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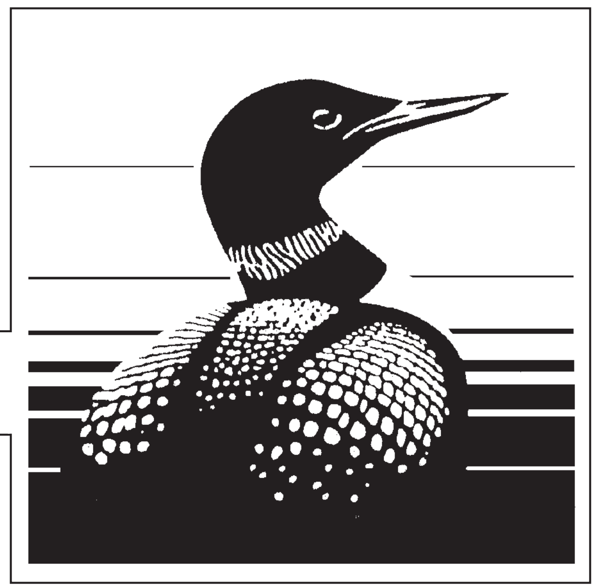

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Abstract.

As part of an investigation into prey resources for birds, spatial scales of variability in invertebrate abundances were examined in the extensive intertidal flats of Boundary Bay, in the Fraser River Estuary, British Columbia. Samples were collected at scales of 1 m, 10 m and 100 m, 1 km and 3.5 km using a hierarchical nested design. Samples were numerically dominated by a few species - amphipods (*Corophium* spp.), podocopid ostracods, the polychaete *Polydora ligni*, and the gastropod *Batillaria zonalis*. Statistical analyses showed, for most species and taxa, significant differences at scales of 10's or 100's of metres, but not at the scale of 1 km. However, at the largest scale examined (3.5 km), there were significant differences in the number of taxa per core and in abundances of *Batillaria zonalis* and *Polydora ligni*. In both species lower numbers were observed in eastern Boundary Bay. In all taxa there was considerable residual variation, suggesting patchiness at smaller spatial scales than the 1 m between replicate cores. These results have implications for future sampling in Boundary Bay and on other intertidal sandflats.

Résumé

Dans le cadre d'une étude des proies à la disposition des oiseaux, nous avons examiné la variabilité spatiale de l'abondance des invertébrés dans les grands platains intertidaux de la baie Boundary, dans l'estuaire du fleuve Fraser, en Colombie-Britannique. Des échantillons ont été recueillis sur des échelles de 1 m, 10 m, 100 m, 1 km et 3.5 km suivant un système hiérarchique de grilles emboîtées. Un petit nombre d'espèces dominaient numériquement les échantillons : amphipodes (*Corophium* spp.), ostracodes podocopid, le polychète *Polydora ligni* et le gastropode *Batillaria zonalis*. Pour la plupart des espèces et des taxa, les analyses statistiques ont montré des différences importantes aux échelles de quelques dizaines et de quelques centaines de mètres mais aucune à l'échelle de 1 km. Néanmoins, pour la plus grande échelle étudiée (3.5 km), nous avons observé des différences importantes dans le nombre de taxa par carotte et dans l'abondance de *Batillaria zonalis* et de *Polydora ligni.* Nous avons observé que ces deux espèces étaient en effectif moindre dans l'est de la baie Boundary. Les variations résiduelles étaient importantes pour tous les taxa, ce qui suggère l'existence d'hétérogénéités à des échelles inférieures à 1 m, distance minimum utilisée entre les échantillons. Ces résultats pourront être utilisés pour la planification des échantillonnages futurs dans la baie Boundary et sur d'autres platains intertidaux.

Introduction.

The Fraser River estuary is composed of extensive intertidal mud and sandflats (ca 681 km^2, Butler and Campbell 1987) adjacent to the city of Vancouver, British Columbia, and can be divided into three geographical sub-areas: Sturgeon Bank, Roberts Bank, and Boundary Bay (Fig. 1). The intertidal marine invertebrates of Roberts and Sturgeon Banks have been the subject of many studies (e.g. Bawden *et al.* 1973, Hoos and Packman 1974, Levings and Coustalin 1975, Otte and Levings 1975, Levings *et al.* 1978, Chapman and Brinkhurst 1981, McGreer 1983, McEwan and Gordon 1985). In contrast, studies in Boundary Bay are more limited and have considered either distributions of selected macrofauna (Kellerhalls and Murray 1969, Swinbanks and Murray 1981, Swinbanks and Luternauer 1987, McEwan and Farr 1986), or have comprised species lists with limited details of distribution or abundance (O'Connell 1975, McEwan and Gordon 1985).

Boundary Bay is an internationally important feeding site for migratory shorebirds and waterfowl (Baldwin and Lovvorn 1994a, Butler 1994, Vermeer *et al.* 1994). In excess of one million migrating Western Sandpiper (*Calidris mauri*) and approximately 60,000 overwintering Dunlin (*C. alpina*) are dependent on the intertidal resources of Boundary Bay and the Fraser River estuary (Butler 1994). Waterfowl such as ducks (*Anas americana, A. acuta, A. platyrhynchos,* and *A. crecca*) can reach total numbers of 80,000 in Boundary Bay in early December (Baldwin and Lovvorn 1994b), and up to 50,000 brant (*Branta bernicla*) use the seagrass beds in the spring (Butler and Campbell 1987).

Investigations of the diets of waterfowl (Baldwin and Lovvorn 1994a) and shorebirds (Sewell 1996, Sutherland *et al.* 2000) in Boundary Bay have shown the importance of a large number of marine invertebrates whose distributions and abundance patterns are relatively unknown. While the distribution of these invertebrates have been described in downshore transects (Baldwin and Lovvorn 1994a, R.W. Elner unpub. data), there is little information on patterns of abundance across the bay. Using a nested hierarchical design this paper considers the distribution patterns and spatial scale of variation in invertebrate abundance across Boundary Bay at five spatial scales ranging from 1 m to 3.5 km.

Methods.

Study Site.

Research was conducted in Boundary Bay, British Columbia, on the inactive southern flank of the Fraser River Delta (Swinbanks and Murray 1981), adjacent to the border with the U.S.A. (Fig. 1). Boundary Bay is protected from the sediment plume of the Fraser River by the Point Roberts Peninsula (Fig. 1), and has low levels of sedimentation (Kellerhals and Murray 1969) with clear marine waters of a salinity typical to the water mass of the southern Strait of Georgia (Waldichuk 1957). Tides in Boundary Bay are of a mixed semi-diurnal type, with a mean tidal range of 2.7 m (Weir 1963).

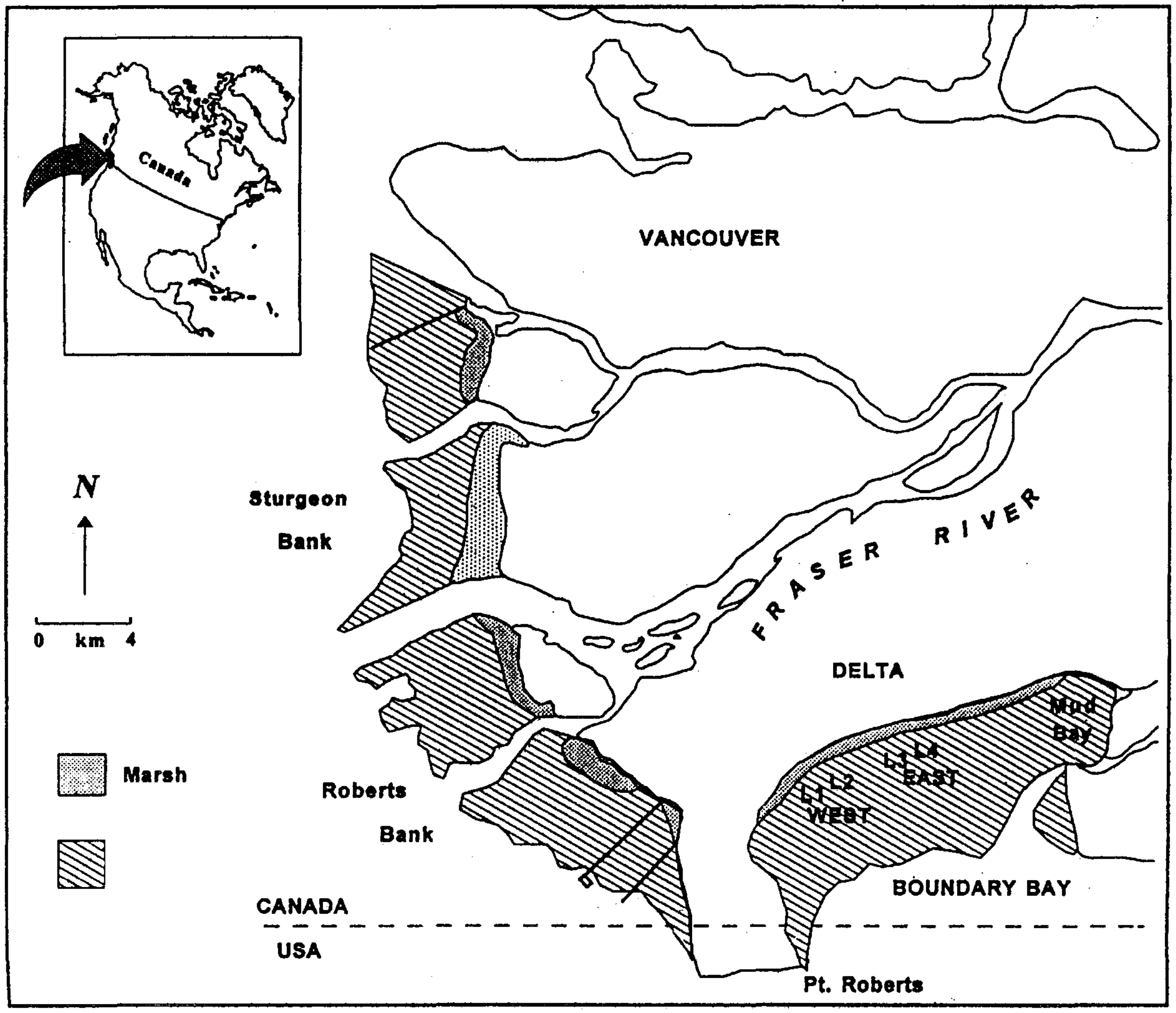
Invertebrate spatial patterns were examined in the upper sandflat zone (Swinbanks and Murray 1981), that is bounded on the northern side by a salt marsh that extends from a tidal height of +3.4 m above Canadian chart datum (= the plane of lowest normal tides) to an artificial dyke (Baldwin and Lovvorn 1994b). The upper sandflats are characterized by an incomplete drainage system, with water remaining in wide, shallow depressions during ebb tide (Kellerhals and Murray 1969). Patterns of surface water remaining at low tide changed with each tidal cycle, so that wet areas on one low tide might be dry on the following low (pers. obs.). The sediments of this part of the tidal flat are primarily sand (mean % sand in surface 0-3 cm = 99.4%, N= 10; unpub. data) with a median ϕ of 2.73 (= 0.15 mm, unpub. data).

Sampling.

The sampling design for this research was the same as that used by Morrisey *et al.* (1992). Invertebrate samples were collected in a transect parallel to the dyke (500 m from the edge of the salt marsh) at a tidal height +3.2 m above chart datum at five spatial scales ranging from 1 m between replicate cores to 3.5 km between the two sides of Boundary Bay (West, East; Fig. 1). The maximum distance to the east, and hence the largest spatial scale, was limited by an increased silt content in the sand of Mud Bay (Kellerhals and Murray 1969).

The design incorporated five spatial scales in a fully nested hierarchical design: (1) Sides of Bay = 3.5 km apart, (2) Locations = 1 km apart; two locations within each side, (3) Sites = 100 m apart; three sites within each location, (4) Plots = random points within each site, on a scale of 10's of metres apart; three plots within each site, (5) Replicates = 1 m apart; three cores within

Fig. 1. The Fraser River Estuary, British Columbia, Canada, showing locations (L1-L4) in West and East Boundary Bay used in sampling. Approximate areas of saltmarsh and extent of intertidal mudflat are shown.



each plot (Fig. 2A). At each site, a wooden stake defined the centre of a 50 m radius circle. The position of the plots within each site was determined using a random compass direction and distance (0 - 50 m) from this stake (Fig. 2B). Replicate cores were taken at the corners of a 1 m sided equilateral triangle defined by a metre rule.

The designation of the two sides of Boundary Bay was determined using major roads in the municipality of Delta, British Columbia (Fig. 1). Locations 1 and 2 in West Boundary Bay, were located 1 km apart on a north-south line running from 72nd St, Delta. Location 3 and 4 in East Boundary Bay were similarly defined from a north-south line from 88th St, Delta.

Samples were collected on August 3 (West Boundary Bay) and August 4, 1994 (East Boundary Bay) using a core 10 cm diameter to 10 cm depth. Samples were frozen on returning from the field. Defrosted sediments were later sieved through a 500 μm 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 (R.W. Elner, unpub. data). The tube-dwelling polychaete *Pygospio elegans* was present in sampled cores but was not included in the current analysis. These spionids construct fragile agglutinated sand tubes which would break during sample processing, making it impossible to consistently determine the numbers of polychaetes per sample. This species is, however, an abundant species in the algal mat zone and upper tidal flats of Boundary Bay (Swinbanks and Murray 1981).

Statistical analyses.

Statistical analyses were performed on the number of invertebrates per 10 cm core for the following categories: (a) Total individuals = the sum of all invertebrates. (b) Number of taxa = defined as the number of orders present (see Table 1) with the higher taxon level used for oligochaetes, the unidentified opisthobranch and the single nemertean. (c) Polychaetes = number of polychaetes excluding *Polydora ligni*. (d) - (g) Single taxa analyses for species that could be consistently identified and were present in >65% of the sampled cores (N= 108). This criteria was met in the gammarid amphipod *Corophium* spp. (95%), *podocopid ostracods* (100%), the polychaete *Polydora ligni* (65%), and the gastropod *Batillaria zonalis* (73%, Table 1). The four-factor nested ANOVAs was calculated using PC-SAS Release 6.03 (SAS Institute, Cary, North Carolina); all factors were random. Violations of the assumptions of the analysis of variance (normality, heterogeneity of variance), were corrected by $\log_{10}(x + 1)$ transformation.

Fig. 2A Hierarchical sampling design used in the Boundary Bay study; and **Fig. 2B** Sampling protocol for Sites A, B, C at each Location (1-4)

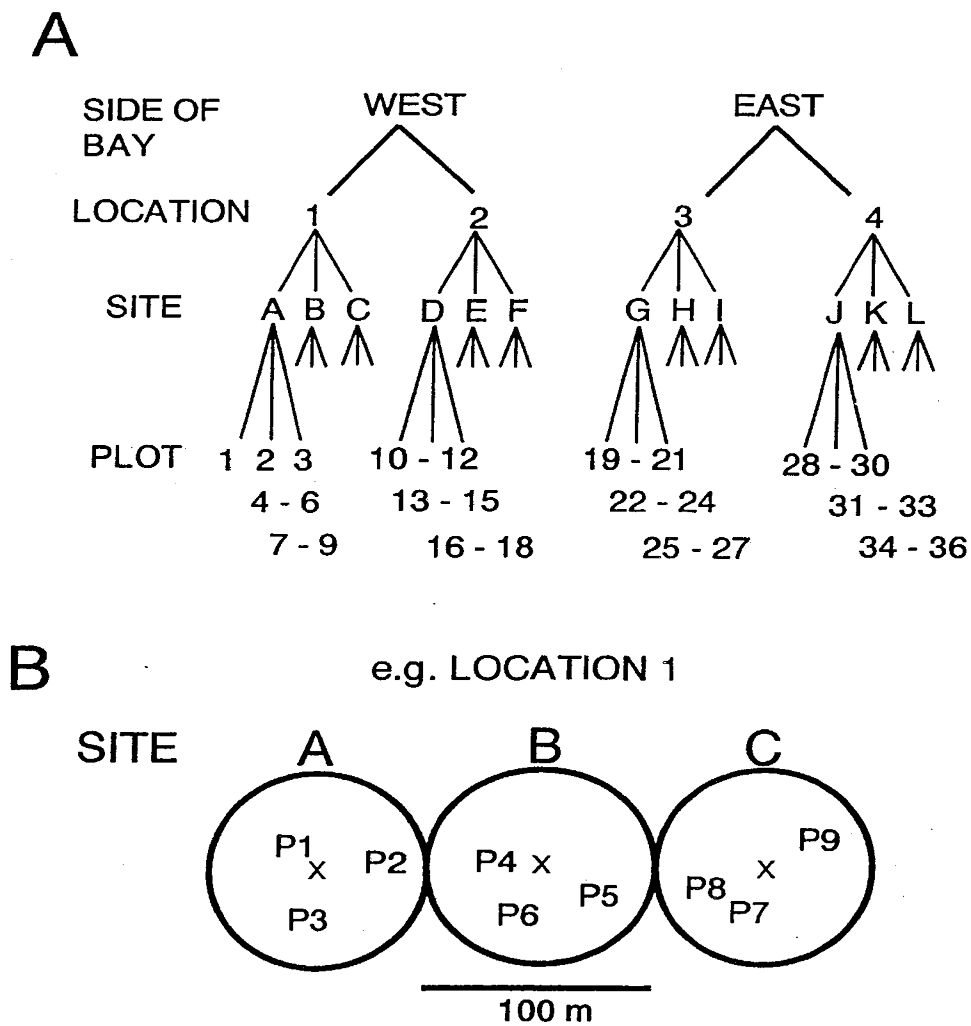


Table 1: Invertebrate macrofauna identified during sampling in Boundary Bay, British Columbia. The mean number per core ± standard deviation is based on N= 54 cores per Side of Bay. No. of cores denotes the number of cores in which the species/taxon was found. ND = no data.

Phylum	Class	Subclass	Order	Species
Mollusca	Gastropoda	Prosobranchia	Mesogastropoda	*Batillaria zonalis*
		Opisthobranchia	Cephalaspidea	*Haminaea vesicula*
		Opisthobranchia	Cephalaspidea	*Acteocina cerealis*
		Opisthobranchia		unknown
	Bivalvia	Heterodonta	Veneroida	*Macoma balthica*
		Heterodonta	Veneroida	*Tapes japonica*
		Heterodonta	Myoida	*Mya arenaria*
		Pteriomorphia	Mytiloida	*Mytilus* spp.
Arthropoda				
Sub-P. Crustacea	Ostracoda	Myodocopa	Myodocopida	*Eusarsiella zostericola*
		Podocopa	Podocopida	unknown
	Malacostraca	Peracarida	Isopoda	unknown
		Peracarida	Tanaidacea	*Sinelobus stanfordi*
		Peracarida	Amphipoda	*Corophium spp.*
		Peracarida	Amphipoda	other gammarids
		Eucarida	Decapoda	*Hemigrapsus* spp.
Annelida	Polychaeta	(Errantia)	Phyllodocida	*Nereis brandti*
			Phyllodocida	*Eteone* spp.
			Phyllodocida	*Glycinde picta*
		(Sedentaria)	Spionida	*Pygospio elegans*
			Spionida	*Polydora ligni*
			Sabellida	*Manayunkia aestuarina*
			Sabellida F. Spirobidae	unknown
			Terebellida	*Hobsonia florida*
			Capitellida	*Capitella* spp.
			Cirratulida	*Paraonella platybranchia*
	Oligochaeta			Unknown
Rhynchocoela				unknown nemertean

Table 1 (cont.).

Mean No. per core ± SD.

West Boundary Bay	No. of cores	East Boundary Bay	No. of cores
4.63 ± 4.12	45	2.20 ±3.09	34
0	0	0.09 ± 0.29	5
0.06 ± 0.23	3	0	0
0.06 ± 0.23	3	0	0
0.20 ± 0.41	11	0.06 ± 0.23	3
0.04 ± 0.19	2	0	0
0.31 ± 0.64	13	0.02 ± 0.14	1
0.09 ± 0.35	4	0.11 ± 0.37	5
0.09 ± 0.35	4	0.26 ± 0.91	7
32.33 ± 29.40	54	42.44 ± 35.34	54
0.04 ± 0.19	2	0	0
0.02 ± 0.14	1	0.02 ± 0.14	1
58.06 ± 59.81	52	54.87 ± 56.71	51
0.19 ± 0.58	6	0.61 ± 1.52	10
0	0	0.04 ± 0.19	2
0.02 ± 0.14	1	0	0
0.56 ± 0.66	25	1.13 ± 2.00	28
0.02 ± 0.14	1	0	0
ND	41	ND	15
6.02 ±6.66	41	0.89 ± 1.04	30
0.04 ± 0.19	2	0.13 ± 0.48	4
0.35 ± 1.20	9	0.09 ± 0.35	4
0.04 ± 0.19	2	0	0
1.13 ± 1.82	24	0.66 ± 0.91	22
1.67 ± 2.43	35	1.39 ± 2.29	29
1.11 ± 2.07	20	0.09 ± 0.35	4
0.02 ± 0.14	1	0	0

Variance components were calculated using the methods of Underwood (1981) based on untransformed analyses.

Results.

Fauna and Flora.

Invertebrate samples from Boundary Bay were numerically dominated by a few species - the gammarid amphipod *Corophium* spp., *podocopid ostracods*, the polychaete *Polydora ligni*, and the gastropod *Batillaria zonalis* (Table 1). An additional 23 species or taxa were identified in sampling; however, the majority of these (13) were found in less than or equal to 5 of the 54 cores on both sides of Boundary Bay (Table 1). Three species (*Macoma balthica, Mya arenaria, Eusarsiella zostericola*), spirobids and oligochaetes were found in less than five cores in either east or west Boundary Bay (Table 1).

While historically the upper sandflat zone of Boundary Bay has been free of vegetation (Kellerhals and Murray 1969, Swinbanks and Murray 1981), the introduced eelgrass *Zostera japonica* is currently found in this zone. Replicate cores taken within the study area (500 m from the salt marsh) commonly included clumps of *Z. japonica*, and plants were also observed shoreward from the area of sampling (pers. obs.). This might be a factor in the occasional presence of species more typically associated with seagrass beds (e.g. *Mytilus* spp., *Haminaea vesicula* and *spirobid polychaetes*).

Spatial Scale Analysis.

Differences in the mean numbers of invertebrates per core were found at all of the spatial scales examined, except for the 1 km between locations (Table 2). At the broadest level of analysis, total individuals, significant differences were found only at the scale of Plots, 10's of metres apart (Table 2, Fig. 3). The number of individuals per plot was influenced primarily by the numbers of crustaceans such as *Corophium* and *podocopid ostracods*, in which numbers per core reached maximum mean values (± SD) of 196 (± 25.5) and 115.7 (± 25.0) respectively (Fig. 3).

Significant differences were observed in the number of taxa per core at the greatest spatial scale, Side of Bay, and between Plots, 10's of metres apart (Table 2, Fig. 3). A significantly lower number of taxa were found in East Boundary Bay (5.44 ± 1.81 taxa per core) than in West

Table 2: ANOVA statistics for taxa and species from Boundary Bay sampling. Analysis variable is number of animals or taxa per 10 cm core. Design is fully nested as described in text. P-values which are significant at $\alpha = 0.05$ are shown in bold.

a) TOTAL INDIVIDUALS; $\log_{10}(x + 1)$ transformed.

Source	df	MS	F	p
Side	1	0.097	0.94	0.435
Location (Side)	2	0.104	0.16	0.856
Site (Location Side)	8	0.654	1.92	0.104
Plot (Site Location Side)	24	0.341	10.81	**0.0001**
Residual	72	0.032		

b) NUMBER OF TAXA; $\log_{10}(x + 1)$ transformed.

Source	df	MS	F	p
Side	1	0.192	21.04	**0.044**
Location (Side)	2	0.009	0.36	0.707
Site (Location Side)	8	0.025	1.13	0.379
Plot (Site Location Side)	24	0.022	3.00	**0.0002**
Residual	72	0.007		

b) POLYCHAETES (excluding *Polydora ligni*); $\log_{10}(x + 1)$ transformed.

Source	Df	MS	F	p
Side	1	0.020	0.30	0.639
Location (Side)	2	0.068	0.90	0.446
Site (Location Side)	8	0.076	0.54	0.818
Plot (Site Location Side)	24	0.142	2.06	**0.010**
Residual	72	0.069		

c) *Batillaria zonalis*; untransformed.

Source	df	MS	F	p
Side	1	158.90	23.67	**0.040**
Location (Side)	2	6.71	0.11	0.899
Site (Location Side)	8	62.35	7.16	**0.0001**
Plot (Site Location Side)	24	8.71	0.91	0.583
Residual	72	9.53		

Table 2 (cont.).

d) *Polydora ligni*; $\log_{10}(x + 1)$ transformed.

Source	df	MS	F	p
Side	1	4.637	46.57	**0.021**
Location (Side)	2	0.099	0.16	0.852
Site (Location Side)	8	0.608	5.51	**0.0005**
Plot (Site Location Side)	24	0.111	1.30	0.198
Residual	72	0.085		

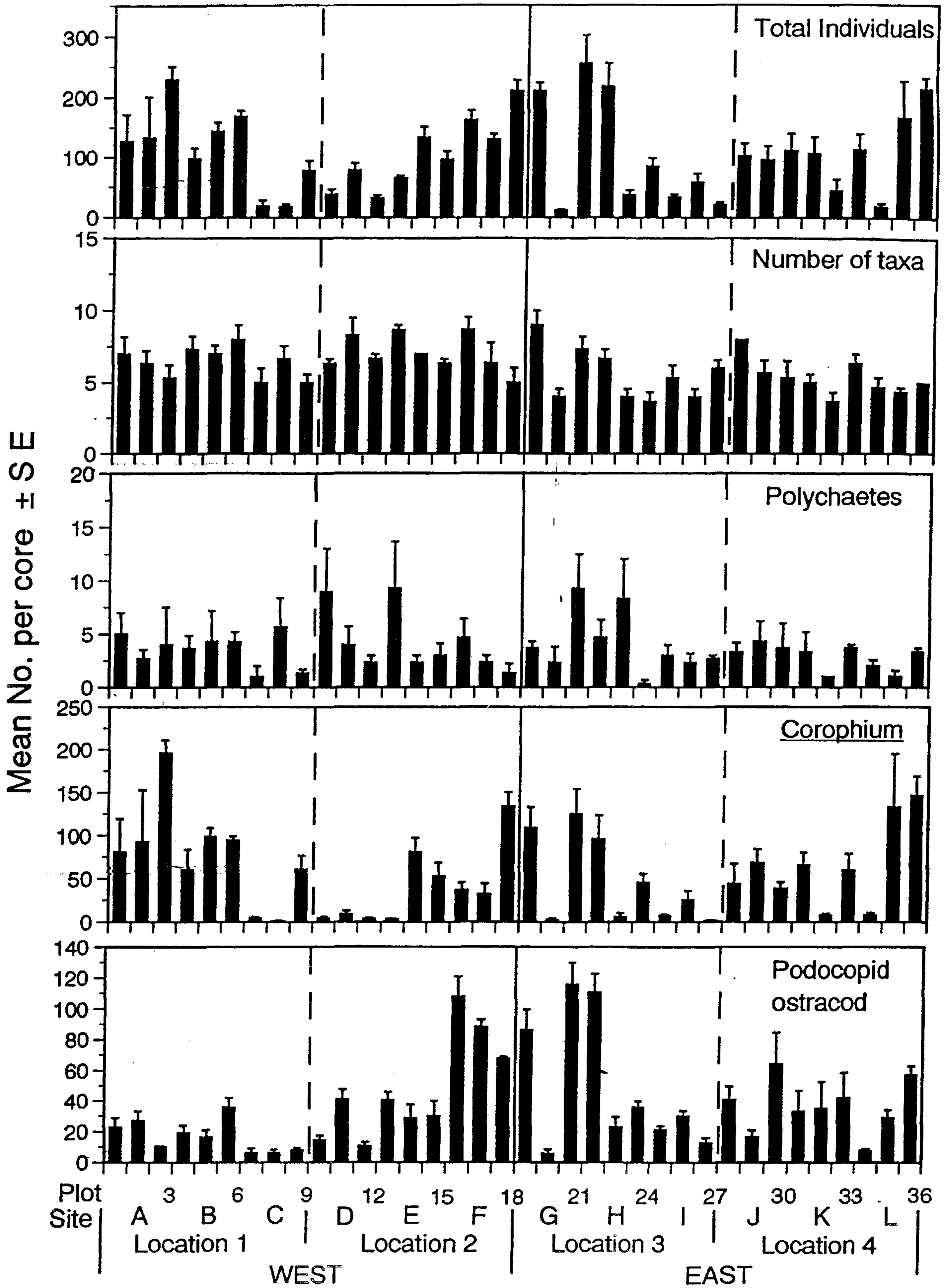
f) *Corophium* spp.; $\log_{10}(x + 1)$ transformed.

Source	df	MS	F	p
Side	1	0.003	0.002	0.969
Location (Side)	2	1.505	0.93	0.433
Site (Location Side)	8	1.617	1.68	0.155
Plot (Site Location Side)	24	0.963	12.63	**0.0001**
Residual	72	0.076		

g) *Podocopid ostracod*; $\log_{10}(x + 1)$ transformed.

Source	df	MS	F	p
Side	1	0.400	0.35	0.616
Location (Side)	2	1.154	2.32	0.160
Site (Location Side)	8	0.497	1.70	0.150
Plot (Site Location Side)	24	0.292	8.06	**0.0001**
Residual	72	0.036		

Fig. 3. Mean number of individuals ± SE per core in Plots (1-36) from Boundary Bay for species and taxa showing significant differences in abundance at the scale of



Boundary Bay (6.72 ± 1.68, Fig. 3). However, the number of taxa had a small range (3 - 10 per core), with a mode of 7 taxa per core.

Significant differences in invertebrate abundance at the scale of Plots (10's of m apart) were seen in the numbers of polychaetes other than *Polydora ligni, Corophium* spp. and *podocopid ostracods* (Table 2, Fig. 3). Plots could differ by two orders of magnitude in the number of *Corophium* spp. or podocopid ostracods present (e.g. Site G, Fig. 3).

Numbers of *Batillaria zonalis* and *Polydora ligni* were significantly different at two spatial scales; Sides of Bay and Site (Table 2, Fig. 4). In both species there were lower numbers in eastern Boundary Bay (Table 1, Fig. 4). Differences in the number of *Batillaria* per core between Sites 100 m apart is most likely related to patterns of standing water on the sandflat. Densities of this species are higher in and around temporary pools of water that remain at low tide (Swinbanks and Murray 1981, pers. obs.), which often extended over areas of the same scale as Sites.

The variance components calculated from the untransformed analyses (Table 3) show a similar pattern of spatial scale as in the analysis of variance (Table 2). As the residual variance differs as a proportion of the total variance between taxa (3.6 to 55.7 %, Table 3), it is not possible to directly compare the relative importance of different spatial scales across taxa (Morrisey *et al.* 1992). Nevertheless, the importance of variation at the spatial scales of Side of Bay (3.5 km) and Site (100 m) in *Batillaria* and *Polydora*, and Plot (10's of m) in *Corophium* and *podocopid ostracods* are seen in the variance estimates (Table 3). Note, however, that there is a considerable variance component for Site in Total individuals and Location in Polychaetes (Table 3) that is not significant in the analysis of variance (Table 2). Additionally, there is considerable residual, or within-plot, variation (Table 3) suggesting that patchiness exists at smaller scales than the 1 m used in the present study.

Discussion.

The upper sandflat zone of Boundary Bay was dominated by four invertebrate species - *Corophium* spp., podocopid ostracods, *Polydora ligni*, and *Batillaria zonalis*. With the exception of *Polydora ligni*, the remaining three species or taxa are components of the diets of both Dunlin and Western Sandpiper in Boundary Bay (K. Vermeer and R.W. Elner unpub. data). Consequently, the results of the present study are important for future research on associations between shorebirds and their marine invertebrate prey.

Fig. 4. Mean number of individuals ± SE per core in Sites (A-L) from Boundary Bay for *Batillaria zonalis* and *Polydora ligni* that show significant differences in abundance

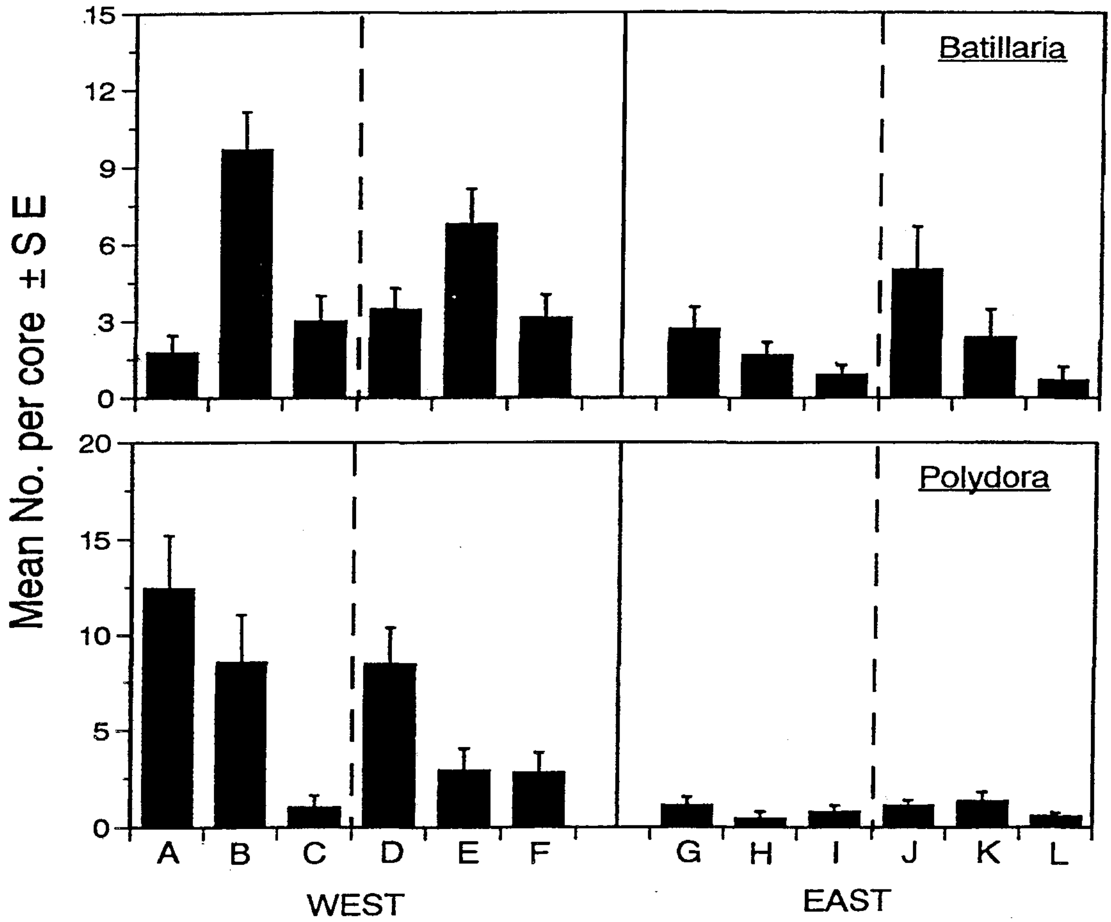


Table 3. Variance component estimates for selected taxa and species from Boundary Bay. Design is fully nested = Side of Bay, Location (Side), Site (Location Side), Plot (Site Location Side). Variance components calculated on untransformed data using methods in Underwood (1981), with negative estimates assumed to be zero.

Source of Variation	**Total Individuals**	**Number of taxa**	**Polychaetes**	***Batillaria***	***Polydora***	***Corophium***	***Podocopid ostracod***
Side	0	43	0	2	11	0	0
Location (Side)	0	1	10	0	0	0	120
Site (Location Side)	23391	5	4	6	9	704	277
Plot (Site Location Side)	11103	5	14	0	3	1582	567
Residual	1825	2	11	10	13	1299	218
Residual as % of total	5.0	3.6	28.2	55.7	36.1	36.2	18.5

The nested hierarchical design used here considered spatial pattern at scales of 1 m, 10 m, 100 m, 1 km and 3.5 km across Boundary Bay. Statistical analyses showed that different patterns of spatial scale were significant in different taxa or species. For example, significant differences were observed at the scale of Plots in most species or taxa studied. The larger scale of Sites (100 m) was significant in *Batillaria* and *Polydora*; while the scale of Side of Bay was significant in both these species and the number of taxa per core.

While the results from Boundary Bay cannot be directly compared to other studies of spatial pattern using hierarchical designs (subtidal, multispecies - Morrisey *et al.* 1992; intertidal, 2 species- Lindegarth *et al.* 1995), a number of similarities are evident. First, as in Boundary Bay, different scales of variation were observed in different taxa

(Morrisey *et al.* 1992) or species (Lindegarth *et al.* 1995). Second, species found in large abundance showed significant differences at the smallest spatial scales (Morrisey *et al.* 1992). The latter pattern was observed in the amphipods *Corophium* spp. and *podocopid ostracods*, which showed significant differences at the scale of Plots, 10's of metres apart. Thirdly, in all cases (Morrisey *et al.* 1992, Lindegarth *et al.* 1995, present study) there was considerable residual variation, suggesting that patchiness exists at smaller spatial scales than the replicate cores.

The design of future sampling programs in Boundary Bay can and should use the results of this spatial study. The primary finding, with respect to the scale of spatial variability, is that there was no significant difference in the abundance of any species or taxon between locations 1 km apart. Consequently, future sampling could focus on smaller areas, 1-10-100's of metres, which could be separated by distances >1 km alongshore, such as sides of the bay. However, because the spatial scales are different in each taxa, an appropriate scale of sampling a gastropod such as *Batillaria* might be inappropriate for crustaceans, such as Corophium, which show significant variability in Plots 10's of metres apart.

Future research may usefully consider the prevalence and abundance of introduced species in Boundary Bay. Examples from the benthic macrofauna include the polychaete *Polydora ligni*, the gastropod *Batillaria zonalis*, and the bivalve *Mya arenaria*. The transport of these species to Canada is almost entirely related to the introduction and maintenance of Atlantic (*Crassostrea virginica*) and Japanese oysters (*C. gigas*) for commercial production during the early part of the twentieth century (Quayle 1964, Waldichuk *et al.* 1994). Transplants of mature oysters to Boundary Bay, and other locations in British Columbia, resulted in the inadvertent introduction of six species of bivalve, seven species of gastropod, four polychaetes and assorted other invertebrates (Waldichuk *et al.* 1994). *Batillaria zonalis*, the most abundant mollusc found in the high intertidal flats of Boundary Bay, was already well established at the time of Quayle's (1964) paper with up to 95 per m^2.

Continued monitoring of invertebrates in the upper sandflat zone of Boundary Bay is also suggested in order to discern the effects of the introduced eelgrass *Z. japonica* on invertebrate abundance in this zone. Data collected in 1991 by Baldwin and Lovvorn (1994b) showed that coverage of *Z. japonica* in Boundary Bay had increased 17-fold to 3845 ha from 211 ha in 1970. However, they did not find *Z. japonica* less than

1 km from the salt marsh (Baldwin and Lovvorn 1994b); whereas in August 1994 plants were present at distances less than 500 m from the salt marsh in the same location as their Transect 1. As previous studies have shown increased invertebrate numbers associated with *Z. japonica* (reviewed in Baldwin and Lovvorn 1994b), it would be of interest to examine changing invertebrate densities in the upper sandflat zone concomitant with colonization of *Z. japonica* in the upper sandflat of Boundary Bay. Future sampling programmes in Boundary Bay will need to consider not only the results of the present study, but also patterns in invertebrate abundance with decreased tidal elevation noted by other authors (Kellerhals and Murray 1969, Swinbanks and Murray 1981, McEwan and Gordon 1985, McEwan and Farr 1986, Baldwin and Lovvorn 1994a). If sampling includes sites seaward of the present study, a necessary prerequisite is a pilot study examining scales of variability stratified into the described faunal zones (Swinbanks and Murray 1981, Baldwin and Lovvorn 1994a). As there are seasonal differences in invertebrate abundances within Boundary Bay (McEwan and Farr 1986) the spatial patterns observed in Boundary Bay might also change temporally. Additional sampling during other seasons is thus required to confirm the importance of the described spatial scales (Morrisey *et al.* 1992).

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