B). Samples were frozen in the syringe after returning from the field and stored until analysis. The upper 3 cm of the core was cut, the sediments dried in a freeze-drier, and particle size analysis performed using standard techniques (Holme & McIntyre 1984). To determine if there was a change in the sediment composition within the enclosure cages during the

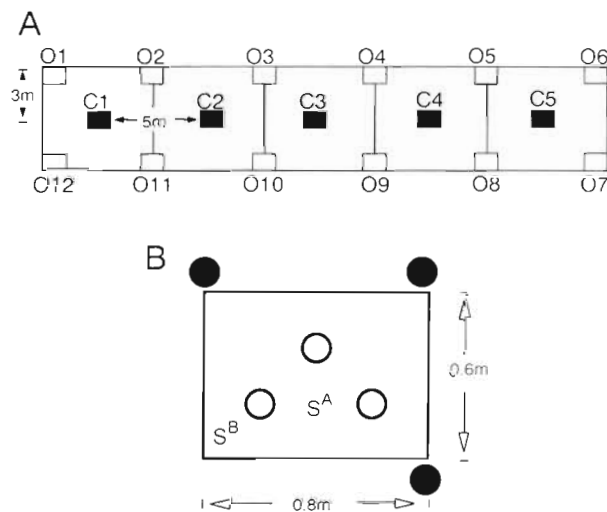


Fig. 2. (A) Arrangement of enclosure Cages (C1 to C5) and Open areas (O1 to O12) at each study site. Enclosure Cages and Open areas were spaced 5 m apart at the same tidal elevation. Square areas surrounding each enclosure Cage (bordered by e.g. O1-O2-O11-O12) are the zones in which shorebird faeces were censused. (B) Sampling protocol for each enclosure Cage or Open area. The  $0.8 \times 0.6$  m area was sampled for sediments at the beginning and end of the experiment ( $S^B$ ,  $S^A$  respectively) and for invertebrates. Samples taken at the beginning of the experiment (Before) were at 3 of the corners of the enclosure Cage (●); at the end of the experiment (After) 3 cores were taken inside the enclosure Cage and in Open areas (○)

experiment, the proportion of silt (<63  $\mu\text{m}$ ) was compared for the Before/After samples at each site using a paired sample *t*-test.

An index of sediment penetrability was obtained in the 29  $\times$  6 m gridded area surrounding the enclosure cages (Fig. 2A) following the method of Kalejta & Hockey (1991). The depth of penetration of a standard 4.8 mm diameter brass rod (0.76 m length, 115 g weight) is measured after being dropped down a 1.5 m PVC tube. The reported index of penetrability is the mean of 10 measurements made in a range of substrate conditions (wetness, texture, etc.) within the grid.

**Before and After study.** Random sampling to test for changes in invertebrate numbers, without an enclosure device, was conducted at the 3 study sites (Boundary Bay, Brunswick Point, Westham Island; Fig. 1) on 1 occasion before (Before; 11 to 15 April) and 1 occasion after the northward migration (After; 25 to 27 May). Sampling was conducted during the same low-tide period as the enclosure experiment at all study sites except Westham Island Before.

Random samples were collected in an area approximately 100 m from Cage 5 at the same tidal elevation as the enclosure experiment. Three sites (A to C) were spaced 100 m apart and marked for the duration of the northward migration of western sandpipers with a wooden stake. At each sampling (Before/After) 3 plots were randomly chosen within each site using a random compass direction and a distance (0 to 50 m) from the

centre stake. In each plot 3 cores were taken within a 0.8  $\times$  0.6 m area, equivalent to the size of the enclosure cage, resulting in a total of 27 cores (3 sites  $\times$  3 plots  $\times$  3 cores) Before and 27 cores After the period of predation at each study site.

In addition to the study sites used for the enclosure experiments, random sampling was conducted at a western sandpiper roost site at Brunswick Point (Brunswick Point-Upper Roost; Fig. 1). This location was adjacent to the salt marsh and was the last part of the shore at Brunswick Point to be covered by the incoming tide. Large numbers of western sandpiper fed in this area (density of faeces and peck/probe marks; author's unpubl. obs.) prior to roosting in the saltmarsh or adjacent fields. Samples were taken Before (19 April) and After (30 May) the northward migration using the sampling protocol described above.

**Statistical analyses.** Statistical analyses were performed on species that were present in at least 65% of the total 66 cores collected in the enclosure experiment and/or were known to be consumed by western sandpiper (Vermeer & Elner unpubl. data; Table 2). The 2 exceptions to the former criteria were *Macoma balthica* at Boundary Bay (39% of cores) and gammarid amphipods at Westham Island (57% of cores). These species were included because of their potential importance in the western sandpiper diet. The measured variable in all analyses was the number of invertebrates per 10 cm core, transformed by  $\log_{10}(x + 1)$  to

Table 2. Range in number of invertebrates per core for species used in analyses at each study site. Diet: asterisk denotes presence of species in stomach contents of western sandpiper from these locations (Vermeer & Elner unpubl. data). Cage Before: range in cores from enclosure Cages 1 to 5 in April 1994 (N = 15). Cage After: range in cores from enclosure Cages 1 to 5 in May 1994 (N = 15). Open After: range in cores from Open areas 1 to 12 exposed to shorebird predation in May 1994 (N = 36)

Location	Species	Diet	Cage Before	Cage After	Open After
Boundary Bay	<i>Batillaria zonalis</i>	•	0–14	0–6	0–11
	<i>Macoma balthica</i>	•	0–5	0–1	0–3
	<i>Eteone</i> spp.		0–5	1–6	0–4
	<i>Manayunkia aestuarina</i>		0–3	0–5	0–10
	Podocopid ostracod	•	5–49	1–14	2–174
Brunswick Point	<i>Macoma balthica</i>	•	6–18	4–15	2–15
	<i>Manayunkia aestuarina</i>		25–699	1–574	3–361
	<i>Eteone</i> spp.		0–5	0–3	0–6
	<i>Hobsonia florida</i>		4–27	2–20	1–24
	<i>Leucon subnasica</i>		6–97	0–42	2–96
	<i>Sinelobus stanfordi</i>		7–58	1–102	1–31
	<i>Corophium</i> spp.	•	0–14	1–37	1–31
Westham Island	<i>Macoma balthica</i>	•	18–51	23–45	26–56
	<i>Mya arenaria</i>		0–10	0–4	0–5
	<i>Manayunkia aestuarina</i>		54–1044	10–654	7–926
	<i>Hobsonia florida</i>		1–31	6–33	2–28
	<i>Leucon subnasica</i>	•	5–41	0–6	0–18
	<i>Sinelobus stanfordi</i>	•	0–34	1–17	0–34
	<i>Corophium</i> spp.	•	8–39	2–27	0–28
	Gammarids	•	0–11	0–6	0–10

conform to the assumptions of ANOVA. Separate analyses were completed for each study site using PC-SAS Release 6.03.

**Exclosure experiment:** The statistical analysis for the exclosure experiment was completed in 2 parts:

(1) The effect of the exclosure cage on invertebrate numbers with no predation by shorebirds (cage effects). The analysis compared invertebrate numbers in the cores taken at the corners of the cage prior to migration (Before) with those taken inside the exclosure cage after the period of predation (After). For each study site and species, differences in invertebrate numbers were compared Before and After predation (B/A), and among exclosure cages (Cage), using a 2-way analysis of variance. The model used in the ANOVA was:

$$X_{ijk} = \mu + B/A_i + Cage_j + B/A \times Cage_{ij} + e_{k(ij)}$$

Both factors were fixed; the effect of all factors was examined against the residual error.

(2) The impact of western sandpiper predation on invertebrate numbers was tested using a nested analysis of variance. For each study site and species, differences in invertebrate numbers were compared in cores taken inside exclosure cages (Predation-) with those in areas open to predation by shorebirds (Predation+) in the After sampling. The model used in the ANOVA was:

$$X_{ijk} = \mu + Predation-/+_i + Position(Predation-/+_{j(i)}) + e_{k(ij)}$$

where Predation = exclosure Cage (Predation-) or Open area (Predation+), and Position = the location of that treatment (Predation- or Predation+) within the predation array (see Fig. 2A). The effect of the Predation-/+ term was examined against the nested term Position(Predation-/+), and the effect of Position(Predation-/+), examined against the residual error.

**Before and After study:** For each study site and species, differences in invertebrate numbers were compared Before and After predation, among sites, and among plots nested within sites using a mixed model analysis of variance. In this analysis the factor Before/After predation was fixed, with Site (A to C) a random factor, orthogonal to time, and Plot a random factor, nested within Site. The model used in the ANOVA was:

$$X_{ijk} = \mu + B/A_i + Site_j + B/A \times Site_{ij} + Plot(Site)_{k(ij)} + B/A \times Plot(Site)_{ik(ij)} + e_{k(ij)}$$

The effect of western sandpiper predation (B/A) was tested against the interaction term  $B/A \times Site$ ; the effect of Site against the term  $Plot(Site)$ ; the effect of  $B/A \times Site$  against the interaction term  $B/A \times Plot(Site)$ ; and the effects of Plot and  $B/A \times Plot(Site)$  were tested against the residual error.

## RESULTS

A summary of the relative abundances of the infaunal invertebrates throughout the Fraser River estuary is given in Table 2. The same general suite of marine invertebrates was found at all study sites, except for the gastropod *Batillaria zonalis* and podocypid ostracods which were found in Boundary Bay only (Table 2). The most numerically abundant species was the small sabellid polychaete *Manayunkia aestuarina* (size 0.5 to 3 mm; Eckman 1979) which forms dense mats of tubes at Brunswick Point and Westham Island, and is rare at Boundary Bay. Other abundant species included the terebellid polychaete *Hobsonia florida*, the crustaceans *Leucon subnasica*, *Sinelobus stanfordi*, *Corophium* spp. and other gammarid amphipods (Table 2).

### Exclosure experiment

#### Cage effects

**Sediment analyses.** The 3 study sites used for the exclosure experiment had different sediment characteristics (Table 1). The sediments in Boundary Bay were almost exclusively sand, with <1% silt, and the lowest mean penetrability (Table 1). Penetrability was, however, higher in wetter areas (maximum 16.7 cm). A high percentage of sand was also found in sediments at Westham Island, with a similar penetrability to that observed at Boundary Bay (Table 1). The 'muddiest' site was Brunswick Point, with over 50% of each sample in sediments <63  $\mu$ m (Table 1). The combination of fine sediments and a high water content in the sediment resulted in the highest index of penetrability (Table 1).

There was no significant change in the percentage of silt in sediment samples taken at the beginning and end of the exclosure experiment at any of the 3 study sites ( $S^A$  vs  $S^B$ , paired  $t$ -tests: Boundary Bay,  $t = 0.256$ ; Brunswick Point,  $t = 0.148$ ; Westham Island,  $t = 0.867$ ;  $df = 4$ ,  $p > 0.05$ ). This suggests that, on the time scale of the exclosure experiment, there was no alteration in sediment composition resulting from the hydrodynamic effect of the exclosure cage.

Deep excavations (ca 5 cm deep) were observed at the corners of each exclosure cage at Westham Island. This scouring resulted from high current flow at this site, but did not affect the central area of the cage used for the After invertebrate and sediment samples (see Fig. 2B).

**Invertebrates.** Changes to the invertebrate numbers in the exclosure cages are described below for the studied species at each study site. In addition, the crab

Table 3. Analyses of variance of the number of invertebrates per core [ $\log_{10}(x + 1)$  transformed] for species at the 3 study sites. Two-way ANOVAs with factors: Before/After (B/A), samples from April and May 1994; Cage, enclosure cage 1 to 5; and the interaction term B/A  $\times$  Cage. Degrees of freedom for F: B/A = 1, 20; Cage = 4, 20; B/A  $\times$  Cage = 4, 20. See model statement in 'Methods'. Significant p-values are shown in bold. Gammarids includes all amphipods except *Corophium* spp.

Location	Species	B/A		Cage		B/A $\times$ Cage	
		F	p	F	p	F	p
Boundary Bay	<i>Batillaria zonalis</i>	9.91	<b>0.005</b>	0.60	0.670	1.95	0.142
	<i>Macoma balthica</i>	4.62	<b>0.044</b>	1.46	0.251	0.95	0.454
	<i>Eteone</i> spp.	3.35	0.082	1.32	0.298	0.42	0.793
	<i>Manayunkia aestuarina</i>	0.01	0.938	2.81	0.053	0.92	0.473
	Podocypid ostracod	19.37	<b>0.0003</b>	1.05	0.405	0.90	0.484
Brunswick Point	<i>Macoma balthica</i>	6.22	<b>0.022</b>	1.78	0.172	2.41	0.083
	<i>Manayunkia aestuarina</i>	4.77	<b>0.041</b>	1.39	0.272	1.48	0.247
	<i>Eteone</i> spp.	1.13	0.301	0.64	0.641	1.38	0.278
	<i>Hobsonia florida</i>	0.95	0.340	4.23	<b>0.012</b>	0.71	0.597
	<i>Leucon subnasica</i>	6.24	<b>0.021</b>	0.98	0.440	0.98	0.441
	<i>Sinelobus stanfordi</i>	16.85	<b>0.0006</b>	3.94	<b>0.016</b>	1.88	0.153
	<i>Corophium</i> spp.	12.92	<b>0.002</b>	3.31	<b>0.031</b>	0.69	0.610
Westham Island	<i>Macoma balthica</i>	1.08	0.311	0.85	0.512	0.91	0.478
	<i>Mya arenaria</i>	0.15	0.699	0.40	0.803	2.02	0.131
	<i>Manayunkia aestuarina</i>	4.26	0.052	0.65	0.632	0.54	0.707
	<i>Hobsonia florida</i>	0.07	0.795	3.20	<b>0.035</b>	1.01	0.427
	<i>Leucon subnasica</i>	116.28	<b>0.0001</b>	0.84	0.514	0.66	0.627
	<i>Sinelobus stanfordi</i>	0.28	0.600	3.17	<b>0.036</b>	0.83	0.523
	<i>Corophium</i> spp.	3.31	0.084	1.00	0.429	0.12	0.973
	Gammarids	0.20	0.657	0.27	0.895	1.14	0.368

*Hemigrapsus* spp., which was absent in the Before samples, was found under the enclosure cages at Boundary Bay and Brunswick Point at the end of the experiment.

(A) Boundary Bay. Five invertebrate species or taxa were examined in Boundary Bay, with significant differences in invertebrate numbers in the area immediately outside (Before, April) and inside the enclosure cage (After, May) in 3 of the species (Table 3). In these 3 species there was a decline in mean numbers between the 2 sampling dates (Fig. 3). This was most marked in the gastropod *Batillaria zonalis* and podocypid ostracods in which the maximum number per core decreased by a factor of 2 between April and May (Table 2). Similarly, *Macoma balthica* showed a significant B/A effect (Table 3) with a decline in mean numbers (Fig. 3). However, in *M. balthica* the mean number per core was usually <1 and no individuals were found at Cage 4 on either sampling date (Fig. 3).

(B) Brunswick Point. Significant B/A effects were found in 5 of the 7 species examined at this study site (Table 3). Again there was a trend for a decline in invertebrate numbers between the April and May sampling dates, except for *Corophium* spp. (Fig. 4). The significant B/A differences in less mobile species such as *Macoma balthica*, and the sabellid polychaete *Manayunkia aestuarina* (Table 3, Fig. 4), probably occurs because the Before samples outside the exclo-

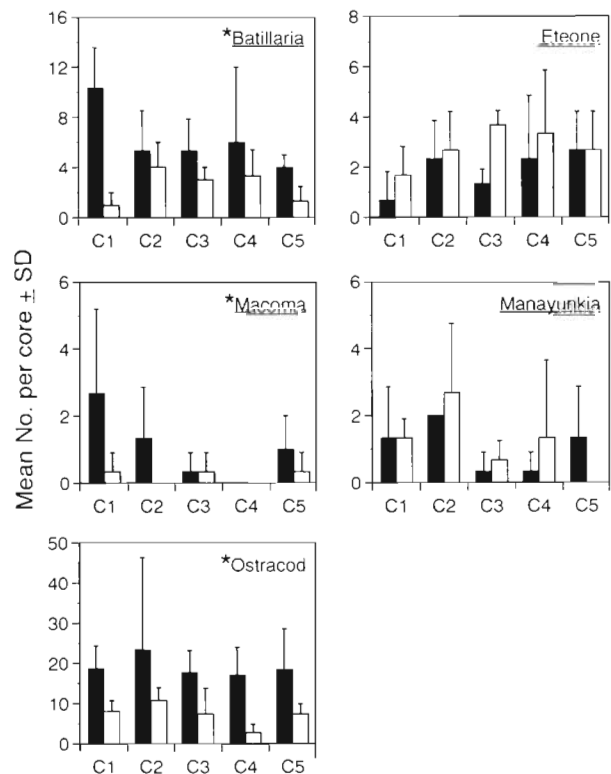


Fig. 3. Invertebrate numbers in Cages 1 to 5 at the beginning (Before, solid bars) and end (After, open bars) of the enclosure experiment from Boundary Bay. Asterisk prior to species name denotes a significant B/A effect in the ANOVA (Table 3)



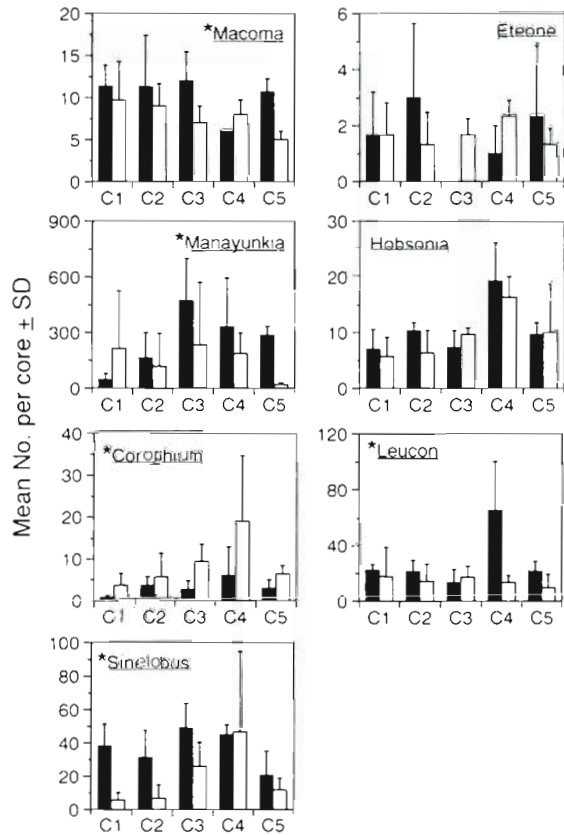


Fig. 4. Invertebrate numbers in Cages 1 to 5 at the beginning (Before, solid bars) and end (After, open bars) of the enclosure experiment from Brunswick Point. Asterisk prior to species name denotes a significant B/A effect in the ANOVA (Table 3)

sure cage did not provide a good estimate of numbers inside. Although declines were seen in most cages, there were B/A increases in Cage 4 for *M. balthica* and Cage 1 in *M. aestuarina* (Fig. 4). Evidence for this small-scale patchiness was also seen in the terebellid polychaete *Hobsonia florida*, which showed a significant difference between cages (Table 3, Fig. 4).

The remaining species that showed significant B/A differences are all mobile crustaceans: the cumacean *Leucon subnasica*, the tanaid *Sinelobus stanfordi*, and the gammarid amphipod *Corophium* spp. (Table 3, Fig. 4). Generally, numbers declined between Before and After samples (*L. subnasica*, *S. stanfordi*; Fig. 4). However, in *Corophium* spp. numbers per core increased up to 3-fold during the experiment (Table 2, Fig. 4). In the latter species, there was also a significant difference between cages (Table 3).

(C) Westham Island. A significant B/A effect was found in 1 species (Table 3), the cumacean *Leucon subnasica*, for which numbers decreased in May to 10% of the April value (Table 2, Fig. 5). There were, however, significant differences between cages in the

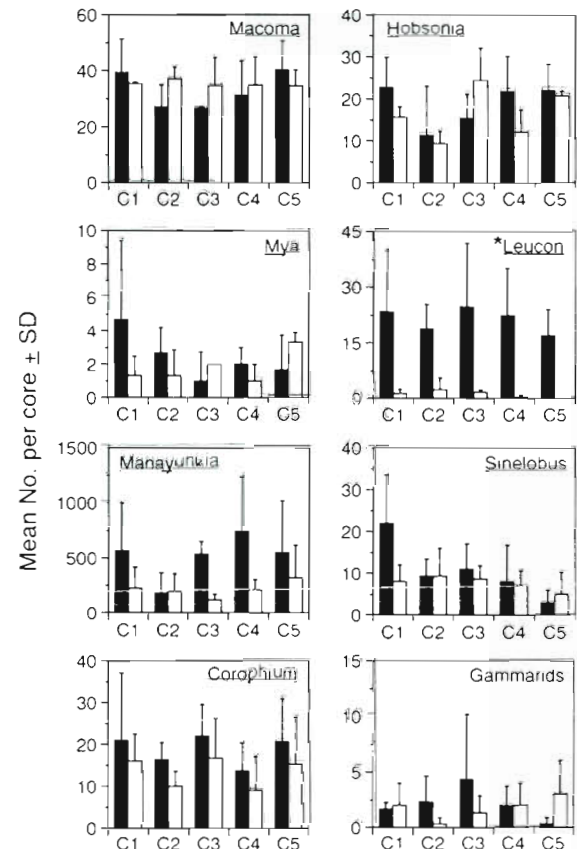


Fig. 5. Invertebrate numbers in Cages 1 to 5 at the beginning (Before, solid bars) and end (After, open bars) of the enclosure experiment from Westham Island. Asterisk prior to species name denotes a significant B/A effect in the ANOVA (Table 3)

terebellid polychaete *Hobsonia florida* and the tanaid *Sinelobus stanfordi* (Table 3, Fig. 5).

#### Predation effect

*Evidence for predation by western sandpiper.* Counts of western sandpiper faeces were made from 19 April to 12 May 1994, to provide a semi-quantitative index of the use by shorebirds of the respective study sites. Feeding western sandpiper produce a faecal pellet every 1 to 3 min (R. Butler pers. comm.), so that faeces within the census area were likely produced from food obtained at that study site, if not in the immediate area surrounding the enclosure cages. This index is an alternate measure to directly observing shorebirds feeding at the study site.

Using the total number of faeces in the 29 × 6 m census area as an index of shorebird predation, the sites are ranked in descending order: Westham Island, Brunswick Point, Boundary Bay (Table 4). There was little evidence for predation at the Bound-



Table 4. *Calidris mauri*. Index of predation by western sandpiper in the gridded area around the enclosure experiment at the 3 study sites in the period 19 April to 12 May 1994. Numbers presented are number of faeces in the 29 × 6 m census area (174 m<sup>2</sup>)

Location	Mean	SD	No. of days censused (N)	Minimum no. of faeces in area	Maximum no. of faeces in area	No. of days with no faeces
Boundary Bay	0.54	0.97	13	0	3	9
Brunswick Point	34.18	47.10	11	0	156	1
Westham Island	50.1	46.6	10	0	116	1

ary Bay site as there were no faeces in the enclosure area on almost 70% of the censused days (Table 4). Westham Island and Brunswick Point had similar levels of predation, although the date with the maximum number of faeces differed (30 April and 6 May respectively). In both cases the single day with no faeces occurred in late May after the majority of western sandpipers had migrated north of the Fraser River estuary.

The ranking of the sites for western sandpiper feeding using the faecal index correlates with observations of western sandpiper flocks in the Fraser River estuary. As the tide rises, flocks of western sandpiper feeding at Westham Island fly south to Brunswick Point where they feed until the rising water covers the mudflats. Flocks then fly to Boundary Bay, or remain at Brunswick Point, to roost in agricultural fields adjacent to the mudflats. On the ebbing tide flocks of western sand-

piper return to Brunswick Point and then to Westham Island (R. Butler pers. comm.). Thus, the primary feeding sites are at Westham Island and Brunswick Point. The low number of faeces at the high shore Boundary Bay site probably reflects the low use of this area for feeding.

No western sandpiper faeces were observed inside the enclosure cages, suggesting that the enclosures were effectively excluding the shorebird predator.

*Invertebrates.* (A) Boundary Bay. A significant difference in invertebrate numbers between Cage (Predation-) and areas Open (Predation+) to predation by western sandpiper was found in only 1 species at Boundary Bay, the phyllodocid polychaete *Eteone* spp. (Table 5). Although there were lower numbers of *Eteone* spp. in the Open area outside the enclosure (Fig. 6), this difference occurred at a study site with little evidence of shorebird predation (Table 4).

Table 5. Analyses of variance of the number of invertebrates per core [ $\log_{10}(x + 1)$  transformed] for species at the 3 study sites. Nested ANOVAs with factors: Predation-/+, enclosure Cage or Open area in May 1994; Position(Predation-/+). Degrees of freedom for *F*: Predation-/+ = 1, 15; Position(Predation-/+) = 15, 34. See model statement in 'Methods'. Significant p-values are shown in bold. Gammarids includes all amphipods except *Corophium* spp.

Location	Species	Predation-/+		Position(Predation-/+)	
		<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Boundary Bay	<i>Batillaria zonalis</i>	0.39	0.541	1.94	0.054
	<i>Macoma balthica</i>	3.06	0.101	1.66	0.108
	<i>Eteone</i> spp.	14.86	<b>0.0016</b>	0.65	0.815
	<i>Manayunkia aestuarina</i>	1.62	0.222	1.17	0.339
	Podocopid ostracod	0.66	0.430	0.99	0.482
Brunswick Point	<i>Macoma balthica</i>	0.36	0.559	1.80	0.076
	<i>Manayunkia aestuarina</i>	0.96	0.342	0.81	0.656
	<i>Eteone</i> spp.	0.02	0.898	0.71	0.758
	<i>Hobsonia florida</i>	1.01	0.331	1.71	0.096
	<i>Leucon subnasica</i>	2.76	0.117	0.71	0.757
	<i>Sinelobus stanfordi</i>	0.75	0.402	1.96	0.051
	<i>Corophium</i> spp.	0.03	0.857	1.96	0.052
Westham Island	<i>Macoma balthica</i>	0.44	0.516	0.73	0.735
	<i>Mya arenaria</i>	0.01	0.923	1.65	0.111
	<i>Manayunkia aestuarina</i>	1.65	0.219	0.46	0.944
	<i>Hobsonia florida</i>	2.44	0.139	1.39	0.207
	<i>Leucon subnasica</i>	0.66	0.430	1.38	0.211
	<i>Sinelobus stanfordi</i>	2.54	0.132	1.06	0.428
	<i>Corophium</i> spp.	1.84	0.196	2.60	<b>0.010</b>
	Gammarids	0.19	0.671	1.99	<b>0.048</b>

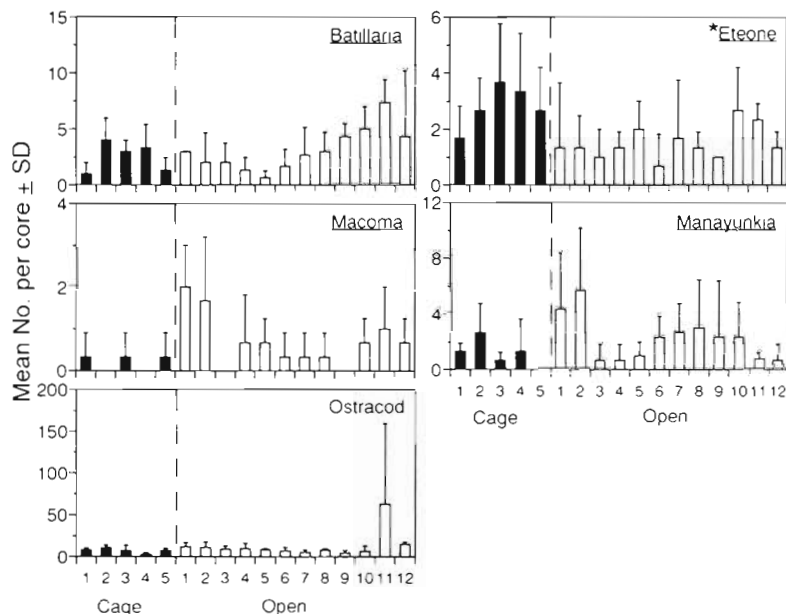


Fig. 6. Invertebrate numbers in Cages (C1 to C5, solid bars) and Open areas (O1 to 12, open bars) after the period of western sandpiper predation at Boundary Bay. Dashed line separates Cage and Open areas. Asterisk prior to species name denotes a significant Predation effect in the ANOVA (Table 5)

The other species tested showed non-significant Predation-/+ effects (Table 5). Cages and Open areas showed a high degree of variability and often showed increases in invertebrate numbers in the presence of predation (Fig. 6).

tested showed similar mean numbers per core in Cage or Open areas (e.g. *Macoma balthica*, *Mya arenaria*, *Hobsonia florida*) or high variability in some Cage or Open areas (e.g. *Manayunkia aestuarina*, *Leucon subnasica*, *Sinelobus stanfordi*; Fig. 8).

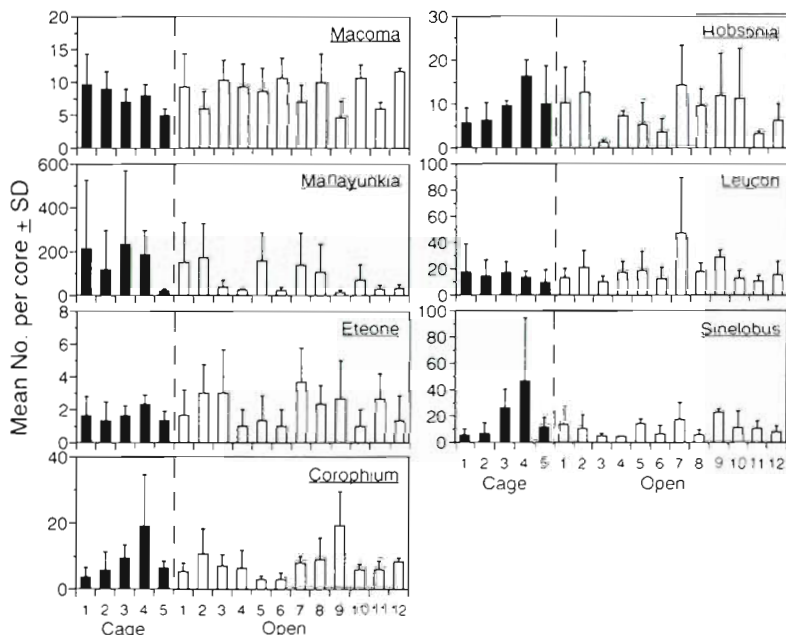


Fig. 7. Invertebrate numbers in Cages (C1 to C5, solid bars) and Open areas (O1 to 12, open bars) after the period of western sandpiper predation at Brunswick Point. Dashed line separates Cage and Open areas. Asterisk prior to species name denotes a significant Predation effect in the ANOVA (Table 5)

(B) Brunswick Point. No significant Predation-/+ effects were seen at Brunswick Point (Table 5), which showed a high index of use for feeding by western sandpiper (Table 4). There were also no significant differences in invertebrate numbers in replicate Cage or Open areas [Position(Predation-/+); Table 5]. High variability was seen in the mean numbers per core for the polychaetes (*Manayunkia aestuarina*, *Hobsonia florida*) and the crustaceans (*Corophium* spp., *Leucon subnasica*, *Sinelobus stanfordi*) in both Cage and Open areas (see SD error bars in Fig. 7).

(C) Westham Island. This site, with the highest index of predation (Table 4), had no significant Predation-/+ effects (Table 5). Significant Position(Predation-/+ ) differences were observed in *Corophium* spp. and gammarid amphipods (Fig. 8). In both cases, numbers per core were higher in Open areas 1 to 4, 11 and 12, on the left half of the predation array (see Fig. 2A). The other species

### Before and After study

Analyses of invertebrate numbers from random samples taken before and after the northward migration of western sandpiper showed few significant B/A differences (Table 6). The bivalve *Macoma balthica* showed significant B/A differences at both Boundary Bay and Westham Island (Table 6, Figs. 9 & 11). A decline in mean numbers of *M. balthica* was observed at Boundary Bay (Fig. 9), where there was little evidence for western sandpiper predation (Table 4). In contrast, at Westham Island, with the highest index of predation (Table 4), the numbers of *M. balthica* increased in the period After predation (Fig. 11).

Significant B/A differences were seen in the polychaete *Manayunkia aestuarina*, the cumacean *Leucon subnasica*, and the tanaid *Sinelobus stanfordi* at Brunswick Point (Table 6, Fig. 10). In these

species there was a dramatic decline in numbers per core in the After samples (Fig. 10). However, these same species showed non-significant B/A effects at Westham Island, which was also used extensively for western sandpiper feeding (Table 6, Fig. 11).

The Brunswick Point-Upper Roost site, which experienced intense use as a roost and feeding site during the period of study (author's pers. obs.), did not show significant B/A differences in any of the species tested (Table 6, Fig. 12). The trend was for a decline or similar numbers per core Before and After predation, with the exception of *Manayunkia aestuarina* for which mean numbers increased in the After samples (Fig. 12).

Evidence for spatial variability in invertebrate numbers was seen at all study sites (Table 6). At Brunswick Point and Westham Island, significant differences were seen at the scale of Sites (100 m apart). However, it was the scale of Plots (10s of metres apart) that was significant in 13 out of 23 cases tested (Table 6).

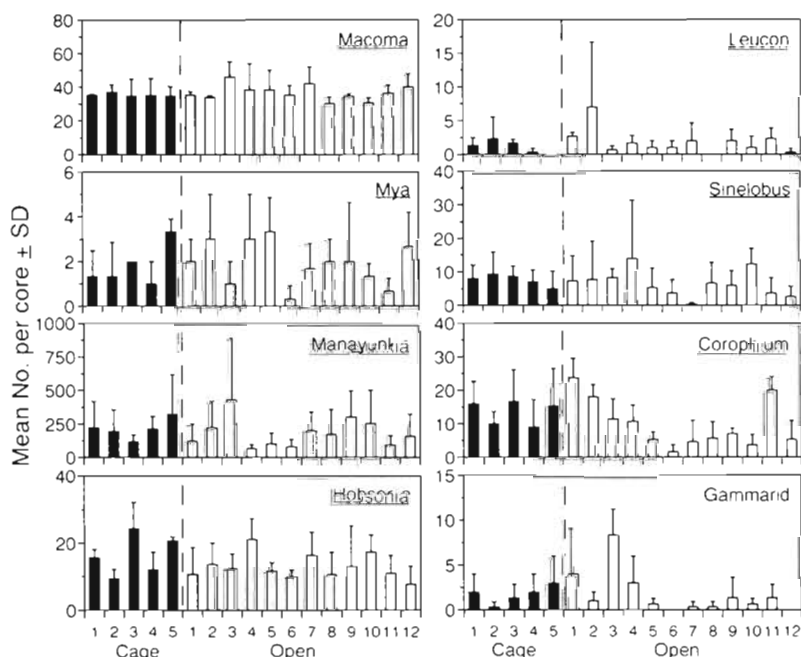


Fig. 8. Invertebrate numbers in Cages (C1 to C5, solid bars) and Open areas (O1 to O12, open bars) after the period of western sandpiper predation at Westham Island. Dashed line separates Cage and Open areas. Asterisk prior to species name denotes a significant Predation effect in the ANOVA (Table 5)

Table 6. Analyses of variance of the number of invertebrates per core [ $\log_{10}(x + 1)$  transformed] for species at the 3 study sites. Mixed model ANOVAs with factors: Before/After (B/A), samples from April and May 1994; Site; B/A  $\times$  Site; Plot(Site); and B/A  $\times$  Plot(Site). Degrees of freedom for F: B/A = 1, 2; Site = 2, 6; B/A  $\times$  Site = 2, 6; Plot(Site) = 6, 36; B/A  $\times$  Plot(Site) = 6, 36. See model statement in 'Methods'. Significant p-values are shown in bold. Gammarids includes all amphipods except *Corophium* spp.

Location	Species	B/A		Site		B/A $\times$ Site		Plot(Site)		B/A $\times$ Plot(Site)	
		F	p	F	p	F	p	F	p	F	p
Boundary Bay	<i>Batillaria zonalis</i>	0.07	0.821	2.06	0.209	3.06	0.122	2.45	<b>0.043</b>	1.47	0.218
	<i>Macoma balthica</i>	45.63	<b>0.021</b>	0.22	0.809	0.09	0.916	2.00	0.091	2.54	<b>0.037</b>
	<i>Eteone</i> spp.	1.20	0.388	0.14	0.873	1.03	0.411	0.99	0.449	2.85	<b>0.022</b>
	<i>Manayunkia aestuarina</i>	0.06	0.832	1.10	0.392	2.53	0.160	2.62	<b>0.033</b>	2.63	<b>0.032</b>
	Podocopid ostracod	9.92	0.088	0.19	0.832	2.23	0.189	2.27	0.059	0.23	0.966
Brunswick Point	<i>Macoma balthica</i>	12.08	0.074	0.10	0.907	0.50	0.631	5.91	<b>0.0002</b>	2.26	0.059
	<i>Manayunkia aestuarina</i>	27.67	<b>0.034</b>	5.88	<b>0.039</b>	1.89	0.231	2.54	<b>0.038</b>	0.65	0.691
	<i>Hobsonia florida</i>	3.50	0.202	0.88	0.461	0.27	0.772	3.78	<b>0.005</b>	3.43	<b>0.009</b>
	<i>Leucon subnasica</i>	22.46	<b>0.042</b>	0.42	0.675	1.34	0.331	4.99	<b>0.0008</b>	5.49	<b>0.0004</b>
	<i>Sinelobus stanfordi</i>	21.94	<b>0.043</b>	1.86	0.236	2.24	0.188	1.98	0.094	1.11	0.376
	<i>Corophium</i> spp.	4.16	0.178	9.64	<b>0.013</b>	2.08	0.206	2.75	<b>0.027</b>	5.74	<b>0.0003</b>
Westham Island	<i>Macoma balthica</i>	1184.17	<b>0.0008</b>	4.28	0.070	0.00	0.999	9.04	<b>0.0001</b>	4.16	<b>0.003</b>
	<i>Mya arenaria</i>	1.41	0.357	2.07	0.207	2.69	0.147	1.09	0.388	0.76	0.604
	<i>Manayunkia aestuarina</i>	8.41	0.101	46.96	<b>0.0002</b>	0.50	0.629	0.99	0.450	1.14	0.362
	<i>Hobsonia florida</i>	0.00	0.988	11.42	<b>0.009</b>	0.12	0.893	9.51	<b>0.0001</b>	11.24	<b>0.0001</b>
	<i>Leucon subnasica</i>	7.46	0.112	9.52	<b>0.014</b>	0.92	0.449	14.02	<b>0.0001</b>	3.71	<b>0.006</b>
	<i>Sinelobus stanfordi</i>	0.03	0.887	6.08	<b>0.036</b>	0.49	0.636	5.19	<b>0.0006</b>	5.54	<b>0.0004</b>
	<i>Corophium</i> spp.	1.52	0.343	1.14	0.382	7.87	<b>0.021</b>	4.96	<b>0.0009</b>	2.26	0.060
Brunswick Point Upper Roost	<i>Macoma balthica</i>	1.47	0.349	7.05	<b>0.027</b>	0.55	0.604	1.20	0.327	3.65	<b>0.006</b>
	<i>Manayunkia aestuarina</i>	12.29	0.072	3.97	0.080	0.35	0.715	1.58	0.182	0.79	0.582
	<i>Hobsonia florida</i>	12.93	0.069	0.65	0.554	2.61	0.153	2.29	0.056	1.89	0.110
	<i>Leucon subnasica</i>	0.47	0.564	3.46	0.100	1.09	0.393	3.64	<b>0.006</b>	1.64	0.164
	<i>Sinelobus stanfordi</i>	9.15	0.094	16.64	<b>0.004</b>	1.44	0.308	0.69	0.661	1.17	0.343

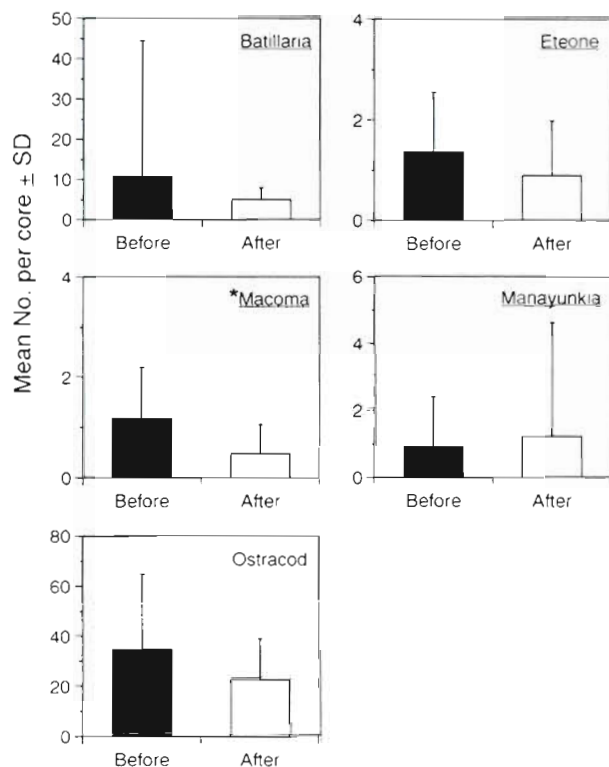


Fig. 9. Invertebrate numbers in Before/After sampling at Boundary Bay. Bars show the mean Before (solid bars) and After (open bars) the western sandpiper migration. Asterisk prior to species name denotes a significant B/A effect in the ANOVA (Table 6)

## DISCUSSION

### Exclosure cage effects

The presence of an exclosure cage in an area of soft sediments may have considerable influence by: altering the physical nature and hydrodynamics of the cage area (e.g. increased sediment removal or deposition); causing larval entrapment; providing substrate for fouling by animals or plants, which may further alter the cage environment; or providing refuges for large motile animals or the studied invertebrates themselves (Virnstein 1978, Peterson 1979, Hulberg & Oliver 1980; see also discussion in Wilson 1991b, Ólafsson et al. 1994).

Two facets of these 'cage effects' need to be considered in an exclosure experiment: (1) changes in the sediment composition, and (2) changes in the invertebrate community beneath the exclosure cage. Consideration of hydrodynamic 'cage effects' on sediment composition have been made in previous shorebird exclosure experiments (Quammen 1981, 1984, Kent & Day 1983, Raffaelli & Milne 1987, Wilson 1989,

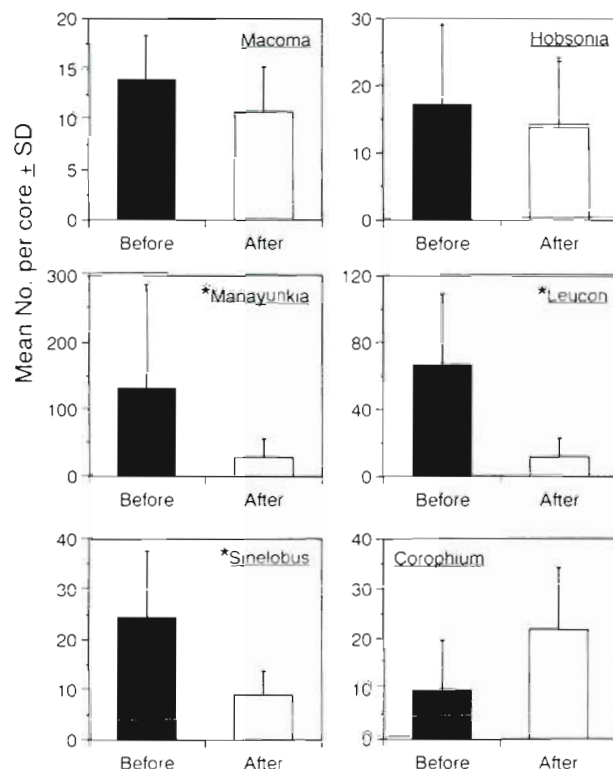


Fig. 10. Invertebrate numbers in Before/After sampling at Brunswick Point. Bars show the mean Before (solid bars) and After (open bars) the western sandpiper migration. Asterisk prior to species name denotes a significant B/A effect in the ANOVA (Table 6)

1994b). However, there are few studies that have considered the latter assumption that there is negligible prey movement during the experiment (Hall et al. 1990b).

In the present study the physical effect of the exclosure cage on the sediment composition was considered by sampling sediments at the beginning and end of the experiment. While no difference was found in the percent of silt present in the cages between times, there was extensive scouring around the stakes at Westham Island as a result of high current flow. The observation of significant scouring without a change in sediment composition in the centre of the cage, also seen by Kent & Day (1983), may be due to the lack of replication in the sediment sampling. As in other shorebird exclosure experiments, only a single core was taken within each cage (Quammen 1981, Kent & Day 1983, but see Raffaelli & Milne 1987,  $N = 3$  cores), and there was no consideration of small-scale spatial variability in sediment composition.

Changes in the invertebrate community beneath the exclosure cage have been less well considered in shorebird exclosure experiments. While there is little



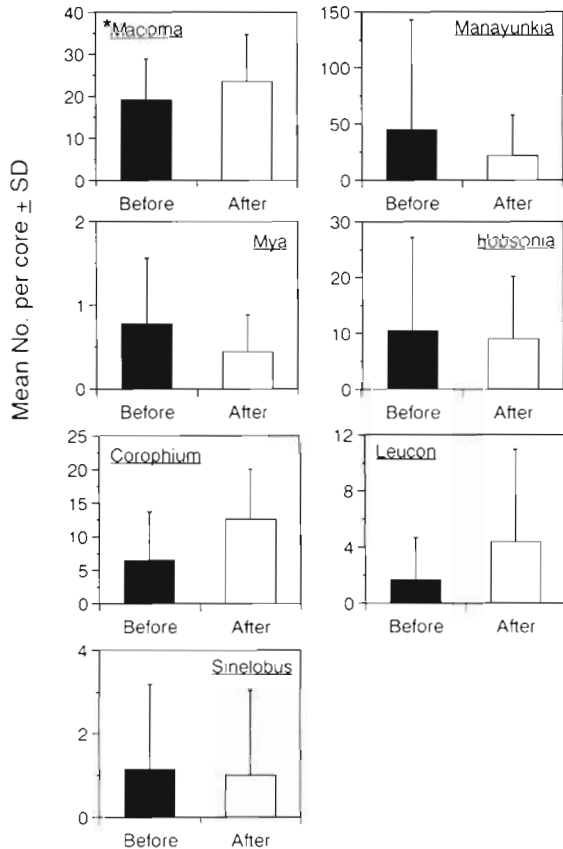


Fig. 11. Invertebrate numbers in Before/After sampling at Westham Island. Bars show the mean Before (solid bars) and After (open bars) the western sandpiper migration. Asterisk prior to species name denotes a significant B/A effect in the ANOVA (Table 6)

information on the distances moved by benthic animals, simulations by Hall et al. (1990b) have demonstrated that random prey movements can confound the results in caging experiments. The one shorebird enclosure experiment that directly examined prey movements found that there was not substantial migration of the polychaete *Ceratonereis pseudoerythraeensis* during the study (Kent & Day 1983). However, prey mobility needs to be considered in enclosure experiments where the prey is highly mobile (e.g. epifaunal species, or infaunal species with high potential for movement such as crustaceans; Hall et al. 1990b).

A more simplistic approach, used in the present research, is to take an initial sample when the enclosure cage is constructed, and compare the invertebrate numbers at this time to those within the cage at the end of the experiment. This method, used by Wilson (1991a, 1994b), assumes that the cores taken at the corners of the enclosure cage are representative of invertebrate numbers inside the cage at the beginning of the exper-

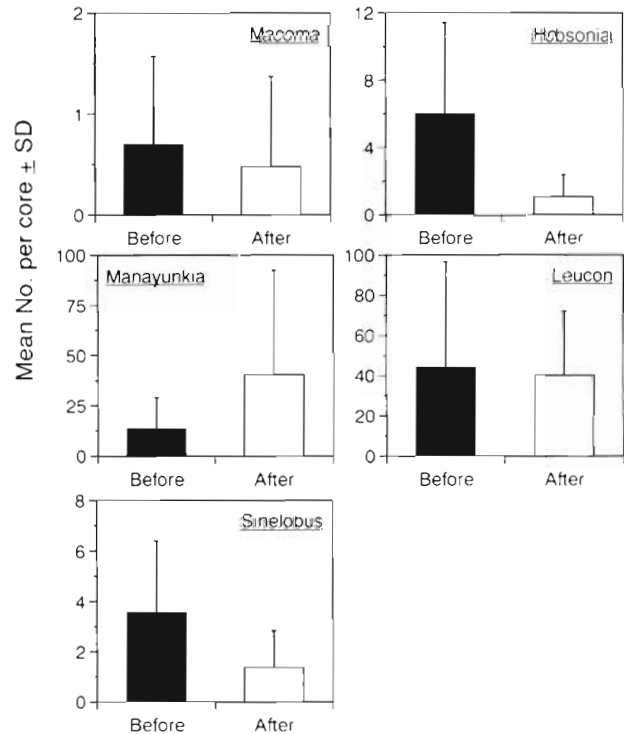


Fig. 12. Invertebrate numbers in Before/After sampling at Brunswick Point-Upper Roost. Bars show the mean Before (solid bars) and After (open bars) the western sandpiper migration. Asterisk prior to species name denotes a significant B/A effect in the ANOVA (Table 6)

iment. In Wilson's enclosure experiments, changes in invertebrate numbers, irrespective of shorebird exclusion, were seen in the amphipod *Corophium spinicorne* (Wilson 1991a, 1994b) and the polychaetes *Streblospio benedicti* (Wilson 1991a) and *Notomastus tenuis* (Wilson 1994b). In *C. spinicorne* in 1 case there was a decline in numbers between the 2 sampling dates (Wilson 1991a). In the other there was an increase, which Wilson (1994b) suggested was due to immigration of *C. spinicorne* under the enclosure cages, an observation made for *Corophium volutator* in other shorebird enclosure experiments (Millard 1975 cited in Baird et al. 1985, Möller & Rosenberg 1982, present study).

Significant differences in invertebrate numbers between cores taken immediately outside the enclosure cage in April (Before) and cores inside the enclosure cage in May (After) were seen in 9 of the 20 species tested (Table 3). Reduced numbers inside the enclosure cage in the After sampling were seen in 8 of these 9 mollusc, polychaete or crustacean species; the amphipod *Corophium* spp. increased in the enclosure cages. Differences could have resulted from 2 factors: (1) the movement of invertebrates into or out of the enclosure cage during the experiment, or (2) small-scale patchiness in invertebrate distributions, i.e. that

cores taken immediately outside the enclosure cage were not good estimates of numbers inside. These factors need to be considered in shorebird enclosure experiments as they influence the Cage value in statistical comparisons to areas Open to predation. For example, the gastropod *Batillaria zonalis*, which is consumed by western sandpiper (Table 2), is associated with temporary pools of water that remain at low tide in Boundary Bay (Swinbanks & Murray 1981, author's pers. obs.). Lower numbers of this species were found in the enclosure cages at the end of the experiment (Fig. 3) as a result of either migration from the enclosure cage or the association of *B. zonalis* with the surface pools. If, in contrast, invertebrate numbers had increased in the enclosure cage (e.g. *Corophium* spp. at Brunswick Point; Fig. 4) this could have produced a spurious predation effect in statistical analysis of the enclosure experiment.

Consideration of changes in invertebrate numbers within enclosure cages is particularly important in long-term enclosure experiments where there may be natural fluctuations in invertebrate prey irrespective of shorebird predation. Long-term studies have been more common at overwintering sites where the shorebird predator may be present for greater than 3 mo (Goss-Custard 1977, Kent & Day 1983, Quammen 1984, Raffaelli & Milne 1987, Kalejta 1993, Mercier & McNeil 1994). The long time-scale of the enclosure experiment introduces 2 additional complexities to the experimental design: (1) the enclosure cage is maintained in the same location for the extended period of predation. Therefore, any cage effects on the sediment composition or infauna can accumulate over an extended time period. For example, there may be extensive fouling of the enclosure cage caused by algae or settled invertebrates, or the inclusion of non-focus predators in the enclosure cage (e.g. crabs; Reise 1978). (2) Regular sampling is required throughout the experiment to determine the influence of invertebrate recruitment, mortality or species migrations, and other predators on invertebrate numbers, exclusive of the shorebird predator. For example, the enclosure cage may modify recruitment patterns in some invertebrates (Kent & Day 1983, Wilson 1989). In these studies increased adult population density in the enclosure cage resulted in a decreased density of newly recruited polychaetes and amphipods respectively (Kent & Day 1983, Wilson 1989). Consequently, there was more recruitment in areas open to shorebird predation with lower numbers of adults, counterbalancing the effect of shorebird predation on invertebrate densities. The importance of such adult-recruit interactions can only be assessed if the size structure of the invertebrate populations is also examined throughout the experiment.

## Effect of shorebird predation

'The interpretation of experiments where no effects are apparent is problematic; the lack of effect may be real, or the experimental design may be inadequate for detecting the effect using inferential statistics.' (Hall et al. 1990b, p. 657).

### Enclosure experiment

The enclosure experiment conducted at 3 study sites on the Fraser River estuary did not detect a significant impact of western sandpiper on the densities of all infaunal marine invertebrate species. Even though shorebird numbers were an order of magnitude above most previous studies (e.g. at Brunswick Point the maximum daily estimate was 1.5 million western sandpiper on 4 May 1994; R. Butler unpubl. data), and the predation occurred over a discrete period (19 April to 12 May), there was a significant predation effect in only 1 of the 20 species tested. Lower numbers of the polychaete *Eteone* spp. were seen in the Open area exposed to shorebird predation at Boundary Bay (Fig. 6), where there was little evidence for western sandpiper feeding.

The enclosure cages used in this experiment appeared to be adequate to test for an effect of predation by western sandpiper. The cages effectively excluded the target predator, did not change the sediment composition, were not excessively fouled, and were not present on the mudflat during periods of invertebrate recruitment. Consequently, comparing invertebrate numbers in the predator exclusion cage to areas exposed to shorebird predation should provide a valid test of the importance of western sandpiper predation to infaunal marine invertebrate populations.

The general non-significance of these enclosure experiments is primarily due to the high variability seen in invertebrate numbers between the 5 Cages or 12 Open areas (Figs. 6 to 8). In this study, the spatial variability of invertebrate distributions was considered by including differences within and between the Cage or Open areas as an integral part of the nested analysis of variance. This is in contrast to other shorebird enclosure experiments where the authors acknowledge that there is spatial variability or patchiness in prey distributions (Kalejta 1993, Mercier & McNeil 1994), but then reduce this variability by pooling the data prior to statistical analysis. Pooling occurs primarily because there are no replicate cores within the enclosure cage (Wilson 1989, 1991a, 1994b, Mercier & McNeil 1994). Consequently, the enclosure cages are considered as 'replicates' in *t*-tests or 1-way ANOVAs that compare the Cage and Open areas (Wilson 1989, 1991a, 1994b,

Kalejta 1993, Mercier & McNeil 1994). The maximum distance apart of the cores used in calculating the Cage mean may, however, be large (20 m: Wilson 1989, 1991a, 1994b; 60 m: Kalejta 1993; 650 m: Mercier & McNeil 1994). In such studies, differences between enclosure cages and areas open to shorebird predation may simply reflect spatial variations in invertebrate abundance that are unrelated to the presence of a shorebird predator.

Consideration of the spatial scale of invertebrate distributions is critical in the design and statistical analyses of future shorebird enclosure experiments. While this study does not provide an exemplary shorebird enclosure experiment, the design tried to maximize the levels of replication (3 study areas, 5 cages, 12 open areas, 3 cores for each mean), within the time constraints posed by sorting invertebrate samples (total 198 cores). The fact that this experiment failed to detect declines in invertebrates in areas open to feeding is considered to be a valid test of the impact of western sandpiper predation on their marine invertebrate prey. The importance of a direct measure of shorebird predation in the Open areas is also emphasised by the potentially spurious decline in *Eteone* spp. at Boundary Bay, where there was little evidence for shorebird feeding.

#### Alternative approaches

An alternative method to assess reductions in invertebrate numbers by shorebirds is to conduct sampling before and after a period of predation. Before and After sampling on the Fraser River estuary did not show consistent declines in invertebrate numbers at sites with a high index of shorebird predation (Westham Island, Brunswick Point) or evidence for high use during the last part of each tidal period (Brunswick Point-Upper Roost). Interpretation of the reduced numbers of some species at Brunswick Point after shorebird predation is complicated by the spatial variability shown in these same species at the scale of Sites (100 m apart) or Plots (10s of metres apart; Table 6). With sampling only on 2 occasions (Before/After), it is impossible to differentiate between the 2 potential sources of decline: (1) that invertebrate numbers have declined as a direct effect of shorebird predation, or (2) that there are spatial and/or temporal differences in invertebrate numbers that occurred regardless of shorebird predation.

The Before/After study described here is effectively similar to an environmental impact study, with a 'natural' rather than a human impact. In this research, sampling was constrained to only 2 sampling dates because of the time required to collect and sort samples (total 216 cores). However, future research should

consider using one of the many BACI (Before/After and Control/Impact) designs described in detail by Underwood (1991, 1992, 1993). This approach would avoid the shortcomings of enclosure experiments (e.g. cage effects, prey movements to or from enclosures), would consider spatial and/or temporal changes in invertebrate numbers, and would allow a rigorous statistical test of the impact of predation by shorebirds on their marine invertebrate prey.

#### General considerations

Baird et al. (1985, p. 576), in a review of shorebird predation, noted that 'the execution and interpretation of enclosure experiments to determine the impact of shorebird predators on benthic invertebrates need to be considered more carefully in the future'. Additionally, the conclusion of significant declines in invertebrate numbers due to shorebird predation in previous enclosure experiments (Schneider 1978, Schneider & Harrington 1981, Kent & Day 1983, Quammen 1984, Mercier & McNeil 1994) should be reevaluated in light of potential flaws in their experimental designs or statistical analyses. Researchers designing enclosure experiments need to carefully consider the replication and interspersal of treatments and, most importantly, include the spatial scale of distribution of the invertebrate prey as a component of the experimental design.

A more general problem with detecting an impact of shorebird predation may be the implicit assumption that the scale at which a scientist samples soft sediments is the same as the impact of the shorebird predator. Sampling in soft sediments typically involves the collection of cores that sample a small discrete area (e.g. 5 cm, 10 cm). In contrast, feeding by shorebirds such as western sandpiper is often in a more irregular fashion with periods of walking and pecking/probing on a larger spatial scale than the sample core. Thus, unless a flock of shorebirds passes through the area of study on a regular basis, reduction in invertebrate numbers may not be detectable using small diameter cores. The discordance in scales between impact and sampling might be one explanation for the lack of agreement between visual observations of high removal rates of invertebrates by shorebirds (e.g. Kalejta 1992) and the failure to detect significant declines in invertebrate numbers using sediment cores (e.g. Kalejta 1993).

Additionally, because soft-bottom macrobenthos generally have clumped distributions (Thrush 1991), to show statistically significant reductions in density by predation there is a need for large sample sizes to reduce the variance about mean invertebrate densities (Baird et al. 1985). Restrictions on the number of sam-

ples that can be collected and processed may, however, result in large standard deviations (e.g. present study) and non-significant predation effects. A *post hoc* power analysis of the enclosure experiment used here shows that the smallest detectable difference ( $\delta$  at a power  $1 - \beta$  of 0.95) between Cage and Open areas, with the observed spatial variability ( $s^2$ ), exceeds the value for the Cage mean in 11 out of 20 species (Table 7). The observed difference between Cage and Open means ( $D$ ) is positive (i.e. shows elevated densities in areas without predation) in 8 of the 15 species and for the total number of individuals per core at Brunswick Point and Westham Island, where there was evidence of significant shorebird predation (Table 7). In contrast,  $D$  is negative (Open > Cage) for all species except *Eteone* spp. (which showed a significant predation effect; Table 5) and for the total number of individuals per core at Boundary Bay (Table 7), where there was little evidence for shorebird predation around the enclosure cages.

Given the level of variation between sample cores, the current analysis detects 11.4 to 52.3% of the difference ( $\delta$ ) required to show a significant predation effect for individual species (Positive  $D$ , excluding the significant value of 100% for *Eteone* spp. at Boundary Bay;

Table 7). To highlight the problem of detecting significant reductions in invertebrate density, the value of  $\delta$  for the total number of individuals per core is greater than the Cage mean at Boundary Bay, and 74 and 71% of the Cage mean at Brunswick Point and Westham Island respectively. This means that a significant predation effect will only be shown if the shorebirds are reducing the total number of invertebrates per core by >70%, a value which greatly exceeds estimates of consumption of shorebirds on the scale of large estuaries (6 to 44% of invertebrate production; Baird et al. 1985).

The conclusion reached from the power analysis is that, given the spatial variability of the invertebrate prey in the Fraser River estuary, it would be very difficult to show significant declines in invertebrate density by western sandpiper predation using the current enclosure design. In a comparable enclosure experiment in subtidal soft sediments, Hall et al. (1990a) concluded that, despite expectations of large reductions in invertebrate densities by predators, the power to detect such effects may be limited because of high within-treatment variances; particularly in soft-bottom habitats where the results can also be confounded by physical and biological cage effects (Hall et al. 1990b).

Table 7. Estimates of smallest detectable difference ( $\delta$ ) between populations means using the present nested design. Calculation of  $\delta$  from Zar (1984):  $\delta = \sqrt{(2ks^2\phi^2)/n}$  with  $k = 2$  (Cage, Open),  $s^2$  = mean square Position(Predation-/+ ) from untransformed ANOVA,  $n = 21.18$  (harmonic mean of  $n = 12$ ,  $n = 36$  for Cage and Open areas respectively), and  $\phi = 29.6 [1 - \beta \text{ of } 0.95]$  with  $v_1 = 1$ ,  $v_2 = 15$ ,  $\alpha = 0.05$  (from Zar 1984, Appendix B, Fig. B.1.a). Actual difference ( $D$ ) = Cage mean – Open mean. Value of  $D$  as a percent of  $\delta [1 - \beta \text{ of } 0.95]$  calculated from the absolute value of  $D$ . Values in parentheses denote that the percentage difference is negative (i.e. Open > Cage)

		Cage mean (N = 15)	Open mean (N = 36)	$s^2$	$\delta$ [1 – $\beta$ of 0.95]	Actual difference ( $D$ )	$D$ as a % of [1 – $\beta$ of 0.95]
Boundary Bay	<i>Batillaria zonalis</i>	2.53	3.11	9.02	3.55	–0.58	(16.3)
	<i>Macoma balthica</i>	0.20	0.69	0.85	1.09	–0.49	(45.0)
	<i>Eteone</i> spp.	2.80	1.50	1.2	1.30	1.30	100
	<i>Manayunkia aestuarina</i>	1.20	2.19	6.45	3.00	–0.99	(33.0)
	Podocypid ostracod	7.20	13.11	561.42	28.01	–5.91	(21.1)
	Total individuals	21.87	31.53	780.27	33.02	–9.66	(29.3)
Brunswick Point	<i>Macoma balthica</i>	7.73	8.69	13.77	4.39	–0.96	(21.9)
	<i>Manayunkia aestuarina</i>	154.00	79.92	14352.01	141.62	74.08	52.3
	<i>Eteone</i> spp.	1.67	2.06	2.80	1.98	–0.39	(19.7)
	<i>Hobsonia florida</i>	9.60	8.14	52.79	8.59	1.46	17.0
	<i>Leucon subnasica</i>	14.53	18.89	244.17	18.47	–4.36	(23.6)
	<i>Sinelobus stanfordi</i>	19.33	10.86	307.31	20.72	8.47	40.9
	<i>Corophium</i> spp.	8.80	7.67	70.16	9.90	1.13	11.4
Westham Island	Total individuals	230.80	145.81	20712.49	170.14	84.99	50.0
	<i>Macoma balthica</i>	35.33	36.78	45.35	7.96	–1.44	(18.1)
	<i>Mya arenaria</i>	1.80	1.92	2.74	1.96	–0.12	(6.1)
	<i>Manayunkia aestuarina</i>	212.87	182.39	29077	201.58	30.48	15.1
	<i>Hobsonia florida</i>	16.40	12.94	59.97	9.15	3.46	37.8
	<i>Leucon subnasica</i>	1.13	1.81	8.09	3.36	–0.67	(19.9)
	<i>Sinelobus stanfordi</i>	7.60	6.50	35.51	7.04	1.10	15.6
	<i>Corophium</i> spp.	13.40	9.75	122.73	13.10	3.65	27.9
	Gammarids	1.73	1.75	13.45	4.34	–0.02	(0.5)
	Total individuals	294.40	255.78	30869.94	207.71	38.62	18.6



Significant predation effects by shorebirds may, therefore, only be found in conditions where: (1) the study area has little environmental dynamics (sediment alteration) and is subject to intense feeding by shorebirds over a short time period (Piersma 1987); (2) the shorebird concentrates its feeding on a particular, abundant infaunal invertebrate [e.g. *Corophium volutator*: Wilson 1989; polychaetes: Kent & Day 1983, Quammen 1984 (muddy sites only), Mercier & McNeil 1994]; (3) the study area has high invertebrate densities so that massive declines can be detected (Székely & Bamberger 1992; Table 7); and (4) the shorebird predator has a high energy demand during the period of study (e.g. during premigratory fattening or moult, at migratory stopovers, or at the end of long flights).

Finally, invertebrate density may not be the ideal measure for quantifying the effect of predation because of the variability inherent in benthic sampling (Grant 1981, Ens et al. 1994). Size-selective predation, as reported in shorebird studies by Wilson (1989), Raffaelli & Milne (1987) and Kent & Day (1983), or bioenergetic approaches may be more suitable in examining food-web interactions between shorebirds and their marine invertebrate prey.

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