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RESEARCH ARTICLE

Biophysical controls on dissolved organic carbon concentrations of Alaskan coastal temperate rainforest streams

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Abstract Coastal carbon cycling models remain incomplete in key continental margins worldwide. Large quantities of labile terrestrial DOC are transferred to the Gulf of Alaska in a flow of freshwater discharge from thousands of watersheds that equals the discharge of the Mississippi River. The coastal margin of southeast Alaska and British Columbia is a potential hotspot of worldwide DOC metabolism and the mass and reactivity of DOC in rivers and estuaries of the region make quantifying and modeling DOC export a priority. Scaling DOC export requires a well-constrained model of streamwater DOC concentrations. We established models for prediction of DOC streamwater concentrations through a broad sampling of streams across a large, diverse landscape in 61 independent watersheds. Stream DOC concentrations were significantly related to the amount of wetlands in a watershed confirming the necessity of understanding the fate of the mass of carbon stored within them. Several measures of slope were useful in predictive models of streamwater DOC concentrations suggesting that slope predicts the presence of wetland soils better than current wetland map layers. We also provide evidence that suggests watersheds with large salmon spawning runs have distinct characteristics that influence the relationship between wetlands and carbon cycling that may provide additional insights into how carbon is processed.

Keywords Dissolved organic carbon · Wetlands · Salmon · Stream biogeochemistry · Slope

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Introduction

The coastal margin of western North America from northern California, through British Columbia, to Kodiak Island in Alaska, contains the largest contiguous expanse of coastal temperate rainforest (CTR) remaining in the world (Waring and Franklin 1979; Fig. 1). These forests have accumulated large amounts of carbon throughout the Holocene and store more organic matter than most other north temperate forests (Gorham et al. 2007). The wettest, or perhumid, region of the CTR includes the central coast of British Columbia and the entire southeast Alaska panhandle (Fig. 1). Wetlands occupy about 22 % of the terrestrial environment of the Alaskan perhumid coastal temperate rainforest (PCTR), compared to 5.5 % in the lower 48 United States (Dahl 2006; USFWS 2009). Wetlands are a major source of DOC to surface waters throughout the world (Mulholland and Kuenzler 1979; Hope et al. 1994; Dillon and Molot 1997; Gorham et al. 1998; Frey and Smith 2005) and the presence of wetlands within a watershed often plays a dominant role in controlling the concentration of DOC in surface waters (Gorham et al. 1998; Aitkenhead and McDowell 2000; Mulholland 2003; Xenopoulos et al. 2003). Given the abundance of carbon and wetlands in the PCTR, the

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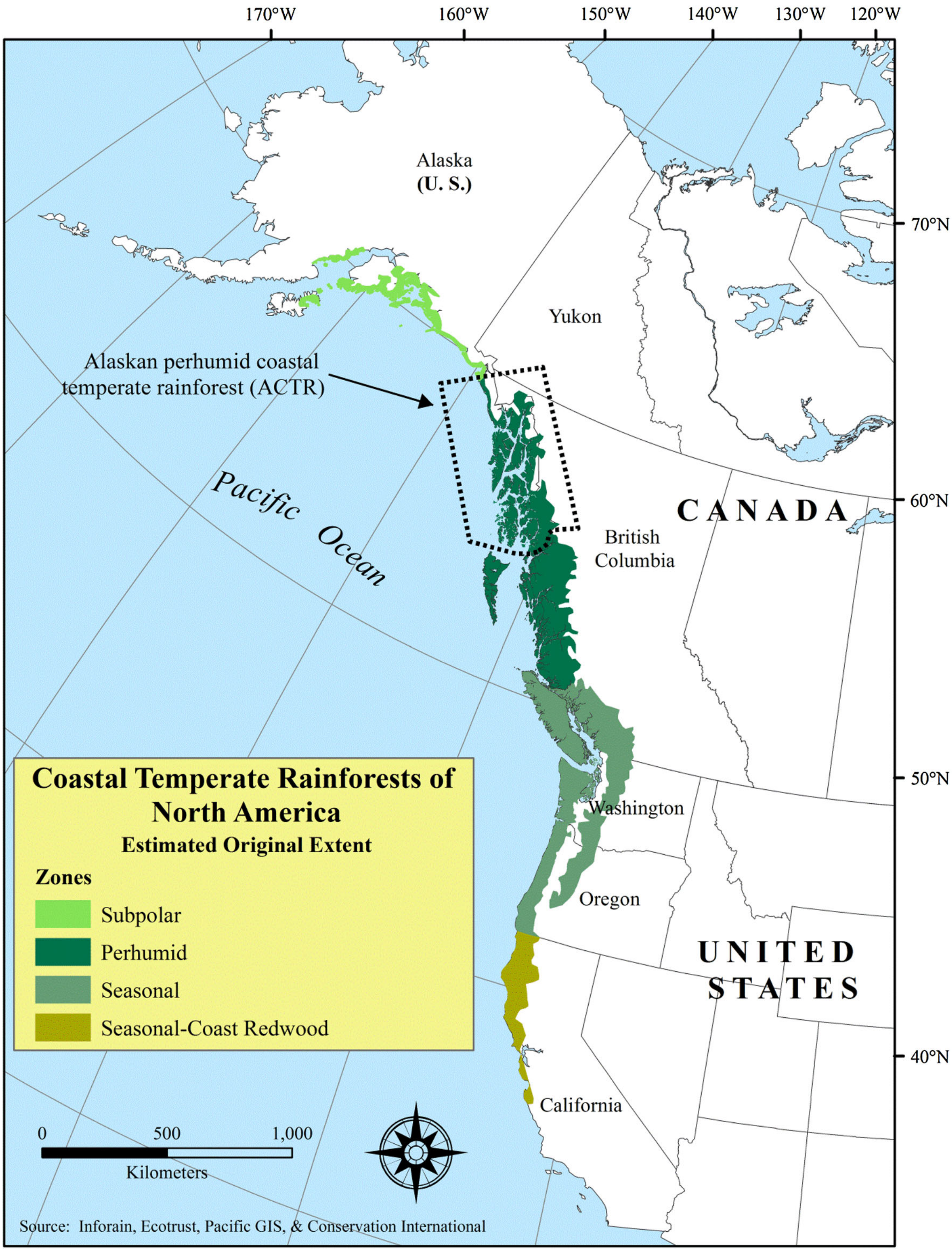

Fig. 1 Distribution of coastal temperate rainforest along the Northeast Pacific coastal margin including the Alaska perhumid coastal temperate rainforest region

primary source of DOC transported through streams to the ocean is likely wetlands. However, although wetlands may contribute significantly to DOC production, other factors may influence DOC concentration such as varying forest stand ages, structures related to windthrow, timber harvest, and the input of carbon from millions of spawning salmon (Nowacki and Kramer 1998; Caouette et al. 2000; Nowacki et al. 2001; Hood et al. 2007).

The vast expanse of the Alaska PCTR is an excellent template to test the strength of association between the extent of wetlands within a watershed and DOC concentration in streamwater and develop quantitative predictive relationships for the diverse landscape components of the region. There is little urban development and the primary anthropogenic disturbance (timber harvest) has been limited to a small portion of the landscape. The exceptionally humid climate of the region creates pervasive soil saturation and water flow from land to streams compared with other areas that have examined terrestrial DOC export. The huge influx of carbon from the ocean in the bodies of hundreds of millions of spawning salmon confounds land-based predictions of stream carbon concentrations and has not been considered in previous research. These factors combine to make testing the assumptions of a controlling relationship between wetlands and DOC critical to a clear understanding of what controls streamwater DOC concentrations and to developing terrestrial carbon flux models for the extensive coastal margin of the Northeastern Pacific coast.

We designed a study to test whether a clear relationship could be detected between wetland coverage and stream DOC concentration at the watershed scale in the Alaska PCTR. We also conducted an exploratory analysis to determine if landscape variables (including percent of wetland coverage) could be used to predict stream DOC. The southeast Alaskan rainforest is surrounded by estuaries or the ocean and terrestrial-marine linkages are omnipresent, yet there are no predictive models for DOC concentration in the region. We tested the influence of wetlands on stream DOC concentration and explored the usefulness of other landscape predictors to develop single and multiple regression models to fill this key carbon cycle information gap.

Methods

Site selection

To assess the relationship between wetland extent and DOC concentration, potential watersheds for sampling were identified using ArcGIS software (ESRI 2005) and geographic information system (GIS) data layers from the U.S. Forest Service (USFS), U.S. Fish and Wildlife Service (USFWS), and the U.S. Geological Survey (USGS). Watersheds were derived from a USFS watershed boundary layer and then filtered by size, GIS data availability, and accessibility. We excluded watersheds smaller than 121.4 ha (300 acres) and watersheds lacking boundary or wetland data from the potential pool. To make synoptic sampling of numerous watersheds across a large and remote area feasible, we also excluded sites that were not reasonably accessible by foot, car, boat, floatplane, or helicopter. Sample sites were then randomly selected from the watersheds remaining in the pool. Our final sample contained 65 independent watersheds draining directly to saltwater (Fig. 2).

Wetlands were identified using the USFWS National Wetlands Inventory (NWI) GIS layer (USFWS 2009). Wetland extent (NWI-Wet; Supplementary Table 1) was calculated as the area of wetlands divided by total land area for each watershed. All NWI terrestrial wetland types (palustrine, lacustrine, riverine, and estuarine) were included in our computation of wetland area. The final set of sample watersheds captured a range of wetland coverage from 1.7 to 95.3 %, reflecting the range found across the Alaska PCTR landscape (Supplementary Tables 1, 2; see supplementary text for detailed site selection methods).

Data collection

Samples were collected from the mainstem stream as close to the watershed saltwater outlet as possible, but above the high tide line. Sampling was conducted once in the spring and once in fall to capture the descending and ascending limbs of the seasonal watershed hydrographs. After unexpected access difficulties and sampling problems, a total of 61 spring, and 55 fall, independent water samples were available for analyses (Fig. 2; Supplementary Table 1). Each sampled location was documented using a global positioning system (GPS) receiver. The position of each collection point was viewed in ArcGIS and watershed boundaries above the actual sample point were redigitized. Subsequent GIS analyses were performed using these updated contributing areas.

Sample streams were identified as nonfish-bearing (NFB) or fish-bearing (FB) based on evidence of large spawning salmon runs (variable FallFish, Supplementary Table 1). Detailed records of spawning run magnitude are not available for the thousands of streams within the Alaska PCTR so readily observable evidence was used to classify a stream. Large spawning runs are dominated by chum and pink salmon and are readily apparent, either by direct observation of spawning fish during a sampling period, or by widespread remains such as skin, heads, or bones, which persist for many months after active spawning. When spawners were observed during the fall sampling, or when bones or other remains were evident, the site was classed as FB. In reaches with thousands of spawners it is not likely we misclassified streams in this way. The timing of our fall sampling was after the normal spawning period for most streams. NFB streams were either at sites above physical barriers to fish movement or above extensive spawning habitat. Sites classified as NFB may also

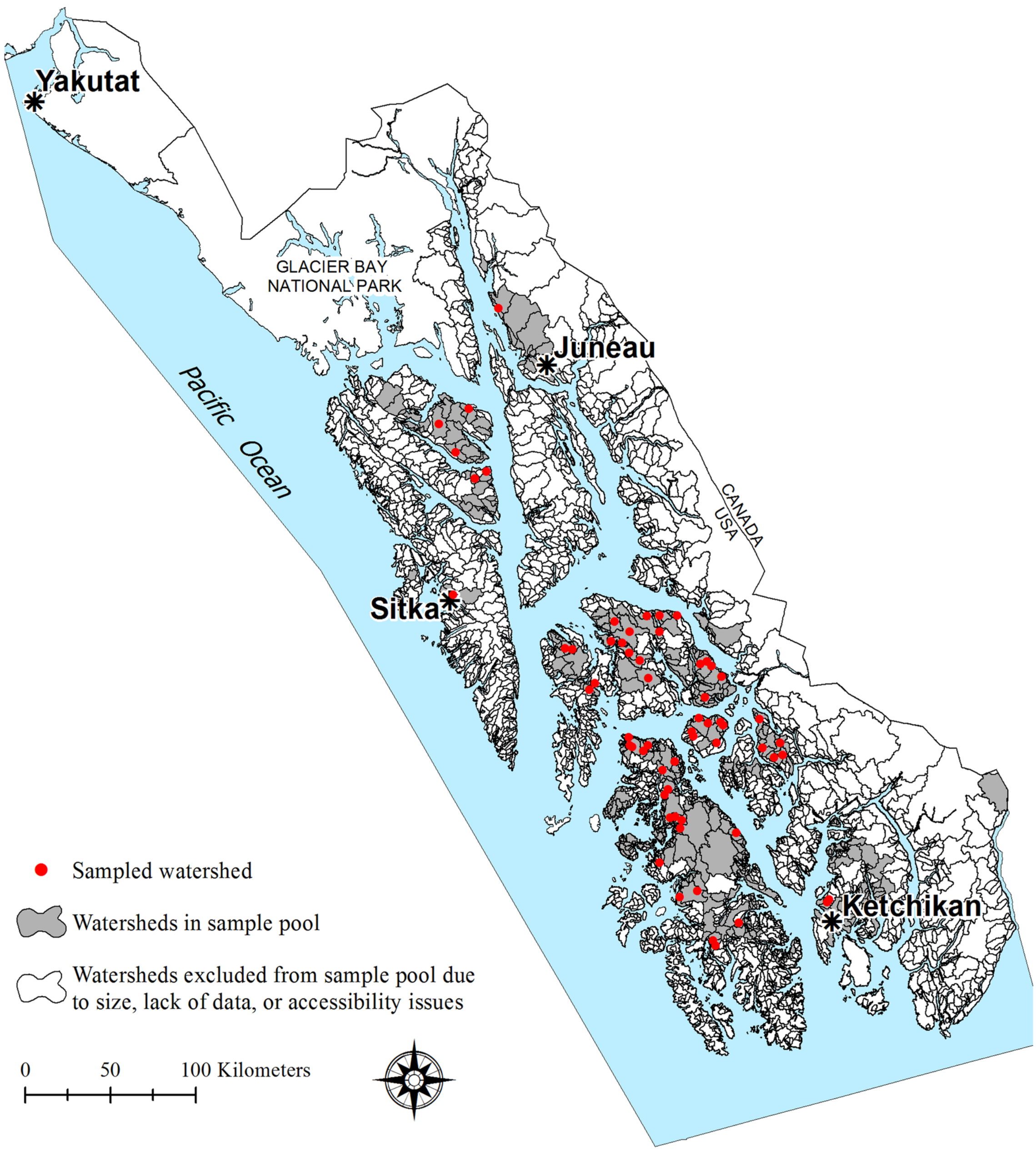

Fig. 2 The Alaska coastal temperate rainforest region with total watershed pool (*white*), candidate watershed pool (*grey*) and sampled watersheds

include streams with coho and king salmon runs, which have many fewer fish, or may include streams with sockeye populations in headwater lakes. Thus our classification is imperfect and biased toward large runs that would leave clear evidence. Because only large numbers of spawners are likely to change stream DOC and nutrient concentrations this bias is not a significant flaw in the analysis, but may contribute to variability in the statistical outcome. Salmon were spawning in large numbers in 19 watersheds sampled in the study.

Laboratory analyses

Streamwater samples were collected in acid rinsed, polyethylene bottles, pre-rinsed with stream water, and filtered in the field through pre-combusted, glass-fiber filters (nominal pore size 0.7 μm) and stored under cool conditions until analyzed within 72 h of sampling. Concentrations of DOC in streamwater were measured by high-temperature combustion using a Shimadzu TOC-V Carbon and Total Nitrogen Analyzer with a lower detection limit of

0.4 mg C L^{-1} for DOC. Specific ultraviolet absorbance (SUVA) was measured using a 1.0 cm quartz cell on streamwater DOC following the procedures of Weishaar et al. (2003). Samples were allowed to warm to room temperature, and then were analyzed on a Genesys 5 Spectrophotometer. SUVA was calculated as the ultraviolet absorbance at 254 nm per L mg C m^{-1}.

Statistical analysis

Influence of wetlands and salmon on DOC and SUVA

The relationships between wetland extent and seasonal stream DOC concentration and SUVA were assessed using partial correlations and linear marginal regression models (SAS Institute Inc., 2011; Proc GLM and Proc Mixed). Marginal models can account for both the correlation between spring and fall samples collected within the same watershed, and the sample variability among watersheds seasonally in a variance–covariance matrix structure (Pinheiro 2006). The marginal model included DOC concentration as the dependent variable, watershed (WSID) as the subject, time (spring or fall) as a repeated measure, and NWI-Wet, time, and the NWI-Wet × time interaction as fixed effects. An identical model was created with SUVA as the dependent variable. We created two additional marginal models by adding the FallFish variable as a fixed effect to the above DOC and SUVA models. Neither the three-way nor the FallFish × time interactions were significant (at $\alpha = 0.05$) and were not retained in the final models.

Model variance–covariance parameters were estimated using residual maximum likelihood (REML). We evaluated the fit of the compound symmetry (CS) and unstructured (UN) covariance structures to the four DOC and SUVA marginal models. For models containing FallFish as a fixed effect, we partitioned the CS and UN matrices into separate covariance parameter estimates for each group, NFB and FB. Fit was assessed by comparing values of the sample-size adjusted Akaike's information criterion (AIC_c) between identical models with different covariance structures, and where appropriate using a likelihood ratio test (Littell et al. 2006). Although covariance parameter estimates differed slightly depending on the covariance structure used, the differences were not large enough to alter the test conclusions or meaningfully change the parameter estimates for the fixed effects. The UN structure was selected as the best balance of fit, number of parameters, and flexibility for describing the covariance in both the DOC and SUVA models. No structural constraints are imposed on the variance–covariance pattern when using the UN matrix, which allows variance heterogeneity to be modelled directly from the data (Wolfinger 1996).

Prior to the analysis we examined scatterplots and Pearson's correlation coefficients of wetland extent with DOC and SUVA to confirm a linear relationship between the variables existed. Residual analyses of the fixed effects for the DOC and SUVA models did not reveal severe departures from normality for the overall marginal model results. However, the reduction in sample size when residuals were grouped by time and FallFish made the histogram distributions harder to interpret. Plots of residuals by predicted values for the overall model did not show any strong patterns for DOC, but were influenced by one or two high residuals (studentized residuals 2.98–4.15) when plots were grouped by spring, fall FB, or spring NFB observations. We had no reason to suspect the data were erroneous for these sites and subsequently left them in the analysis. Residual plots for SUVA were slightly funnel-shaped in the fall and SUVA variance was clearly different between seasons. However, because variance heterogeneity was accounted for in the UN covariance structure for the DOC and SUVA models, we were satisfied regression assumptions were met.

Predictive models for DOC concentration

We used ordinary least squares regression to construct predictive models of average fall and spring DOC concentration for Alaska PCTR watersheds. A pool of potential explanatory variables relating to watershed physical characteristics and land-use activities was selected a priori based on literature from similar studies (Eckhardt and Moore 1990; Gergel et al.1999; Mulholland 2003; Frost et al. 2006; Johnston et al. 2008; Kreutzweiser et al. 2008). Additional landscape variables that we reasoned had potential to influence DOC production and delivery were also included in the pool for exploratory analysis (Supplementary Table 2). Variables describing watershed size, shape, topography, karst extent, wetland type, lakes, and stream attributes were extracted from USFS, USFWS, and USGS GIS datasets. USGS (60 m) National Elevation Dataset (NED) digital elevation models (DEMs) were used to calculate slope, elevation, and surface shape variables. GIS datasets from the USFS, Sealaska Native Corporation, and the State of Alaska provided timber harvest and road information.

Pearson's correlation coefficients and scatterplots helped to initially identify strong linear relationships between DOC and watershed variables and potential collinearity among explanatory variables (Supplementary Table 3). Using all-subsets multiple regression, with AIC_c and adjusted R-squared (adjR^2) as criteria, we identified the best n-variable model subsets from all explanatory variables (Burnham and Anderson 2002; Supplementary Table 4, see supplementary text for model selection details).

To check regression assumptions, residual plots and normal probability plots were examined for indications of non-constant variance and for residual distribution(Cook and Weisberg 1982). Studentized residuals and the Cook's D statistic were used to assess outliers and influential observations. Using a cutoff value of Cook's $D = 1$ (Weisberg 1985), no watersheds were considered influential in any of the candidate models (highest $D = 0.43$, highest studentized residual 2.7). Models having a scaled condition index ≥ 18, combined with two or more variables having variance-decomposition proportions > 0.5, were considered to be at least moderately affected by collinearity (Belsley 1991).

Fall DOC was normally distributed and analysis of fall model residuals did not indicate a need to transform the dependent variable (DOC). The distribution of spring DOC values was positively skewed, and although some spring models did not violate regression assumptions, others raised concerns with non-constant variance of the residuals. Although transformations of spring DOC stabilized the variance, we chose to retain the original scale of the data for ease of model interpretation and comparison with fall results. To correct for suspected non-constant variance in spring models, the heteroscedasticity-consistent covariance matrix (HCCM; method HC3) was used to generate standard errors, P values, and 95 % confidence limits for spring model parameter estimates (Long and Ervin 2000).

Results and discussion

Wetland influence on DOC concentration

The hypothesis that DOC concentration in Alaska PCTR watersheds is influenced by wetland coverage is well supported by our data, as indicated by the partial correlation of DOC with NWI-Wet of 0.57 ($df = 114$; $P < 0.001$) when controlling for time. DOC concentration increased with wetland extent during both seasons (Fig. 3a). Although DOC concentrations converged at low wetland coverage, concentration increased with wetland coverage more rapidly in the fall than spring ($F_{(1,59)} = 5.55$; $P = 0.022$; Table 1, first model; Fig. 3a; Supplementary Table 5). Mean DOC concentrations were higher in fall (7.9 ppm) than in spring (5.7 ppm), with 80 % of the sampled streams showing a fall increase (Supplementary Table 1).

These results are consistent with smaller-scale studies within southeast Alaska. Enhanced soil organic matter mineralization increases DOC concentrations in soils during warm summer periods (D'Amore et al. 2015). Increased fall precipitation in non-glacial watersheds flushes stored DOC from soils into adjacent streams increasing both discharge and concentration (Schmiege et al. 1974; Fellman et al. 2009b; Edwards et al. 2013). Studies in other wetland-rich locations have also demonstrated similar processes, including higher seasonal DOC production, increased DOC solubility, and hydrologic flushing from carbon-rich, saturated soil horizons (Worrall et al. 2002; Pastor et al. 2003; Worrall and Burt 2008).

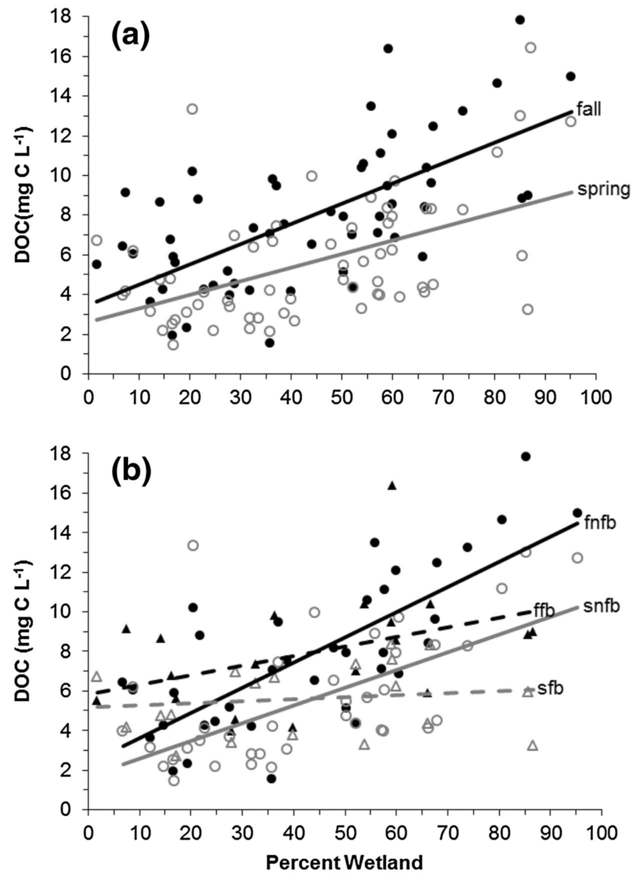

Fig. 3 **a** Relationship of stream DOC concentration with percent wetland cover in watersheds throughout the Alaska PCTR for spring, *open circles*, and fall, *filled circles*; and **b** relationship of DOC with percent wetland cover in watersheds for spring nonfish-bearing (snfb; *open circles*), spring fish-bearing (sfb; *open triangles*), fall nonfish-bearing (fnfb; *filled circles*), and fall fish-bearing streams (ffb; *filled triangles*). The regression lines from Table 1 are shown for each case

Our study expands the scale of inference for the relationship between the areal extent of wetlands and stream DOC concentration, and we believe it to include the widest range of wetland coverage (2–95 %) reported in the literature. We analyzed 61 completely independent streams from a pool of hundreds of largely undisturbed watersheds. The study design was also uncomplicated by variable nesting or longitudinal effects associated with sampling sub-catchments at different locations within larger basins (e.g. Frost et al. 2006). That the relationship between wetland extent and DOC concentration holds over 87,700 km^2, encompassing $> 4°$ latitudinal gradient and diversity in geologic history, landforms, and plant communities underscores the important role of wetland carbon export in controlling stream DOC concentrations.

Carbon quality and wetlands

Understanding the fate of exported DOC in the region requires an estimate of the quality of the organic matter to support metabolism. Whether carbon delivered to the marine system enters the food web or long-term storage pools is important in evaluating the impact of organic carbon flux to estuaries and coastal waters. We measured carbon quality as the SUVA of DOC at 254 nm (SUVA). Low SUVA values suggest less aromatic, more labile carbon (higher quality), whereas higher values indicate more aromatic, less biologically available DOC (lower quality). Carbon quality was higher overall during the spring, with a mean concentration of 3.29 L mg C^{-1} m^{-1}, compared to 4.63 L mg C^{-1} m^{-1} in the fall (Supplementary Table 1), reflecting a seasonal change in carbon quality also found in other streams (Laudon et al. 2004; Agren et al. 2007; Fellman et al. 2008, 2009a).

The partial correlation between SUVA and wetland extent, controlling for time, was 0.59 ($df = 108$; $P < 0.001$), indicating that the quality of carbon exported from watersheds was strongly related to the presence of wetlands. Carbon quality decreased with increasing wetland coverage during both sample periods (Fig. 4a). The marginal model analysis of SUVA, time, and wetland coverage showed that the relationship between carbon quality and wetlands depended on the time of sampling ($F_{(1,56)} = 11.37$; $P = 0.001$; Supplementary Table 5) and that quality decreased with wetland coverage at a higher rate in the spring compared to fall (Table 1; Fig. 4a). The lower SUVA values we measured during spring in watersheds with small areas of wetland likely reflect increased in-channel microbial production during the early growing season combined with lower exports from soils during low discharge, drier conditions. Exported aromatic compounds from soils (Fellman et al. 2009a) appear to overwhelm the SUVA signal at high wetland coverage. During increased fall runoff, even watersheds with fewer wetlands export large amounts of wetland-derived DOC as peat surface horizons and overland flow paths fill and water is discharged directly from wetland to stream (Gibson et al. 2000; Fitzgerald et al. 2002; Emili et al. 2006; Fellman et al. 2009b; D'Amore et al. 2010).

Wetlands, spawning salmon, and stream DOC

The annual spawning migration of hundreds of millions of salmon transfers carbon and other materials from the Gulf of Alaska back into the terrestrial ecosystem (Gende et al. 2002; Rex et al. 2014). Most of our sampled watersheds host various species of salmon, but 19 of the watersheds support autumn runs of thousands of pink and chum salmon, which bring large masses of carbon into the lower watershed. Adding FB or NFB streams to the marginal model revealed that the relationship between wetland extent and DOC concentration was different in FB versus NFB streams ($F_{(1,53)} = 9.18$, $P = 0.004$; Fig. 3b; Supplementary Table 5). In NFB streams, DOC concentrations increased with wetlands at rates similar to the model that did not consider fish. However, in FB watersheds fall DOC increased with wetland coverage ($t(53) = 2.22$, $P = 0.031$; Table 1) at only one-third that rate. In the

Table 1 Estimates of fixed effects for DOC and SUVA linear marginal models

Model	Class	Intercept (SE)	Slope (SE)	DF	*t* Value	*P* value
DOC = NWIwet time	Fall	3.43 (0.800)	10.28 (1.614)	59	6.37	<0.001
NWIwet × time	Spring	2.63 (.749)	6.86 (1.498)	59	4.58	<0.001
DOC = NWIwet time	Fall, NFB	2.36 (0.888)	12.71 (1.809)	53	7.03	<0.001
FallFish NWIwet × time	Fall, FB	5.77 (1.088)	4.89 (2.206)	53	2.22	0.031
NWIwet × FallFish	Spring, NFB	1.71 (0.826)	8.94 (1.697)	53	5.27	<0.001
	Spring, FB	5.12 (1.045)	1.12 (2.119)	53	0.53	0.600
SUVA = NWIwet time	Fall	4.10 (0.139)	1.20 (0.281)	56	4.27	<0.001
NWIwet × time	Spring	1.91 (0.236)	3.11 (0.470)	56	6.63	<0.001
SUVA = NWIwet time	Fall, NFB	4.28 (0.169)	0.93 (0.340)	50	2.74	0.009
FallFish NWIwet × time	Fall, FB	3.79 (0.202)	1.62 (0.409)	50	3.96	<0.001
NWIwet × FallFish	Spring, NFB	2.11 (0.251)	2.84 (0.512)	50	5.56	<0.001
	Spring, FB	1.62 (0.276)	3.53 (0.561)	50	6.3	<0.001

NWIwet is the proportion of a watershed mapped as wetland in the USFWS National Wetlands Inventory

Time represents the two sample periods, spring and fall. The variable FallFish describes whether a stream has large fall runs of spawning salmon and has two classes: nonfish-bearing (NFB) or fish-bearing (FB). The *t* test is testing whether the regression slope is different from zero spring the wetland–DOC relationship is not significant in FB streams ($t(53) = 0.53$, $P = 0.600$; Table 1; Fig. 3b).

No strong impact of large spawning runs on carbon quality was detected in our study. SUVA values in FB streams behaved similarly to those in NFB streams with regard to season and wetland coverage (Fig. 4b). DOC quality decreased with increasing wetland coverage in FB and NFB streams during spring and fall (Fig. 4b). The presence of fall salmon did not have a strong influence on the relationship between wetlands and SUVA in the marginal model analysis ($F_{(1,50)} = 2.12$, $P = 0.151$; Supplementary Table 5).

Although the annual influx of salmon is thought to have a dramatic influence on the productivity of natal streams, and even upland forests, in salmon watersheds (Naiman et al. 2009), a simple regional flux budget suggested that salmon derived nutrient inputs are dwarfed by the massive flux of materials from terrestrial soils to ocean (Edwards et al. 2013). Our results suggest that, although salmon carbon inputs may be high in some locations, there is no unambiguous impact of salmon carbon on stream DOC concentration at larger scales. High spawner densities and low discharge can increase stream DOC concentrations during spawning (Hood et al. 2007), but there is little evidence that the phenomenon is widespread or persistent (Janetski et al. 2009). Invoking salmon carbon inputs to explain the increased concentrations at low wetland coverage would not explain how salmon inputs could simultaneously reduce concentrations at higher wetland abundances. In addition, the trend that streams hosting large spawning runs influenced the wetland–DOC link in spring is even harder to explain. The large salmon spawning runs occur in late summer and autumn, months before our spring sampling. Although we have observed short term storage and release of salmon-derived nutrients during a flood in a salmon stream in southeast Alaska (Fellman et al. 2008), and over-winter storage zones exist, there is no evidence that enough salmon carbon is stored over winter to increase stream concentrations the following spring.

Carbon quality, as indicated by SUVA, also failed to show a clear influence of salmon inputs. The increase in SUVA with increasing wetland coverage and increased discharge suggests that the quality of DOC in the Alaska PCTR is controlled by inputs of lower quality dissolved organic matter from wetland soils, which vary seasonally as changes in hydrology control the amount of soil carbon exported to streams. This result is straightforward and expected, but the lack of significance of salmon on fall SUVA runs counter to conventional wisdom about the importance of salmon-derived nutrients on natal streams. The differences we observed in the seasonal trends for SUVA and wetland coverage are more simply explained as a consequence of an overwhelming input of more aromatic DOC from wetland soils that varies seasonally with well described variations in soil DOC availability, and hydrologic connectivity (e.g. Fellman et al. 2008).

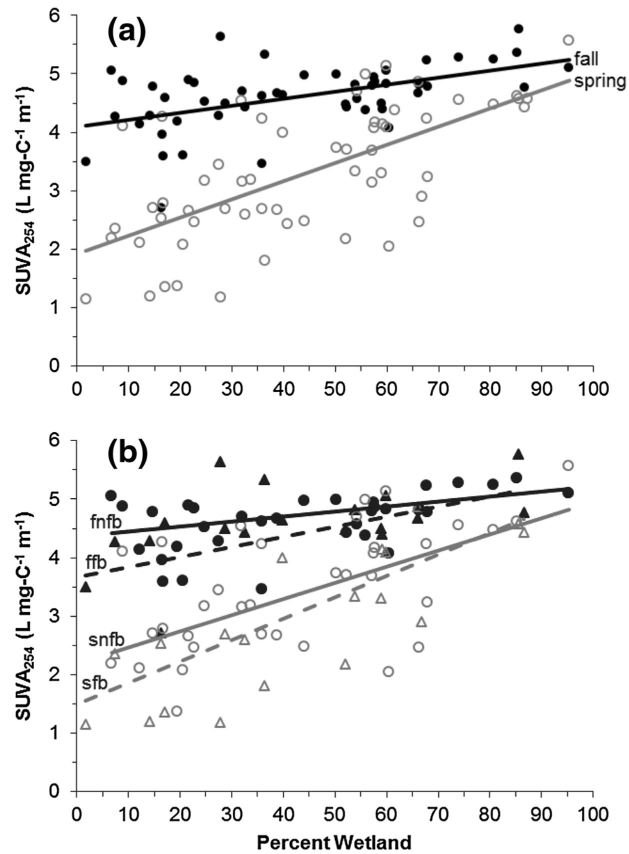

Fig. 4 **a** Relationship of SUVA with percent wetland cover in watersheds throughout the Alaska PCTR for spring, *open circles*, and fall, *filled circles*; and **b** relationship of SUVA with percent wetland cover in watersheds for spring nonfish-bearing (snfb; *open circles*), spring fish-bearing (sfb; *open triangles*), fall nonfish-bearing (fnfb; *filled circles*), and fall fish-bearing streams (ffb; *filled triangles*). The regression lines from Table 1 are shown for each case

We conclude that broader watershed characteristics may control both the suitability of the lower watershed for mass spawners and the dynamics of release, transport and uptake of wetland-derived carbon. The spatial and temporal resolution of our fish observation data does not provide a clear mechanism for the "spawner" effect on the relationship between stream carbon concentrations and wetlands. Therefore, we did not attempt to create predictive regression models based on these data. However, the importance of both carbon and salmon in the Alaska PCTR ecosystem suggests research on these relationships should be a priority for the future.

Table 2 Top-ranked single and multiple regression models for predicting spring and fall DOC concentrations for Alaska PCTR watersheds

Time	# Independent variables	Equation	adjR^2
Spring	1	$DOC_{(ppm)} = 2.80 + 11.99(Slopes0–5)$	0.622
	2	$DOC_{(ppm)} = 7.28 + 9.61(Slopes0–5) - 0.104(SlopeRnge)$	0.686
	3	$DOC_{(ppm)} = 3.25 + 12.78(Slopes0–5) - 0.112(StrmLen) + 2.74(karst)$	0.727
Fall	1	$DOC_{(ppm)} = 4.77 + 13.53(Slopes0–5)$	0.519
	2	$DOC_{(ppm)} = 4.08 + 12.11(Slopes0–10) - 9.00(HarvAll)$	0.593
	3	$DOC_{(ppm)} = 5.37 + 13.90(Slopes0–5) - 7.67(HarvAll) + 260.28(NWI\text{-}PUB)$	0.633
	4	$DOC_{(ppm)} = 8.48 + 12.26(Slopes0–5) - 9.27(HarvAll) - 3.95(ElevRnge) + 253.79(NWI\text{-}PUB)$	0.669

See Supplementary Table 2 for explanatory variable definitions and Supplementary Tables 6 and 7 for additional model details

Building predictive models for watershed DOC concentration

Although wetlands are clearly a dominant source of DOC to surface waters, they are not the only landform or location for DOC production and processing (Blöschl and Sivapalan 1995). We generated alternative single and multiple regression models using watershed variables derived from GIS datasets. The additional variables fell into several broad classes: physical attributes of the watershed that might control the distribution of wet soils or water movement, geology, land cover, and human activities such as timber harvest and road construction. Separate predictive models were constructed for spring and fall because DOC concentration differed significantly between the two seasons in the marginal model analysis. The top-ranked models from this set of candidate models (Supplementary Table 4) are reported for each time period in Table 2 and regression results for all candidate 1-, 2-, and 3-variable spring and 1-, 2-, 3-, and 4-variable fall models are presented in Supplementary Tables 6 and 7.

Wetlands and slope as predictors for DOC

Proportion of the watershed covered by wetlands (NWI-Wet) explained a significant amount of variation in stream DOC concentration for both spring and fall (25 and 40 %, respectively) and has a clear functional link to biogeochemistry, but it was not the best candidate as a predictive variable. Measures of watershed slope explained more of the variation in DOC in all models, regardless of time or number of explanatory variables (Table 2, Supplementary Tables 4, 6, 7). Three slope variables, proportion of watershed in 0°–5° slopes (Slopes0–5), proportion of watershed in 0°–10° slopes (Slopes0–10), and average basin slope (SlopeAvg), consistently outperformed various wetland variables. Slopes0–5 explained 63 and 53 % of the variation in spring and fall DOC concentration, respectively (Supplementary Tables 6, 7). Slopes0–5 was the clear, top 1-variable model for both spring and fall, with AIC_c weights > 90 % (Supplementary Table 4).

The superiority of slope variables over NWI derived wetland coverage as a predictor of stream DOC may be explained by: (1) the extensive area of soils within the Alaska PCTR that do not meet the jurisdictional definition of wetlands but which are rich in carbon, wet, and act as DOC sources (D'Amore et al. 2015), and (2) the presence of wetland areas beneath the forest canopy that are not visible on remotely sensed images and therefore not mapped in the NWI (Creed et al. 2003). We have documented that wetlands export large amounts of DOC, and catchment slope itself does not produce carbon, therefore we interpret our results as an indication that slope is a better predictor of functional wetland, and carbon-rich, wet soil abundance, than the NWI layer.

Other predictor variables

Landscape physiography plays a large role in determining hydrologic flow paths and connectivity that influence vegetation types and wetland formation, which in turn control DOC concentration in surface waters (Boyer et al. 1997; Mulholland 1997; 2003; Wilson and Xenopoulos 2008; Winn et al. 2009). Average basin slope or area of basin in low slopes have appeared in other studies as important predictors of DOC concentration and flux for streams and lakes in local, regional, and global models (Rasmussen et al. 1989; Claire et al. 1994; Ludwig et al. 1996; Frost et al. 2006; Winn et al. 2009; Teisserenc et al. 2010; Jankowski et al. 2014). The prevalence of variables describing watershed slope, elevation, and topographic variability in all our single and multiple regression models (Supplementary Table 4) is consistent with this concept of landscape influence on processes that generate and export DOC.

Other predictor variables repeatedly appear alongside slope in the candidate multiple regression models (Supplementary Table 4). Due to the exploratory nature of the predictive model analysis spurious results are possible, so we caution against over-interpretation of the results (Anderson et al. 2001). However, for interest and to suggest possible areas for future research, we discuss some of these predictors below and compare them to results found in other studies.

Mainstem stream length (StrmLen) appears as a significant predictor in a 2-variable model and in the top-ranked 3-variable model in the spring (Table 2, Supplementary Tables 4, 6). Frost et al. (2006) reported a significant correlation between stream DOC concentration and stream length ($r(60) = -0.47$). However, we found very little relationship between spring DOC and StrmLen ($r(61) = -0.06$). We believe that StrmLen may be functioning as a suppressor variable in the regression model due to its correlation with Slopes0–5 ($r(61) = 0.25$), which is another predictor in the 2- and 3-variable models (Pandy and Elliott 2010).

Proportion of the watershed harvested for timber (HarvAll) was the second most important variable after slope attributes (Slopes0–5, Slopes0–10, or SlopeAvg) in all but four fall multiple regression models (Supplementary Table 7). In those four candidate models, proportion of the watershed roaded (Roads) replaced HarvAll as a predictor; however, roads are highly correlated with harvest ($r(55) = 0.92$) and likely reflect the timber harvest impact. Another harvest variable, proportion of watershed harvested during the 5 years prior to sampling (Harv5), is a significant predictor in three candidate fall regression models. The coefficient for HarvAll and Harv5 in our fall models was negative, suggesting timber harvest may decrease fall stream DOC concentrations.

In coniferous forests of the North American Pacific Northwest, where vegetation and climate are similar to the Alaska PCTR, two studies found no difference in stream DOC concentration between logged and old-growth catchments 1–10 years after harvest (Bilby and Bisson 1992; Sorensen and Heise 2008). In contrast, Dahm (1980) found stream DOC to increase in the first 2 years following logging, then observed no effect during the third year of a 3-year study. At the same site, Hood et al. (2006) observed decreased stream DOC concentration from logged watersheds during two storm events 28 and 40 years post-harvest.

The influence of timber harvest on stream DOC within the Alaska PCTR is of interest because timber harvest is the dominant land-use in the region. However, comparing our modeling results to existing studies of logging effects on stream DOC concentrations is problematic because most logging effects studies have occurred in watersheds that differ substantially from our study watersheds in size, representativeness (headwater or lake subcatchments vs. entire basins to coastal outlet), disturbance history, management practices, and harvest treatment. Although we can comment on observed patterns, this study was not designed to experimentally test how logging influences DOC concentrations; therefore, we cannot make any statistical inferences on cause and effect. Complicating any observed patterns is that HarvAll and Roads appear to be participating in a cooperative suppression relationship with other slope variables in the models (Sharpe and Ali 2009).

Along with topographic variables and timber harvest, proportion of watershed area in the NWI class *palustrine unconsolidated bottom* (NWI-PUB) was a significant predictor in the 3- and 4-variable fall regression models (Supplementary Table 7). In the Alaska PCTR the PUB wetland class represents the typical brownwater ponds found in fen habitats, but also includes small, shallow lakes (< 8 ha). This result agrees with the findings from a multiple regression analysis of NWI wetland types and DOC in northern Michigan, USA (Johnston et al. 2008), where a positive relationship was observed between stream DOC concentration and the extent of small ponds and lakes in a watershed.

Another NWI wetland type, palustrine emergent wetlands (NWI-PE), appears as a significant predictor in two of the candidate fall 3-variable regression models (Supplementary Table 7). The direction of the relationship between DOC and NWI-PE changes from positive in the zero-order correlation ($r(55) = 0.17$) to negative in the regression equation ($\beta = -0.22$ to -0.26). This sign change, combined with standardized regression coefficients for NWI-PE that are greater than the zero-order correlation with DOC, is an indication that NWI-PE is a suppressor variable (Tzelgov and Henik 1991). This finding differs from a study in the Ontonagon River drainage in Michigan, USA (Frost et al. 2006) where NWI-PE had a negative correlation with DOC concentration ($r(60) = -0.50$, after transforming both variables) and a significant strong negative effect on DOC in regression models. However, stream samples from the Ontonagon study were collected in the fall, which is the low-flow period for that system, compared to the fall high-flow condition of Alaska PCTR streams. Our spring sample, collected during near base-flow conditions, showed no relationship between DOC and NWI-PE ($r(61) = 0.00$) and did not appear in any of the spring candidate models.

Conclusions

Our study emphasizes the important relationship between wetlands and DOC concentration in streams across a large and heterogeneous landscape and highlights relationships with seasonality, topography, salmon populations and forest management. A primary motivation for this research was the need to develop scalable models to estimate DOC concentrations for the thousands of watersheds along the Alaska PCTR draining to coastal waters. Such estimates are difficult because the large number of watersheds, spatial variability and remoteness make direct measurement impractical. Consequently research on the significance of terrestrial outputs on coastal oceans has focused on large rivers with single outlets (Raymond et al. 2007; Holmes et al. 2012; McClelland et al. 2012) and the larger flux from broadly distributed small drainages has been poorly recognized. The models we developed will be applied to future flux estimates for the Alaska PCTR.

A second motivation for this study was to understand the primary controls on riverine DOC concentrations to guide development of scenarios for response to climate change. The Alaska PCTR is predicted to warm by up to 6 °C by the end of the century (National Climate Assessment 2014), which will have significant effects on the biogeochemical processes that produce, transport and transform terrestrial and aquatic nutrients (Groffmann et al. 2012). In southwest Alaska, for example, Jankowski et al. (2014) found that CO_2 respiration from sediments in high DOC streams draining flatter watersheds increased with temperature faster than sediments from low DOC streams in steeper watersheds. The results from southwest Alaska suggest that the respiratory response to warming in Alaska PCTR streams may also vary widely depending upon watershed geomorphology and wetland distributions. Research in the Alaska PCTR has shown that wetland soil carbon cycles are highly responsive to variations in soil wetness and temperature (Emili et al. 2006; D'Amore et al. 2015). That important wetland influences persist at scales ranging from individual site studies to the entire region as shown in this study confirms the need to incorporate wetland function in any assessment of future change. Although landscape slope was the best predictor of DOC concentrations, changes in carbon cycling and transport will be driven not by changes in watershed morphology but by changes in temperature-sensitive plant communities, soil carbon cycling, wetlands, and hydrologic flow paths that play out across the inherited physical landscape. Understanding the key role that wetlands play in generating carbon export and what additional variables influence retention and transport is critical in building process-based models that can predict carbon export patterns. Intriguing relationships such as the differences in FB watersheds, or the influence of timber harvest will be integrated into future research designs that can better address how the amount and quality of organic carbon delivered to one of the largest estuaries in the world will be affected by changes in climate.

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