

# Associations Between Arthropods and the Supralittoral Ecotone: Dependence of Aquatic and Terrestrial Taxa on Riparian Vegetation

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**ABSTRACT** We evaluated the family-level richness and abundance of aquatic and terrestrial arthropods in marine supralittoral habitats and related arthropod assemblages to the presence and composition of supralittoral vegetation. Using pan traps, we collected 12,226 arthropods in 24 taxa. Collembolans (Entomobryomorpha, Hypogastruridae), amphipods (Talitridae), and midges (Chironomidae) were the most abundant taxa. Regardless of habitat associations, arthropod abundance was higher in sites with supralittoral vegetation than in the site where vegetation had been removed for townhouse development. This was true for both aquatic and terrestrial arthropods. Our results suggest that removal of supralittoral vegetation may have cascading effects on supralittoral arthropod communities and may adversely affect the productivity of both aquatic and terrestrial arthropods.

**KEY WORDS** algal wrack, estuarine, insects, riparian vegetation, supralittoral

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IN THIS PAPER, WE PRESENT a structural analysis of the abundance and distribution of arthropods in relation to supralittoral vegetation in the ecotone between the sea and the land. As pointed out by Richardson et al. (1997), such transitional habitats are often ignored because of the different backgrounds of marine and terrestrial ecologists. However, these ecotones are important for species and processes that encounter them as boundaries. For example, Polis and Hurd (1995, 1996) and Anderson and Polis (1998) found that production from the marine ecosystem subsidized terrestrial arthropods (spiders and scorpions) living near the coast relative to those that lived farther inland.

There is increasing evidence that altering freshwater transitional ecotones affects the structure and function of the aquatic ecosystems they border (Young 2000). For example, reductions in leaf litter have been shown to limit the abundance of detritivores, thereby reducing population size of both aquatic and terrestrial insect prey available for freshwater fish (Wipfli 1997). The structure and function of marine and terrestrial ecotones may also be important for arthropods associated with the marine supralittoral, a transitional ecotone. Removal of supralittoral vegetation may have cascading effects on both the aquatic and terrestrial components of the supralittoral ecotone. However, there have been no studies on the importance of supralittoral vegetation to the productivity and composition of aquatic or terrestrial arthropods in temperate intertidal zones.

In this paper we document associations between both vegetated and unvegetated supralittoral zones and their associated arthropod fauna in Howe Sound, British Columbia. The purpose of the study was (1) to determine if the presence of supralittoral vegetation affected the diversity and composition of arthropod communities in the supralittoral ecotone and (2) to identify associations between supralittoral vegetation, unvegetated supralittoral habitats, and arthropod communities.

## Materials and Methods

Three sites in Howe Sound, British Columbia were chosen for this study: Furry Creek South (FCS), Furry Creek North (FCN), and Porteau Cove (PC) (Fig. 1, A and B). FCS and PC are vegetated supralittoral habitats. FCS has been partially developed as a golf course, with a buffer zone of  $\approx 10$ –30 m depending on the location along the beach left uncut. PC has been developed as a Provincial Park camping site. The supralittoral vegetation in PC has been partially removed to build camping sites; however, a buffer zone of  $\approx 2$ –10 m has been left partially intact. While both FCS and PC are considered vegetated supralittoral, PC is generally more disturbed than FCS, primarily because of its use as a camping site. At PC, gravel- and dirt-covered campsites occupy most of the area along the beach. The mature trees that comprise the canopy are similar at FCS and PC, except for Sitka spruce (*Picea sitchensis*), which was rare at PC and common at FCS, and big-leaf maples (*Acer macrophyllum*), which were only present at PC. The third site, FCN, was clear-cut for a townhouse development before the

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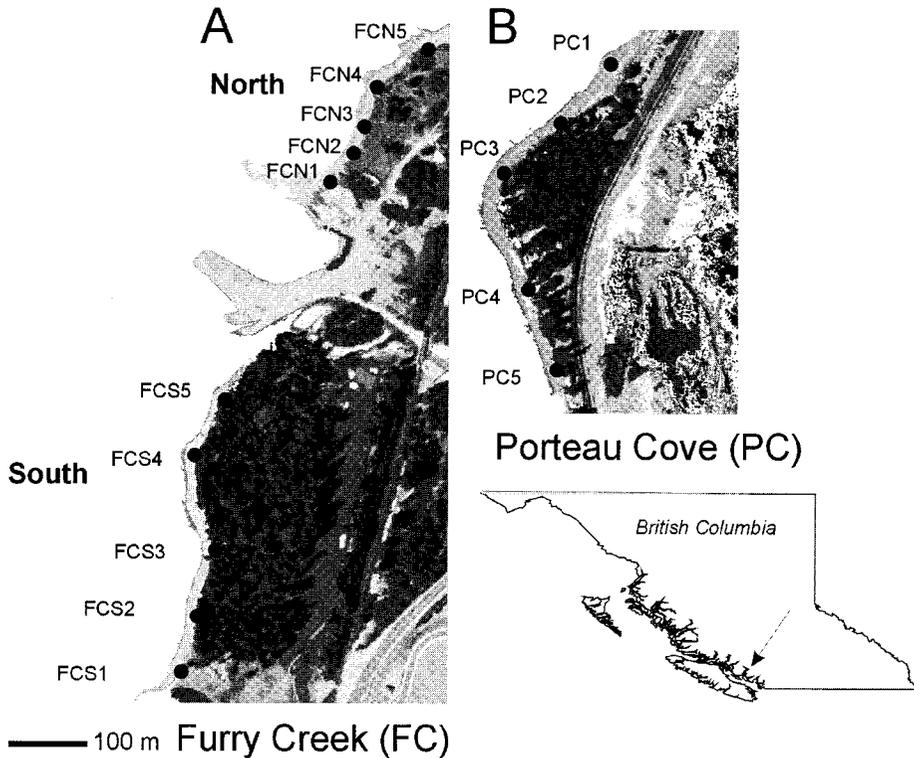


Fig. 1. Aerial photos of pan trap locations for FCN, FCS, and PC. Location of traps are shown by dots. In FCN, the unvegetated area located directly behind the traps has been replaced with a townhouse development and all riparian vegetation has been removed.

start of the study and represents an unvegetated supralittoral habitat where the vegetation was replaced with revetment.

To assess arthropod diversity, we sampled the supralittoral community over a 2-mo period in February and March 2001 using pan traps. Pan traps were established in five locations in all sites. Each trap was set out four times, twice in February and twice in March, except for the PC traps, which were only deployed twice in March. Pan traps were located at the seaward edge of the vegetated supralittoral, which corresponds to the line of the higher high water large tide (HH-WLT), which is the average of the highest high waters, one from each of 19 years of observation (Forrester 1983) for FCS and PC, or for FCN, the HHWLT. Each trap was set out for 24 h. Traps were filled with water and  $\approx 5$  ml of liquid soap to reduce surface tension. Traps were clear plastic 4.2-l containers (W 188 by L 321 by H 82 mm). In FCS and PC, pan traps were partially dug into the sand or gravel substrate. In FCN, pans were set on top of the revetment. FCN and FCS were separated by  $\approx 1$  km. PC was located  $\approx 10$  km south of FCS. Within each location, a transect of  $\approx 500$  m was arrayed along the drift line parallel to the shoreline, and the five traps were located  $\approx 100$  m apart. After collection, traps were brought back to the laboratory, and the arthropods were washed on a 250-micron sieve and rinsed to remove the soap. Materials

retained on the sieve were backwashed into a vial and preserved in 5% formalin. Vial contents were then sorted and identified using an illuminated lens and a dissecting microscope.

Identification was done to family for all taxa except for Acari, Araneae, Opiliones, Thysanoptera, and Collembola (Brusca and Brusca 1990, Merritt and Cummings 1996), and taxa were classified as aquatic or terrestrial according to Merritt and Cummings (1996). Collembola have traditionally been considered an Order within the Class Insecta; however, recent revisions (Bellinger et al. 1996–2003, Nardi et al. 2003) suggest that Collembola has the same taxonomic rank (Class) as Insecta. We identified three Orders of Collembolans in five families: Entomobryomorpha (Tomoceridae, Isotomidae), Symphyleona (Sminthuridae, Dicytomidae), and Poduromorpha (Hypogastriridae). Collembola are primarily inhabitants of soil, litter, and moist vegetation (Christiansen 1996), and the adults cannot survive submersion (Joosse 1976); thus, we have treated all Collembola in the statistical analyses as terrestrial.

Supralittoral vegetation was assessed during the same period as the arthropod sampling. All vegetation landward from the pan trap within a  $100\text{-m}^2$  area was classified to type, identified to species, and percent cover was determined. The  $100\text{-m}^2$  area of vegetation sampling was done landward on either side of the pan

Table 1. List of riparian vegetation identified in Furry Creek South (FCS) and Porteau Cove (PC)

Type	Origin	Common name	Latin name	Frequency <sup>a</sup>	
				FCS	PC
Tree	Native	Douglas-fir	<i>Pseudotsuga menziesii</i>	4	2
Tree	Native	Western red cedar	<i>Thuja plicata</i>	5	4
Tree	Native	Big-leaf maple	<i>Acer macrophyllum</i>	0	2
Tree	Native	Sitka spruce	<i>Picea sitchensis</i>	5	0
Tree	Native	Western hemlock	<i>Tsuga heterophylla</i>	5	0
Shrub	Native	Rose	<i>Rosa sp.</i>	3	5
Shrub	Native	Salal	<i>Gaultheria shallon</i>	5	5
Shrub	Native	Red huckleberry	<i>Vaccinium parvifolium</i>	4	1
Shrub	Native	Oval-leaved huckleberry	<i>Vaccinium ovalifolium</i>	3	1
Shrub	Native	Salmonberry	<i>Rubus spectabilis</i>	4	1
Shrub	Native	Oceanspray	<i>Holodiscus discolor</i>	1	4
Shrub	Introduced	Cherry	<i>Prunus sp.</i>	0	2
Shrub	Native	Red-flowering currant	<i>Ribes sanguineum</i>	1	0
Shrub	Introduced	English ivy	<i>Hedera sp.</i>	0	1
Shrub	Native	Sitka willow	<i>Salix sitchensis</i>	0	1
Shrub	Native	Trailing blackberry	<i>Rubus ursinus</i>	1	1
Shrub	Native	Red alder	<i>Alnus rubra</i>	5	3
Shrub	Native	Snowberry	<i>Symphoricarpos albus</i>	0	4
Shrub		Black twinberry	<i>Lonicera involucrata</i>	1	0
Shrub		Indian Plum	<i>Oemleria cerasiformas</i>	1	0
Herbaceous	Native	Herb-Robert	<i>Geranium robertianum</i>	0	1
Herbaceous	Native	False lily-of-the-valley	<i>Maianthemum dilatatum</i>	3	2
Herbaceous	Native	Sword fern	<i>Polystichum munitum</i>	0	1
Herbaceous	Native	Pearly everlasting	<i>Anaphalis margaritacea</i>	2	0
Herbaceous	Native	Beach pea	<i>Lathyrus japonicus</i>	5	0
Herbaceous	Native	Dunegrass	<i>Elymus mollis</i>	4	0
Herbaceous	Introduced	Wall lettuce	<i>Lactuca muralis</i>	3	0
Herbaceous	Introduced	Hairy cat's-ear	<i>Hypochaeris radicata</i>	2	0
Herbaceous	Introduced	Grass	European species	1	0

Shown are type of vascular plant, origin (native versus introduced), common and latin name, and frequency (number of times a species was recorded for each of the 5 pan trap locations in FCS and PC).

<sup>a</sup> Frequency refers to the number of vegetation sampling plots within a site where a species occurred.

trap, with the pan set at the seaward edge of the plot. Percent cover of sand/gravel, large organic debris (LOD), and cobble were also determined in the 100-m<sup>2</sup> area landward of each trap. Percent cover of sand/gravel refers specifically to cover landward of the pan trap. Seaward of the pan traps in FCS and PC the substrate is sandy beach merging into cobble toward the lower littoral. At FCN, seaward of the pan traps is revetment and cobble merging into sand and cobble toward the lower littoral. Beach wrack, composed of decaying macroalgae and terrestrial material such as leaves and wood, was ubiquitous at all three sites; however, the composition of the wrack differed between sites with and without supralittoral vegetation from primarily macroalgae (FCN) to a mix of macroalgae and terrestrial material (FCS, PC). Because the presence of wrack did not differ between the sites, wrack was not used as a variable in the analyses; however, many of the arthropod taxa identified in the supralittoral are strongly associated with wrack (Jędrzejczak 2002a, b).

Two types of ordination analysis, canonical correspondence analysis (CCA) and detrended correspondence analysis (DCA), were used to relate arthropod assemblages to riparian vegetation and substrate. Ordination analysis arranges or orders taxa and sample units along environmental gradients (ter Braak 1986, Palmer 1993) and extracts the underlying factors (or axes) that distinguish the taxa or sample units. Each

axis is a linear combination of the original variables and can be thought of as a hypothetical environmental gradient. These hypothetical axes are then subsequently interpreted in terms of the measured environmental gradients used in the analysis (ter Braak 1986). A two-step approach was used to determine associations between arthropod taxa and riparian vegetation as suggested by ter Braak (1986). CCA was used to directly relate arthropod abundance to environmental factors. DCA was used to extract from the taxa data the dominant pattern of variation in community composition without environmental factors. This combined approach allowed us to determine whether the patterns extracted by taxa information alone coincided with the patterns extracted by using taxa-environment associations. Both CCA and DCA result in a set of eigenvalues between 0 and 1 and the sum of the eigenvalues corresponds to the total explained variance.

DCA was used to order arthropod taxa without using environmental variables at FCS. Because it is possible that the measured environmental factors may be different from the most important gradients, DCA is useful to ensure that the measured environmental factors represent the most important gradients. If the results from the CCA and DCA are similar, the environmental factors used in the DCA are likely the most important factors to explain taxa-environmental associations (ter Braak 1986).

**Table 2.** List of arthropod taxa collected at Furry Creek South (FCS), Furry Creek North (FCN), and Porteau Cove (PC)

Family	Order	Habitat	Total (n)	PC (n)	FCS (n)	FCN (n)	CODE
Entomobryomorpha	Collembola	Terrestrial	5509	4511	929	69	ENTO
Talitridae	Amphipoda	Aquatic	3260	2820	406	34	TALI
Hypogastruridae	Collembola	Terrestrial	1776	80	1691	5	HYPO
Chironomidae	Diptera	Aquatic	1,151	335	526	290	CHIA
Ligiidae	Isopoda	Aquatic	250	246	4	0	LIGI
Acari	Acari	Terrestrial	87	47	38	2	ACAR
Symphyleone	Collembola	Terrestrial	66	14	50	2	SMIN
Araneae	Araneae	Terrestrial	29	1	23	5	ARAN
Canacidae	Diptera	Aquatic	25	2	11	12	CANA
Ceratopogonidae	Diptera	Aquatic	16	4	11	1	CERA
Aphididae	Homoptera	Terrestrial	16	0	15	1	APHI
Cicadellidae	Homoptera	Terrestrial	8	2	6	0	CICA
Mymaridae	Hymenoptera	Aquatic	5	4	1	0	MYMA
Empididae	Diptera	Aquatic	5	3	2	0	EMPI
Diplopoda	Diplopoda	Terrestrial	6	2	1	3	DIPL
Staphylinidae	Coleoptera	Aquatic	3	3	0	0	STPA
Tipulidae	Diptera	Aquatic	4	1	3	0	TIPU
Sciomyzidae	Diptera	Aquatic	2	2	0	0	SCIO
Opiliones	Opiliones	Terrestrial	2	1	1	0	OPIL
Thysanoptera	Thysanoptera	Terrestrial	2	1	1	0	THYS
Hebridae	Hemiptera	Aquatic	1	0	1	0	HEBR
Tingidae	Hemiptera	Terrestrial	1	0	1	0	TING
Ichneumonidae	Hymenoptera	Aquatic	1	0	0	1	ICHN
Muscidae	Diptera	Aquatic	1	0	0	1	MUSC

Shown are taxonomic level of identification (family, order), habitat type (aquatic, terrestrial) based on Merritt and Cummins (1996), sites where the taxa were collected, and total abundance of taxa across all three sites, total abundance of the taxa at PC, FCS, and FCN, and the CODE used in the DCA and CCA ordinations diagrams.

Two CCAs were performed. The first related arthropod abundance to supralittoral vegetation in FCS. This analysis was performed to determine whether there were associations between arthropod taxa and percent cover, species richness, and type (i.e., canopy, understory, herbaceous plants) of supralittoral vegetation. A vegetation index (VI) was calculated for each site as the average percent cover for each type of vegetation, e.g., canopy, shrub/tree-understory, herbaceous-understory, and herbaceous-beach  $\times$  the number of plant species in each category. The rationale for using a VI as opposed to using percent cover for each species was because in CCA the environmental variables must be fewer than the number of sites (in this case, there were five pan trap locations in FCS,  $n = 5$ ). Twenty-nine plant species were identified in the supralittoral; thus, it was necessary to collapse the vegetation data into four or fewer environmental variables that captured vegetation characteristics.

The second CCA related arthropod abundance to environmental factors for all three sites (PC, FCS, FCN). This analysis was performed to determine whether arthropod taxa differed between vegetated versus unvegetated sites. The environmental variables used in the analysis include total plant richness, total plant cover (ranked in order of cover), percent cover of (1) LOD, (2) sand/gravel, (3) cobble, (4) canopy species, (5) shrub/tree-understory, (6) herbaceous-understory, and (7) herbaceous-beach.

Results of ordination analyses are shown on an ordination diagram or triplot, which simultaneously displays species or taxa scores and sample or site scores as points, and environmental gradients as arrows (for review, see ter Braak 1986). For all ordination analy-

ses, triplots were rescaled to show the maximum spread between taxa to facilitate interpretation. Taxa abundances were untransformed. For the FCS analysis, taxa abundances were cumulative (total per site) across all sampling periods. For the ordination of all three sites (PC, FCS, FCN), average abundance was used, as there were fewer sampling periods in PC ( $n = 2$ ) than either FCS or FCN ( $n = 4$ ). All ordination analyses were performed using PC-Ord for Windows v. 4.01 (McCune and Mefford 1999). Cumulative taxa richness and cumulative taxa abundance refer to the total number of individuals or taxa from all pan traps within a site over all sampling dates. Differences between sites in taxa richness and abundance were assessed using *t*-tests.

## Results

Vegetation in the supralittoral included a total of 29 taxa represented by 5 tree species, 16 shrub species, and 9 species of herbaceous plants (Table 1). To conform to the literature on freshwater riparian habitats, we restricted our consideration of vegetation to vascular plants. However, algae, mosses, and lichen are often dominant features of the seaward edge of the supralittoral ecotone. Mosses and lichens were common at FCS but were not abundant (there were some patches at PC but none at FCN) at FCN or PC.

Twenty-four taxa of arthropods in four classes (Hexapoda, Diplopoda, Crustacea, Arachnida) were collected at the three sites (Table 2). Of these, 11 taxa were only collected from sites with supralittoral vegetation (FCS, PC). Ten taxa were common to all three sites. A number of taxa were exclusive to only one site. Two taxa were exclusive to FCS, two taxa were ex-

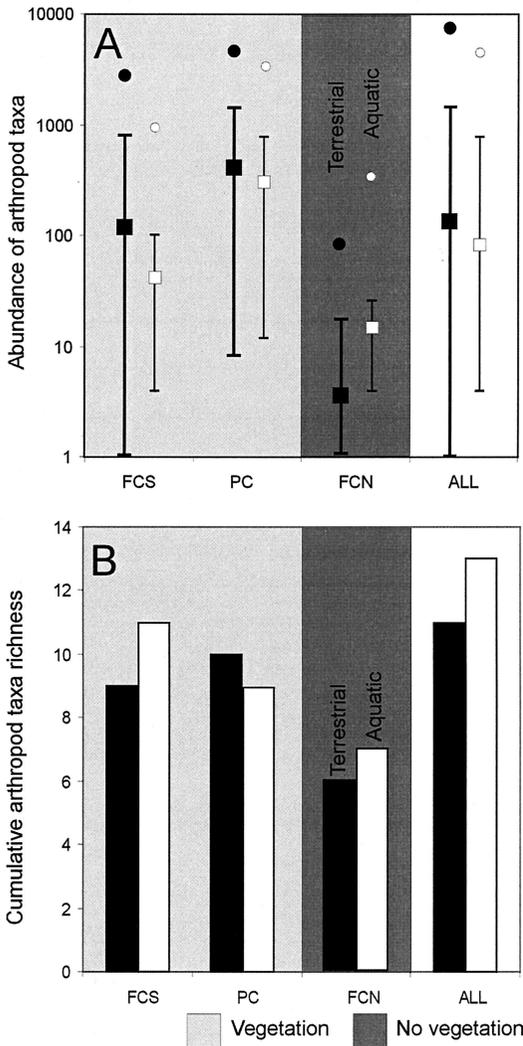


Fig. 2. Aquatic and terrestrial arthropods in the marine supralittoral. Terrestrial arthropods are shown in bold (A) or in black (B), aquatic arthropods are shown in white. Light gray background shows sites with supralittoral vegetation (PC, FCS), and dark gray background shows the site with no supralittoral vegetation (FCN). White background shows all sites combined. (A) Abundance of aquatic and terrestrial arthropods at FCS, PC, and FCN. Circles represent total abundance, squares represent mean abundance, and ranges represent minimum and maximum abundance. (B) Cumulative taxa richness of aquatic and terrestrial arthropods. Sites are the same as for A.

clusive to PC, and two taxa were exclusive to FCN (Table 2).

Of the 24 arthropod taxa collected, 11 were terrestrial, or in the case of Collembola, the taxa contained terrestrial species, and 13 were aquatic (Merritt and Cummings 1996). Terrestrial taxa were more abundant numerically at FCS ( $P = 0.018$ ) than aquatic taxa (Fig. 2A). Aquatic taxa were more abundant at FCN ( $P = 0.003$ ) than terrestrial taxa (Fig. 2A). There was

no difference in abundance of terrestrial versus aquatic taxa at PC ( $P = 0.277$ ; Fig. 2A). Aquatic taxa richness was highest at FCS and lowest at FCN; however, the difference in taxa richness across the three sites was not significant ( $P > 0.05$ ; Fig. 2B).

CCA of riparian vegetation-arthropod associations at FCN showed that riparian vegetation (VI) explained 96.4% of the total variance in the patterns of arthropod taxa (Fig. 3). The first two eigenvalues were 0.240 and 0.048, indicating that the first axis explained most of the variability (74.8% explained variance). Axis 2 explained 14.9% of the variability. Axis 1 represents the overall trend in association between arthropods and supralittoral vegetation. Axis 1 was positively correlated with cover of herbaceous plants on the beach ( $r = 0.678$ ) and herbaceous plants in the understory ( $r = 0.654$ ), and negatively correlated with shrubs in the understory ( $r = -0.554$ ). Axis 2 represents a gradient of increasing canopy cover and positively correlated with herbaceous cover in the understory ( $r = 0.456$ ) and negatively correlated with canopy cover ( $r = -0.450$ ).

The placement of sites along the first CCA axis revealed how the supralittoral vegetation of the five sites was distinct (Fig. 3). FCS1 and FCS4 were located in areas with greater coverage of supralittoral vegetation, with both a dense understory and high canopy cover. FCS2 and FCS3 were located in areas with dense understory. In contrast, FCS5 was associated with greater cover of herbaceous plants on the beach and herbaceous plants in the understory.

The riparian vegetation-arthropod associations shown in the CCA were supported by DCA where only taxa data were used in the ordination (Fig. 4). DCA showed that the eigenvalues of the first and second axes, 0.240 and 0.008, respectively, closely coincided with the eigenvalues from CCA. Eigenvalues for axis 1 for both DCA and CCA were 0.240. This similarity is partly shown by concordance between Figs. 3 and 4 and suggests that the environmental variables chosen to represent vegetation characteristics are similar to those identified by DCA. Similar to the CCA, the first DCA axis represented 97% of the total variance in the taxa data.

Correlation analysis of the total abundance ( $\log_{10}$ ) of each of the taxa with the first axis of the DCA showed that 30% of the variability in total arthropod taxa abundance could be explained by the first axis. Thus, as supralittoral vegetation increases in both richness and cover, arthropod abundance increases ( $R = 0.548$ ,  $P = 0.01$ ).

To determine which arthropod taxa were associated with supralittoral vegetation and which were associated with unvegetated supralittoral habitat, we used arthropod abundance data from all three sites (PC, FCS, and FCN) and total plant richness, total plant coverage (rank), and percentage cover of (1) LOD, (2) canopy, (3) shrub/tree-understory, (4) herbaceous-understory, (5) herbaceous-beach, (6) sand/gravel, and (7) cobble. The first three eigenvalues were 0.493, 0.159, and 0.052. The first CCA axis represents a substrate gradient and explained 42.8% of the

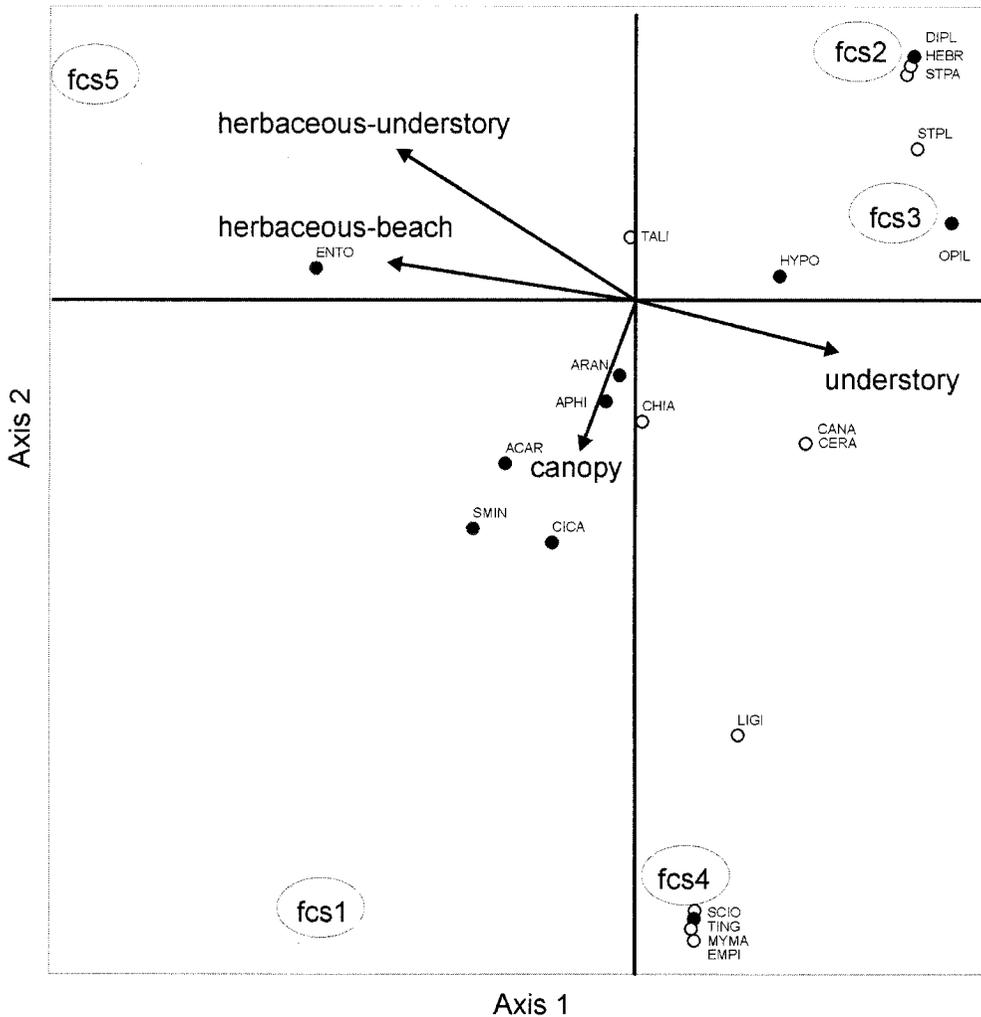


Fig. 3. Canonical correspondence analysis (CCA) of riparian vegetation-arthropod associations for FCS. Arthropod taxa are shown by circles. Black circles denote terrestrial arthropods, open circles denote aquatic arthropods. Sites are shown by fcs1-5. See Table 2 for taxa codes.

variance in arthropod taxa (Fig. 5). Axis 1 was strongly positively correlated with percent cover of sand and gravel ( $r = 0.622$ ) and negatively correlated with all variables representing supralittoral vegetation. The strongest negative correlations for axis 1 were for percent cover of canopy ( $r = -0.724$ ) and total cover of all plants ( $r = -0.727$ ). Axis 2 represented a gradient of vegetated to unvegetated supralittoral and explained 13.8% of the variance. Axis 2 was strongly negatively correlated with percent cover of cobble ( $r = -0.899$ ) and positively correlated with plant richness ( $r = 0.4$ ).

The positioning of the three sites (PC, FCS, FCN) along axes 1 and 2 shows both the difference between the two vegetated sites (PC and FCS) and the difference between FCS and FCN (Fig. 5). PC and FCS differ primarily along axis 1, which represents a gradient of unvegetated supralittoral such as sand/gravel cover (PC) to supralittoral vegetation (FCS). FCS and

FCN differ primarily on axis 2, which represents a gradient of unvegetated supralittoral cobble cover (FCN) to supralittoral vegetation (FCS).

Correlation analysis of the average arthropod abundance per site showed that axis 2, rather than axis 1, was significantly related to arthropod abundance ( $R = 0.888$ ,  $r^2 = 0.79$ ,  $P < 0.001$ ). Likewise, 83% of the variability in average arthropod richness was explained by axis 2 ( $R = 0.913$ ,  $P < 0.001$ ). Thus, across all three sites, arthropod taxa abundance and richness are highest in sites with more riparian vegetation.

## Discussion

The associations between vegetation and arthropod communities have received considerable attention in the riparian ecotone of streams (Erman 1984, Nakano et al. 1999), primarily because of the importance of the riparian ecotone as a habitat for juvenile salmonids

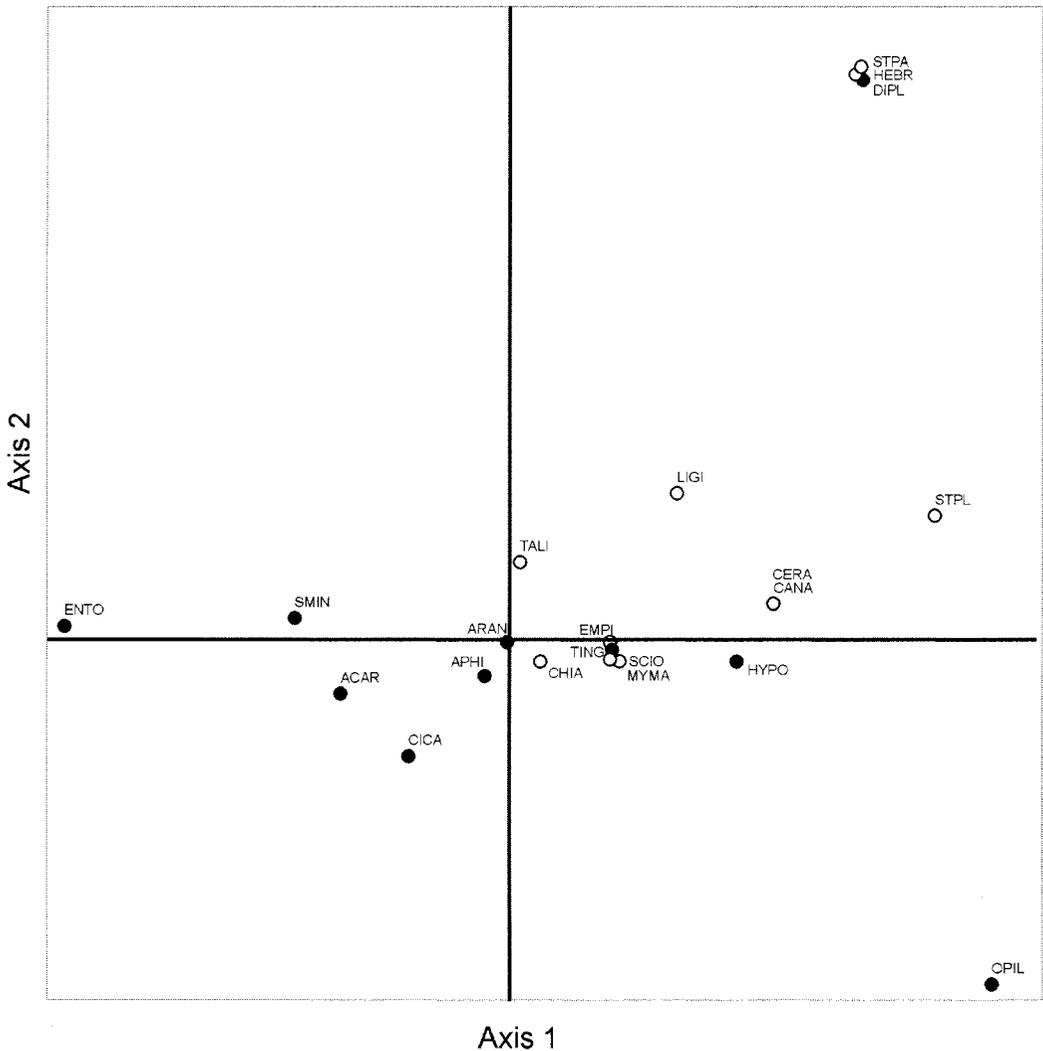


Fig. 4. Detrended correspondence analysis (DCA) for riparian vegetation-arthropod associations for FCS. Arthropod taxa are shown by circles. Black circles denote terrestrial arthropods, open circles denote aquatic arthropods. See Table 2 for taxa codes.

(Naiman and Decamps 1997). In contrast, there is no available information on the impact of removal of supralittoral vegetation on arthropod communities in marine supralittoral ecotones. It is well established that clear-cutting of riparian vegetation in streams alters the composition of invertebrate communities (Golladay and Webster 1988) through changes in either food choice (Mutch et al. 1983, Dobson et al. 1992, Richardson 1992, Dobson 1994) or habitat (Voshell and Simmons 1977, Webster and Simmons 1978, Winterbourne 1978, Street and Titmus 1982, Scarsbrook and Townsend 1994). Similar to freshwater riparian vegetation, marine and estuarine supralittoral vegetation may provide temperature and microclimate control, habitat complexity and prey refuges, increases in the abundance of food, and increased nutrient input (Cummins et al. 1989, Inoue et al. 1997).

Of the 24 arthropod taxa collected, 11 were identified as terrestrial and 13 were identified as aquatic (Merritt and Cummings 1996). Across all taxa, arthropod taxa richness and abundance was higher in the vegetated sites than in the unvegetated site. Aquatic arthropods were eight times more abundant on average at the vegetated sites as opposed to the unvegetated site and terrestrial arthropods were 65 times more abundant at the vegetated sites. This suggests that supralittoral vegetation may provide important functions for both aquatic and terrestrial arthropods associated with the supralittoral ecotone. Because both terrestrial and aquatic taxa were more abundant and diverse at sites with supralittoral vegetation, habitat complexity and prey refuges associated with terrestrial vegetation are probably not the primary cause of increased arthropod abundance and richness in

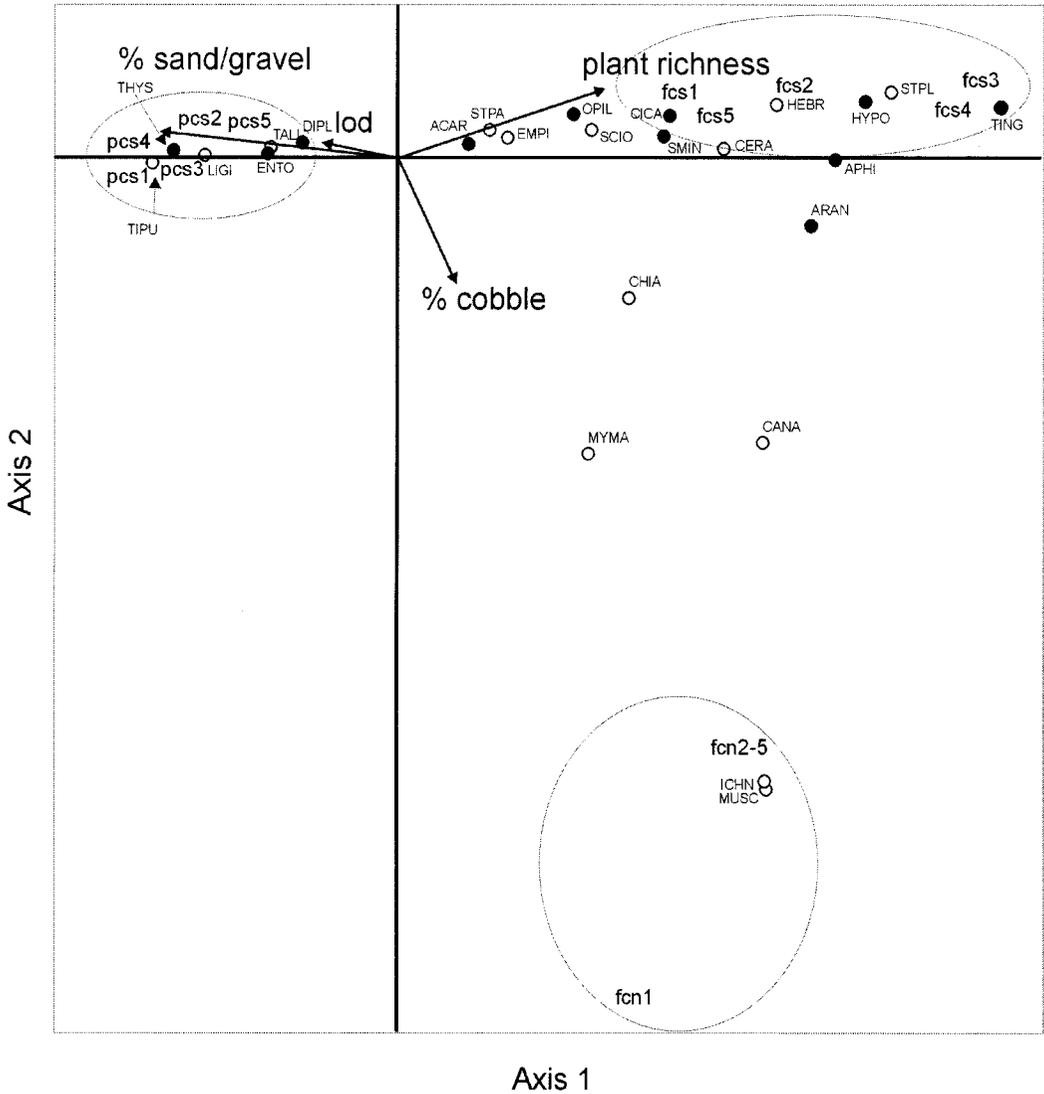


Fig. 5. CCA of arthropod associations with environmental factors for all three sites: PC (vegetated riparian), FCS (vegetated riparian), and FCN (unvegetated riparian). Arthropod taxa are shown by circles. Black circles denote terrestrial arthropods, open circles denote aquatic arthropods. Sites are shown by pcs1–5 (PC), fcs1–5 (FCS), and fcn1–5 (FCN). See Table 2 for taxa codes. Large circles show site relationships.

sites with supralittoral vegetation. Instead, increases in arthropod abundance and richness in sites with supralittoral vegetation are likely caused by a combination of increases in the abundance and diversity of prey, increased allochthonous inputs to the supralittoral ecotone from terrestrial leaf litter drop, temperature and microclimate control, increased habitat complexity of beach wrack, and differences in local chemical conditions and microbial communities associated with beach wrack in vegetated supralittoral sites.

Ten arthropod taxa were associated with unvegetated supralittoral habitats. These taxa are primarily inhabitants of algal wrack (Joosse 1976, Richardson et al. 1997, Jędrzejczak 2002b). For example, Talitridae

(amphipods) are commonly found in algal wrack (dry algae) in the supralittoral (Richardson et al. 1997). Algal wrack is a common feature in supralittoral habitats and provides food and shelter for both aquatic and terrestrial arthropods, particularly amphipods, isopods, and dipteran larvae (Jędrzejczak 2002b). On a beach in Poland where the basal food supply was provided entirely from the sea, Jędrzejczak (2002b) reported that Amphipoda, Diptera, Chilopoda, and Coleoptera (Staphylinidae, Ptiliidae, Histeridae, Anthicidae, Coccinellidae) were the most abundant macrofaunal taxa in algal wrack. The wrack meiofaunal community was composed primarily of Nematoda, Oligochaeta, Turbellaria, Gastrotricha, Dipteran larvae, Acarina, and Collembola.

In our study, Talitridae, Entomobryomorpha, Hydropogonidae, Symphyleone, Canaceidae, Ceratopogonidae, Chironomidae, Diplopoda, Acari, and Araneae, were present at all three sites suggesting associations with algal wrack or other nonvegetated supralittoral microhabitats rather than terrestrial vegetation. However, except for Chironomidae (midges) all taxa common to both vegetated and unvegetated supralittoral had lower abundances in the unvegetated site. This suggests that the reduced productivity of arthropods in the unvegetated supralittoral site may be caused by a combination of differences in (1) microclimate conditions such as moisture regimen and temperature that affect arthropod taxa directly as well as indirectly by mediating chemical conditions and microbial communities in algal wrack (Jędrzejczak 2002a), (2) complexity and composition of the wrack, and (3) the abundance and composition of allochthonous inputs.

Beaches are generally nutrient-poor systems (Bouchard and Bjorndal 2000), receiving nutrients and energy from both the sea and the land. For example, macrophytes, macroalgae, and carrion washing ashore have been found to be a significant source of marine-derived nutrients (Heatwole 1971, Allaway and Ashford 1984, McLachlan and McGwynne 1986, Polis and Hurd 1995, 1996). However, decomposition of algal wrack and plants in the supralittoral is strongly affected by temperature and moisture regimen (Wachendorf et al. 1997, Jędrzejczak 2002a). Because the composition of macro- and meiofaunal communities inhabiting algal wrack are related to the chemical conditions and microbial communities of decomposing wrack (Jędrzejczak 2002b), temperature and moisture related differences between sites with and without supralittoral vegetation might indirectly affect supralittoral arthropod communities (Jędrzejczak 2002b).

We found differences in the species composition of the arthropod communities not associated with supralittoral vegetation consistent with this hypothesis. Of the 13 aquatic taxa, only 4 taxa, three dipterans and the talitrid amphipods, were common to all 3 sites (Table 2). Two taxa, Muscidae and Ichneumonidae, were only found at FCN. The other six taxa were only found at sites with supralittoral vegetation, despite being aquatic. Staphylinidae and Sciomyzidae were only found at PC, and Ligiidae, Mymaridae, Empididae, and Tipulidae were found at both PC and FCS. For example, representatives of the isopod Family Ligiidae are commonly found scavenging on beach wrack and dead animals high up in the supralittoral or in the intertidal zone. This habitat preference of Ligiidae suggests that a member of this family would be present along shores regardless of the presence of terrestrial vegetation; however, Ligiidae were only found in sites with supralittoral vegetation.

Terrestrially derived sources of nutrients are also important to supralittoral ecotones. Coastal forests are particularly important in providing spatial subsidies to the land-sea ecotone in estuaries (Polis and Hurd 1996). For example, in La Perouse Bank, which is 75 miles off the west coast of Vancouver Island, 29% of

the total particulate organic matter is of terrestrial origin (Wu et al. 1999). However, different forest stands may have varying inputs of nutrients because of soil and species composition. For example, old-growth forests around the west coast of Vancouver Island have been shown to release more nitrogen in their leaf litter than secondary-growth forests (Prescott et al. 1993). This is especially true for Sitka spruce, western hemlock, and western red cedar, which are relatively poor at retaining nutrients (Vitousek and Reiners 1975).

There were large differences in the composition and percent cover of vegetation between the two vegetated supralittoral sites in this study that would likely have had a strong effect on the amount of allochthonous leaf litter entering the supralittoral ecotone as well as on the nutrient concentration in the leaf litter itself. At FCS the canopy was dominated by Sitka spruce, western red cedar, and western hemlock, whereas at PC western red cedar, Douglas fir, and big-leaf maple dominated the canopy. Furthermore, at FCS, the average percent cover of canopy species was 89% while at PC the average percent cover of canopy species was only 25%. These differences also affected the composition of the wrack. At FCS and PC the wrack included both marine and terrestrially derived sources (e.g., leaves, twigs, seeds, wood), while at FCN the wrack was composed primarily of macroalgae (C.D.L., unpublished data).

Dipterans are the most successful insects to colonize marine environments (Merritt and Cummings 1996). We collected seven families of dipterans in the marine supralittoral. Chironomidae were the most dominant dipteran family by two orders of magnitude and the only dipteran family to have similar abundances in all three sites. Of the 1,115 individuals collected at all three sites, 45, 29, and 25% of chironomids were collected at FCS, PC, and FCN, respectively. This similarity in abundance between the three sites suggests that at the family level the abundance of Chironomidae was not related to the presence of supralittoral vegetation. However, identification to genus or species level would likely have revealed significant differences between sites in composition. Chironomidae, which were the most abundant taxa at FCN, are an exclusively aquatic family, with 13 genera containing marine representatives found in intertidal habitats (Ward 1992). This suggests that as a family they should be less dependent on the presence and composition of supralittoral vegetation than terrestrial dipterans or other terrestrial arthropods. However, despite this, the abundance of chironomids was still lowest at the site with no supralittoral vegetation.

Collembola, which are considered primarily a terrestrial taxa with some aquatic species (Ward 1992), were numerically the most dominant taxa in the vegetated supralittoral sites and the second most dominant taxa in the unvegetated site (after Chironomidae). Five families comprised 60% of the total abundance across all sites and taxa. A random subset of 24 individuals identified to species showed a range of habitat associations including two exclusively terrestrial species [*Anurophorous pacifica* (Potapov), *Ptenothrix maculosa* (Schott)], and six

species that are often found on the water surface [*Hypogastrura viatica* (Tullberg), *Hypogastrura* (*Ceratophylla*) *pseudarmata* (Folsom), *Tomocerus* (*Pogonognathellus*) *flavescens* (Tullberg), *Sminthurinus maculosus* (Snider), *Archistoma besselsi* (Packard), *Isotoma* (*Haliotoma*) *marisca* (Christiansen and Bellingger)].

Despite this range of habitat associations, all Collembola have an affinity for microhabitats with high humidity and are often found in marginal (damp) habitats (Ward 1992). In the intertidal zone, dense clouds of Collembola can be found on algal wrack throughout the spring and summer (C.D.L., unpublished data). However, adult collembolans cannot tolerate complete submergence and must seek out terrestrial habitats or microhabitats such as air bubbles attached to aquatic plants when the tide comes in (Joose 1976).

Several studies have found no direct relationship between plant species and the compositions of collembolan communities (Wood 1966, Curry 1978, Addison 1980). However, there may be a relationship between the abundance of collembolans and plant species. Berch et al. (2001) found that the abundance of collembolans was highest under Sitka spruce (32,000 individuals/m<sup>2</sup>) and Douglas fir (30,000 ind./m<sup>2</sup>), followed by western hemlock (20,000 individuals/m<sup>2</sup>) and western red-cedar (10,000 individuals/m<sup>2</sup>) in a study of the soil communities associated with conifer species on Southern Vancouver Island. Sterzyńska and Ernsberger (2000) found higher abundances of Collembola in an older intertidal salt marsh with dense cover of *Salicornia* spp. than in a younger one with poorer vegetation cover. *P. maculosa*, one of the two terrestrial collembolans we found in the supralittoral, was significantly more abundant at FCS, the site with the greatest overall conifer canopy cover and the only site with Sitka spruce and western red-cedar.

Other studies suggest that vegetation type, soil type, moisture, and temperature contribute to the overall composition of collembolan fauna (Vannier and Verhoef 1978, Verhoef and Witteveen 1980, Lek-Ang et al. 1999). Of the 5,509 individuals of Entomobryomorpha that were collected at all three sites, only 1.3% were found at the site with no supralittoral vegetation. Furthermore, while six of the eight collembolans identified to species are often found on the water surface (Merritt and Cummings 1996) in beach zones and tidal margins, their abundances were highest in the sites with supralittoral vegetation. This suggests that the presence of supralittoral vegetation may have provided important control of microclimate conditions such as lower water temperature and shade (Vannier and Verhoef 1978, Verhoef and Witteveen 1980, Lek-Ang et al. 1999).

In conclusion, regardless of terrestrial versus aquatic habitat associations, arthropods collected in pan traps in the supralittoral ecotone are more abundant in sites with supralittoral vegetation than sites where vegetation had been removed for townhouse development. These results suggest that loss of supralittoral vegetation may reduce the productivity of both aquatic and terrestrial insects, possibly by adversely affecting the amount of

allochthonous material entering the supralittoral and microclimate conditions.

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