

## ***Relationships between fish and supralittoral vegetation in nearshore marine habitats***

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### ABSTRACT

1. This study was conducted to determine whether there were significant differences in the species richness and community composition of fish assemblages in coastal nearshore habitats with differing compositions of supralittoral vegetation.

2. We sampled fish assemblages and conducted supralittoral vegetation surveys at 27 beaches on the west coast of Vancouver Island, British Columbia. Thirteen of the beaches had supralittoral vegetation characteristic of old-growth coastal forests and 14 had been previously subjected to logging or other disturbances.

3. Physical features (e.g. substrate, salinity, etc.) were recorded at each beach to determine whether there were significant associations between supralittoral vegetation and beach characteristics as well as between beach characteristics and fish assemblages.

4. Across all 27 beaches, 1832 individuals of 31 species of nearshore fish were collected, primarily juvenile cottids and salmonids. Mean species richness did not differ between beaches with old-growth versus secondary-growth supralittoral vegetation; however, a higher cumulative number of species was found at beaches with old-growth supralittoral vegetation.

5. Canonical Correspondence Analysis (CCA) showed that beach characteristics and supralittoral vegetation were not significantly associated. Separate CCA for fish associations with beach characteristics and fish associations with supralittoral vegetation explained ~55% of the variance in fish assemblage composition, suggesting that fish assemblage composition is significantly affected by substrate, submerged vegetation, and physico-chemical conditions as well as by the community composition of vegetation in adjacent supralittoral habitats.

6. Specifically, we found associations between supralittoral vegetation and penpoint gunnels (*Apodichthys flavidus* Girard), tidepool sculpins (*Oligocottus maculosus* Girard), Pacific staghorn sculpins (*Leptocottus armatus* Girard), arrow gobies (*Clevelandia ios* Jordan and Gilbert), shiner perch (*Cymatogaster aggregata* Gibbons) and kelp perch (*Brachyistius frenatus* Gill). Juvenile chum (*Oncorhynchus keta* Walbaum) and coho (*Oncorhynchus kisutch* Walbaum) salmon were strongly associated with supralittoral vegetation characteristic of mature coastal forests such as mosses and

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western red cedar (*Thuja plicata*) suggesting that some nearshore fish species may be affected by processes originating in terrestrial ecosystems.

7. Our results suggest that some nearshore fish species may be affected by removal of supralittoral vegetation.

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KEY WORDS: coastal; logging; intertidal; salmon; sculpins; temperate rainforest

## INTRODUCTION

Studies looking at the potential impacts of alterations in terrestrial vegetation on fish communities in adjacent aquatic habitats have primarily focused on fish assemblages in streams (Gowns *et al.*, 1998, 2003) or estuaries (Peterson *et al.*, 2000), with a particular focus on salmonids (Everest *et al.*, 1987; Scrivener and Brownlee, 1989; Hartman *et al.*, 1996; Bérubé and Lévesque, 1998; St Onge and Magnan, 2000; Sobocinski, 2003). No similar information is available on associations between supralittoral vegetation and fish communities in coastal regions; however, two lines of evidence suggest that supralittoral vegetation may affect fish assemblages in nearshore marine habitats. First, nearshore marine fish assemblages have been shown to be resource-limited (Grossman, 1982, 1986). Second, removal of supralittoral vegetation reduces leaf litter drop which may result in declines in freshwater invertebrate productivity (Culp, 1988), and may decrease terrestrial insect drop into nearshore marine environments (Attrill *et al.*, 1999; Romanuk and Levings, 2003). Both of these effects of removal or modifications of supralittoral vegetation have the potential to affect food supply to fishes in nearshore environments.

We conducted a study to determine if the extent and composition of supralittoral vegetation is related to fish community composition in nearshore marine habitats. Specifically, our goal was to determine whether there were significant differences in species richness and community composition of nearshore marine fish assemblages between beaches characterized by mature or old-growth supralittoral vegetation and beaches on which supralittoral vegetation had been altered through logging or other disturbances. Our research was on the west coast of Vancouver Island, British Columbia, (BC), which has been subjected to intensive hand and industrial logging for over a century (MacKinnon and Trofymow, 1998).

## METHODS

### Site descriptions

Barkley Sound (48° N, 125° W) is a large embayment (~522 km<sup>2</sup>) located on the west coast of Vancouver Island, British Columbia, Canada. Twenty-three beaches were sampled along the Trevor Channel, which is located on the eastern side of the Sound, and four beaches located along Alberni Inlet from 4 May to 11 May 2003 (Figure 1). Trevor Channel is a narrow and deep channel (~150 m) heavily influenced by the freshwater outflow from Alberni Inlet (Taylor and Haigh, 1996). In our survey, surface salinity ranged from 4 to 33 ppt (mean 25.8 ± 6.9 SD). Surface water temperature ranged from 9.5 to 21°C (mean 13 ± 2 SD; Table 1).

Fourteen of the 27 beaches were adjacent to areas where the supralittoral had been disturbed at various times over the past century and were at various stages of succession. We chose beaches a priori based on visual inspection of the tree canopy as either old-growth (OG) or disturbed (D). A site was designated OG if it had a substantial tree canopy characteristic of mature or old-growth forests. Beaches were chosen on the east or north sides of the islands in the Trevor Channel (e.g. Helby Is., Diana Is., Tzartus Is.) as well as on the mainland of Vancouver Island (Table 1). In addition to beaches along the Trevor Channel, four sites were also sampled in Alberni Inlet. Five of the sites were located on beaches that had a stream or creek.

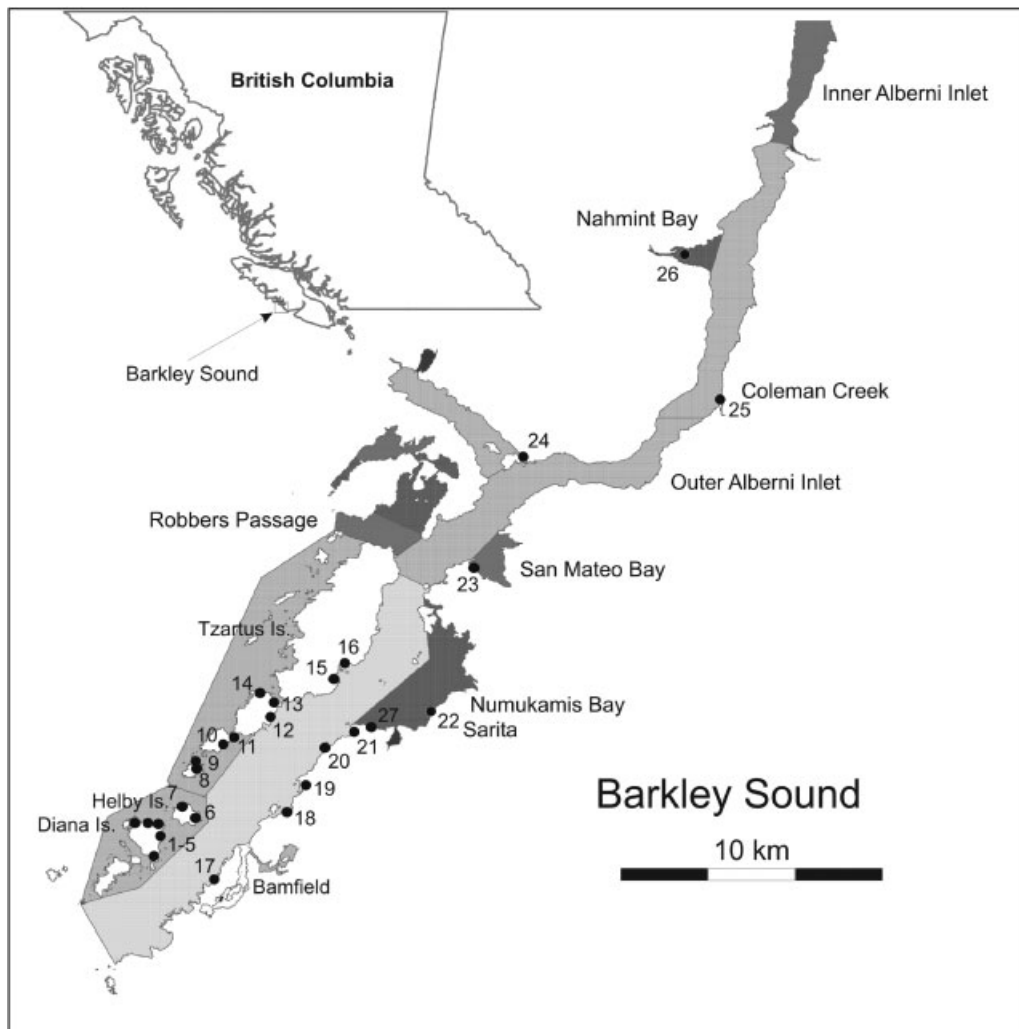


Figure 1. Map of British Columbia and sites in Barkley Sound. Shading indicates average spring salinity (darker shading shows lower salinity).

Beaches spanned a range of conditions from shallow mudflats to steeper cobble beaches (Table 1). Beaches were approached by boat. Only gently sloping beaches that could be beach seined by wading were chosen.

### Fish sampling

Fish were collected using beach seines deployed by wading. The beach seine was  $3 \times 1$  m with a mesh size of 6 mm. The net was set parallel to the shore  $\sim 1$  m from the water line. The deeper drag line was always set at a depth of less than  $\sim 1$  m. For most beaches, sampling was initiated at one end of the beach, furthest away from where the boat was beached, and continued to the other end of the beach. Beach seines are effective and non-selective for sampling nearshore fish from areas with relatively flat sand or mud bottoms (Cailliet *et al.*, 1986). However, when beach seines are deployed off beaches where the subtidal and intertidal has rocky substrate or submerged vegetation the effectiveness and non-selectiveness of beach seining can be

Table 1. Site descriptions arranged in order of CPUE, percentage of total abundance including site code number, situation on an island (I) versus on the mainland (M), location (L) in Trevor Channel (TC) or in Alberni Inlet (AI), designation as an old-growth (OG) or logged (D) site, fish abundance by percentage of total caught, number of species caught, number of seines conducted, and description and location name of the beach for each of 27 sites

Site no.	I or M	L	Creek	Salinity (ppt)	Temperature (°C)	Logging	Abundance (% of total)	Species (#)	Seines (#)	Beach description
24	M	AI	YES	15	21.0	OG	13.88	7	6	Mud beach in Limestone Bay
9	I	TC	NO	30	13.0	D	10.42	4	15	Cobble and gravel beach on Ross Is.
14	I	TC	NO	28	14.0	D	9.31	7	9	Gravel and sand beach in Robbers Passage
6	I	TC	NO	30	12.0	D	8.75	8	7	Boulder and rock beach on Helby Is.
4	I	TC	NO	32	12.0	OG	7.46	1	9	Sand beach on Diana Is.
1	I	TC	NO	28	13.0	OG	5.28	9	12	Cobble and sand beach on Diana Is.
18	M	TC	NO	23	12.0	D	5.26	6	5	Steep rocky beach
16	M	TC	NO	25	15.0	OG	4.89	10	9	Gravel and mud beach in Sprout Bay
15	I	TC	NO	24	15.0	OG	4.66	10	15	Gravel beach Tzartus Is.
2	I	TC	NO	30	14.0	OG	4.46	5	13	Sand beach on Diana Is.
22	M	TC	NO	17	13.0	D	4.44	8	15	Gravel and sand beach in Sarita Bay
23	M	AI	YES	23	13.0	D	3.65	7	15	Cobble and gravel beach in San Mateo Bay
26	M	AI	YES	4	9.5	D	3.40	5	15	Gravel and bedrock beach in Alberni Inlet
25	M	AI	YES	12	12.0	OG	2.28	3	12	Cobble and gravel beach near Coleman Creek
8	I	TC	NO	29	13.0	D	1.61	4	15	Boulder and gravel beach on Ross Is.
13	I	TC	NO	29	13.0	OG	1.58	3	15	Cobble beach in Robbers Passage
7	I	TC	YES	31	13.0	OG	1.54	5	15	Gravel beach on Helby Is.
20	M	TC	NO	30	11.0	D	1.47	7	15	Cobble beach
11	I	TC	NO	24	12.0	OG	1.33	9	15	Cobble beach on Fleming Is.
19	M	TC	NO	25	13.0	D	0.97	9	15	Steep cobble beach
3	I	TC	NO	33	12.0	OG	0.93	4	15	Sand beach on Diana Is.
10	M	TC	NO	26	13.0	OG	0.86	7	15	Cobble beach
17	M	TC	NO	30	11.5	D	0.63	3	11	Brady Beach; sand
12	I	TC	NO	30	13.0	D	0.50	4	15	Cobble beach on Fleming Is.
21	I	TC	NO	30	12.0	D	0.29	3	15	Gravel beach
5	I	TC	NO	33	12.0	OG	0.14	3	15	Sand beach on Diana Is.
27	M	TC	NO	20	12.0	D	0.00	0	15	No fish caught. Rocky beach near Sarita Bay

Table 2. Common and scientific names for each fish species ordered according to percentage of total abundance. Also shown is number of sites a species was caught at (column headed by 'All') and the number of OG and D sites a species was caught at. Code refers to the codes used for species in the CCA (Figures 4–6)

Common name	Family	Species name	% of total	All	OG	D	Code
Tidepool sculpin	Cottidae	<i>Oligocottus maculosus</i> (Girard)	46.5	25	13	12	TPS
Pacific staghorn sculpin	Cottidae	<i>Leptocottus armatus</i> (Girard)	16.4	7	3	4	PSS
Chum salmon	Salmonidae	<i>Oncorhynchus keta</i> (Walbaum)	10.0	16	7	9	CHM
Butter sole	Pleuronectidae	<i>Isopsetta isolepsis</i> (Lockington)	7.7	15	6	9	BTS
Buffalo sculpin	Cottidae	<i>Enophrys bison</i> (Girard)	4.8	10	4	6	BFS
Arrow goby	Gobiidae	<i>Clevelandia ios</i> (Jordan and Gilbert)	2.6	2	1	1	GO
Penpoint gunnel	Pholidae	<i>Apodichthys flavidus</i> (Girard)	2.1	9	5	4	PG
Coho salmon	Salmonidae	<i>Oncorhynchus kisutch</i> (Walbaum)	1.8	3	1	2	COH
Shiner perch	Embiotocidae	<i>Cymatogaster aggregata</i> (Gibbons)	1.4	6	4	2	SP
Pacific sanddab	Bothidae	<i>Citharichthys sordidus</i> (Girard)	1.3	3	2	1	PSD
Kelp perch	Embiotocidae	<i>Brachyistius frenatus</i> (Gill)	1.3	4	3	1	KP
Kelp clingfish	Gobiesocidae	<i>Rimicola muscarum</i> (Meek and Pierson)	0.6	4	4	0	KC
Bay pipefish	Syngnathidae	<i>Syngnathus leptorhynchus</i> (Girard)	0.6	8	5	3	BP
Sharpnose sculpin	Cottidae	<i>Clinocottus acuticeps</i> (Gilbert)	0.6	6	1	5	SNS
Surf smelt	Osmeridae	<i>Hypomesus pretiosus pretiosus</i> (Girard)	0.4	6	3	3	SS
Three-spined stickleback	Gasterosteidae	<i>Gasterosteus aculeatus</i> (L.)	0.4	3	1	2	STI
Pacific sand lance	Ammodytidae	<i>Ammodytes hexapterus</i> (Pallas)	0.3	2	1	1	PSL
Striped kelpfish	Clinidae	<i>Gibbonsia metzi</i> (Hubbs)	0.3	2	2	0	SK
Whitespotted greenling	Hexagrammidae	<i>Hexagrammos stelleri</i> (Tilesius)	0.2	3	0	3	WPG
Tube-snout	Aulorhynchidae	<i>Aulorhynchus flavidus</i> (Gill)	0.1	1	0	1	TS
Kelp greenling	Hexagrammidae	<i>Hexagrammos decagrammus</i> (Pallas)	0.1	2	2	0	KG
Pacific herring	Clupeidae	<i>Clupea harengus</i> (pallasi Valenciennes)	0.1	2	1	1	PH
Speckled sanddab	Bothidae	<i>Citharichthys stigmæus</i> (Jordan and Gilbert)	0.1	2	1	1	SSD
Spotted snailfish	Liparidae	<i>Liparis callyodon</i> (Pallas)	0.1	1	0	1	SSF
Cabezon	Cottidae	<i>Scorpaenichthys marmoratus</i> (Ayres)	0.1	2	1	1	CAB
Calico sculpin	Cottidae	<i>Clinocottus embryum</i> (Jordan and Starks)	0.1	1	1	0	CS
Northern spearnose poacher	Agonidae	<i>Agonopsis vulsa</i> (Jordan and Gilbert)	0.1	1	1	0	NSP
Crevice kelpfish	Clinidae	<i>Gibbonsia montereyensis</i> (Hubbs)	≤0.1	1	0	1	CKF
Lingcod	Hexagrammidae	<i>Ophiodon elongatus</i> (Girard)	≤0.1	1	1	0	LC
Pacific sandfish	Trichodontidae	<i>Trichodon trichodon</i> (Tilesius)	≤0.1	1	1	0	PSF
Red Irish lord	Cottidae	<i>Hemilepidotus hemilepidotus</i> (Tilesius)	≤0.1	1	1	0	RIL

affected. To account for this we used a sampling protocol where either 15 seines were deployed or ~100 individual fish were collected. Thus, for mud beaches such as site #24 only seven seines were deployed to reach ~100 individuals, whereas for cobble or rock beaches the maximum ( $n = 15$ ) number of seines were usually deployed (Table 2). Of the 27 sites sampled, 16 sites required the maximum number of seines ( $n = 15$ ); the other 11 sites, needed between five and 13 seines (Table 2). Each seine sample covered ~9 m<sup>2</sup> of beach. This collection method was also used to minimize the impact of the sampling protocol. The very high abundances of some species, e.g. tidepool sculpins (*Oligocottus maculosus*), in some seines would have resulted in considerable mortality. Fish were kept in a cooler during the fieldwork then frozen at the end of the sampling day. In the laboratory, they were thawed, identified to species according to Lamb and Edgell (1986) and enumerated. Immature fish that could not be identified conclusively to species were not included in the analysis.

### Vegetation surveys

Supralittoral vegetation and beach substrate were recorded at the same time as the fish sampling. For supralittoral vegetation, two 10 × 10 m plots were surveyed at each site. Plots were established from the

'wrack line', the band of terrestrial and marine detritus that represents the upper range of tidal heights, and extended into the forest. Typically, plots were separated by ~10 m perpendicular to the beach; however, as some beaches had atypical vegetation such as a garden or non-vegetated areas, plots were established up to 100 m apart.

We used percentage cover to quantify trees (>4 m height), shrubs (woody vegetation <4 m height), herbs (all herbaceous species), ferns, mosses and lichens within the plots. We did not identify liverworts, and with the exception of three grass and sedge species (Lyngbyei's sedge (*Carex lyngbyei*), European beachgrass (*Ammophila arenaria*), dune grass (*Elymus mollis*)), we grouped grasses to one group, sedges (*Carex* spp.) to one group, and rushes to one group. Additionally, we did not attempt to resolve willows (*Salix* spp.), roses (*Rosa* spp.), species in the genus *Veronica* or species in the genus *Aster* spp., owing to a lack of fruiting characters to assist in identification. We identified all mosses to species with the exception of the genera *Dicranum*, *Mnium*, *Plagiothecium* and *Rhizomnium*. Vegetation-habitat associations were taken from Pojar and Mackinnon (1994; Table 3).

Table 3. Beach-vegetation and supralittoral vegetation taxa used in the ordination analyses. Taxa are listed alphabetically within structural vegetation layers

Species	Common name	Ecological associations <sup>a</sup>	Vegetation layer
<i>Alnus rubra</i>	Red alder	D	Tree, shrub
<i>Picea sitchensis</i>	Sitka spruce	Ma,R	Tree, shrub
<i>Prunus emarginata</i>	Bitter cherry	D	Tree, shrub
<i>Salix</i> spp.	Willow	D	Tree, shrub
<i>Thuja plicata</i>	Western red cedar	G,R	Tree, shrub
<i>Tsuga heterophylla</i>	Western hemlock	G,S	Tree, shrub
<i>Gaultheria shallon</i>	Salal	G	Shrub
<i>Lonicera involucrata</i>	Black twinberry	G,M	Shrub
<i>Rubus parviflorus</i>	Thimbleberry	D	Shrub
<i>Rubus spectabilis</i>	Salmonberry	D,W	Shrub
<i>Vaccinium</i> spp.	Blueberry and huckleberry	G,D,S	Shrub
<i>Blechnum spicant</i>	Deer fern	D,W	Fern
<i>Polystichum munitum</i>	Sword fern	G,M	Fern
<i>Carex</i> spp. <sup>a</sup>	Sedges	Es,O	Herb
<i>Elymus mollis</i> <sup>a</sup>	Dune grass	I,S,B	Herb
<i>Maianthemum dilatatum</i>	False lily-of-the-valley	S,W	Herb
<i>Potentilla anserina</i> <sup>a</sup>	Silverweed	W,S	Herb
<i>Vicia gigantia</i>	Giant vetch	D,E	Herb
<i>Dicranum</i> spp.	Moss	S,Or	Moss
<i>Hookeria lucens</i>	Clear moss	S,M,Or	Moss
<i>Hypnum circinale</i>	Coiled-leaf moss	G,S	Moss
<i>Isothecium myosuroides</i>	Cat's tail moss	G,S	Moss
<i>Kindbergia oregana</i>	Oregon beaked moss	G,S	Moss
<i>Kindbergia praelonga</i>	Slender beaked moss	G,S	Moss
<i>Plagiothecium</i> spp.	Moss	S, Or	Moss
<i>Rhizomnium</i> spp.	Moss	W,S,Or	Moss
<i>Rhytidodelphus loreus</i>	Lanky moss	G,S	Moss
<i>Usnea longissima</i>	Methuselah's beard	O(F),E	Lichen

<sup>a</sup> Denotes vegetation taxa used in the beach-characteristics CCA. Codes are as follows: **D** disturbed habitats of all kinds; **Ma** mature conifer forests; **R** exceptionally rich soils like those occurring in lowland flood plains; **G** generally distributed throughout region; **E** often found at forest edges; **W** occurring on soils with high water content; **M** occurring on moist soils; **A** occurring on acidic soils; **O** associated with open, high light areas (not necessarily frequently disturbed, though); **O(F)** open areas but generally within forested habitat, e.g. canopy gaps and trails; **S** occurring only under substantial shade; **I** isolated distribution; **R** known to occur on rocky surfaces; **Es** known especially from estuaries; **B** associated specifically with beaches; **S** occurring on sandy soils; **X** occurring on exceptionally dry sites; **Or** organically rich sites, especially with much woody debris; **Ca** calcium rich sites. Taken from ecological annotation given in Pojar and Mackinnon (1994).

For beach substrate and beach characteristics two 10 × 10 m plots were surveyed for each site to assess beach vegetation cover (dune grass, sedges and silverweed (*Potentilla ansifera*), substrate type (bedrock, boulder, cobble, gravel, sand, mud), organic debris (mostly conifer logs) as either small organic debris (SOD) greater than 20 cm or large organic debris (LOD) less than 20 cm diameter, intertidal attached algae (primarily rockweed, *Fucus gardneri*) and presence of oysters (*Crassostrea gigas*). Plots were set up at the wrack line adjacent to the vegetation plots and extended into the intertidal. Additional measurements collected during the seining included surface salinity, temperature, and geographical location. Salinity was measured with a refractometer. We also recorded the presence of eelgrass (*Zostera marina*) and kelp (*Macrocystis* spp.).

### Data analysis

Accumulation curves were plotted to show how the number of fish species recorded at each beach changed as sampling progressed. Because species richness (the number of species recorded) is strongly influenced by sample size (the number of individuals recorded), rarefaction was also used to investigate whether there were differences in species richness between OG and D beaches. Rarefaction curves show the expected species richness for samples of different sizes if these samples were drawn at random from the pooled samples for all beaches. Individual-based rarefaction curves were calculated using EstimateS (Colwell, 1997) and sample-based rarefaction curves were calculated using EcoSim7 (Gotelli and Entsminger, 2003). *t*-Tests were used to determine significant differences between accumulation and rarefaction curves between OG and D beaches. Sorenson's similarity index was used to determine the magnitude of compositional differences in fish species identifies between OG and D beaches (Colwell, 1997).

### Ordination

Canonical correspondence analysis (CCA) was used to ordinate taxa and sample units along environmental gradients and extract the underlying factors (or axes) that distinguished the taxa or sample units (ter Braak, 1986; Palmer, 1993). In CCA, 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). CCA results in a set of eigenvalues between 0 and 1 and the sum of the eigenvalues corresponds to the total explained variance. Results of ordination analyses are shown on an ordination diagram or biplot, 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). Monte Carlo permutation tests were used to determine whether the explained variance was significantly different from the null hypothesis of no relationship between matrices. We only present results for axes that were significantly different from random at  $p < 0.05$ . For all CCA, biplots were rescaled to show the maximum spread between taxa to facilitate interpretation. Ordination analyses were performed using PC-Ord for Windows v. 4.01 (McCune and Mefford, 1999). Three CCA were performed. The first related beach characteristics to the composition of supralittoral vegetation. This CCA was performed to determine whether beach characteristics determined the composition of supralittoral vegetation and thus whether relationships between fish community composition and supralittoral vegetation were spurious resulting from secondary relationships to beach site characteristics. The second CCA related fish community composition to beach characteristics including vegetation on the beach (e.g. dune grass; as opposed to vegetation in the supralittoral), substrate, and physico-chemical conditions. The third CCA related fish community composition to supralittoral vegetation.

Owing to the unevenness of our sampling protocol we could not use raw population abundances in the CCA. Instead, for each site we calculated mean density per seine and then estimated population abundances for each beach by multiplying density by the total census area. This calculation provides an estimate of the population numbers collected from each beach based on the uneven sampling protocol. We

performed CCA using both the entire fish data set (i.e. all 31 species) as well as only species that were present at more than six of the 26 sites where fish were collected (i.e. 11 species). This cut-off point was chosen to focus on patterns for fish species that made greater than 1% of the total abundance.

For the beach characteristics CCA, the environmental variables included cover of dune grass, silverweed, sedges, cover of bedrock, boulder, cobble, gravel, sand, mud, SOD (small organic debris), LOD (large organic debris), algae (primarily *Fucus gardneri*), presence of oysters, temperature, salinity, geographical location and presence of a creek or stream. For the supralittoral vegetation CCA, all species that were present at < four sites were removed from the analysis, reducing the environmental matrix for supralittoral vegetation to 25 plant species or taxa (Table 3). The three species of *Vaccinium* (oval-leaved blueberry, evergreen huckleberry, and red huckleberry), identified in the plots were analysed according to genus rather than for each species separately to reduce the number of variables in the environmental matrix. All environmental variables were standardized before analysis. Abundance was calculated as above and was standardized before analysis.

## RESULTS

Fish were caught at 26 of the 27 beaches. None were caught at site 27 and data from this location were excluded from all subsequent analyses. 1832 individuals of 31 species were recorded from all beaches (Table 2). The most abundant species across all beaches were tidepool sculpin (*Oligocottus maculosus* Girard) (46.5%), Pacific staghorn sculpin (*Leptocottus armatus* Girard) (16.4%), and chum salmon (*Oncorhynchus keta* Walbaum) (10.0%) (Table 2). The species that were caught at the greatest number of beaches were tidepool sculpin (*O. maculosus*), chum salmon (*O. keta*), and butter sole (*Isopsetta isolepis* Lockington) (Table 2). On average, 5.8 species ( $\pm 2.53$  SD) were found at each beach, ranging from one species to 10 species (Table 1).

Mean species richness was not significantly different between OG and D beaches ( $t = 0.07$ ,  $p = 0.94$ ). However, species accumulation curves based on the cumulative number of individuals, showed that cumulatively more species were caught at OG beaches ( $t = 4.49$ ,  $p = 0.01$ ; Figure 2(b)). Similarly, rarefaction curves showed that a higher cumulative number of species were caught at OG beaches ( $t = 3.64$ ,  $p = 0.02$ ; Figure 2(b)). Across all beaches, observed cumulative species richness was within the 95% confidence intervals predicted by rarefaction up until the last few samples. This difference between observed and predicted species richness suggests that observed species richness was lower than predicted by chance with increasing sampling effort (Figure 2(a)).

Sorenson's similarity index showed that fish assemblages across all beaches had on average 39% of species in common, ranging from no species in common to 89% species similarity ( $\pm 18\%$  SD). There was no difference in similarity between OG and D beaches ( $F_{1, 154} = 0.344$ ,  $p = 0.558$ ). Species composition differed between OG and D beaches although the differences in species composition between OG and D beaches were dominated by rare species (Table 2). Species caught only at OG beaches included: kelp clingfish (*Rimicola muscarum* Meek and Pierson), striped kelpfish (*Gibbonsia metzi* Hubbs), kelp greenling (*Hexagrammos decagrammus* Pallas), northern spearnose poacher (*Agonopsis vulsa* Jordan and Gilbert), lingcod (*Ophiodon elongatus* Girard), red Irish lord (*Hemilepidotus hemilepidotus* Tilesius) and Pacific sandfish (*Trichodon trichodon* Tilesius) (Table 2). Four species were only caught at D beaches: whitespotted greenling (*Hexagrammos stelleri* Tilesius), tube-snout (*Aulorhynchus flavidus* Gill), spotted snailfish (*Liparis callyodon* Pallas) and the crevice kelpfish (*Gibbonsia montereyensis* Hubbs).

### Relations between beach characteristics and supralittoral vegetation

CAA for beach characteristics–supralittoral vegetation showed that beach characteristics explained 38.8% of the total variance in the community composition of supralittoral vegetation (Figure 3). However,

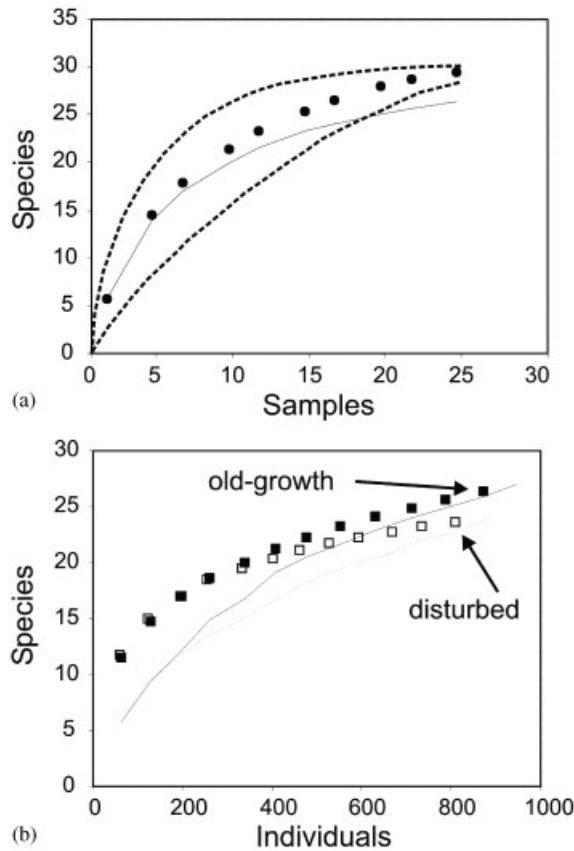


Figure 2. Rarefaction and species accumulation curves for fish species richness. Lines represent accumulation curves and circles or squares represent rarefaction curves. (a) sample-based accumulation and rarefaction curves showing 95% confidence intervals. (b) individual-based accumulation and rarefaction curves calculated separately for OG beaches (black squares) and D beaches (open squares).

Monte Carlo permutation tests for both eigenvalues and species–environment correlations showed that none of the beach characteristics axes were significantly related to the composition of supralittoral vegetation ( $p > 0.05$ ).

### Beach characteristics

CCA of beach characteristics–fish associations showed that beach characteristics explained 51.2% of the total variance in the patterns of fish taxa (Figure 4(A)). Monte Carlo simulation showed that the eigenvalue of the first axis was significant ( $p = 0.02$ ) and the species–environment correlation was significant for axis 1 ( $p = 0.02$ ) and axis 2 ( $p = 0.01$ ). The first three eigenvalues were 0.774, 0.549 and 0.419. Axis 1 explained 22.8% of the variability and represented the overall trend in association between fish and herbaceous plants on the beach as well as between shallow muddy sites with creeks versus higher salinity sites. Axis 1 was positively correlated with cover of sedges ( $r^2 = 0.84$ ), silverweed ( $r^2 = 0.85$ ), water temperature ( $r^2 = 0.82$ ), mud ( $r^2 = 0.685$ ), sites with a creek ( $r^2 = 0.607$ ) and negatively correlated with salinity ( $r^2 = 0.457$ ) and percentage gravel ( $r^2 = 0.399$ ). Axis 2 explained 16.1% of the variability and represented a gradient of marine to estuarine sites. Axis 2 positively correlated with salinity ( $r^2 = 0.655$ ) and negatively correlated with the presence of creeks ( $r^2 = 0.582$ ), mud ( $r^2 = 0.482$ ), eelgrass ( $r^2 = 0.394$ ) and dune grass ( $r^2 = 0.381$ ).

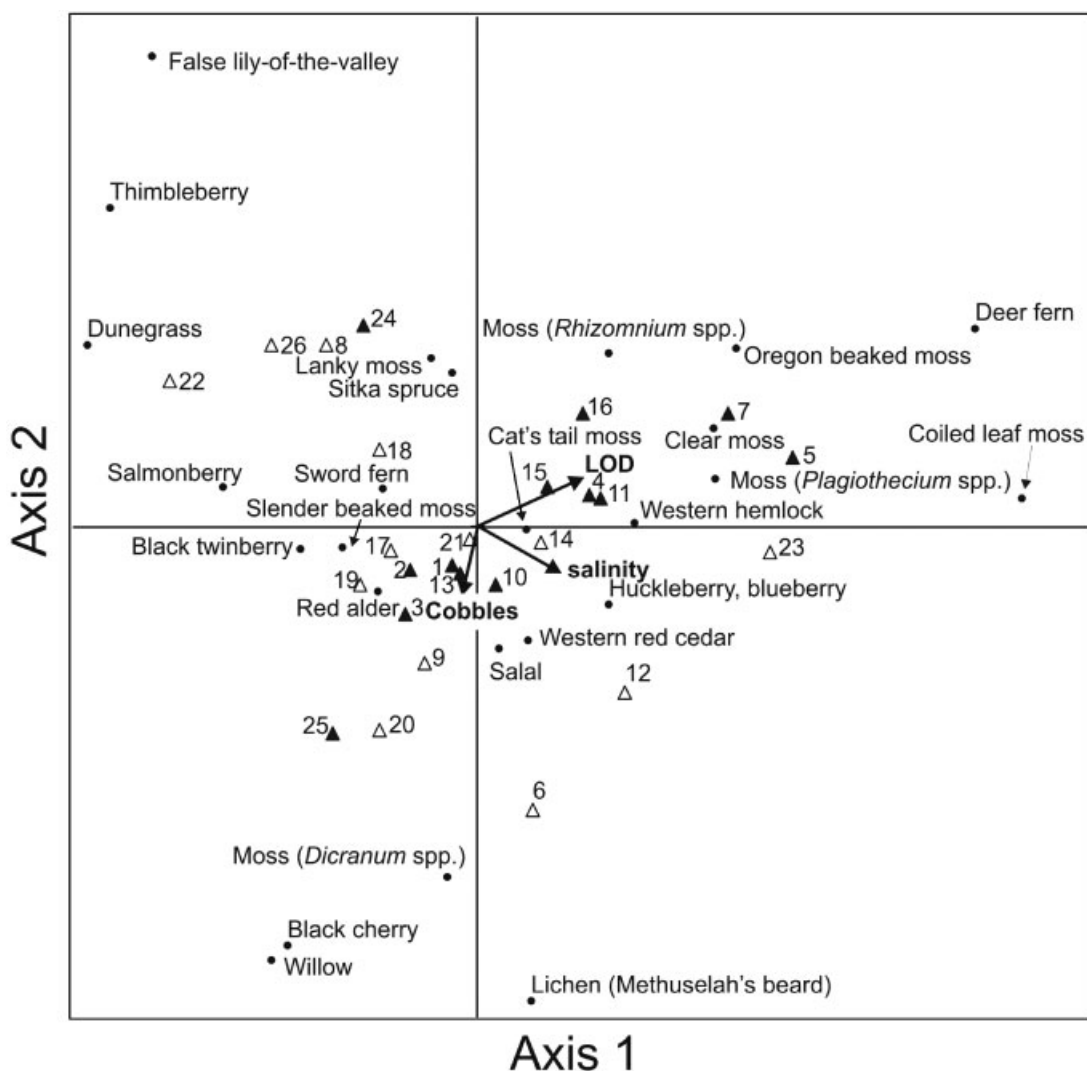


Figure 3. CAA of beach characteristics–vegetation associations showing beach characteristics vectors for axis 1 and 2. Arrows denote variables from the beach characteristics matrix. Site codes are given in Table 1 and species names for vegetation are given in Table 3. OG beaches denoted by black triangles and D beaches by open triangles.

Six of the 11 most abundant species (> 1% of total catch) showed strong loadings (i.e.  $r > 0.4$ ) onto the significant beach characteristics axes (Table 4). The CCA for species that occurred greater than 1% of the total catch was very similar in terms of site scores and vectors to the ordination for all 31 species (Figure 4(B)). The primary difference was in the explained variance of the CCA which increased to 60.5% and in the increase in the significance of the eigenvalue for the second axis ( $p = 0.01$ ).

### Supralittoral vegetation

In total our survey yielded 97 categories of vegetation with 87 definitive species (partial list, Table 3). CCA of supralittoral vegetation–fish associations showed that supralittoral vegetation explained 56% of the total

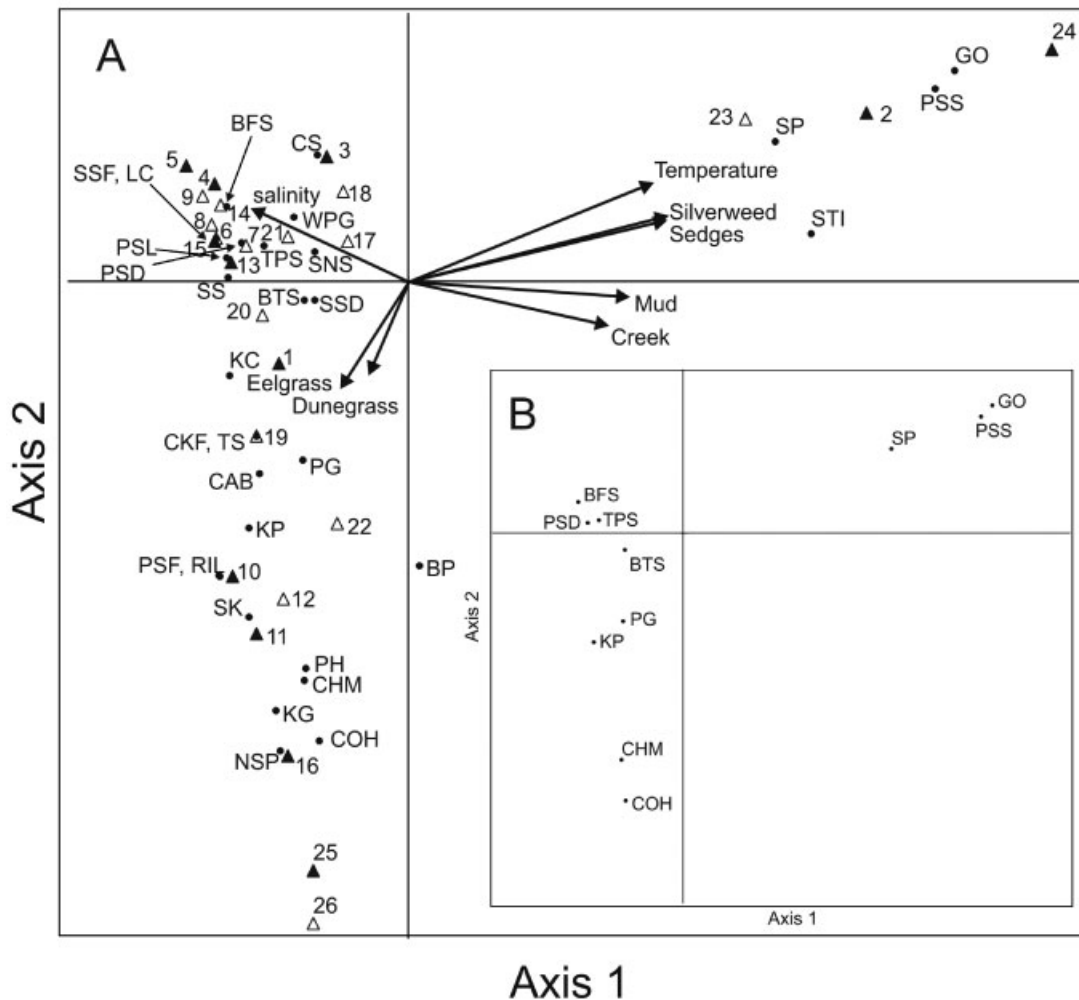


Figure 4. CCA of beach characteristics–fish assemblages showing species and site loadings on axis 1 and 2. (A) All 31 fish included in the ordination. (B) Ordination with only the 11 most abundant fish. Arrows denote variables from the environmental matrix with strong axis loadings. Site codes are given in Table 1. Species codes are given in Table 2. Dots represent fish species positions on the ordination diagram. Ellipses show distinct fish assemblages. OG beaches denoted by black triangles and D beaches by open triangles.

variance in the patterns of fish taxa (Figures 5 and 6). Monte Carlo permutation tests for both eigenvalues and species–environment correlations showed that all three axes significantly related the composition of supralittoral vegetation to fish assemblage composition ( $p = 0.01$ ). The first three eigenvalues were 0.777, 0.584 and 0.548 indicating that all three axes were relatively important in explaining the variability in fish community composition. Axis 1 explained 22.9% of the variability and represented the overall trend in association between fish and dominant canopy cover. This axis was positively correlated with cover of sitka spruce (*Picea sitchensis*) ( $r^2 = 0.810$ ), false lily-of-the-valley (*Maianthemum dilatatum*) ( $r^2 = 0.608$ ) and salmonberry (*Rubus spectabilis*) ( $r^2 = 0.342$ ), and negatively correlated with western red cedar (*Thuja plicata*) ( $r^2 = 0.417$ ), western hemlock (*Tsuga heterophylla*) ( $r^2 = 0.432$ ), blueberry and huckleberry ( $r^2 = 0.398$ ) and cat's tail moss (*Isoetes myosuroides*) ( $r^2 = 0.314$ ). Axis 2 explained 17.2% of the variability and probably represented a gradient of logging disturbance as it was positively associated with cat's tail

Table 4. Axis loadings for the 11 most common species for the beach characteristics – and supralittoral vegetation–fish associations CCA. Only axis loadings greater than  $r = 0.4$  are shown. Values in brackets denote the axis that species loaded on. X denotes an association less than  $r = 0.4$

Common name	Beach characteristics	Supralittoral vegetation
Tidepool sculpin	0.426 (2)	X
Pacific staghorn sculpin	−0.702 (1)	0.836 (1)
Chum salmon	−0.848 (2)	−0.857 (3)
Butter sole	X	X
Buffalo sculpin	X	X
Arrow goby	−0.654 (1)	0.775 (1)
Penpoint gunnel	X	−0.414 (2)
Coho salmon	−0.587 (2)	−0.585 (3)
Shiner perch	−0.512 (1)	0.682 (1)
Pacific sanddab	X	X
Kelp perch	X	−0.953 (2)

moss ( $r^2 = 0.18$ ) and negatively correlated with salal (*Gaultheria shallon*) ( $r^2 = 0.271$ ). Axis 3 explained 16.1% of the variability and also probably represented a disturbance gradient (Figure 6) as it was positively correlated with blueberry and huckleberry ( $r^2 = 0.502$ ) and salal ( $r^2 = 0.331$ ), which are found across a wide range of habitats in the region (Table 3). Axis 3 was negatively correlated with the moss *Rhizomnium* spp. ( $r^2 = 0.486$ ) and lanky moss (*Rhytidodelphus loreus*) ( $r^2 = 0.593$ ), which are usually associated with organically rich, shady sites (Table 3). Axis 3 was also negatively correlated with salmonberry ( $r^2 = 0.55$ ), which can either be associated with disturbed sites or sites with high water content (Table 3). Of the 11 species of fish with abundances greater than 1% of the total catch, seven of them had strong (i.e.  $r > 0.4$ ) associations with at least one of the vegetation axes (Table 4). The CCA for species that occurred greater than 1% of the total catch was very similar in terms of site scores and vectors to the ordination for all 31 species (data not shown). The primary difference was in the explained variance of the CCA which increased to 67.3%.

## DISCUSSION

### Supralittoral vegetation–fish associations

There was no difference in mean species richness of nearshore fish between OG and D sites. In contrast, cumulative fish species richness was enhanced on the OG beaches relative to D sites because the former were characterized by rare species that accounted for greater than 1% of the total abundance. This suggests that beaches with old-growth supralittoral vegetation may provide different ecosystem functions compared to beaches with more disturbed supralittoral vegetation. The number of generalist or abundant species was similar at OG and D sites, suggesting that both ecosystem types were providing functions for this suite of species.

It is generally thought that terrestrial habitat specialists may be more sensitive to disturbance than generalists (Brook *et al.*, 2003) but there are few data on this topic for marine species. In our study, some general observations on fish species caught only at OG beaches support the idea that they may be specialists. Specifically, kelp clingfish, kelp greenling, striped kelpfish and northern spearnose poacher are associated with submerged kelp or eelgrass; Pacific sandfish and juvenile lingcod (Cass *et al.* (1990), but they did not study intertidal areas) are associated with sand or muddy bottoms; and calico sculpin and red Irish lord are associated primarily with rocky shores (Eschmeyer and Herald, 1983). In contrast, the more

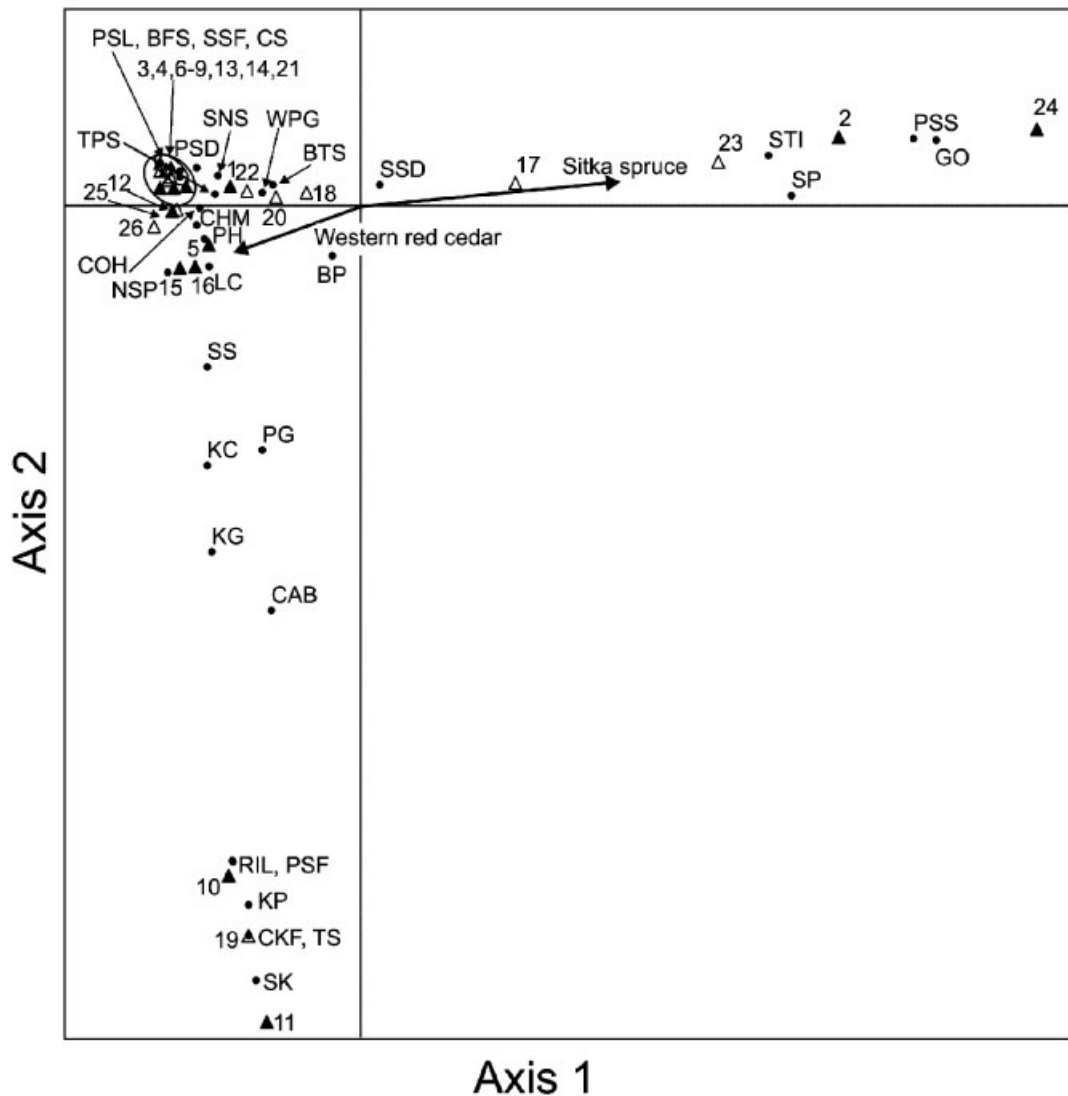


Figure 5. CCA supralittoral vegetation–fish assemblages showing species and site loadings on axis 1 and 2. See Figure 4 for codes and symbol descriptions. OG beaches denoted by black triangles and D beaches by open triangles.

abundant fish species can be considered habitat generalists. For example, tidepool sculpin and Pacific staghorn sculpin were the two most abundant species found in this study. Sculpins are generally thought to be habitat generalists and are often the dominant fishes found in both tidepool and nearshore subtidal habitats (e.g. Green, 1971; Szabo, 2002). Likewise, juvenile chum, which use a range of nearshore habitats during their early marine residency (Levings and Tompkins, 1985), were found at 16 of 27 sites and were the third most abundant species. Three apparently specialist species (e.g. tube-snout, spotted snailfish and crevice kelpfish) were only caught at disrupted sites, suggesting these habitats may have been providing ecosystem functions they were adapted to.

Previous studies in streams have shown that riparian zones with banks with little or no vegetation sometimes support fewer fish species compared to riparian zones with well-vegetated banks (Gronns *et al.*,

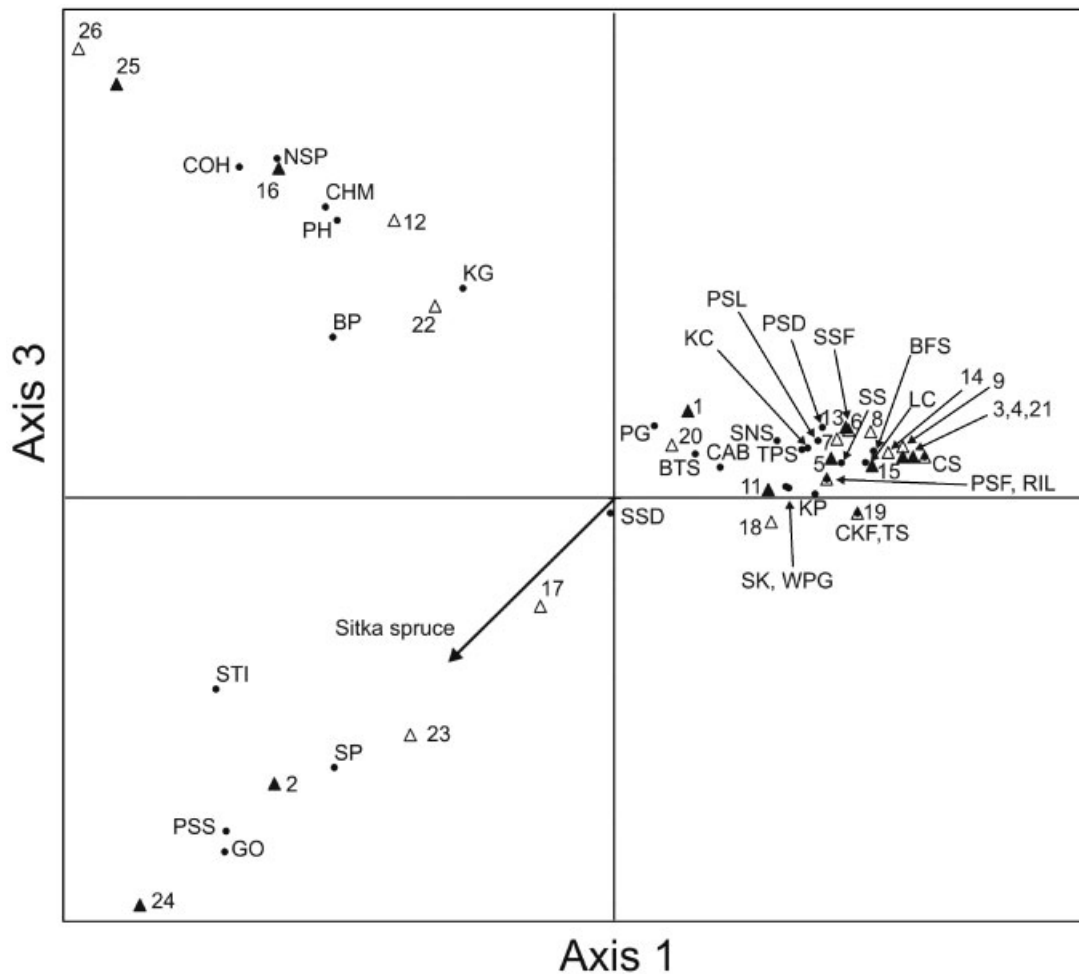


Figure 6. CCA supralittoral vegetation–fish assemblages showing species and site loadings on axis 1 and 3. See Figure 4 for codes and symbol descriptions.

1998); however, this is not always the case (Growth *et al.*, 2003). While there are no available studies for comparison with similar marine systems, it is likely that nearshore fish could be affected by vegetation in adjacent terrestrial habitats. Two lines of evidence support this hypothesis based on the effects of removal of supralittoral vegetation on food supply to nearshore fishes.

First, several authors working on intertidal fish in our study area (Mgaya, 1992; Szabo, 2002) and elsewhere (Grossman, 1982, 1986) have argued that intertidal fish species compete intra- and inter-specifically for food, not space as some previous authors have suggested (Cross, 1981; Yoshiyama *et al.*, 1986), and that productivity is the most important factor in survivorship of juvenile intertidal fish. If intertidal fish compete strongly for resources, when resources are high more species should be able to coexist. The diet of nearshore fish, and in particular their juvenile stages, is frequently dominated by small crustaceans. Because the secondary productivity of small crustaceans can be regulated by primary productivity and fluctuations in detrital food webs (Laur and Ebeling, 1983), reductions in litter drop or other organic material have the potential to disrupt energy flow from the terrestrial to the marine environment. For example, population densities of amphipods at a sandy beach near Bamfield responded

quickly to local fluctuations in productivity and provision of algae in wrack (Richards, 1984), suggesting that these taxa are resource-limited.

Second, terrestrially derived carbon may represent an important carbon contribution in nearshore habitats, increasing the productivity of intertidal and terrestrial arthropods. Old-growth forests in the Pacific Northwest are among the most productive forests globally and terrestrial debris (dissolved and particulate carbon) is an important external source of carbon in oceanic margins (Valiela, 1984). While the increases in secondary productivity from litter drop to marine beaches are probably localized (cf. mangroves, Jennerjahn and Ittekkot (2002)) and carbon flux is greater for phytoplankton and algae than for supralittoral vegetation, old-growth forests have the potential to contribute substantial amounts of litter as many coniferous species drop needles through much of the year (Richardson *et al.*, 2004). In contrast, most deciduous trees only drop litter in autumn and winter (Petersen and Cummins, 1974). One notable exception is red alder, which also drops litter through much of the year and has very high rates of decomposition (Richardson *et al.*, 2004). However, conifer litter also decomposes more slowly than deciduous litter (Richardson *et al.*, 2004), which may result in a more constant source of detritus. Furthermore, a variety of high intertidal invertebrates such as isopods, decapod crabs and gastropod molluscs, have been shown to feed directly on, or influence the decomposition of, vascular plant material, including leaves of the live oak (e.g. *Quercus virginiana*, Zimmer *et al.*, 2004).

In marine coastal habitats there is no previous literature available on whether supralittoral vegetation might be important for nearshore fish. However, our results showed that gradients in coverage of sitka spruce, western red cedar and western hemlock were dominant CCA vectors for nearshore fish, suggesting that fish community composition was associated with dominant canopy cover. Old-growth forests are also characterized by diverse moss and lichen communities (Lesica *et al.*, 1991) whereas secondary supralittoral vegetation often has a dense undergrowth of salal, a low shrub whose leaf litter may not be as widely distributed compared to conifer needles and deciduous tree leaves. We found that juvenile chum and coho were strongly associated with gradients in cover of moss. Most of the beaches with disturbed supralittoral vegetation were in a stage of secondary growth that corresponded to a more intermediate stage of development (i.e. canopy dominated by both western red cedar and western hemlock). For example, two of the three sites with the highest abundance of juvenile chum salmon had been subjected to some logging disturbances; however, none of these sites had red alder as the dominant canopy species, and they were all characterized by high moss cover.

A number of the fish species caught in the nearshore areas of Barkley Sound are known to feed on both marine and terrestrial arthropods. In particular, the diets of both juvenile chum in estuaries and nearshore habitats (Healey, 1982; Romanuk and Levings, 2005) and coho salmon at the Carnation Creek estuary on Trevor Channel (Tschaplinski, 1987) have been shown to contain a mixture of aquatic and terrestrial prey species. Our analysis suggested that the dominant tree canopy species association for juvenile chum and coho salmon was western red cedar.

### **Beach characteristics–fish associations**

It is not possible to ascertain in a descriptive study whether the associations between fish assemblages and supralittoral vegetation were direct or caused by an underlying correlation with another habitat variable. However, it is notable that the beach characteristics and supralittoral vegetation CCA explained similar proportions of variation in the fish assemblage structure. While this could have been due to correlations between beach characteristics and supralittoral vegetation, our analysis failed to detect any such significant associations. This suggests that the significant supralittoral vegetation–fish associations were not the result of spurious correlations between beach characteristics and supralittoral vegetation. This result also suggests, at least for the beach characteristics that we quantified, that backshore vegetation composition is not correlated with beach characteristics such as structural composition (e.g. cobble, sand).

In the beach characteristics CCA, some fish assemblages were strongly associated with intertidal plants (e.g. silverweed, sedges) and temperature. In particular, arrow gobies, shiner perch and Pacific staghorn sculpins, all showed strong positive associations with beach vegetation as well as with increased water temperature. This was probably due to associations between beach vegetation and insects in the more estuarine sites and suggests that beaches with high cover of both supralittoral vegetation as well as intertidal vegetation may provide the highest quality nearshore habitat for some nearshore fish. Previous studies in freshwater tidal habitats have found higher densities of fallout insects in vegetated versus non-vegetated habitats (Whitehouse *et al.*, 1993; Tanner *et al.*, 2002).

Very few studies have examined ecological patterns or processes in marine-supralittoral ecotones in temperate coastal regions; however, recent studies have suggested that processes operating in the supralittoral may have a significant effect on communities on both sides of the ecotone (Romanuk and Levings, 2003). Ecological research to improve management strategies has been recommended in the Pacific Northwest where timber harvesting, urbanization and foreshore developments can damage or remove supralittoral vegetation (Lemieux *et al.*, 2004). Knowledge of how processes operating in the supralittoral might affect nearshore communities will be important in developing management strategies for buffer widths and other guidelines. To date, almost all existing guidelines have been derived from freshwater studies. For example in the United States the Forest Ecosystem Management Assessment Team developed generalized curves of percentage cumulative effectiveness for particular riparian effects and functions as a function of buffer width (Farrell, 2004). This type of guideline is sorely needed to manage supralittoral vegetation using strategies that protect key fish habitat (King County, 2004). Applied research such as experiments to test effects of vegetation removal on fish community structure is clearly needed, as well as further work to describe structure and energy flow to from supralittoral to the nearshore habitats.

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## REFERENCES

- Attrill MJ, Bilton DT, Rowden AA, Rundle SD, Thomas RM. 1999. The impact of encroachment and bankside development on the habitat complexity and supralittoral invertebrate communities of the Thames Estuary foreshore. *Aquatic Conservation: Marine and Freshwater Ecosystems* **9**: 237–247.
- Bérubé P, Lévesque F. 1998. Effects of forestry clear-cutting on numbers and sizes of brook trout, *Salvelinus fontinalis* (Mitchill), in lakes of the Mastigouche Wildlife Reserve, Quebec, Canada. *Fisheries Management and Ecology* **5**: 123–137.
- Brook BW, Sodhi NS, Ng PKL. 2003. Catastrophic extinctions follow deforestation in Singapore. *Nature* **424**: 420–423.
- Cailliet GM, Love MS, Ebeling AW. 1986. *Fishes: A Field and Laboratory Manual on their Structure, Identification, and Natural History*. Wadsworth: Belmont, CA; 132–134.
- Cass AJ, Beamish RJ, McFarlane GA. 1990. Lingcod (*Ophiodon elongatus*). *Canadian Special Publication Fisheries and Aquatic Sciences* **109**: 40.
- Colwell RK. 1997–2000. EstimateS: Statistical estimation of species richness and shared species from samples. <http://viceroy.eeb.uconn.edu/EstimateS>.
- Cross JN. 1981. Structure of a rocky intertidal fish assemblage. PhD thesis. University of Washington: Seattle, WA.
- Culp JM. 1988. The effects of streambank clearcutting on the benthic invertebrates of Carnation Creek, British Columbia. In *Proceedings of the Workshop: Applying 15 years of the Carnation Creek Results, January 13–15, 1987, Nanaimo, B.C.*, Chamberlin TW (ed.). Pacific Biological Station: Nanaimo, BC; 87–92.
- Eschmeyer WN, Herald ES. 1983. *A Field Guide to Pacific Coast Fishes of North America*. Houghton Mifflin: Boston, MA.

- Everest FH, Beschta RL, Scrivener JC, Koski KV, Sedell JR, Cederholm CJ. 1987. Fine sediment and salmonid production: a paradox. In *Streamside Management: Forestry and Fishery Interactions*, Salo EO, Cundy TW (eds). Contrib. No. 57. Institute of Forest Resources, University of Washington, Seattle, WA; 98–142.
- Farrell M. 2004. Current marine riparian setback standards used by DFO in B.C., In *Proceedings of the DFO/PSAT Sponsored Marine Riparian Experts Workshop, Tsawwassen, B.C., February 17–18, 2004*, Lemieux JP, Brennan JS, Farrell M, Levings CD, Myers D (eds). Canadian Technical Report Fisheries and Aquatic Sciences no. 2680; 58–62.
- Gotelli NJ, Entsminger GL. 2003. EcoSim: Null models software for ecology. Version 7. Acquired Intelligence Inc. and Kesity-Bear. Burlington, VT 05465. <http://homepages.together.net/~gentsmin/ecosim.htm>.
- Green JM. 1971. High tide movements and homing behavior of the tidepool sculpin *Oligocottus maculosus*. *Journal of the Fisheries Research Board of Canada* **28**: 383–389.
- Grossman GD. 1982. Dynamics and organization of a rocky intertidal fish assemblage: the persistence and resilience of taxocene structure. *American Naturalist* **119**: 611–637.
- Grossman GD. 1986. Resource partitioning in a rocky intertidal fish assemblage. *Journal of Zoology, London (B)* **1**: 317–355.
- Growns IO, Pollard DA, Gehrke PC. 1998. Changes in river fish assemblages associated with vegetated and degraded banks, upstream of and within nutrient-enriched zones. *Fisheries Management and Ecology* **5**: 55–69.
- Growns I, Gehrke PC, Astles KL, Pollard DA. 2003. A comparison of fish assemblages associated with different riparian vegetation types in the Hawkesbury–Nepean River system. *Fisheries Management and Ecology* **10**: 209–220.
- Hartman GF, Scrivener JC, Miles MJ. 1996. Impacts of logging in Carnation Creek, a high-energy coastal stream in British Columbia, and their implication for restoring fish habitat. *Canadian Journal of Fisheries and Aquatic Sciences* **53**: 237–251.
- Healey MC. 1982. Juvenile Pacific salmon in estuaries: the life support system. In *Estuarine Comparisons*, Kennedy VS (ed.). Academic Press: New York; 315–341.
- Jennerjahn TC, Ittekkot V. 2002. Relevance of mangroves for the production and deposition of organic matter along tropical continental margins. *Naturwissenschaften* **89**: 23–30.
- King County. 2004. Juvenile salmonid composition, timing, distribution, and diet in marine nearshore waters of Central Puget Sound in 2001–2002. <http://dnr.metrokc.gov/wlr/watersheds/puget/nearshore/juvenile-salmonid-report.htm>.
- Lamb A, Edgell P. 1986. *Coastal fishes of the Pacific Northwest*. Harbour Publishing: British Columbia, Canada.
- Laur DR, Ebeling AW. 1983. Predator–prey relationships in surfperches. *Environmental Biology of Fishes* **8**: 217–229.
- Leuieux JP, Brennan JS, Farrell M, Levings CD, Myers D (eds). 2004. *Proceedings of the DFO/PSAT Sponsored Marine Riparian Experts Workshop, Tsawwassen, British Columbia, February 17–18, 2004*. Canadian Manuscript Report of Fisheries Aquatic Sciences 2680.
- Lesica P, McCune B, Cooper S, Hong WS. 1991. Differences in lichen and bryophyte communities between old-growth and managed second-growth forests. *Canadian Journal of Botany* **69**: 1745–1755.
- Levings CD, Tompkins A. 1985. Habitats of Fraser River chum—an overview. In *Proceedings 1985 Northeast Pacific Pink and Chum Salmon Workshop*, Shepherd BG (Rapporteur). Dept. of Fish. and Oceans: 1090 West Pender Street, Vancouver, BC; 162–167.
- MacKinnon A, Trofymow JA. 1998. Structure, Processes, and Diversity in Successional Forests of Coastal British Columbia. In *Proceedings of a Workshop on Structure, Process, and Diversity in Successional Forests of Coastal British Columbia, February 17–19, 1998, Victoria, British Columbia*, Trofymow JA, MacKinnon A (eds). *Northwest Science*, **72** (special issue no. 2): 1–3.
- McCune B, Mefford MJ. 1999. PC-ORD: Multivariate analysis of ecological data (version 4). MjM Software Design, Gleneden Beach, Oregon.
- Mgaya YD. 1992. Density and production of *Clinocottus globiceps* and *Oligocottus maculosus* (Cottidae) in tidepools at Helby Island, British Columbia. *Marine Ecology Progress Series* **85**: 219–225.
- Palmer MW. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. *Ecology* **74**: 2215–2230.
- Petersen RC, Cummins KW. 1974. Leaf processing in a woodland stream. *Freshwater Biology* **4**: 343–368.
- Peterson M, Comyns B, Hendon J, Bond P, Duff G. 2000. Habitat use by the early life-history stages of fishes and crustaceans along a changing estuarine landscape: differences between natural and altered shoreline sites. *Wetlands Ecology and Management* **8**: 209–219.
- Pojar J, MacKinnon A. 1994. *Plants of the Pacific Northwest Coast*. Lone Pine: Vancouver, BC.
- Richards LJ. 1984. Field studies of foraging behavior of an intertidal beetle. *Ecological Entomology* **9**: 189–194.
- Richardson JS, Shaughnessy CR, Harrison PG. 2004. Litter breakdown and invertebrate association with three types of leaves in a temperate rainforest stream. *Archiv für Hydrobiologie* **159**: 309–325.
- Romanuk TN, Levings CD. 2003. Associations between arthropods and supralittoral ecotone: dependence of aquatic and terrestrial taxa on riparian vegetation. *Environmental Entomology* **32**: 1343–1353.

- Romanuk TN, Levings CD. 2005. Stable isotope analysis of trophic position and terrestrial versus marine carbon sources for juvenile Pacific salmonids in nearshore marine habitats. *Fisheries Management and Ecology* **12**: 113–121.
- St Onge I, Magnan P. 2000. Impact of logging and natural fires on fish communities of Laurentian Shield lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **57**: 165–174.
- Scrivener JC, Brownlee MJ. 1989. Effects of forest harvesting on spawning gravel and incubation survival of chum (*Oncorhynchus keta*) and coho salmon (*O. kisutch*) in Carnation Creek, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* **46**: 681–696.
- Sobocinski KL. 2003. The impact of shoreline armoring on supratidal beach fauna of central Puget Sound. Master of Science thesis, University of Washington, Seattle, WA.
- Szabo AR. 2002. Experimental tests of intercohort competition for food and cover in the tidepool sculpin (*Oligocottus maculosus* Girard). *Canadian Journal of Zoology* **80**: 137–144.
- Tanner CD, Cordell JR, Rubey J, Tear LM. 2002. Restoration of freshwater intertidal habitat functions at Spencer Island, Everett, Washington. *Restoration Ecology* **10**: 564–576.
- Taylor FJR, Haigh R. 1996. Spatial and temporal distributions of microplankton during the summers of 1992–1993 in Barkley Sound, British Columbia, with emphasis on harmful species. *Canadian Journal of Fisheries and Aquatic Sciences* **53**: 2310–2322.
- ter Braak CJF. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* **67**: 1167–1179.
- Tschaplinski PJ. 1987. Comparative ecology of stream-dwelling and estuarine juvenile coho salmon (*Oncorhynchus kisutch*) in Carnation Creek, Vancouver Island, British Columbia. PhD thesis, University of Victoria: Victoria, BC.
- Valiela I. 1984. *Marine Ecological Processes*. Springer-Verlag: New York.
- Whitehouse TR, Levings CD, MacDonald JS. 1993. Chironomid (Diptera) insects from natural and transplanted estuarine marshes in British Columbia. In *Proceedings of the 1993 Canadian Coastal Conference May 4–7, 1993, Vancouver, British Columbia*. Coastal Zone Engineering Program of the National Research Council: Ottawa; 499–524.
- Yoshiyama RM, Sassaman C, Lea RN. 1986. Rocky intertidal fish communities of California: temporal and spatial variation. *Environmental Biology of Fishes* **17**: 23–40.
- Zimmer M, Pennings SC, Buck TL, Carefoot TH. 2004. Salt marsh litter and detritivores: a closer look at redundancy. *Estuaries* **27**: 573–769.