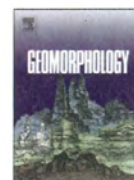




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Holocene soil-geomorphic surfaces influence the role of salmon-derived nutrients in the coastal temperate rainforest of Southeast Alaska

David V. D'Amore^{a,*}, Nicholas S. Bonzey^b, Jacob Berkowitz^c, Janine Rüegg^d, Scott Bridgman^e^a Forest Service, U.S. Department of Agriculture, Pacific Northwest Research Station, Juneau, AK 99801, USA^b Virginia Polytechnic Institute and State University, Department of Forest Resources and Environmental Conservation, Blacksburg, VA, 24601 USA^c Environmental Research and Development Center, U.S. Army Corps of Engineers, Vicksburg, MS, USA^d University of Notre Dame, Department of Biological Sciences, Notre Dame, IN 46556, USA^e University of Oregon, Center for Ecology and Evolutionary Biology and Environmental Studies Program, Eugene, OR 05405, USA

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ABSTRACT

The influence of salmon-derived nutrients (SDN) is widely accepted as a potential factor in the maintenance of aquatic and terrestrial productivity in North American Coastal rainforests. Holocene alluvial landforms are intimately connected with the return of anadromous salmon, but the influence of the soils that occupy these landforms and support this important terrestrial–aquatic ecological coupling have not been examined in SDN studies. We used paleo-ecologic information, soil resource inventories and measurements of soil morphology to construct a soil-geomorphic model for alluvial landforms along salmon spawning channels on Prince of Wales Island, Southeast Alaska, USA. Post-glacial sea-level rise, crustal uplift and subsidence combined with Holocene sediment deposition have formed alluvial terraces and floodplains along rivers on Prince of Wales Island. These alluvial landforms have soils that are mapped as Entisols (Tonowek soil series) and Spodosols (Tuxekan soil series). We propose a soil-geomorphic model where the Spodosols located on terraces are estimated to derive from sediments deposited after the stabilization of landscape approximately 8 kybp to 6 kybp. The stability of these soils is reflected through mature soil development with organic matter accumulation and podzolization. Our model identifies Entisols on floodplains developed from alluvial deposition in the latter Holocene that have soil morphologic features consistent with recent deposition and limited soil development. We used this soil-geomorphic model to test the hypothesis that the terrestrial end-member value commonly used to quantify nitrogen (N) loading on soils through stable isotope analysis differs by soil type and found that the two soil types had significantly different N isotopic ($\delta^{15}\text{N}$) values more consistent with soil development than SDN loading. The use of a soil-geomorphic model provides a means to stratify alluvial landforms and constrain the natural variability encountered in studies of riparian nutrient cycles associated with the feedbacks between SDN and terrestrial ecosystems to improve estimates of the fate of SDN in soils and vegetation.

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1. Introduction

The influence of salmon-derived nutrients (SDN) is widely accepted as a potential factor in the maintenance of aquatic and terrestrial productivity in nutrient-limited forests of the North American Pacific Coastal rainforests (Ben-David et al., 1998; Bilby et al., 1998; Willson et al., 1998; Wipfli et al., 1998; Naiman et al., 2002). The biogeomorphological interaction among alluvial landforms, riparian vegetation and stream channels provides spawning

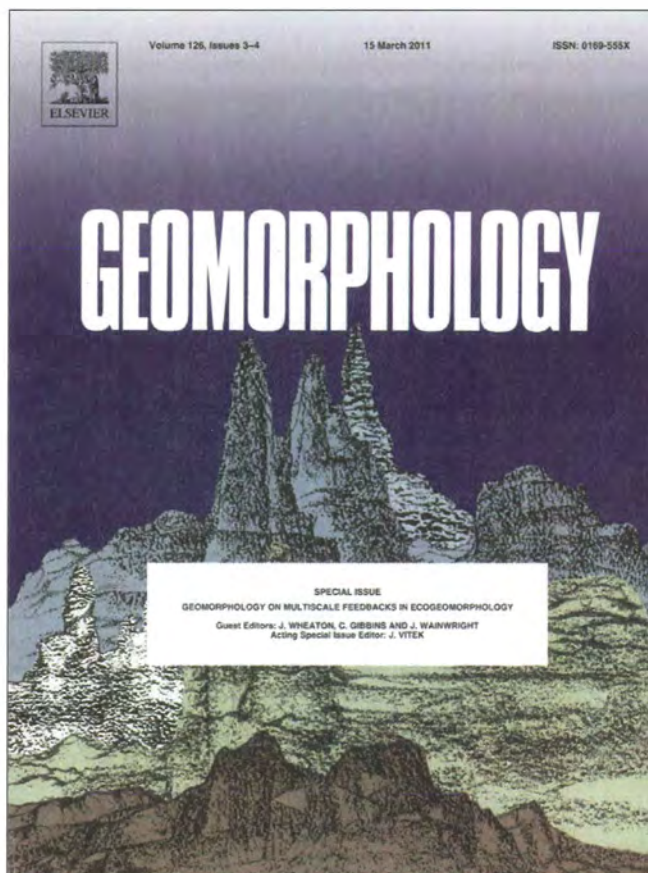
habitat for salmon, and the nutrients from salmon promote the growth and maintenance of trees that perpetuate stream channel attributes conducive to the successful rearing of young salmon (Naiman et al., 2002). Understanding the specific mechanisms related to the biogeomorphological feedback associated with SDN is complicated by soil heterogeneity and the potential for vastly different cycling and storage of nutrients in the terrestrial system. Post-glacial chronosequences of soils and ecosystems have provided a model for soil-geomorphic development in glacially derived soils in post-glacial valleys of the North Pacific Coastal rainforests (Crocker and Major, 1955; Ugolini, 1968; Chapin et al., 1994), but we have not found any studies that provide a model for Holocene soil geomorphology and alluvial landforms connected with the return of anadromous salmon.

The mass spawning of chum (*Oncorhynchus keta*) and pink salmon (*O. gorbuscha*) occurs in low-gradient river systems that can be

* Corresponding author. Tel.: +1 907 586 7955; fax: +1 907 586 7848.

E-mail addresses: ddamore@fs.fed.us (D.V. D'Amore), nbonzey@vt.edu (N.S. Bonzey), jacob.f.berkowitz@usace.army.mil (J. Berkowitz), jruegg@nd.edu (J. Rüegg), bridgman@uoregon.edu (S. Bridgman).

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identified by geomorphic, soil, and vegetation attributes (Naiman et al., 2005). The SDN from these mass spawning salmon is transferred from the aquatic to the terrestrial ecosystem via multiple pathways including bears (Quinn et al., 2009) and other piscivores (Merz and Moyle, 2006), as well as floods (Ben-David et al., 1998; Fellman et al., 2008). The SDN can be directly applied to the soil through the deposition of carcasses, or indirectly through feces and urine of piscivorous animals. The consumption of carcasses by insects and subsequent re-distribution through multiple trophic pathways can also spread SDN in the terrestrial ecosystem (Reimchen et al., 2003). Therefore, SDN are distributed on soils in irregular patterns with varying amounts of material and nutrient concentration. The most consistent patterns associated with SDN are concentration plumes that are greatest at the stream edge near the spawning salmon and decrease in a perpendicular direction away from the stream (Ben-David et al., 1998).

Quantifying the impact of the SDN nutrient subsidy on plant growth uses several approaches that either directly or indirectly measure some aspect of soils. The 'Riparian zone' is often invoked as a homogeneous soil-geomorphic surface associated with alluvial landforms. However, homogeneity in terrestrial plant communities often masks soil variability on alluvial landforms (Merrill and Benning, 2006). Reference reaches above barriers to salmon migration (e.g., waterfalls) are also used as 'control' reaches, thus allowing a comparison of stream reaches with and without the influence of SDN. However, natural barriers to salmon migration, such as waterfalls, reflect distinct geomorphic changes that influence soil and vegetation communities that can confound SDN studies. In zones above barriers, the classic floodplain is often limited by the physiography of steep valley sides and constrained channels (Montgomery, 1997). Greater growth rates of trees have been noted in salmon reaches compared to non-salmon-bearing reaches above a barrier (Helfield and Naiman, 2001). However, these growth rates may have been related to differences in vegetation communities rather than the presence of SDN (Kirchhoff, 2003) and subsequent speculation noted that vegetation differences and growth rates above and below the salmon barrier may have been due to geomorphologic and soil factors, not necessarily the presence of salmon (Naiman et al., 2002). Higher N concentrations were found in a non-salmon-bearing reach compared to a salmon-bearing reach, contrary to the hypothesized influence of SDN (Bartz and Naiman, 2005). However, the potential influence of specific soil types was not investigated that may have impacted the N variability in the riparian zone.

Transects that extend perpendicular to the stream channel capture the diffusion of SDN distribution, but can cross various soil types (Ben-David et al., 1998; Bilby et al., 2003; Bartz and Naiman, 2005). Nitrogen concentrations varied with distance from the stream across four landform categories in one SDN study, but there was no identification of soil type or evaluation of nutrient concentrations related to soil factors (Bilby et al., 2003). Soil map units identified in regional soil surveys have not provided the resolution for partitioning specific soil types for field studies (see Bartz and Naiman, 2005 use of Reiger et al., 1979). The only study we have encountered with a specific soil type identified and isolated as an experimental unit highlighted how soil heterogeneity in texture, pH, and cation exchange capacity may have influenced SDN cycling (Drake et al., 2005).

The $\delta^{15}\text{N}$ natural abundance method is commonly used in SDN research as a tracer to determine the source and sinks of N in riparian zones (Drake et al., 2006; Gende et al., 2007). However, variable soil-geomorphic features associated with the cycling of nitrogen can confound the use of tracers such as $\delta^{15}\text{N}$. Nitrogen has two stable (i.e. non-radioactive) isotopes, ^{14}N and ^{15}N , with the vast majority being ^{14}N . Because of the relatively small difference in the proportion of $^{15}\text{N}/^{14}\text{N}$ relative to a standard, N isotopes can be effective tracers in ecological studies (Rundel et al., 1989; Lajtha and Michener, 1994). The $\delta^{15}\text{N}$ source is assumed to be provided by the salmon, while the

sinks for $\delta^{15}\text{N}$ are assumed to be vegetation, microbial communities, and soil surfaces. A mixing model can determine the amount of N provided by SDN through a mathematical expression with known values of the $\delta^{15}\text{N}$ for the marine and terrestrial end-members (adapted from Kline et al., 1990, 1993):

$$\% \text{SDN} = \frac{\text{SAM} - \text{TEM}}{\text{MEM} - \text{TEM}} \times 100\%$$

Where the %SDN is the percentage of salmon-derived N in the sample of vegetation or soil, SAM is the $\delta^{15}\text{N}$ of a representative sample of vegetation or soil, TEM is the $\delta^{15}\text{N}$ of the terrestrial end-member (assumed to be a sample that has obtained 100% of its N from terrestrial sources), and MEM is the $\delta^{15}\text{N}$ of the marine end-member (assumed to be a sample that has obtained 100% of its N from marine sources). The N loading rate provided by SDN is calculated from measured or estimated values for the end-members.

Natural fractionation through nitrification, denitrification and NH_4^+ volatilization influence the isotopic fractionation of $\delta^{15}\text{N}$ and cause problems in determining augmentation of N by salmon in soils and vegetation with the $\delta^{15}\text{N}$ method (Högberg, 1997). Högberg (1997) notes that $\delta^{15}\text{N}$ is not a "conservative, unchanging tracer" and the texture, moisture conditions and abundant carbon substrate in riparian soils lead to intense, sustained nitrogen cycling (Bedard-Haughn et al., 2003; Pinay et al., 2003; Luxhøj et al., 2004) that causes a pronounced fractionation of N (Naiman et al., 2005). Trees may discriminate against the heavier $\delta^{15}\text{N}$ isotope when forest growth is not N-limited, such as riparian zones (Nadelhofer and Fry, 1994) leaving an enriched $\delta^{15}\text{N}$ signature. Therefore, both vegetation and soil processes lead to fractionation and concentration of $\delta^{15}\text{N}$, which diminishes the isotopic ratio and can render the $\delta^{15}\text{N}$ natural abundance method ineffective in determining N loading through SDN.

Recent attempts have been made to link the ecological aspects of ecosystems, such as stream systems, to geomorphology (Renschler et al., 2007). The study of eco-geomorphology describes the integration of physical, chemical, and biological components of ecosystems (Thoms and Parsons, 2002). The related field of soil geomorphology has emerged as an important study of the linkage between soils and landforms (Birkeland, 1999; Wysocki et al., 2000) and the soil-geomorphic approach provides a means to build models that can address the confounding influence of soil variability in studies of SDN. Soil geomorphology combines landform arrangement and differentiation with the process of soil formation and provides a means to constrain the variability in ecological function related to soils (Daniels and Hammer, 1992; Gerrard, 1992). While soil state-factor theory (Jenny, 1941; Amundson and Jenny, 1997) can be applied to alluvial soils in riparian zones in order to understand ecological function (Van Cleve et al., 1991), the soil geomorphological template can link the biological feedback mechanisms to the paleo-environmental template of Holocene landscape evolution. The eco-geomorphological feedback between SDN and terrestrial ecosystems can be improved through an understanding of alluvial soil geomorphology.

This study was designed to address the need for integrating alluvial soil geomorphology with the deposition of SDN on terrestrial ecosystems in North Pacific coastal rainforests. Our goal was to establish a model for soil geomorphology of Holocene alluvial landforms in salmon spawning streams of Southeast Alaska. We established relationships between soil attributes and landforms through replicated descriptions and characterization of several soils in Holocene alluvial deposits along salmon spawning streams on Prince of Wales Island, Southeast Alaska, USA. We then used these alluvial soil types to test the hypothesis that the concentration of isotopic nitrogen ($\delta^{15}\text{N}$), commonly used as a tracer of SDN, was related to alluvial soil type.

2. Methods

2.1. Site selection and description

The study was conducted on Prince of Wales Island, part of the extended island archipelago located in the North American coastal temperate rainforest (Fig. 1). The climate is cool and moist with annual precipitation of 2500–3000 mm yr⁻¹ and average temperature of 6° C (Western Regional Climate Center, 2008). Seven watersheds were chosen for sampling from a pool of potential watersheds identified on Prince of Wales Island in Southeast Alaska (Fig. 1; Tiegs et al., 2008; Table 1). The U.S. Geological Survey Hydrologic Unit Code (HUC 5/6/7) layer was used to determine total watershed area.

Landform sample locations were identified by delineating the overlap of floodplain channel types (Tongass National Forest Channel Type User Guide, FP 4,5; USDA Forest Service, 1992) with the alluvial soil map unit that is closely associated with low-gradient floodplain channel types along salmon spawning reaches (Tonowek/Tuxekan soil association; USDA Forest Service, 1996). The Tonowek/Tuxekan soil association is the primary alluvial soil map unit on Prince of Wales Island and covers 12,269 ha (USDA Forest Service, Tongass National Forest Database). This soil association is found on nearly level, alluvial floodplain landforms that occupy valley floors in large third and fourth order streams (USDA Forest Service, 1996). The soil association has two soil types including an Entisol on a lower topographic surface in the alluvial floodplain and a closely associated Spodosol located on

alluvial terraces. There are also inclusions of soils similar to the Tonowek and Tuxekan that are somewhat poorly drained. The soil association is primarily associated with alluvial landforms near streams, but is also found on footslope landforms in alluvial fans. The potential area of alluvial landforms associated with anadromous salmon habitat was determined by the intersection of the Tonowek/Tuxekan soil complex with anadromous salmon streams defined by stream class (USDA Forest Service, Tongass National Forest anadromous stream GIS database).

The soil map unit is a soil association comprised of two soils, the Tonowek and Tuxekan soil series. The association designation does not provide delineation for each soil type, therefore, the individual soil taxa were identified in the field by shovel and auger surveys. One Tonowek soil was identified and described in six watersheds and an additional two pedons were identified and described in one watershed at different locations along the stream ($n=8$). Tuxekan soils were identified and described in four watersheds ($n=4$) (Table 2). We completed soil profile descriptions and sampled by horizon at each site. Soil particle size was determined by size separation (Kettler et al., 2001). Bulk density was determined by intact cores from soil profile faces in 233 cm³ rings. Field samples were taken in triplicate, weighed, dried and reported as dry weight per unit volume (g cm⁻³). Carbon and nitrogen values were determined on pulverized samples in a LECO CHN analyzer. Soil pedons were classified at each site using soil descriptions and laboratory data (Soil Survey Division Staff, 1999). Water table levels were measured with pressure transducers placed in duplicate 50 cm deep wells in each soil type at the Indian Creek site.

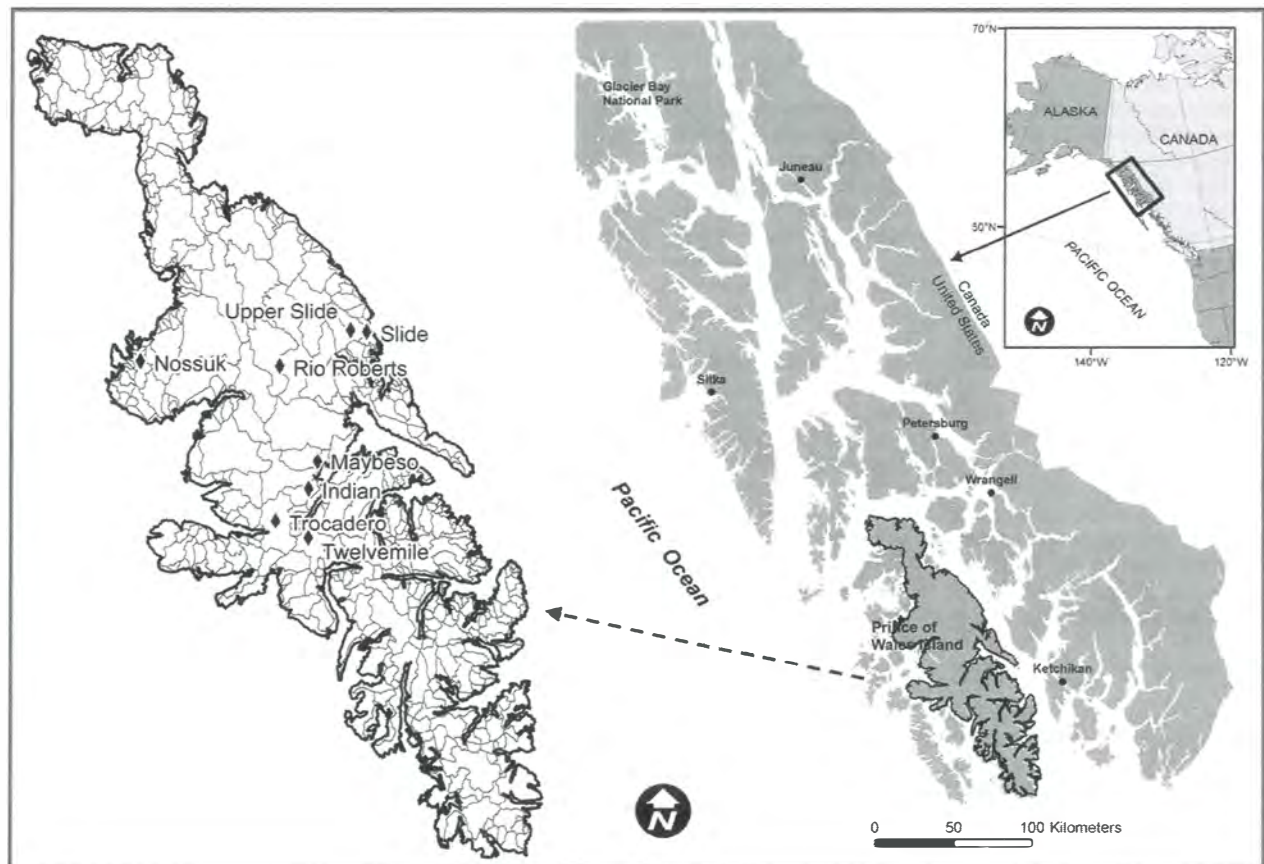


Fig. 1. The North American coastal temperate rainforest of southeast Alaska (inset) is dominated by large islands known collectively as the Alexander Archipelago. The largest island in this region is Prince of Wales Island, which is located on the outer coast of the Alexander Archipelago. Study locations on Prince of Wales Island are identified in the enlarged image of Prince of Wales Island.

Table 1

Site locations with type of soil sampled, watershed location and watershed and harvest area.

Site name	Soils examined	Watershed area (km ²)	Harvest area (%)	Latitude	Longitude
Nossuk	Tonowek	19.5	5.4	55°42'10.3"N	133°17'20.6"W
Indian	Tonowek/Tuxekan	25.9	9.3	55°26'18.3"N	132°42'58.5"W
Trocadero	Tonowek	44.8	11.2	55°22'34.0"N	132°50'40.7"W
Maybeso	Tonowek/Tuxekan	38.7	21.8	55°29'32.8"N	132°40'57.8"W
Slide	Tonowek	25.9	57.9	55°44'52.6"N	132°29'42.8"W
12-mile	Tonowek/Tuxekan	31.1	68.3	55°20'23.8"N	132°43'21.5"W
Rio Roberts	Tonowek/Tuxekan	31.1	0	55°41'08.5"N	132°48'15.8"W
Upper Slide	Tonowek	10.5	40.6	55°45'07.3"N	132°33'05.2"W

The study sites contained Sitka spruce (*Picea sitchensis* (Bong.) Carr.), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and red alder (*Alnus rubra* (Bong.)) as the major overstory tree species with understory dominated by blueberry (*Vaccinium* spp.). Pink salmon, chum salmon, and coho salmon (*O. kisutch*), were present in the study streams (Tiegs et al., 2008).

2.2. Paleo-landscape development

We used information from the Queen Charlotte islands, located south of Prince of Wales (Josenhans et al., 1997) and local observations in Southeast Alaska (Twenhofel, 1952; Swanston, 1969; Mobley, 1988) as well as recent observations from Prince of Wales Island (Jim Baichtal, Tongass National Forest, personal communication) as a guide for establishing the paleo-landscape evolution on Prince of Wales Island. The best estimate for former shorelines on Prince of Wales Island is at 12.5 m above present mean high tide (Swanston, 1969; Jim Baichtal, Tongass National Forest, personal communication). We used the 60 m digital elevation model of Prince of Wales Island to determine the potential location of the maximum sea-level associated with the Tonowek/Tuxekan soil map unit. This analysis provided a means to assess the extent of the soil map unit that overlies former marine terraces. We used this as a guideline for establishing an outline of potential paleo-shorelines that intersected with the Tonowek/Tuxekan soil map unit in the floodplains of major river systems on Prince of Wales Island.

2.3. ¹⁵Nitrogen measurement of soils

Soil samples were taken from each horizon in each pedon sampled in the study and analyzed for isotopes of nitrogen ($\delta^{15}\text{N}$). Nitrogen has two naturally occurring stable isotopes, ^{15}N to ^{14}N where the variation in the absolute abundance of ^{15}N to ^{14}N is small. Nitrogen isotopic composition is expressed in δ notation in units of parts per thousand (‰). The $\delta^{15}\text{N}$ values is defined as $\delta^{15}\text{N} (\text{‰}) = [R_{\text{sample}} - R_{\text{standard}}] \times 1000$, where R is $^{15}\text{N}/^{14}\text{N}$ for $\delta^{15}\text{N}$ and the standard is atmospheric N_2 . Samples for ^{15}N isotopes were analyzed at the University of California, Davis. A two-way ANOVA was used to analyze $\delta^{15}\text{N}$ concentration in which soil type and mean horizon sample depth were used as fixed effects (PROC GLM, SAS, V. 9.2). Three depth classes were assigned to the $\delta^{15}\text{N}$ values for each horizon from each pedon: shallow (mean depth of 7 cm), medium (mean depth of approximately 18 cm) and deep (mean depth of approximately 37 cm).

3. Results

3.1. Soils and landforms

The soils located and described on the low terrace and alluvial floodplain landform in the research watersheds had A–C horizon sequences typical of Entisols (Table 2). These soils were all classified as Typic Cryofluvents that formed in deep, well-drained deposits of

alluvium. The soils correspond closely to the description of the Entisol (Tonowek soil series) map unit component (Fig. 2), which has a modal soil pedon classified as a coarse-loamy over sandy or sandy-skeletal, mixed, nonacid Typic Cryofluvent (USDA NRCS, 2010, official Series description). There were slight variations in the soils described in this study including several organic horizons (Oi, Oe) described over A horizons and two cambic (Bw) horizons. The lower C horizons of the Entisols tend to be coarser in texture than those above with all textures coarser than silt loam (Table 2). The coarse deposits found in lower horizons of the floodplain soils correspond to modal pedon descriptions of very coarse, skeletal, and sandy-skeletal textures. There is an irregular carbon and nitrogen content with depth that is characteristic of episodic carbon accumulation on exposed soil surfaces and subsequent burial during flood events on the alluvial floodplain landforms.

The soils from the upper terraces at the research sites had reddish-brown Bs horizons with accumulations of organic matter, Fe, Al, and Si in ratios that met spodic horizon criteria and were all classified as Spodosols (Soil Survey Division Staff, 1999; Table 2). There were also evident E horizons below the organic horizons (Table 2). The C horizons of the Spodosols had similar textures to the B horizons indicating a more uniform textural distribution in the pedons than the floodplain soils. Carbon and nitrogen concentrations were generally higher in the Bhs and Bs horizons than the surface mineral or C horizons of the upper terrace soils (Table 2). The modal description of the Spodosol (Tuxekan soil series) component of the alluvial landform map unit (Fig. 2) consists of deep, well-drained soils formed on alluvial fans and terraces and is classified as a coarse-loamy over sandy or sandy-skeletal, mixed Typic Humicryod (USDA NRCS, 2010, official Series description). We noted the presence of a variant to the modal Spodosol (Tuxekan soil series) at the research sites. The modal description has deep, surface organic matter accumulation with a folistic epipedon with greater than 25 cm of unsaturated organic material over mineral soil. The variant had less organic material due to irregular forest floor organic matter accumulations and was most often found in close association with the Tonowek series.

The morphological properties of the soils were consistent with patterns in the physical measurements of individual horizons (Table 3). Mean bulk density variation in both soils is low with mean values slightly lower in the Tuxekan soils corresponding to higher organic matter content. The Tuxekan tends to finer particle size classes, while the Tonowek is very coarse. The variability in texture in the Bw and Bs horizons is high with standard errors greater than 10% in most cases (Table 3). The Tuxekan soils have lower sand contents and higher silt and clay content than the Tonowek soil horizons. Carbon and nitrogen concentrations tend to be higher in the Tuxekan soils compared to the Tonowek soils (Table 3).

3.2. Soil geomorphic reconstruction of the Tonowek/Tuxekan map unit

The arrangement of the alluvial terraces on the landscape conforms to the superposition of the Tuxekan surface as an initial alluvial

Table 2

Soil profile descriptions of Tonowek and Tuxekan soil profiles from Prince of Wales Island, Southeast Alaska.

Site	Horizon	Depth (cm)	Munsell color	Bulk density (g/cm ³)	Texture ^a	N (%)	C (%)	C/N
Tonowek Indian	A	0–13	7.5 YR 3/2	0.44	SiCL			
	C	13–25	7.5 YR 3/2	0.59	SL	0.40	6.24	15.70
	2C	25–54	10 YR 3/3	0.65	SL	0.18	3.07	16.97
	3C	54–69	10 YR 3/3	0.78	LS	0.07	1.34	17.93
	4C	69+	10 YR 3/3	nd ^b		0.12	2.26	18.81
Maybeso	A	0–16	7.5 YR 3/2	0.43	SL	0.08	1.58	19.99
	C	16–27	10 YR 4/4	0.58	LS	0.35	6.93	19.73
	C2	27–41	7.5 YR 3/4	0.39	SL	0.04	0.68	17.28
	C3	41+	7.5 YR 4/2	0.52	SL	0.11	2.04	18.96
Nossuk	A	0–7	7.5 YR 2.5/2	0.24	L	0.11	1.96	17.79
	Bw	7–19	7.5 YR 3/3	0.50	SL	0.52	10.41	20.06
	C	19–25	10 YR 3/2	nd	LS	0.12	1.96	16.93
	C2	25+	10 YR 3/2	nd	S	0.00	0.14	nd
Rio Roberts	A	0–7	10 YR 2/2	0.58	SiL	0.00	0.05	nd
	C	7–36	10 YR 3/4	0.40	L	0.66	11.11	16.73
	2C	36–69	10 YR 3/6	nd	S	0.19	2.90	15.28
	3C	69+	Nd	nd	S	0.00	0.00	nd
Slide	A	0–8	10 YR 3/2	0.57	SL	0.00	0.00	nd
	C1	8–32	7.5 YR 3/2	0.37	LS	0.24	3.71	15.80
	C2	32–61	7.5 YR 3/2	nd	S	0.06	1.11	17.95
	2C	61+	10 YR 3/3	nd	S	0.00	0.00	nd
Trocadero	Oa	0–2	7.5 YR 3/2	0.17		0.00	0.00	nd
	A	2–11	10 YR 3/3	0.28	SL	0.94	27.48	29.18
	Bw	11–27	7.5 YR 4/4	0.39	SL	0.30	7.23	24.04
	C	27–34	10 YR 4/4	nd	LS	0.15	3.27	21.22
12-mile	C2	34+	nd	nd	LS	0.05	1.23	23.56
	Oi	0–2	7.5 YR 2.5/2			0.04	0.72	19.07
	A	2–11	10 YR 3/2	0.70	L	0.53	7.79	14.61
	C	11–27	10 YR 3/3	0.42	SL	0.30	4.27	14.27
Upper slide	C2	27–55	10 YR 3/4	0.54	SL	0.18	2.24	12.63
	C3	55–82	10 YR 3/3	0.65	SL	0.28	3.44	12.30
	C4	82+	10 YR 4/1	0.61	SL	0.33	4.86	14.55
	A	0–7	7.5 YR 2.5/2	0.65	SL	0.30	4.64	15.40
	C	7–18	10 YR 3/2	0.73	SL	0.13	2.52	19.02
	C2	18–36	10 YR 3/3	0.85	S	0.00	0.52	nd
	C3	36–52	10 YR 3/4	0.74	SL	0.08	2.11	26.10
	C4	52–60	10 YR 3/3	0.56	L	0.28	6.01	21.10
	C5	60–69	10 YR 3/3	0.59	SiL	0.25	4.48	18.12
	C6	69–89	10 YR 4/2	0.93	SL	0.00	0.00	nd
	C7	89+	nd	nd		0.03	0.66	22.83
Tuxekan Indian	Oi	0–4	5 YR 2.5/2	0.11	S	1.75	50.82	29.02
	Oe	4–11	7.5 YR 2.5/2	0.08	S	1.90	49.92	26.33
	E	11–14	7.5 YR 5/2	nd	L	0.41	8.55	21.10
	Bs	14–19	5 YR 3/3	0.43	SL	0.10	2.63	26.46
	Bw	19–32	7.5 YR 4/6	0.46	SL	0.04	1.57	34.92
	C1	32–65	10 YR 4/3	nd	nd	nd	nd	nd
	C2	65+	nd	nd	nd	nd	nd	nd
	A	0–19	7.5 YR 3/3	0.36	SL	0.27	4.97	18.37
	E	19–22	7.5 YR 4/2	nd	L	0.12	1.97	15.89
	Bs	22–24	5 YR 3/3	nd	L	0.15	2.92	19.95
	Bw	24–37	7.5 YR 3/4	0.36	SL	0.17	3.70	22.39
	C	37+	7.5 YR 4/1		SL	0.15	2.93	19.18
	Oe	0–4	7.5 YR 2/2	0.11	O	1.44	44.51	30.91
	E	4–9	5 YR 5/2	nd	nd	nd	nd	nd
	Bs	9–18	5 YR 5/4	0.31	SiL	0.26	4.56	17.79
	Bw	18–24	5 YR 3/3	0.31	SiCL	0.22	3.63	16.27
12-mile	C1	24–32	7.5 YR 4/3	nd	nd	nd	nd	Nd
	C2	32–43	7.5 YR 4/4	0.37	SiCL	0.17	3.23	18.48
	C3	43+	nd	nd	nd	nd	nd	Nd
	Oa	0–9	7.5 YR 2.5/2	0.16	O	1.48	22.87	15.41
	E	9–12	7.5 YR 5/2	nd	nd	nd	nd	Nd
	Bhs	12–18	5 YR 4/6	0.38	SiL	0.28	5.19	18.68
	Bs	18–86	7.5 YR 4/4	0.38	SiL	0.16	2.79	17.08
	C1	86–116	5 GY 5/1	0.58	SiL	0.07	0.17	2.57
	C2	116+	5 GY 6/1	0.52	L	0.04	0.12	2.70

^a O = organic; S = Sand; LS = loamy sand; SL = sandy loam; SiL = silt loam; SiCL = silty clay loam.^b nd = no data.

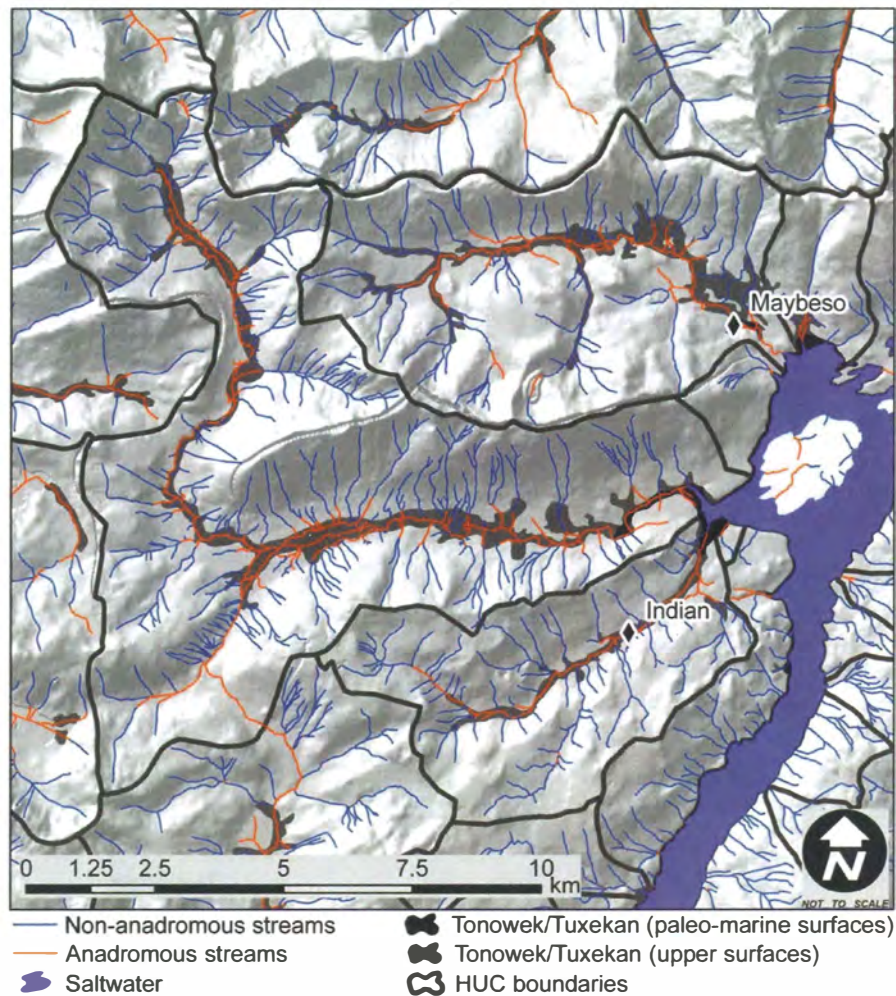


Fig. 2. Tonowek/Tuxekan map unit association showing the extent of the map unit along with the overlap of the map unit with potential paleo-marine surfaces in several watersheds on Eastern Prince of Wales Island, Alaska, including the Maybeso and Indian River sample sites (see Fig. 1). Anadromous and non-anadromous stream channels are identified to display the overlap of spawning channels and the soil map unit association.

Table 3

Soil horizon summaries for comparison of properties of Tonowek and Tuxekan soils on Prince of Wales Island. Values for means and associated standard errors are given for attributes by horizon designation. Data from all horizons identified as C material were also combined for comparison between the two soil types.

Tonowek							Tuxekan					
Horizon	Db ^a (g cm ⁻³)	Sand	Silt	Clay (%)	Carbon	Nitrogen	Db (g cm ⁻³)	Sand	Silt	Clay (%)	Carbon	Nitrogen
Oi							0.11	91.2	1.1	7.7	50.8	1.8
Oe	0.58	64.4	11.4	24.1	11.1	0.007	0.09 (0.02)	90.3	2.8	6.8	47.2	1.7
Oa	0.17	86.6	6.6	6.6	27.5	0.9	0.16				22.8	1.5
A	0.47 (0.07)	66.9 (3.9)	18.3 (3.5)	14.9 (1.4)	6.7 (0.01)	0.4 (0.04)	0.36	57.3	28.4	14.2	5.0	0.3
E							0.46 (0.03)	36.3 (4.9)	17.9 (1.9)	0.3 (0.1)	5.3 (3.3)	0.4 (0.3)
Bw	0.45 (0.06)	75.0 (0.3)	12.9 (0.2)	12.1 (0.5)	2.6 (0.7)	0.1 (0.02)	0.38 (0.05)	49.1 (18.5)	32.6 (13.3)	18.2 (5.2)	3.0 (0.7)	0.1 (0.05)
Bhs							0.38	22.4	53.8	23.8	5.2	0.3
Bs							0.38 (0.03)	34.0 (12.8)	46.9 (10.6)	19.0 (3.5)	3.2 (0.4)	0.2 (0.03)
C	0.55 (0.06)	71.3 (6.5)	18.1 (5.8)	10.6 (0.9)	2.1 (0.6)	0.1 (0.04)	0.59	59.7	28.2	12.0	2.9	0.2
C1	0.37	85.2	5.6	9.1	1.1	0.1	0.58	23.3	57.5	19.1	0.20	0.07
C2	0.59 (0.14)	84.5 (3.0)	7.2 (2.4)	8.3 (0.7)	0.9 (0.4)	0.04 (0.03)	0.44 (0.07)	25.1 (10.5)	48.6 (7.0)	26.3 (3.5)	1.7 (1.5)	0.1 (0.07)
C3	0.64 (0.06)	72.3 (4.2)	18.9 (6.2)	8.8 (2.2)	2.5 (0.4)	0.2 (0.06)						
C4	0.59 (0.02)	53.7 (5.1)	30.6 (4.8)	15.7 (0.4)	5.4 (0.6)	0.3 (0.02)						
2C	0.65	77.9	10.4	11.7	0.3 (0.5)	<0.01						
3C	0.78	80.1	8.6	10.5	1.1 (1.1)	0.05 (0.07)						
All C	0.61 (0.04)	72.7 (3.5)	16.8 (3.0)	10.4 (0.6)	1.7 (0.3)	0.1 (0.02)	0.49 (0.06)	33.3 (9.8)	45.7 (6.8)	20.9 (3.7)	1.6 (0.9)	0.1 (0.03)

^a Db = bulk density.

deposit in post-glacial valleys. The position and soil attributes of the Tonowek indicates that this surface was formed by alluvial deposition adjacent to the remnants of the Tuxekan surface that was eroded during stream downcutting into the channel. A representative soil profile reconstruction at Indian Creek supports this relationship where C horizon sediments are similar in color and texture and are likely to be derived from a series of early depositional phases (Fig. 3). The stream channel has incised to the point indicated by the measured water table depth that corresponds to the threshold between the recent floodplain deposit and the original surface.

3.3. Proximity of soil mapping unit to salmon spawning streams

The Tonowek/Tuxekan soil association comprises a mean area of 0.80% in watersheds on Prince of Wales Island, but 75% of the soil map unit complex is found along anadromous salmon-bearing reaches (Fig. 2). The proximity of the Tonowek and Tuxekan soils to salmon streams receiving large inputs of spawning salmon suggests that these are the primary soil surfaces that receive annual inputs of SDN through both overbank flooding and animal activity. Moderate to high availability of spawning habitat for pink and chum salmon was identified in 80% of anadromous stream reaches that occur in conjunction with the Tonowek/Tuxekan soil association. A component of the overlap between salmon streams and the soil map unit occurs at low elevation, distal stream reaches near estuaries which coincides with the estimate for buried marine sediments (Fig. 2)

3.4. $\delta^{15}\text{N}$ in Tonowek and Tuxekan soils

The $\delta^{15}\text{N}$ was significantly different between the Tonowek and Tuxekan soils ($p < 0.001$; Fig. 4). There was no interaction between soil

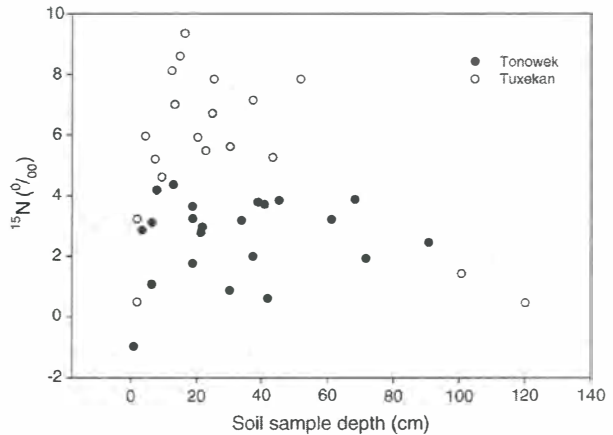


Fig. 4. Nitrogen isotope ($\delta^{15}\text{N}$) measurements by depth from Tonowek (filled circles) and Tuxekan (open circles) soils on Prince of Wales Island, Southeast Alaska. Sample depths were assigned at the midpoint of the measured horizon to provide a continuous depth profile on the x-axis.

type and depth ($p = 0.099$), but the $\delta^{15}\text{N}$ was significantly related to the depth of sampling within a soil profile ($p < 0.01$). The $\delta^{15}\text{N}$ values for the Tonowek soils range between approximately 1 and 4‰ with a mean of 2.2‰ (Fig. 4). The Tuxekan soils have values that are nearly all above 4‰ with a mean of 6.1‰ (Fig. 4). The within site variation in the Tuxekan soil is evident from the values less than 4‰ that occur at the soil surface or deeper than 100 cm.

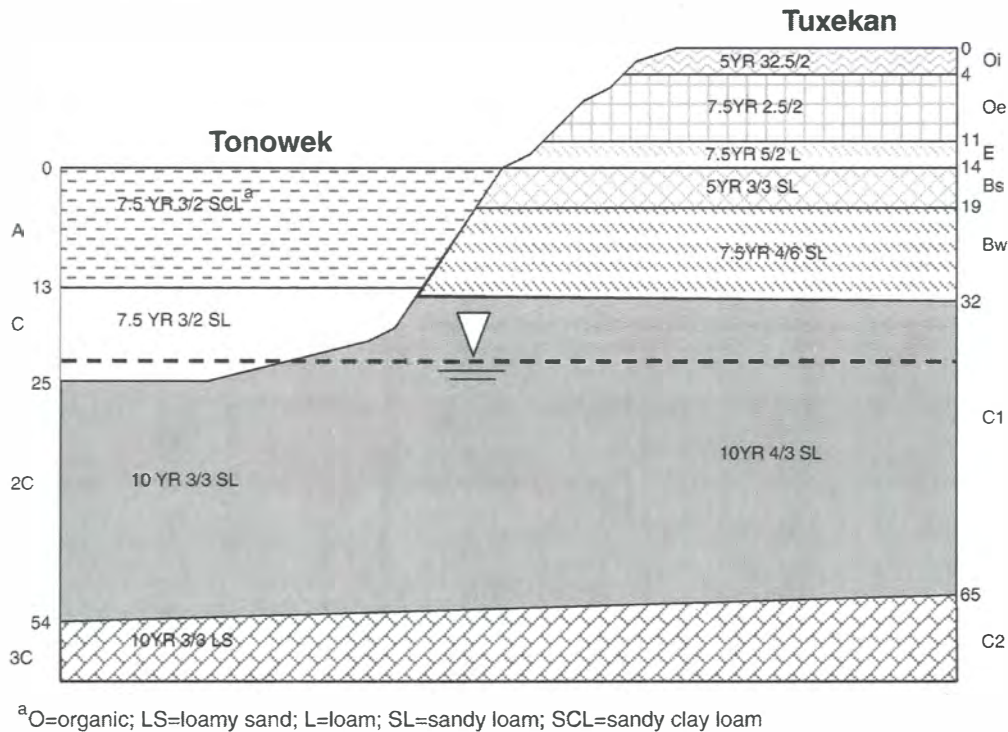


Fig. 3. Stratigraphic profile of the Tonowek and Tuxekan soil sequence from the Indian River site, Prince of Wales Island. The horizon designation and depth are shown on the vertical axes for each type of soil. The Tonowek soil (left) is incised into the older Tuxekan soil (right). The dashed line represents the measured depth of the water table across the alluvial terrace.

4. Discussion

4.1. A soil geomorphic model for Holocene alluvial landforms

A preliminary soil geomorphic model of alluvial landforms on Prince of Wales Island can be derived from paleo-landscape research from Southeast Alaska, British Columbia and Washington State. The landscape position and description of the Tonowek and Tuxekan soils is similar to the Holocene terraces in Washington State, which formed through a combination of tectonic and erosional forces during the Pleistocene and Holocene (Pazzaglia and Brandon, 2001; Benda et al., 1992). The Northern Pacific Coast, including the mainland fringe and island archipelago of Southeast Alaska and British Columbia, was subject to large continental ice-sheets that extended from the mainland to the outer coastal islands (Mann and Hamilton, 1995). The retreat of glacial ice in Southeast Alaska was rapid in the late-Pleistocene, and most of the Prince of Wales Island was ice-free as early as 12,000 ^{14}C years before present (ybp) (Mann and Hamilton, 1995; Carrerra et al., 2007). The deposition of alluvium along low-gradient stream channels driven by erosion and transport of sediment from high-gradient streams likely formed the primary alluvial terrace in the HUC 5, 6, and 7 class watersheds on Prince of Wales Island. The Tuxekan soils are composed of silt-loam material over gravelly sands and most likely formed in the deposits from early Holocene alluvial deposition.

We speculate that the Tuxekan soils located on the upper terrace stabilized approximately 6500 ^{14}C ybp due to evidence from paleo-shoreline reconstructions of post-glacial isostatic adjustment and equilibrium with sea level. Evidence from shell bed deposits in fjords and uplifted estuaries has calibrated the maximum post-glacial sea-level rise at approximately 8500 ^{14}C ybp on Prince of Wales Island (Swanston, 1969; Josenhans et al., 1997; Hastings, 2005). Sea-level rise equilibrated with uplift approximately 6500 ^{14}C ybp leading to stable river and estuarine systems on Prince of Wales Island (Josenhans et al., 1997; Hastings, 2005). The major rivers of Prince of Wales Island most likely began a period of downcutting through the primary alluvial surface (Tuxekan) and established a new alluvial surface (Tonowek) after 6500 ^{14}C ybp. Cooler conditions, snow accumulation and increased rainfall in the mid-Holocene (Heusser et al., 1985) promoted a period of less vigorous erosion and sedimentation that formed the low terraces and floodplains (Tonowek soils) during the mid to late Holocene. Therefore, we conclude that the Tuxekan surface has been stable for approximately 6000 years, while the Tonowek surface has been subject to channel altering forces such as flooding and debris jams from the mid- to late Holocene. These conclusions are supported by the degree of soil development in the Tuxekan soils compared to the Tonowek soils. The accumulation of organic material and podzolization in the Tuxekan soils would not have been possible unless the alluvial landform was stable. Further, the lack of evidence for soils on multiple terraces confirms that the landscape stabilized shortly after the Tuxekan terrace was abandoned.

4.2. Evidence and rationale for a paleo-estuary landform designation

There is evidence for a potential distinction in alluvial landforms located near estuaries that formed over glacio-marine deposits in paleo-estuaries from alluvial surfaces created further upstream. Coastal refugia were formed due to the upward crustal displacement on the eastern part of Prince of Wales due to crustal depression of the western portion of Prince of Wales similar to the process documented for the Queen Charlotte Islands (Josenhans et al., 1997). Potential coastal refugia have been identified on the outer margins of the Alexander archipelago, including Prince of Wales Island, through reconstruction of ice sheet routes (Josenhans et al., 1997; Kaufman and Manley, 2004; Carrerra et al., 2007). Paleo-estuaries were formed when isostatic rebound was outpaced by glacial meltwater after glacial retreat and lower portions of the landscape were inundated from approximately 9700–8500 ^{14}C ybp

(Mobley, 1988; Josenhans et al., 1997; Barrie and Conway, 2002). The paleo-shoreline associated with the maximum sea-level inundation has been calculated to be approximately 12.5 m above the present tide line for Prince of Wales Island (Jim Baichtal, Forest Service, Tongass National Forest, unpublished; Hastings, 2005). The presence of seawater in these estuaries probably deposited glacio-marine sediment similar to the Gastineau formation near Juneau, Alaska (Miller, 1973). Glacio-marine sediments form the base level for many stream reaches near estuaries in watersheds on Prince of Wales Island and other areas throughout Southeast Alaska. Isostatic rebound continued from 8500–6500 ^{14}C ybp leading to the emergence of the land surface and deposition of alluvial sediment along the lower reaches of the rivers over the glacio-marine sediments. The Tonowek/Tuxekan map unit overlaps the zones of paleo-estuaries that are now freshwater alluvial stream terraces in many locations (Fig. 2).

The presence of the paleo-estuarine geomorphic feature presents the potential for interaction with the ecological development of the post-glacial landscape. The Holocene was one of the most dramatic times of change over the course of salmonid evolution (Waples et al., 2009). Salmon are adapted to systems subject to rapid change, and the various modes of stream geomorphic development provided a variety of habitats for post-glacial stream colonization. The diversity in geomorphic development of streams and estuaries provided areas for niche differentiation in the post-glacial environment on Prince of Wales Island and paleo-estuaries may have played a role in the development of salmon populations that are believed to use estuaries as part of their life-history strategy (Koski, 2009). Competition may also have been a factor, given the presence of endemic chum salmon that may have persisted in coastal refugia during the Pleistocene (Kondzela et al., 1994). The use of soil geomorphic methods in this study provides an approach to sub-divide the landscape into discrete units in order to adequately test the feedback mechanisms that may have contributed to the diversity of salmon species that presently occupy watersheds of Prince of Wales Island.

4.3. Use of the soil geomorphologic template in watershed research

The proposed alluvial soil geomorphic model can be used to address the soil variability encountered in measurements of terrestrial nutrient cycling associated with the deposition of SDN. The natural deposition of salmon cannot be easily controlled in observations of SDN nutrient cycles. Spawning salmon are most abundant along floodplain channels where salmon biomass is distributed by flooding and bears, but bears also feed on salmon at specific locations that may be located several or tens of meters beyond the stream edge (Hilderbrand et al., 1999; Gende et al., 2002; Helfield and Naiman, 2006) creating a high degree of spatial variability in the deposition of salmon in the riparian zone (Wilkinson et al., 2005). Identification and delineation of soil types can be used in experiments and observational studies in riparian zones. Experiments can be designed to manipulate the application rate of SDN stratified across the Tonowek and Tuxekan soils to determine the fate of nutrients in both soils and vegetation. Surveys of riparian zones should include soil delineations that can control sources of natural variation in soil nutrient concentrations and cycling. The varying ages and modes of formation can also be used to potentially calculate loading rates with more specific studies of soil age. The stable Tuxekan surface has provided a template for the distribution and accumulation of SDN over the latter half of the Holocene, while the Tonowek soil has been subject to frequent disturbance.

4.4. Soil geomorphic feedbacks to SDN: A specific example using $\delta^{15}\text{N}$

Internal N cycling dynamics within an ecosystem can have equal or greater effects on the stable isotope signature of N in soils and plants. Moreover, the size and composition of various soil N pools changes over time periods of ecosystem succession (Cole and Rapp, 1981; Kaye

et al., 2003). Therefore, the soil type can have a distinct ecological feedback under conditions of SDN additions. Evidence for the varying feedback and fate of N is given in the results of the $\delta^{15}\text{N}$ analysis. The $\delta^{15}\text{N}$ values in the Tuxekan soil are contrary to the expected decrease in SDN signature from the edge of the stream as shown in previous SDN research (Ben-David et al., 1998; Hilderbrand et al., 1999; Bartz and Naiman, 2005). The increasing $\delta^{15}\text{N}$ values are, however, consistent with the differences associated with the factors of formation for each soil. Processes such as ammonia volatilization, denitrification, and leaching of nitrate lead to a loss of the lighter ^{14}N isotope from the ecosystem, leaving behind a soil N pool progressively enriched in ^{15}N (Högberg, 1997; Hobbie and Ouimet, 2009). The greater age and loamy texture of the Tuxekan soil is consistent with higher $\delta^{15}\text{N}$ values due to N processing and denitrification that promotes selective fractionation (Pinay et al., 1995) relative to the younger age and coarser texture of the Tonowek soil.

The potential influence of soil type can be illustrated with an example using the SDN mixing model to calculate the nitrogen contribution from SDN in soils (e.g. Gende et al., 2007). If we apply the SDN loading model to each soil and use a value of 2‰ for the terrestrial end-member (TEM), 12‰ for the marine end-member (MEM), and the mean measured values from the Tonowek (2.2‰) and Tuxekan (6.1‰) soils, the SDN loading equations are as follows:

$$\% \text{SDN} = \frac{\text{SAM} - \text{TEM}}{\text{MEM} - \text{TEM}} \times 100\%$$

$$\% \text{SDN}(\text{Tonowek}) = \frac{2.2 - 2.0}{12.0 - 2.0} \times 100\% = 2\% \text{SDN}$$

$$\% \text{SDN}(\text{Tuxekan}) = \frac{6.1 - 2.0}{12.0 - 2.0} \times 100\% = 41\% \text{SDN}$$

These results demonstrate the potential for a nearly 40% discrepancy in the calculation of N loading between the soil types. This problem can be addressed by adjusting the value of the terrestrial end-member through the use of reference and treatment sites (e.g. Morris et al., 2005). However, the fate of the SDN would still vary by specific soil type, and each soil would need its own appropriate reference site to control the site specific variation. This example pertains to the soil N concentrations, but vegetation is often used as the primary source of material for analysis of $\delta^{15}\text{N}$ loading. The $\delta^{15}\text{N}$ values for vegetation are influenced by the isotope ratio of the external nitrogen source (i.e. soils) and the physiological mechanisms within the plant (Evans, 2001). Therefore, different soil types that vary in the fractionation of N isotopes and cycling of SDN inputs can influence the $\delta^{15}\text{N}$ signature in plants. These findings highlight the potential for SDN experiments stratified by soil type to improve estimates of N loading using terrestrial and marine end-member mixing models.

5. Conclusions

Two distinct soils are located on Holocene alluvial landform on Prince of Wales Island, Alaska. The presence of these two soil types is related to Holocene landscape evolution combined with the time of soil development since deposition. These two soil types have significantly different nitrogen isotopic signatures on Prince of Wales Island that appears to be more related to soil development than the proximity to SDN. Soil geomorphology provides a means to stratify riparian landscapes to reduce variability in probabilistic sampling strategies for ecosystem function. The use of specific soil types as sample units can serve to constrain the natural variability found in alluvial soils. Therefore, the fate of SDN in the terrestrial ecosystem should incorporate soil geomorphology in the design and execution of future studies to reduce the uncertainty in the magnitude of the terrestrial response to the SDN subsidy.

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References

- Amundson, R., Jenny, H., 1997. On a state factor model of ecosystems. *Bioscience* 47, 536.
- Barrie, J.V., Conway, K., 2002. Rapid sea-level change and coastal evolution on the Pacific margin of Canada. *Sedimentary Geology* 150, 171–183.
- Bartz, K., Naiman, R.J., 2005. Effects of salmon-borne nutrients on riparian soils and vegetation in southwest Alaska. *Ecosystems* 8 (5), 529–545.
- Bedard-Haughn, A., van Groenigen, J., van Kessel, C., 2003. Tracing ^{15}N through landscapes: potential uses and precautions. *Journal of Hydrology* 272, 175–190.
- Benda, L., Beechie, T.J., Wissmar, R.C., Johnson, A., 1992. Morphology and evolution of salmonid habitats in a recently deglaciated river basin, Washington State, USA. *Canadian Journal of Fisheries and Aquatic Sciences* 49, 1246–1256.
- Ben-David, M., Hanley, T.A., Schell, D.M., 1998. Fertilization of terrestrial vegetation by spawning Pacific salmon: the role of flooding and predator activity. *Oikos* 83, 47–55.
- Bilby, R.E., Fransen, B., Bisson, P., Walter, J., 1998. Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*O. mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, USA. *Canadian Journal of Fisheries and Aquatic Sciences* 55, 1909–1918.
- Bilby, R.E., Beach, E., Fransen, B., Walter, J., Bisson, P., 2003. Transfer of nutrients from spawning salmon to riparian vegetation in western Washington. *Transactions of the American Fisheries Society* 132, 733–745.
- Birkeland, P.W., 1999. *Soils and Geomorphology*. Oxford University Press, New York.
- Carrera, P.E., Ager, T.A., Baichtal, J.F., 2007. Possible refugia in the Alexander Archipelago of southeastern Alaska during the late Wisconsin glaciation. *Canadian Journal of Earth Science* 44, 229–244.
- Chapin, F.S., Walker, L.R., Fastie, C.L., Sharman, L.C., 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecological Monographs* 64 (2), 149–175.
- Cole, D.W., Rapp, M., 1981. Elemental cycling in forest ecosystems. In: Reichle, D. (Ed.), *Dynamic Properties of Forest Ecosystems*. International Biological Program, 23. Cambridge University Press, Cambridge, pp. 341–409.
- Crocker, R.L., Major, J., 1955. Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. *Journal of Ecology* 43, 427–448.
- Daniels, R.B., Hammer, R.D., 1992. *Soil Geomorphology*. John Wiley and Sons, New York.
- Drake, D., Smith, J., Naiman, R.J., 2005. Salmon decay and nutrient contributions to riparian forest soils. *Northwest Science* 79 (1), 61–71.
- Drake, D., Naiman, R.J., Bechtold, J.S., 2006. Fate of nitrogen in riparian forest soils and trees: an ^{15}N tracer study simulating salmon decay. *Ecology* 87 (5), 1256–1266.
- Evans, R.D., 2001. Physiological mechanisms influencing plant nitrogen isotope composition. *Trends in Plant Science* 6, 121–.
- Fellman, J.B., Hood, E.H., Edwards, R.T., D'Amore, D.V., 2008. Return of Salmon-derived nutrients from the riparian zone to the stream during a storm in southeastern Alaska. *Ecosystems* 11, 537–544.
- Gende, S., Edwards, R.T., Willson, M., Wipfli, M., 2002. Pacific salmon in aquatic and terrestrial ecosystems. *Bioscience* 52 (10), 917–928.
- Gende, S.M., Miller, A.E., Hood, E., 2007. The effects of salmon carcasses on soil nitrogen pools in a riparian forest of southeastern Alaska. *Canadian Journal of Forest Research* 37 (7), 1194–1202.
- Gerrard, A., 1992. *Soil Geomorphology: An Integration of Pedology and Geomorphology*. Chapman Hall, London, 269 pp.
- Hastings, K., 2005. Long-term Persistence of Isolated Fish Populations in the Alexander Archipelago, University of Montana, Missoula, MT, PhD Dissertation.
- Helldorf, J., Naiman, R.J., 2001. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. *Ecology* 82 (9), 2403–2409.
- Helldorf, J., Naiman, R.J., 2006. Keystone interactions: salmon and bear in riparian forests of Alaska. *Ecosystems* 9 (2), 167–180.
- Heusser, C., Heusser, L., Peteet, D., 1985. Late-Quaternary climatic change on the American North Pacific coast. *Nature* 315, 485–487.
- Hilderbrand, G., Hanley, T., Robbins, C., Schwartz, C., 1999. Role of brown bears (*Ursus arctos*) in the flow of marine nitrogen into a terrestrial ecosystem. *Oecologia* 121, 546–550.

- Hobbie, E.A., Ouimette, A.P., 2009. Controls of nitrogen isotope patterns in soil profiles. *Biogeochemistry* 95, 355–371.
- Högberg, P., 1997. Tansley Review No. 95 15 N natural abundance in soil-plant systems. *New Phytologist* 137 (2), 179–203.
- Jenny, H., 1941. *Factors of Soil Formation*. McGraw-Hill, New York.
- Josenhans, H., Fedje, D., Pienitz, R., Southon, J., 1997. Early Humans and Rapidly Changing Holocene Sea Levels in the Queen Charlotte Islands-Hecate Strait. British Columbia, Canada.
- Kaufman, D.S., Manley, W.F., 2004. Pleistocene maximum and late Wisconsinan glacier extents across Alaska, USA. In: Ehlers, J., Gibbard, P.L. (Eds.), *Quaternary Glaciations-Extent and Chronology, part II, North America: Developments in Quaternary Science, Vol. 2b*. Elsevier, pp. 9–27.
- Kaye, J.P., Binkley, D., Rhodes, C., 2003. Stable nitrogen accumulation and flexible organic matter stoichiometry during primary floodplain succession. *Biogeochemistry* 63, 1–22.
- Kettler, T.A., Doran, J.W., Gilbert, T.L., 2001. Simplified method for soil particle-size determination to accompany soil-quality analyses. *Soil Science Society of America Journal* 65 (3), 849–852.
- Kirchhoff, M., 2003. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity: comment. *Ecology* 84 (12), 3396–3399.
- Kline, T.C., Goering, J.J., Mathisen, O.A., Poe, P.H., Parker, P.L., 1990. Recycling of elements transported upstream by runs of Pacific salmon: I. 15 N and 13 C evidence in Sashin Creek, southeastern Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 47, 136–144.
- Kline, T.C., Goering, J.J., Mathisen, O.A., Poe, P.H., Parker, P.L., Scalan, R.S., 1993. Recycling of elements transported upstream by runs of Pacific salmon: II. 15 N and 13 C evidence in Kvichak River Watershed, Bristol Bay, Southwestern Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 50, 2350–2365.
- Kondzela, C.M., Guthrie, C.M., Hawkins, S.L., Russell, C.D., Helle, J.H., Gharrett, A.J., 1994. Genetic relationships among chum salmon populations in southeast Alaska and Northern British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 51, 50–64.
- Koski, K., 2009. The fate of coho salmon nomads: the story of an estuarine-rearing strategy promoting resilience. *Ecology and Society* 14, 4 online <http://ecologyandsociety.org/vol14/iss1/art4/>.
- Lajtha, K., Michener, R.H. (Eds.), 1994. *Stable Isotopes in Ecology and Environmental Science*. Blackwell Scientific Publications, Cambridge, MA.
- Luxhoi, J., Nielsen, N.E., Jensen, L.S., 2004. Effect of soil heterogeneity on gross nitrogen mineralization measured by 15 N-pool dilution techniques. *Plant and Soil* 262 (1), 263–275.
- Mann, D.H., Hamilton, T.D., 1995. Late Pleistocene and Holocene paleoenvironments of the North Pacific Coast. *Quaternary Science Reviews* 14, 449–471.
- Merrill, A.G., Benning, T.L., 2006. Ecosystem type differences in nitrogen process rates and controls in the riparian zone of a montane landscape. *Forest Ecology and Management* 222 (1–3), 145–161.
- Merz, J.E., Moyle, P.B., 2006. Salmon, wildlife, and wine: marine-derived nutrients in human-dominated ecosystems of central California. *Ecological Applications* 16, 999–1009.
- Miller, R.D., 1973. Gastineau channel formation: a composite glaciomarine deposit near Juneau, Alaska. USGS report B 1394-C. C1–C20, Reston, VA.
- Mobley, C.M., 1988. Holocene sea levels in southeast Alaska: preliminary results. *Arctic and Alpine Research* 41, 261–266.
- Montgomery, D., 1997. The influence of geological processes on ecological systems. In: Schoonmaker, P., von Hagen, B., Wolf, E. (Eds.), *The Rain Forests of Home*. Island Press, Washington DC, pp. 43–68.
- Morris, A.E.L., Stark, J.M., Gilbert, B.K., 2005. Evaluation of isotopic fractionation error on calculations of marine-derived nitrogen in terrestrial ecosystems. *Canadian Journal of Forest Research* 35, 1604–1616.
- Nadelhofer, K.J., Fry, B., 1994. Nitrogen isotope studies in forest ecosystems. In: Lajtha, K. (Ed.), *Stable Isotopes in Ecology and Environmental Science*. Blackwell Science, O, pp. 22–44.
- Naiman, R.J., Bilby, R.E., Schindler, D.E., Helfield, J., 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. *Ecosystems* 5, 399–417.
- Naiman, R.J., Decamps, H., McClain, M., 2005. *Riparia*. Elsevier, Amsterdam, 430 pp.
- Pazzaglia, F.J., Brandon, M.T., 2001. A fluvial record of long-term steady-state uplift and erosion across the Cascadia forearc high, Western Washington State. *American Journal of Science* 301, 385–431.
- Pinay, G., Ruffinoni, C., Fabre, A., 1995. Nitrogen cycling in two riparian forest soils under different geomorphic conditions. *Biogeochemistry* 30, 9–29.
- Pinay, G., O'Keefe, T., Edwards, R.T., Naiman, R.J., 2003. Potential denitrification activity in the landscape of a Western Alaska drainage basin. *Ecosystems* 6 (4), 336–343.
- Quinn, T.P., Carlson, S.M., Gende, S.M., Rich Jr., H.B., 2009. Transportation of Pacific salmon carcasses from streams to riparian forests by bears. *Canadian Journal of Zoology* 87, 195–203.
- Reiger, S., Schoephorster, D.B. and Furbush, C.E., 1979. Exploratory soil survey of Alaska. In: USDA (Editor). *Soil Conservation Service*.
- Reimchen, T., Mathewson, D., Hocking, M., Moran, J., 2003. Isotopic evidence for enrichment of salmon-derived nutrients in vegetation, soil, and insects in riparian zones in coastal British Columbia. In: Stockner, J. (Ed.), *Nutrients in Salmonid Ecosystems: Sustaining Production and Biodiversity*. American Fisheries Society, Bethesda, MD.
- Renschler, C.S., Doyle, M.W., Thoms, M., 2007. Geomorphology and ecosystems: challenges and keys for success in bridging disciplines. *Geomorphology* 89, 1–8.
- Rundel, P.W., Ehleringer, J.R., Nagy, K.A. (Eds.), 1989. *Stable Isotopes in Ecological Research*. Springer-Verlag, New York.
- Soil Survey Division Staff, 1999. *Soil Taxonomy: A Basic System of Soil Classification for Making and Interpreting Soil Surveys*. USDA Natural Resources Conservation Service, Handbook No. 436.
- Swanston, D.N., 1969. A late-Pleistocene glacial sequence from Prince of Wales Island, Alaska. *Arctic* 22, 25–33.
- Thoms, M.C., Parsons, M.E., 2002. Ecogeomorphology: an interdisciplinary approach to river science. *International Association of Hydrological Sciences* 227, 113–119.
- Tiegs, S.D., Chaloner, D.T., Levi, P., Ruegg, J., Tank, J.L., Lamberti, G.A., 2008. Timber harvest transforms ecological roles of salmon in southeast Alaska rain forest streams. *Ecological Applications* 18, 4–11.
- Twenhofel, W.S., 1952. Recent shore-line changes along the Pacific coast of Alaska. *American Journal of Science* 250, 523–548.
- Ugolini, F.C., 1968. Soil development and alder invasion in a recently deglaciated area of Glacier Bay, Alaska. In: Trappe, J.M., Franklin, J.F., Tarrant, R.F., Hansen, G.M. (Eds.), *Proceedings, Biology of Alder*. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, Pullman, WA, pp. 115–139.
- USDA Forest Service, 1992. Channel type user guide, Tongass National Forest, Southeast Alaska. Alaska Region report R10-TP-26, April, 1992. 179 pp.
- USDA Forest Service, 1996. Landforms of the Alaska region classification guide. Alaska Region, December 1996. 74 pp.
- USDA NRCS, 2010. <http://soils.usda.gov/technical/classification/osd/index.html>.
- Van Cleve, K., Chapin, F.I., Dyrness, C.T., Viereck, L., 1991. Element cycling in Taiga forests: state-factor control; a framework for experimental studies of ecosystem processes. *Bioscience* 41 (2), 78–88.
- Waples, R.S., Beechie, T., Pess, G.R., 2009. Evolutionary history, habitat disturbance regimes, and anthropogenic changes: what do these mean for resilience of Pacific salmon populations? *Ecology and Society* 14, 3 online <http://www.ecologyandsociety.org/vol14/iss1/art3/>.
- Western Regional Climate Center, 2008. <http://www.wrcc.dri.edu/>.
- Wilkinson, C.E., Hocking, M.D., Reimchen, T.E., 2005. Uptake of salmon-derived nitrogen by mosses and liverworts in coastal British Columbia. *Oikos* 108 (1), 85–98.
- Willson, M.F., Gende, S.M., Marston, B.H., 1998. Fishes and the forest: expanding perspectives on fish-wildlife interactions. *Bioscience* 48 (6), 455–462.
- Wipfli, M.S., Hudson, J., Caouette, J., 1998. Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, USA. *Canadian Journal of Fisheries and Aquatic Sciences* 55, 1503–1511.
- Wysocki, D.A., Schoenenberger, P.J., LaGarry, H.E., 2000. *Geomorphology and landscapes*. In: Sumner, M.E. (Ed.), *Handbook of Soil Science*. FL, CRC Press, Boca Raton, pp. E5–E39.