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ARTICLE

Implications of legacy watershed disturbances for channel structure and salmon habitat availability under different low-flow levels: an analysis of 45 years of discharge–habitat relationships at Carnation Creek, British Columbia

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Abstract: In streams where water availability is limited, conservative flow ranges are often adopted by water managers to ensure that streamflow is available to meet the ecological requirements of aquatic organisms. However, a variety of natural and anthropogenic disturbances can influence stream channel morphology and in-stream wood characteristics through time, potentially altering the availability of habitat at a given flow level. Using a 2D hydrodynamic modelling approach incorporating 45 years of detailed channel morphology data from Carnation Creek, British Columbia, this paper examines relationships between legacy (forestry-driven) watershed disturbance, changes to channel morphology, and habitat availability for juvenile coho salmon (*Oncorhynchus kisutch*) under nine flow levels. Results indicate that substantial variability in the abundance of salmonid habitat is present through time, even when modelled flow levels are held constant. Additionally, trade-offs were observed between availability of habitat types as discharge increased. Finally, modelling results indicate that habitat availability is reduced following historical harvesting. These findings suggest that legacy watershed disturbances affecting stream channel form and function are worth considering when allocating streamflow.

Résumé : Dans les cours d'eau où la disponibilité d'eau est limitée, des fourchettes de débit axées sur la conservation sont souvent adoptées par les gestionnaires de l'eau afin d'assurer la disponibilité d'un écoulement suffisant pour répondre aux besoins écologiques d'organismes aquatiques. Diverses perturbations naturelles et d'origine humaine peuvent toutefois influencer la morphologie du chenal d'un cours d'eau et les caractéristiques du bois dans le cours d'eau au fil du temps, modifiant ainsi potentiellement la disponibilité d'habitats à un débit donné. En utilisant une approche de modélisation hydrodynamique en 2D qui intègre 45 années de données détaillées sur la morphologie du chenal pour le ruisseau Carnation (Colombie-Britannique), l'article examine les relations entre les perturbations passées (causées par l'exploitation forestière) du réseau hydrographique, les changements de la morphologie du chenal et la disponibilité d'habitats pour les saumons cohos (*Oncorhynchus kisutch*) juvéniles pour neuf niveaux de débit. Les résultats révèlent une variabilité considérable de l'abondance d'habitats de salmonidés au fil du temps, même quand les débits modélisés sont maintenus constants. Des compromis entre la disponibilité de différents types d'habitats sont en outre observés à mesure qu'augmentent les débits. Enfin, les résultats de la modélisation indiquent que la disponibilité d'habitats baisse après des coupes passées. Ces constatations donnent à penser qu'il est pertinent de tenir compte, au moment d'établir les débits à allouer, des perturbations passées du réseau hydrographique qui ont une incidence sur la forme et la fonction du chenal. [Traduit par la Rédaction]

Introduction

The quality and quantity of aquatic habitat supporting juvenile salmonids can be conceptualized as a product of five primary components in stream channels and in the broader surrounding landscape: hydrology, biology, geomorphology, water quality, and connectivity (Annear et al. 2004). These components interact to create temporal variability in habitat through changes in the daily, seasonal, and annual inputs of energy and resources as well as changes in the structural elements provided by the stream channel and adjacent riparian area. A common watershed management priority is to ensure that the quantity and timing of flows required for different aquatic species, their life stages, and varied life histories are maintained (Jowett 1997; Richter et al. 1997; Bradford and Heinonen 2008). However, changes in stream channel morphology and associated structural elements can influence the quantity and quality of suitable habitats available for a given flow level (Fabris et al. 2017; Reid et al. 2020). Similarly, watershed disturbances that alter stream channel form via changes in sediment regimes or riparian function can enact long-lasting disruptions to aquatic habitat conditions, regardless of water availability and timing (Chapman 1962; Murphy et al. 1986; Tschaplinski et al.

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2004; Tschaplinski and Pike 2010, 2017; Moore and Richardson 2012).

Streamflow timing and volume can be affected through land cover changes (Moore and Wondzell 2005), variations in climate (Hodgkins 2009; Wu et al. 2012), flow diversions (Nilsson et al. 2005; Gibeau et al. 2017), and direct stream and aquifer withdrawals (Shank and Stauffer 2015). However, the explicit effects of this variability in streamflow on salmonid habitats depend strongly on many factors, including localized physical stream channel characteristics (Cederholm et al. 1997; Hafs et al. 2014), watershed-specific hydrologic storage and release mechanisms, time of year (Tschaplinski and Pike 2017), and, importantly, sensitivity of the local aquatic species to flow reductions or consequent water temperature changes (Eliason et al. 2011). Commonly, streams in forested mountain environments are in a state of adjustment to episodic and spatially discrete formative processes such as landslides and debris flows, which may be a product of both natural and anthropogenic disturbances (Nakamura and Swanson 1993; Hoffman and Gabet 2007; Reid et al. 2019). In these environments, land surface changes can lead to variation in the abundance and characteristics of in-stream wood (Murphy and Koski 1989; Hassan et al. 2016) and channel stability, geometry, substrate texture, and morphology (Hoffman and Gabet 2007).

To ensure that adequate streamflow is available to maintain functionality of stream habitats, a variety of methods have been developed to estimate the timing and quantity of discharge required (Tharme 2003; Annear et al. 2004; Linnansaari et al. 2013), often termed in-stream flow needs or requirements (hereinafter just IFN) and also environmental flow needs. Common across many of the routine IFN methods is the adoption of a series of conservative flow levels or preferred flow ranges outside of which habitat conditions are considered suboptimal. Importantly, most of these flow-based approaches assume that the quantity and quality of habitat produced at each flow level is constant through time, regardless of variability in channel form or other elements important for habitat. However, relatively few studies (Thompson and Lee 2000; Rice et al. 2001; Pess et al. 2002; Benda et al. 2004; Rice 2017) have assessed the relationship between geomorphic variability and habitat availability, providing clues about how channel or watershed disturbance history might affect this interaction with streamflow and habitat availability at a given flow level.

To explore this topic, this study uses a 2D hydrodynamic modelling approach incorporating 45 years of channel bed survey data from Carnation Creek, British Columbia, a small salmon-bearing stream on southwestern Vancouver Island, Canada. This study builds upon two previous papers that have examined (*i*) long-term change in channel morphology in Carnation Creek (Reid et al. 2019) and (*ii*) connections among sediment supply conditions, channel morphology, and temporal habitat variability (Reid et al. 2020). The primary focus of the present work is to evaluate the implications of morphology-driven habitat change (via five flow-based variables) in relation to nine common IFN flow levels and to explicitly investigate the effect of legacy watershed disturbance on habitat availability at these flow levels. This study concentrates on habitat metrics relevant to juvenile coho salmon (*Oncorhynchus kisutch*) during summer low-flow conditions from 1 May to 30 September. These metrics include a range of habitat types ranging from low-velocity pool areas with wood cover important for juvenile coho rearing to high-velocity flow areas that juveniles tend to avoid (Bjornn and Reiser 1991; Beecher et al. 2002).

This paper has three broad objectives: (*i*) to briefly describe the Carnation Creek watershed experiment, evolution of stream channel morphology, and disturbance state over the 45-year data record; (*ii*) to examine the trends and implications of variability across five flow-driven aquatic habitat metrics for nine management flow levels ranging from very low (the lowest 7-day flow occurring once every 10 years — 7Q10) to higher than average (400% of mean annual discharge — MAD); and (*iii*) to compare and contrast pre- and postharvest channel disturbance conditions with focus on relationships between habitat area and streamflow.

This study aims to address the following research questions:

(1) Are certain IFN flow levels more sensitive to temporal variability in channel morphology than others?

(2) Do higher flow levels always produce improved or increased habitat availability?

(3) What are the trade-offs between habitat metrics as flow levels change?

(4) Can a channel with legacy watershed disturbances provide similar habitat to an undisturbed channel?

Methods and data

Study area

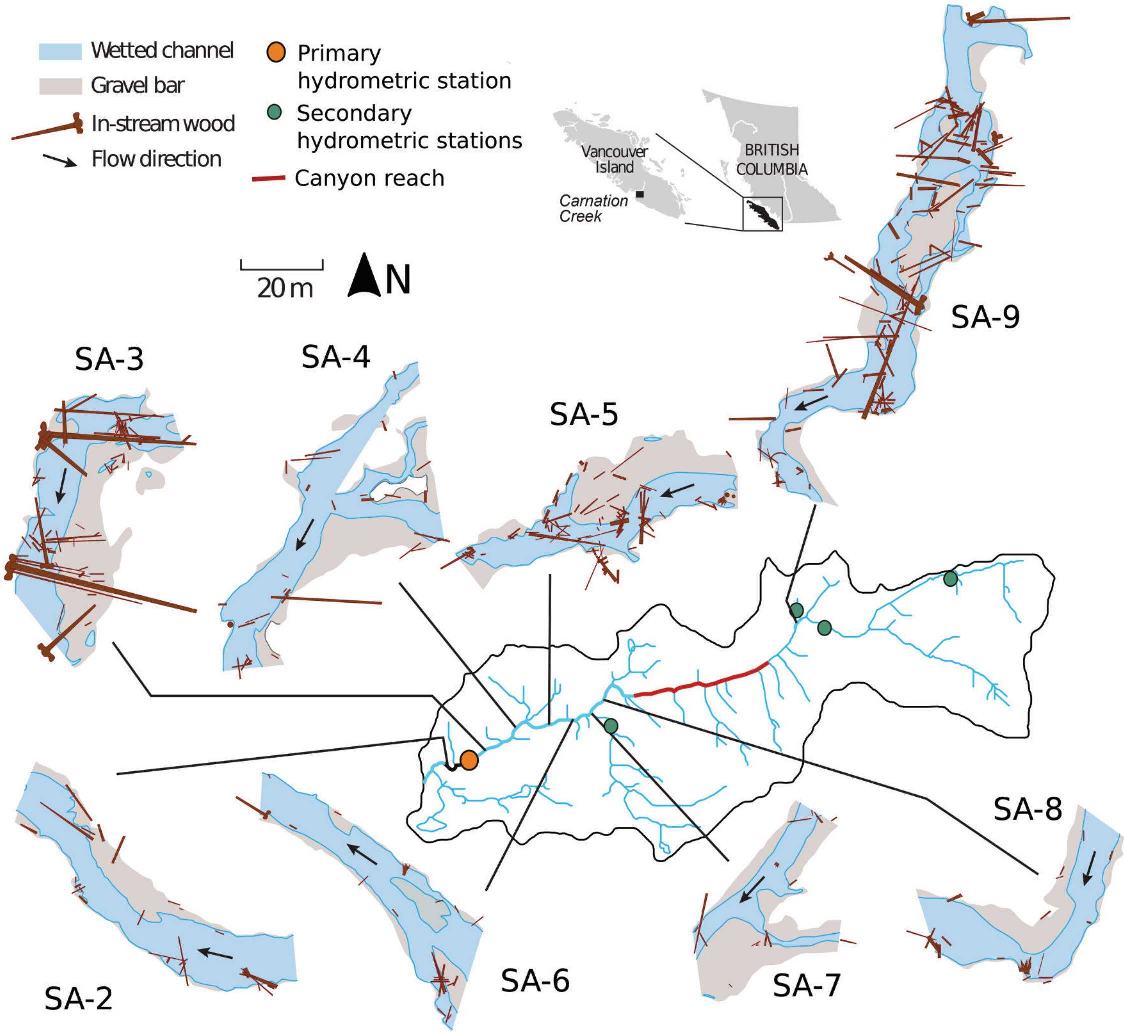
This study uses data collected within the Carnation Creek Experimental Watershed. This research site was established in 1970 to investigate the influence of forest practices of the day on physical and biological watershed processes and salmon populations (Hartman and Scrivener 1990; Tschaplinski and Pike 2017). Component studies of this ongoing project include examination of channel morphology, aquatic ecology, and linkages among climate, hydrology, and watershed processes (Tschaplinski and Pike 2017). The 11.2 km^2 basin (Fig. 1) is located on the southern shore of Barkley Sound, on southwestern Vancouver Island, British Columbia. Several anadromous salmon species inhabit Carnation Creek, including chum salmon (*Oncorhynchus keta*), coho salmon, steelhead trout (*Oncorhynchus mykiss*), and sea-run cutthroat trout (*Oncorhynchus clarkii*) (Tschaplinski and Pike 2017).

The Carnation Creek watershed was glaciated during the most recent glacial maximum, and till varying in depth from 0.15 to >2 m covers Jurassic volcanic bedrock. Catchment relief exceeds 900 m, and steep gradients greater than 40% are found throughout the watershed (Hartman and Scrivener 1990; Tschaplinski and Pike 2017). This glacial legacy has resulted in a catchment configuration with hillslope–channel coupling (Nakamura and Swanson 1993) and colluvial sediment delivery in headwater regions and in a confined section of channel referred to as the "canyon reach" (Zimmermann et al. 2004; Reid et al. 2019; see Fig. 1). Sediment delivery events have occurred sporadically over the period of record, with the largest debris flows associated with a large storm in 1984 (Hartman and Scrivener 1990; Reid et al. 2019). The lower 2.9 km of stream is generally buffered from direct hillslope processes by a floodplain that is up to 200 m wide.

The climate of the watershed is temperate and humid, and the hydrological regime is rain-dominated. Annual precipitation ranges from ~2900 mm near sea level to more than 4800 mm at higher elevations. Most rainfall occurs during autumn and winter storms, often resulting in flows above 20 $m^3 \cdot s^{-1}$ (Reid et al. 2019). Flows during summer months are generally low, usually below 0.1 $m^3 \cdot s^{-1}$ (Fig. 2). The primary channel morphology is pool–riffle, with gradients typically less than 1%, and active channel width averages ~ 15 m. Numerous wood accumulations (logjams) and individual pieces can be found within the channel and are often associated with both pools and sediment accumulations. Apart from sporadic small sand patches, streambed sediment texture ranges from gravel (median size 20–40 mm) near the river mouth to cobbles and boulders (median size > 128 mm) in the canyon reach and headwaters. Large bars spanning over one-half the channel width are common both upstream and downstream of the canyon reach.

The Carnation Creek watershed experiment is a pre- versus postharvest observational study design that focusses on both watershed- and channel-scale processes. After 5–6 years of preharvest baseline data collection (starting 1970–1971 depending on the variable studied), 41% of the watershed was logged over a 6-year period from 1976 to 1981 (Hartman and Scrivener 1990), with the postlogging phase of the experiment extending to present time

Fig. 1. Carnation Creek watershed and location of hydrometric stations and eight channel morphology study areas. Maps shown correspond to 2015 channel survey at ~200% mean annual discharge (MAD; 1655 L·s⁻¹). The confined canyon reach is illustrated as a red line. Maps were created using the R programming language and ArgGIS 10.6; map data were collected by the authors. [Colour online.]



(Tschaplinski and Pike 2017). Three riparian harvest treatments were included in the study. A riparian buffer varying in width from 1 to 70 m was left along the lowermost 1300 m of stream, followed by two clear-cut treatments each 900 m long. The first clear-cut segment entailed harvesting to the stream's edge, with cross-stream falling and yarding and limited in-stream salvage of windthrown trees (termed intensive clear-cutting). The second clear-cut segment involved harvesting up to the banks, but no cross-stream or in-stream activity was permitted (termed careful clear-cutting). Given the complex riparian disturbance history and relatively narrow retention strips, the logging effect along the channel is treated as a binary for this study, with preharvest conditions up to 1976 and postharvest thereafter.

Hydrometric, channel morphology, and wood data

Carnation Creek datasets include detailed information on hydrologic, geomorphic, and in-stream wood. This study uses a portion (45 years, 1971–2015) of the ongoing collected data record. Channel topography surveys have been conducted annually in eight study channel areas (referred to as "SA" hereinafter) since 1973 and since 1971 in four of the eight sites (Fig. 1; Table 1). Seven of these (SA-2 to SA-8) are spaced 300–500 m apart along the lower 3 km of channel, overlapping with anadromous fish presence. The eighth (SA-9) is located ~5.6 km upstream from the river mouth and is upstream of anadromous fish activity. Individual study areas range in length from 5 to 15 bankfull channel width (w_b) equivalents, possess gradients of between 0.5% and 1.5%, and vary in topographic complexity and wood abundance (Reid et al. 2020).

Topographic channel data were collected along cross-sections spaced 1–3 m apart in each SA until 2008, when the cross-section survey approach was replaced with a feature-based total station survey. Survey errors are low, typically in the order of 1–2 cm. No data were collected in 2010 in any study area, nor in SA-9 in 1990. Digital elevation models (DEMs) of 10-cm resolution were generated from interpolated annual survey data using the R programming language (R Core Team 2019) and the "Raster" package (Hjimans 2019).

Data on wood piece positions and dimensions have also been collected in all SAs since 1973 (since 1971 in SA-2, SA-3, SA-6, and SA-8). To incorporate wood data into the analysis of the 2D hydrodynamic model output, wood pieces were digitized from annual study area maps. However, it was not possible to locate some original wood piece maps from the mid- and late 1990s for some SAs, and no maps were available for 1999 and 2000. Where wood data are absent, maps before and after the gap were examined for similarity in wood abundance and position, and if similar, the record was filled with the last year of data prior to the gap to

Fig. 2. Daily average flows over the 45-year period of record collected at the primary hydrometric station between SA-2 and SA-3 (see Fig. 1). Note the period of low flows from 1 May to 30 September. [Colour online.]

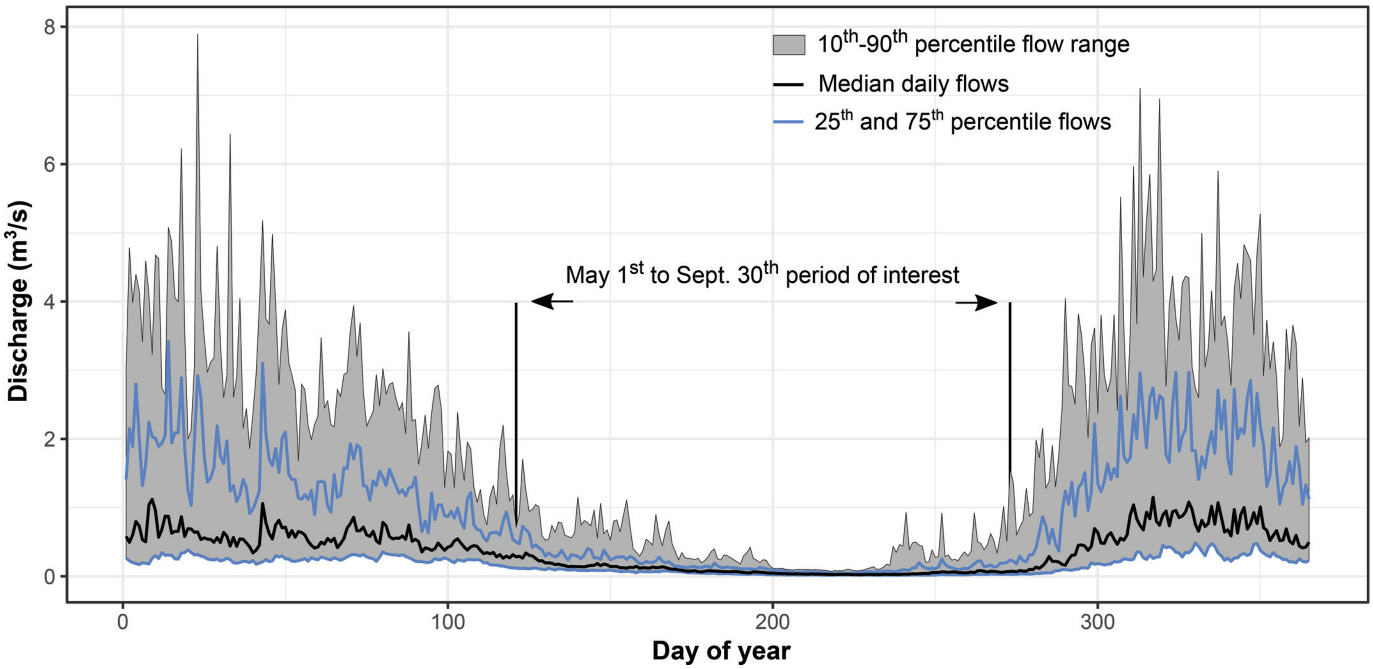


Table 1. Study area characteristics (1971–2015 average values).

Study area	Length (m)	w_b[a]	d_b[b]	Slope (%)[c]	Wood pieces	Wood vol. ($m^3 \cdot m^{-2}$)	Treatment	Riparian harvest date	Surveyed since
SA-2	82	13.8	0.99	0.73	35	0.03	Buffer	1976[d]	1971
SA-3	68	19.6	0.97	0.36	40	0.07	Buffer	1978[d]	1971
SA-4	62	21.2	0.42	1.35	44	0.04	Buffer	1978[d]	1973
SA-5	75	13.7	0.61	0.91	47	0.04	Intensive	1976[e]	1973
SA-6	70	14.9	0.74	0.53	24	0.01	Intensive	1976[e]	1971
SA-7	51	19.6	0.77	0.86	23	0.01	Intensive	1976[e]	1973
SA-8	58	16.9	0.87	0.95	39	0.05	Careful	1978[f]	1971
SA-9	148	11.0	0.59	1.90	95	0.08	Careful	NA[g]	1973

[a]Average channel width (m).
[b]Average bankfull depth (m).
[c]Slope calculated from fit line along thalweg.
[d]Variable riparian buffer strip left (2–70 m).
[e]Intensive harvesting treatment: all riparian vegetation removed inside and outside of stream channel.
[f]Careful harvesting treatment: woody riparian vegetation removed, no instream activities or yarding.
[g]No riparian harvesting occurred along SA-9.

approximate the record. Further details of geomorphic and wood data collection can be found in Reid et al. (2019).

Hydrological data have been collected at several locations in the watershed, including from a Water Survey Canada hydrometric station (Station ID WSC–08HB048, Carnation Creek at the mouth). Discharge data from this station was used to generate flow level statistics. Nine flow levels were calculated as input for the hydrological modelling scenarios, ranging from 7Q10 to 400% MAD or 6 to 3310 $L \cdot s^{-1}$ near the river mouth (Table 2). These flow levels encompass nearly the full range of flow conditions typical of the period from 1 May to 30 September (Fig. 2). As flow data were not recorded directly in most study areas, discharge at the Water Survey Canada hydrometric station was scaled by contributing source area upstream of the midpoint of each study area (Table 2). This relationship was derived by fitting flows from the primary and four secondary hydrometric stations (Fig. 1) against contributing area upstream of each station.

Depth and velocity simulations

To evaluate the availability of aquatic habitat at different flow levels through time, we used the Nays2DH hydrodynamic model (Nelson et al. 2016) to simulate 2D depths and velocities in all study areas. While the input data for this model do not capture details of all structural channel elements relevant to salmonid habitat (e.g., overhanging and undercut banks, grain-scale features), the long temporal record of channel bed topography is valuable for assessing patterns in aquatic habitat. Approximately 2700 individual model simulations were run, incorporating nine flow levels of interest for each SA for each year (Table 2). As with other 2D hydrodynamic models, boundary conditions include a channel bed DEM and downstream water surface elevation for each flow level and a roughness value (Manning's n). All simulations were run through the International Rivers Interface Cooperative (Nelson et al. 2016).

Empirical stage–discharge rating curves were generated from historical channel survey and discharge data to obtain downstream water surface elevations for each flow level in each SA. Simulation runtimes ranged between 800 and 1000 s, depending on the specific SA and flow level. Model timestep was 0.01 s, the default for the program, and calculation grid with cells of 1 m^2 were used during simulations. A Manning's n value of 0.04 was

Table 2. Flow level parameters.

Study area	Area[a] (km²)	7Q10	95P[b]	3% MAD	5% MAD	10% MAD	20% MAD	40% MAD	100% MAD	400% MAD
SA-2	10.1	6.0	19.0	24.8	41.4	82.8	165.5	331.0	827.5	3310.1
SA-3	9.3	5.9	18.8	23.1	38.5	77.0	153.9	307.8	769.6	3078.3
SA-4	8.7	5.8	18.6	21.8	36.3	72.7	145.3	290.6	726.5	2906.2
SA-5	8.1	5.7	18.1	20.1	33.5	66.9	133.9	267.8	669.4	2677.8
SA-6	7.8	5.7	17.8	19.5	32.4	64.9	129.7	259.5	648.7	2595.0
SA-7	7.6	5.7	17.6	18.9	31.5	63.1	126.1	252.2	630.5	2522.2
SA-8	7.4	5.6	17.4	18.3	30.5	61.0	122.0	243.9	609.8	2439.4
SA-9	3.8	5.1	11.3	9.5	15.8	31.5	63.0	126.1	315.2	1260.8

Note: All units for discharge are in litres per second.
[a]Contributing area to centre of the study area.
[b]95th percentile flow represents a flow that is equal to or exceeded 95% of the time in May to September flow record.

used for all sites and simulations, a typical value for high-roughness gravel bed streams. While Nays2DH has the option to include features such as wood pieces as flow obstacles, uncertainty surrounding wood contact with the channel bed led to the decision to exclude wood from the simulations and to reincorporate the wood information in the analysis stage. Based on field observations of wood in the SAs, a presumption was made that, at the low modelled flows, wood pieces would have minimal effect on the flow field. Further details of hydrodynamic modelling approach and implementation with Carnation Creek data can be found in Reid et al. (2020).

Assessment of model performance

Given the impracticality of calibrating the large number of simulations individually, model output was instead compared with field-measured water depths and velocities. In the summer and fall of 2017, over 60 depth and velocity point measurements were taken in three study areas (SA-2, SA-3, and SA-7) using a SonTek Flow Tracker Acoustic Doppler Velocimeter in flow conditions ranging from 12 to 1300 L·s^{-1}. Velocity measurements were taken at positions of 0.6 times the depth below the water surface. Nays2DH simulations were run using the same flows and bed surfaces as those present during the field data collection, and results were compared. To best capture temporal and spatial variability, we also checked reach-averaged widths, depths, and velocities against 30 DEMs and historical flow conditions sampled from the 45-year record. Width and depths were extracted from the water surface elevations at the times of surveys, and velocities (V) were calculated as $V = Q/w_b \times D$, where Q is study area discharge (scaled), w_b is the bankfull channel width, and D is the mean depth. In addition, an assessment of model output sensitivity to study area length was performed by duplicating and appending DEMs in SA3, SA-6, and SA-8 to generate double-length segments and comparing output of simulations in these reaches with simulation results from the regular model output.

Model performance is summarized in Fig. 3. Overall, the model performed well when evaluated against field depth and velocity point measurements. Mean prediction error in depth was ±0.12 m, and velocity was ±0.23 m·s^{-1}. Nays2DH tends to slightly overpredict low velocities and underpredict higher velocities. Reach length (Fig. 3*f*) did not have a meaningful effect on model output, with differential results in the order of 1% of channel area. While the model performed well when evaluated against field data, the authors are aware of the limitations of such an approach in small streams with rough boundaries but deem it acceptable for the purposes of exploring the study objectives.

Model output analysis

To evaluate temporal and disturbance-driven dynamics in modelled habitat, five flow-based habitat variables were selected: (*i*) total pool area (Tp); (*ii*) pool area with wood cover (Pwc); (*iii*) high-velocity wetted area (Hv); (*iv*) shallow water area (Sw); and (*v*) mean wetted width (Ww) (Table 3). Collectively, these variables capture a range of aquatic conditions, both optimal and suboptimal, for juvenile coho salmon (see Bjornn and Reiser 1991).

To quantify the availability of habitat for each variable, depth and velocity rasters of 1 m² resolution were produced from the model output for each simulation. Once generated, raster areas were selected within the defined value range of each variable, and the area of each variable was calculated. To determine the quantity of pool area overlain by wood pieces (Pwc), we cropped areas of flow rasters falling into the pool criteria by wood piece polygons, and the cropped areas were subsequently quantified. The resulting dataset includes time series of each variable, at each flow level, for each study area, over the 45-year record. All analysis was completed with the R programming language using packages "Raster" (Hjimans 2019) and "RGDAL" (Bivand 2019).

To evaluate the effect of timber harvesting on habitat availability and to characterize the relationship between discharge and habitat abundance, we used a nonlinear mixed-effects (NLME) modelling approach. Mixed-effects models account for both a lack of independence among repeated measures within groups and for differences in variation due to group characteristics. For the Carnation Creek dataset, the data are grouped by study area; each study area contains 45 observations for each of the nine flow levels, corresponding to a series of annual observations. The "mixed effects" of such models therefore include a combination of fixed and random effects. In this analysis, the fixed effect quantifies habitat area by discharge, while two random effects account for variance attributed to study area and to the harvest state. This structure also allows the entire dataset to be analysed in a single model (per habitat variable), negating the need for multiple comparisons. Following initial analysis, the relationship between discharge and habitat was found to be strongly nonlinear, and a logistic-growth function was deemed a more appropriate model. A model of this type will take the following form:

$$(1) \qquad y = \frac{a}{1 + e^{-\left(\frac{x-b}{c}\right)}}$$

where a represents the model asymptote, b is the sigmoid midpoint, c is the logistic growth rate (or scale), and x is the independent variable. Additional details of nonlinear mixed effects models can be found in Stegmann et al. (2018).

To assess the role of watershed disturbance history on habitat availability at different flow levels, input data were characterized as either preharvest (before 1976) or postharvest (after 1976) time periods, regardless of the specific riparian treatment. To fit the models, we used the R package "lme4" (Bates et al. 2019), and data attributes were assigned into fixed (discharge) and random (study area, harvest state) effects. The significance of harvesting on habitat availability was assessed using a likelihood ratio test between a model fit with "harvest state" as a predictor and a model where "harvest state" was omitted.

Fig. 3. Evaluation of model performance: (*a*) modelled versus measured depth, point measurements; (*b*) modelled versus measured velocity, point measurements; (*c*) modelled versus measured depth, SA-averaged; (*d*) modelled versus measured velocity, SA-averaged; (*e*) modelled versus measured wetted width, SA-averaged; (*f*) model performance comparing areas extended versus regular reaches.

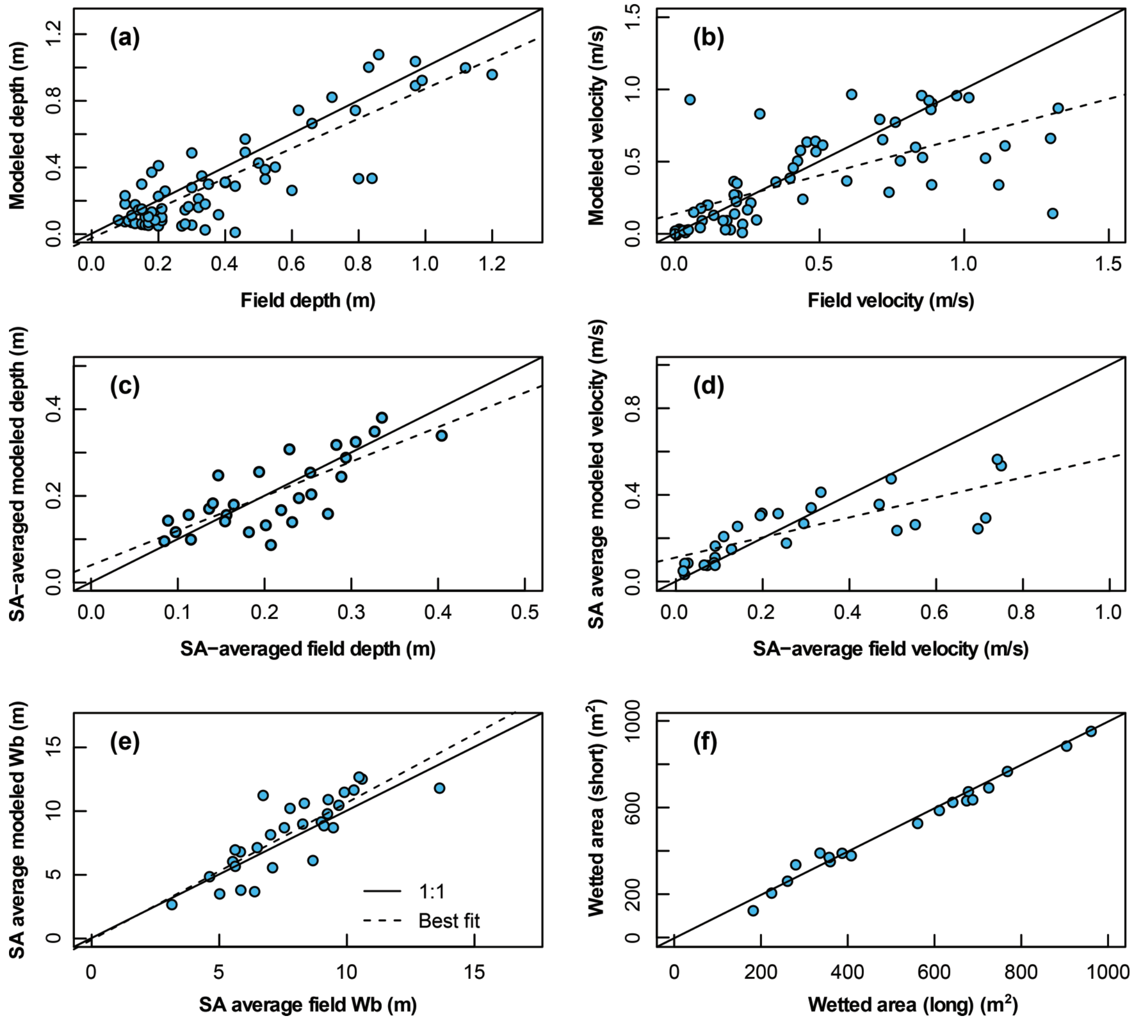


Table 3. Habitat variables and definitions.

Variable	Symbol	Definition
Total pool area	Tp	All wetted area of depth > 0.1 m and velocities < 0.6 $\mathrm{m \cdot s^{-1}}$
Pool area with wood cover	Pwc	Tp overlain by wood pieces
High-velocity water area	Hv	All wetted area of velocities > 0.6 $\mathrm{m \cdot s^{-1}}$
Shallow water area	Sw	All wetted area < 0.1 m depth
Mean wetted width	Ww	Modeled wetted area > 0.02 m depth divided by reach length

Results

Temporal trends and variability of modelled habitat

Overall, channel morphology and in-stream wood at Carnation creek varied through time for all study areas (Fig. 4). Normalized bed elevation averaged over all study areas (Fig. 4*a*) increased by ~0.2 m between 1978 and the late 1980s, remaining elevated until the late 1990s, and then degraded to preharvest levels by 2002. Departures in sediment storage (Fig. 4*b*), the combination of change in elevation and width, shows no trend until 1978, when an increase occurred, peaking in 1989. There was a decline in storage from 1997 to 2001, followed by small-scale fluctuation. Channel width (Fig. 4*c*) generally increased to a maximum positive departure of 2.5 m in 1997, followed by a rapid narrowing to 2000, and another reduction near 2005. Finally, departures in wood storage (Fig. 4*d*) show a general increase until 1985, a decline to 1998, and relatively stable values until 2011.

The variation in channel morphology and in-stream wood translates to differences in habitat availability during the study period (Figs. 5*a*–5*d*). Total pool area (Tp) declined gradually for all flow levels ≥ 5% MAD. From 40% to 400% MAD, Tp displayed a distinct (decadal) oscillating downward trend. At 400% MAD, up to 47% of the active channel area can be occupied by pool habitat, while only 2%–3% of the study area is occupied at the 7Q10 flow level.

Pool area with wood cover (Pwc) showed a complex temporal pattern (Fig. 5*b*) with two rapid declines. At most flow levels, similar patterns to Tp were detected, with an increase in Pwc through the late 1970s, followed by a period of fluctuating values to the late

Fig. 4. Plots of departures in (*a*) bed elevation, (*b*) sediment storage (scaled to channel area), (*c*) channel width, and (*d*) wood volume. All panels show results grouped across all study areas. The dashed line corresponds to the start of timber harvesting activities in the Carnation Creek watershed.

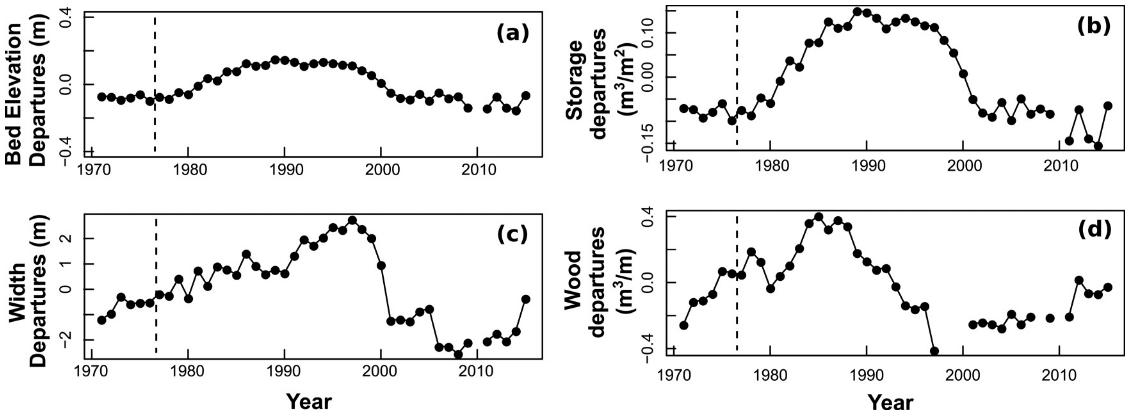
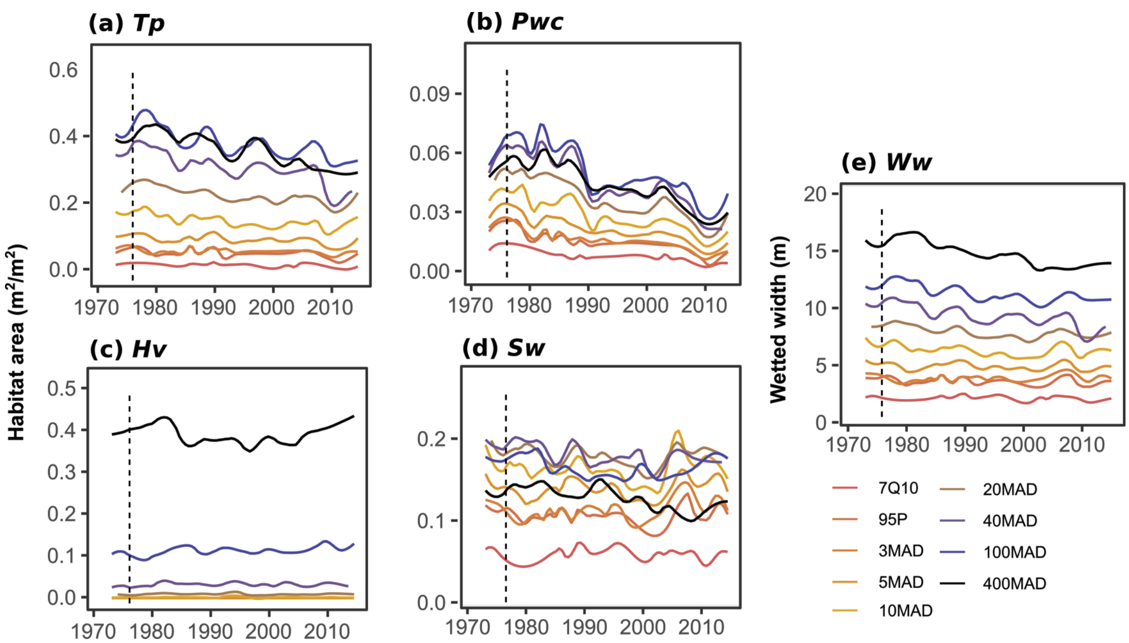


Fig. 5. Time series of modelled habitat for the five variables of interest: (*a*) Tp = total pool area; (*b*) Pwc = pool area with wood cover; (*c*) Hv = high-velocity wetted area; (*d*) Sw = shallow water area; (*e*) Ww = mean wetted width. Plots have been smoothed with a loess function of span 1.7 for ease of interpretation. Vertical dashed line corresponds to beginning of harvesting period at Carnation Creek. Results are grouped across all study areas. [Colour online.]



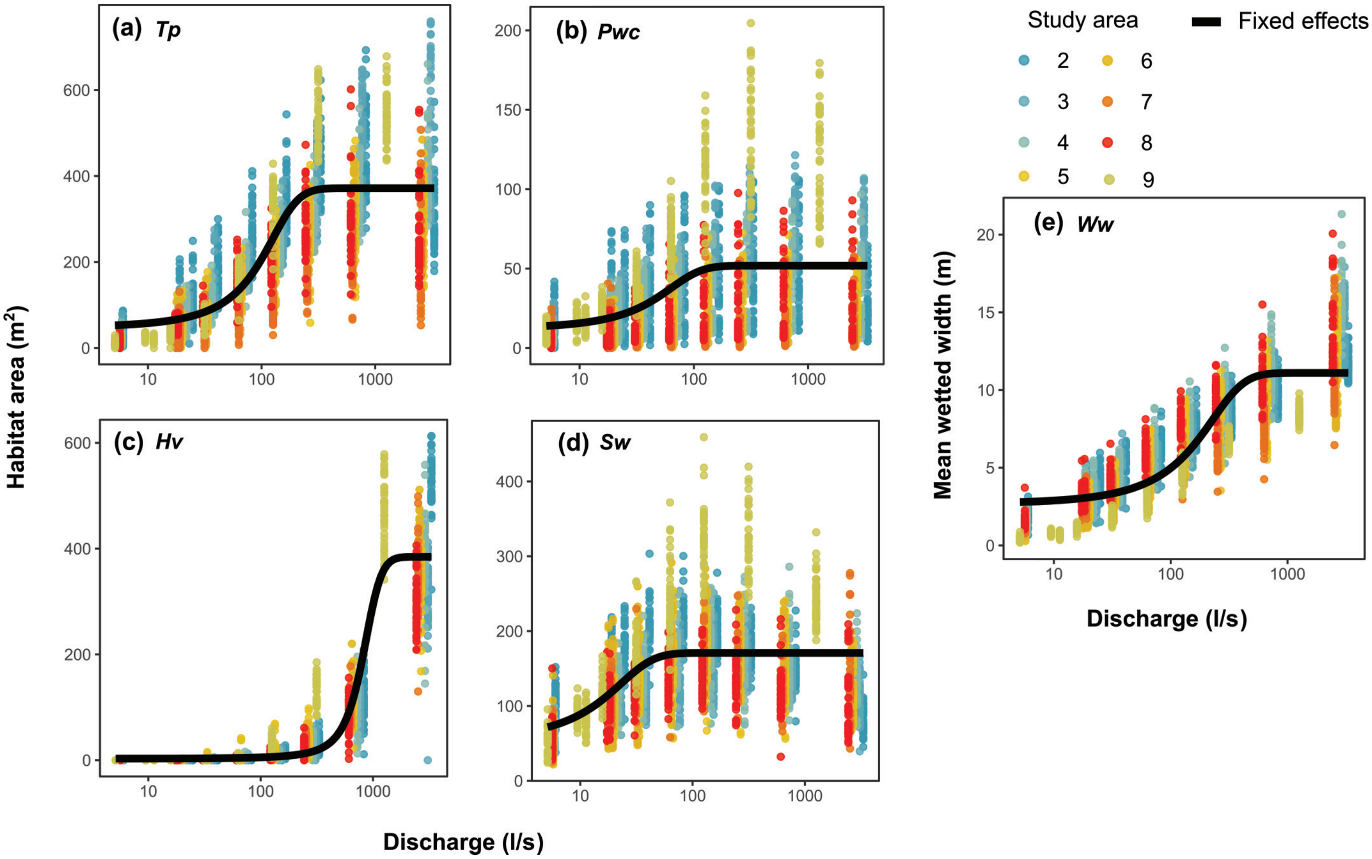
1980s, and then a rapid decline. Post-1990, Pwc remained relatively constant but declined rapidly (for the highest flow levels) again after 2005 with a slight increase post 2012. Trends at flows less than 10% MAD were relatively subtle, while flow levels from 40% to 400% MAD produced similar Pwc availability. Overall, less than 7% of the active channel area is typically occupied by Pwc at the highest flows.

High-velocity (Hv) wetted areas (i.e., >0.6 m·s^{-1}; Fig. 5*c*) displayed a different temporal pattern to the pool-related variables (Tp and Pwc). Below 40% MAD, minimal Hv was present, but occupied up to 43% of channel area at 400% MAD. At 400% MAD, availability of Hv increases to the early 1980s, declined rapidly, then remained similar until the mid-2000s, after which it increased above preharvest levels. At 100% MAD, Hv displayed minor fluctuations with no discernable trend through time. From 2000 to 2015, opposite trends are apparent between Tp (Fig. 5*a*) and Hv (Fig. 5*c*) at 400% MAD.

Shallow water (Sw) habitat area (Fig. 5*d*) displayed the most variable and complex interannual temporal patterns. Flow levels below 20% MAD displayed an oscillating pattern that spiked in the mid- to late 2000s. Flow levels ≥ 40% MAD displayed different long-term patterns, with Sw declining through time at 400% MAD, but increasing slightly after 2000 for 100% MAD. Modelled Sw ranged between 5% and 20% of the active channel area, depending on flow level.

Mean wetted width (Ww) (Fig. 5*e*) displayed the lowest degree of temporal variability. Maximum Ww occurred at the highest flow levels (i.e., 400% MAD). From 40% to 400% MAD, a minor increase in width occurred to 1980, after which a consistent decline is observed. Flows at 20% and 10% MAD displayed a similar pattern, with minor declines until the late 1990s and then an increase to the mid-2000s. Results for flows < 5% MAD display little evidence of a long-term trend. At 400% MAD, width averaged up to 15 m. At 7Q10, Ww averages were close to 2 m.

Fig. 6. Raw data from Nays2DH model output with logistic growth model fit overlaid for (*a*) pool area; (*b*) pool area with wood cover; (*c*) high-velocity wetted area; (*d*) shallow water area; and (*e*) mean wetted width. Each coloured point corresponds to a single year of data for each study area and flow level. Model fit includes all data; individual study area models can be found in the online Supplementary materials, Figs. S1–S5[1]. [Colour online.]



Relationships between flow level and habitat availability

Relationships between habitat availability and flow level across the full dataset are shown in Fig. 6, with study area relationships shown in the online Supplementary Figs. S1–S5[1]. Overall, the logistic growth models fit the data well, but the shape of the models differ between variables. For Tp (Fig. 6*a*), values steadily increase from low flows and reach an asymptote (i.e., average maximum habitat provided across study areas) of 372 m² near 400 L·s⁻¹ (50% MAD) near the river mouth. The most rapid increase in habitat with added flow is between 60 and 120 L·s⁻¹, ~7% and 15% MAD near the river mouth.

The model fit for Pwc (Fig. 6*b*) illustrates a similar steady increase from low flows from a site-average minimum near 15 m², but reaches the asymptote sooner, close to 190 L·s⁻¹ with a value of 52 m². This corresponds to a maximum occurring between 20% and 40% MAD, depending on position along the channel. The most rapid increase in Pwc with added flow is between 20 and 70 L·s⁻¹ or ~3% to just below 10% MAD.

The model for Hv (Fig. 6*c*) displays a distinct shape from the pool-based variables. Very little Hv is present at flows below 200 L·s⁻¹ (~25% MAD), but area increases rapidly between 600 and 1100 L·s⁻¹ (~75% to 130% MAD) and reaches the site mean asymptote of 383 m² near 2000 L·s⁻¹, or ~240% MAD, again depending on location along the channel.

The relationship between flow level and Sw habitat area (Fig. 6*d*) shows an elevated minimum near 75 m² at the lowest flows and a rapid increase to the asymptote. The most rapid gains in Sw area are at the lowest flows, with continually diminishing returns at higher discharges. The asymptote of 171 m² is reached at ~100 L·s⁻¹, slightly above 10% MAD.

For mean wetted width (Ww; Fig. 6*e*), the logistic shape of the model fit is more subtle, approaching a log-linear form. Ww increases most rapidly between 60 and 180 L·s⁻¹, or between 10% and slightly more than 20% MAD. The Ww model asymptote is reached near 700 L·s⁻¹ (85% MAD near the river mouth) with a SA-averaged value of 11.1 m.

While the logistic growth model fits the data well, in some cases a decrease in habitat area is apparent at higher flows. This is apparent in several individual study areas for Pwc (Fig. 6*b*) but is more pronounced for Sw (Fig. 6*d*; also see Fig. 7*d*), where most study areas display some degree of reduction in Sw area.

Habitat response to historical forest harvesting

The significance of legacy forestry disturbances in affecting habitat was examined using a likelihood ratio test, with discharge and study area as the control variables and harvesting state as the test variable (Table 4). For all variables, the nonlinear mixed effects models fit with "harvest state" as a predictor yielded significantly different predictions from models fit without "harvest state" as an explicit variable. Generally, the fixed effects show that harvesting reduced the asymptote or the stable amount of habitat area reached once flow exceeded a given threshold. This difference in habitat availability following harvesting is further summarized in Fig. 7. In the case of Tp (Fig. 7*a*), preharvest values are

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2020-0120.

Fig. 7. Boxplots of habitat availability pre- and postharvesting for the average habitat availability in all study areas for (*a*) total pool area; (*b*) pool area with wood cover; (*c*) high-velocity wetted area; (*d*) shallow water area; and (*e*) mean wetted width. Note that a direct test for significance between pre- and postharvest periods is not possible with a nonlinear mixed effects model. See Table 4 for an evaluation of significance. [Colour online.]

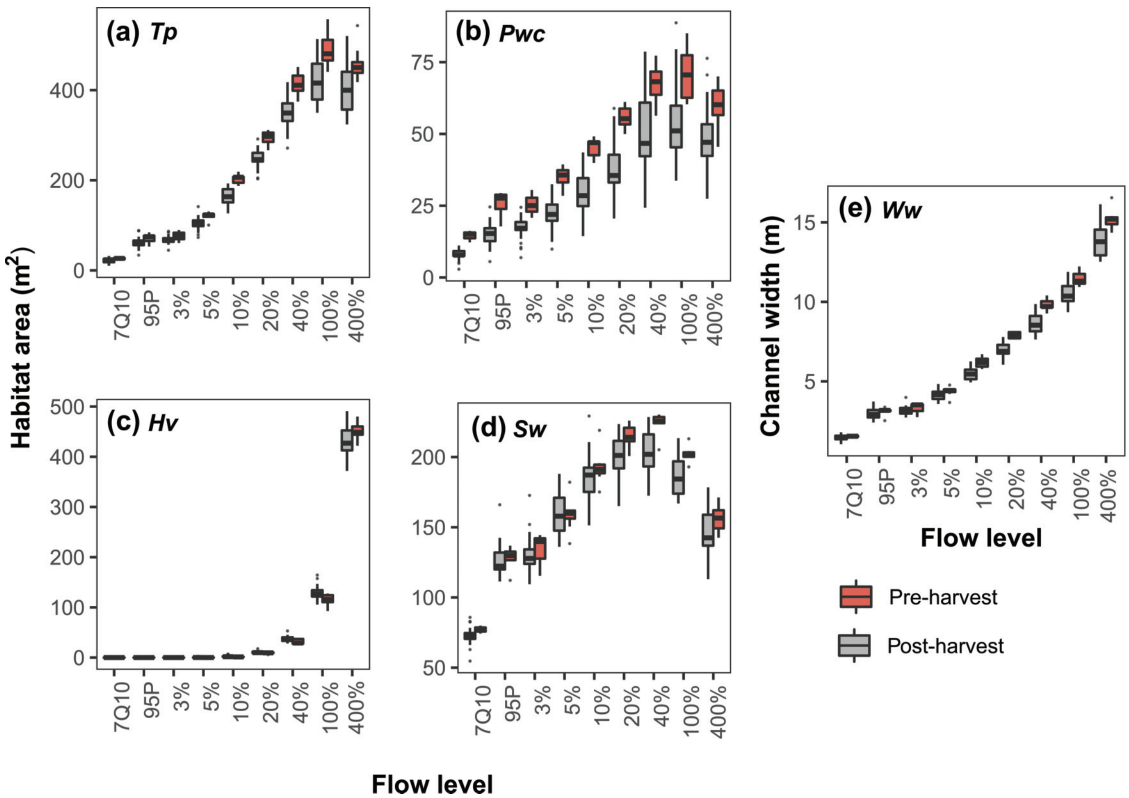


Table 4. Logistic growth model parameters for the fixed effect — with and without harvesting.

	Full model			Reduced[a] model			ANOVA	
Variable	Asymptote	Midpoint	Scale	Asymptote	Midpoint	Scale	*F*	*p*
Tp	372	89.3	46.9	357.8	90.25	46.9	96.9	<0.00002
Pwc	51.8	34.5	29.3	46.1	35.1	29.3	707.8	<0.00002
Hv	384	805	166	382.5	794.4	163.7	107.7	<0.00002
Sw	171	9.07	12.2	168.55	8.9	12.3	140.7	<0.00002
Ww	11.1	122	107	10.79	124.33	107.5	109.1	<0.00002

[a]Harvesting omitted as a predictor variable.

elevated above postharvest values at all flow levels and with little overlap, suggesting a consistent reduction in available habitat postharvesting. Of all variables, Pwc (Fig. 7*b*) displays the greatest difference between pre- and postharvest habitat availability, with a substantial reduction in postharvest area and little overlap between pre- and postharvest data. Hv area (Fig. 7*c*) shows much subtler differences pre- and postharvest, with slightly greater areas postharvest for 20%–100% MAD. Sw area (Fig. 7*d*) again shows a general reduction in habitat area after harvesting, but the postharvest difference is less pronounced at flows below 20% MAD. Ww (Fig. 7*e*) also shows greatest differences at flows above 5% MAD, where preharvest wetted width for a given flow is elevated notably above postharvest width.

The effect of legacy watershed disturbances on habitat availability can be further examined through a comparison of asymptotes from the NLME model (Fig. 8). For Tp (Fig. 8*a*), preharvest asymptotes are greater than postharvest asymptotes in all cases except for SA-8, which changes very little over time. Pwc asymptotes (Fig. 8*b*) are greater preharvest in all sites but SA-3 and SA-8, with the largest reductions in SA-2 and SA-7. Hv (Fig. 8*c*) asymptotes show both increases and decreases, with greater high-velocity area postharvest in SA-7 and SA-8 and slightly more in SA-2. Asymptotes for Sw models (Fig. 8*d*) are similar before and after harvesting for four of eight sites, with notable increase in postharvest asymptotes for SA8 and decreases in SA5–SA7. Finally, asymptotes for Ww (Fig. 8*e*) are greater preharvest with the exception of SA-8.

To determine whether legacy forest practice disturbances have a detectable effect on habitat availability when real hydrological data are considered, the pre- and postharvest logistic growth models were used to predict habitat at the study area level using the full hydrological record (May through September, 1972–2015). For each variable, this analysis results in two predicted time series: one series predicted from the preharvest and one from the postharvest flow–habitat relationship (Fig. 9). For Tp (Fig. 9*a*), the average postharvest reduction in daily average habitat area is 16.5% but ranges from 14% to 23% depending on the flow characteristics of a given season. For Pwc (Fig. 9*b*), a more dramatic reduction of 31.3% occurs, but ranges from 28% to 38% year to year. For daily mean Hv (Fig. 9*c*), there is little difference between pre- and postharvest values, with an average increase of 3.3%, ranging from an increase of less than 1% to 8%. For Sw area (Fig. 9*d*), postharvest

Fig. 8. Asymptotes (i.e., maximum attainable habitat) fit for pre- and postharvest data periods for each study area: (*a*) total pool; (*b*) pool area with wood cover; (*c*) high-velocity wetted area; (*d*) shallow water area; and (*e*) mean wetted width. Values below the 1:1 line indicate greater maximum habitat under preharvest conditions. [Colour online.]

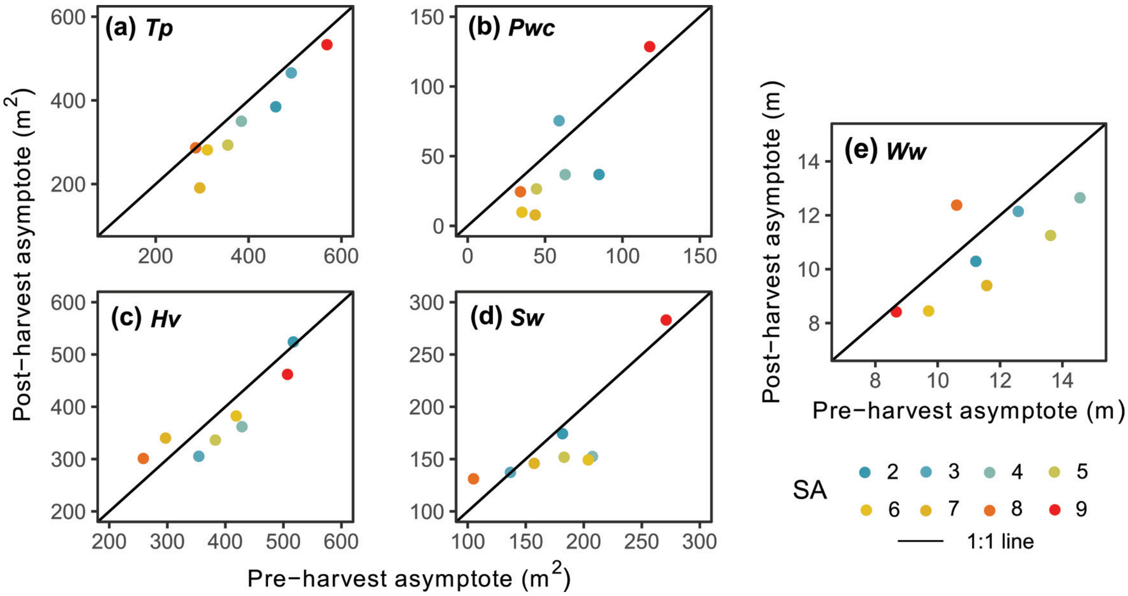
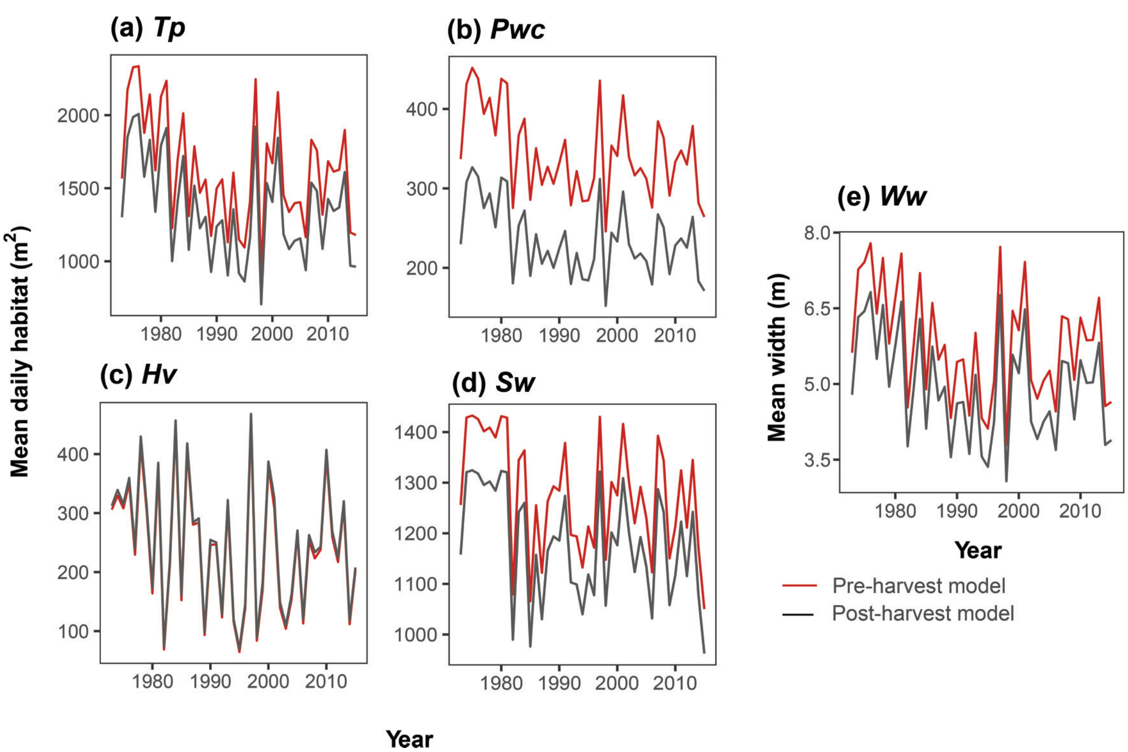


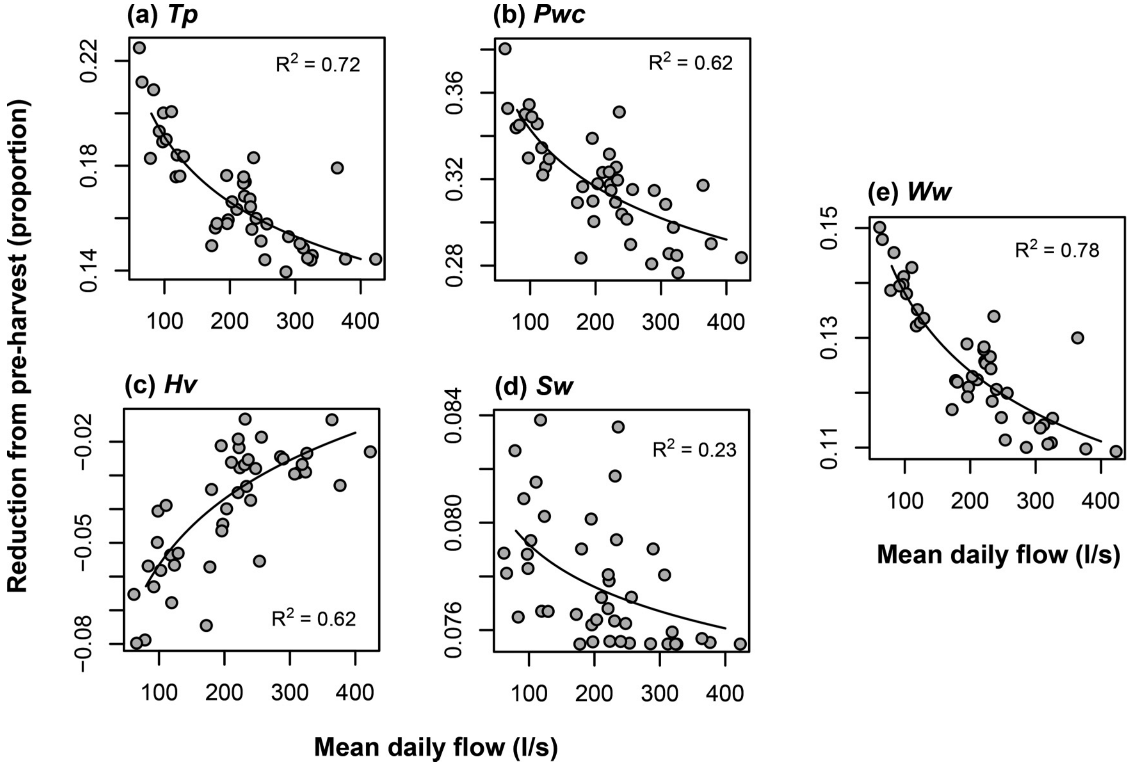
Fig. 9. Mean daily habitat values across 1 May to 30 September over the 45-year period of record for (*a*) total pool area; (*b*) pool area with wood cover; (*c*) high-velocity wetted area; (*d*) shallow water area; and (*e*) mean wetted width. Daily habitat values are predicted using pre- and postharvest logistic growth models for individual study areas, and the results are summed across all study areas, with the exception of mean wetted width (*e*), which was calculated as the average across the study areas. [Colour online.]



models resulted in a reduction of 7.7% and ranges from 7% to 8.5%. Finally, Ww (Fig. 9*e*) was reduced by 12.5% on average, ranging from 11% to 15%.

For all variables, the effect of legacy watershed disturbances on habitat availability over a given season is strongly related to the mean flow conditions for that season (Fig. 10). In the cases of Tp, Pwc, and Ww (Figs. 10*a*, 10*b*, and 10*e*, respectively), the effects are most pronounced during the driest seasons and least pronounced during the wettest. For Sw (Fig. 10*d*), there is a high degree of scatter in the data, but the wettest seasons consistently experience lower potential losses from harvesting. For Hv (Fig. 10*c*), the overall effect of legacy harvesting disturbance at Carnation Creek is low, but a significant positive relationship is found between average daily flow and change in available habitat.

Fig. 10. Relationships between change in habitat availability predicted from the pre- and postharvest logistic growth models and mean daily flow level over each 1 May to 30 September season from 1972 to 2015 for (*a*) total pool area; (*b*) pool area with wood cover; (*c*) high-velocity wetted area; (*d*) shallow water area; and (*e*) mean wetted width. Relationships are significant with $p < 0.05$ in all panels.



Discussion

Temporal patterns in channel form and habitat availability

Field and model data presented in Figs. 4 and 5 illustrate that channel morphology, in-stream wood, and modelled habitat variables did not remain static through time. Given that flow levels are held constant throughout the simulations, temporal variability in habitat is therefore driven by direct changes to channel morphology and, in the case of Pwc, also from changes in wood abundance (see Fig. 4). Therefore, the adoption of static threshold IFN standards in these instances is likely to yield differing quantities of habitat through time. The sensitivity of modelled aquatic habitat to channel morphology change is, however, variable-dependent. For instance, Sw is most sensitive to changes in channel shape and structure, while Ww and Hv were found to be comparatively stable through time (Fig. 5).

The declining pattern of wetted width (Fig. 5*e*) is likely a product of in-stream wood loss, associated reduction in sediment storage, and reduction in sediment supply after a period of elevated input in the early to mid-1980s (Reid et al. 2019). Reduced supply and abundance of wood will often lead to a simplified channel, which may incise and lead to reduced topographic relief (Nakamura and Swanson 1993). The cascading morphological effects of wood loss may also explain the overall reduction in several habitat variables with time (particularly Tp), as wood is often associated with pool areas (Abbe and Montgomery 1996).

With the exception of Sw, temporal patterns in all habitat variables display a partial dependency on flow level, with habitat availability at lower flows (<10% MAD) generally fluctuating less through time. While basic principles of hydraulic geometry (e.g., Leopold and Maddock 1953) will dictate the relationships between discharge and specific channel hydraulics, changes to smaller-scale and transient features, such as bars and pools, appear to exert a strong influence on the temporal patterns of modelled habitat. Given that the abundance of Tp, Pwc, and Hv area is very low at the lowest flows (<5% MAD), changes in morphology appear to have comparatively little effect on small-scale variation, but longer-term trends are still apparent. While few studies (e.g., Lapointe 2012; Rice 2017) have examined connections between geomorphic variability and habitat availability, results from Carnation Creek further support the finding that changes in channel morphology are important factors in regulating habitat availability through time.

The habitat variables selected for this study represent ranges of hydraulic conditions for juvenile coho. While the specific criteria for these variables are based largely on published literature for the species (e.g., Bjornn and Reiser 1991; Beecher et al. 2002), definitions for what constitutes optimal and marginal habitat will vary by species, and details of patterns in habitat will vary as a function of the habitat variable definition. For instance, the definition for Sw, chosen to illustrate patterns in shallow water areas, is relatively subjective, but the consequence of a different threshold can be inferred in part from the patterns observed in the other variables. Future work could consider flow-based definitions of morphological units (e.g., Wyrick and Pasternack 2014) as an alternative approach to characterizing hydraulic variability over time.

Relationships between flow level and habitat availability

Differing shapes of the habitat–discharge relationships for each variable (Figs. 6 and 7) demonstrate that all modelled variables are maximized at different flow levels, and therefore singular IFN levels do not yield optimal availability for all variables. The logistic growth form of the flow–habitat relationships (Fig. 6) indicates that additional streamflow generally increases habitat quantity rapidly at flow levels equal to and lower than 20% MAD, with the exception of Hv, which increases most above 20% MAD.

Evidence of trade-offs in habitat availability between variables is observable as discharge increases (Figs. 6 and 7). In general, the primary trade-off is between the pool-based variables (Tp and Pwc, which contain a velocity component) and Sw and Hv. For instance, maximizing the area of suitable Tp (Figs. 6*a* and 7*a*) may result in an unacceptable quantity of Hv (Figs. 6*c* and 7*c*). Given that many natural channels in mountainous environments have steep banks, once the bed area has been mostly wetted, it is likely that additional discharge will primarily increase depths and velocities, reducing Sw area and increasing Hv area. Pwc displays diminishing returns with added streamflow beginning near 10% MAD, as most wood appears to be within the wetted channel at this flow level, and additional streamflow does not create pool areas in the vicinity of wood. Therefore, as discharge increases, flow in pool areas becomes too swift and falls outside of the Tp criteria, thus leading to few additional gains and in some cases (Figs. 6*b* and 7*b*) reductions in rearing habitat with preferred velocities (Bjornn and Reiser 1991; Beecher et al. 2002). While clear inflection points in the flow–habitat relationships are not always obvious, the rapid increase in Hv above 20% MAD, combined with the relatively minor increases in Tp above 20%–40% MAD, indicate that targets between 10% and 20% MAD are producing at least a moderate quantity of suitable habitat and that below 10% MAD sharp losses in habitat availability will occur in Carnation Creek. In Carnation Creek and many other streams in seasonally dry climates, streamflow may drop to very low levels even in the absence of any direct withdrawals (Reid et al. 2020). Though streamflow may naturally drop below 10% MAD, these results support the conservation of streamflow for aquatic habitat below this level where possible to limit major declines in habitat availability.

Legacy watershed disturbances and habitat availability

In Carnation Creek, the legacy of watershed and riparian disturbance from historical timber harvesting appears to have significantly influenced the availability of aquatic habitat through time, and this effect is likely persisting even 30 years after the disturbance has occurred. A combination of removal of vegetation in the riparian zone and colluvial processes following harvesting appears to be associated with a general reduction in the availability of Tp, Pwc, Sw, and Ww, with a slight increase in Hv. While our selection of variables represents a subset of hydraulic conditions relevant for juvenile coho, the changes to the pool-based variables imply a reduction in low-velocity rearing habitat, while high-velocity areas avoided by juveniles (Beecher et al. 2002) are comparatively less affected.

The relative reduction in habitat is most pronounced during drier than average low-flow seasons (Fig. 10), suggesting that the effect of legacy harvesting may be exacerbated at lower flows (<10% MAD), though the greatest absolute differences between pre- and postharvest habitat production occur at the highest flow levels (Fig. 7). These findings are important for water management considerations, suggesting that maintenance and conservation efforts at the lowest of flows (<10% MAD) ensure consistent habitat provision regardless of channel condition. Collectively, these results highlight the importance of channel status evaluation as part of the process of defining critical and optimal environmental flow levels. These findings have direct implications for the establishment of presumptive flow standards in regions with a history of timber harvesting or other watershed disturbances that affect fluvial processes, suggesting that evaluation of channel status may be required to periodically adjust target flow levels to maintain constant habitat availability while providing water for societal use.

The primary mechanisms through which historical logging influenced habitat in Carnation Creek are likely tied to the reduction in wood supply through riparian harvesting and changes to sediment and debris delivery from hillslopes. In addition to providing direct cover, wood pieces (particularly logjams) serve to retain sediment (Hogan et al. 1998; Wohl and Scott 2017) and increase the topographic complexity of stream channels through the creation of pools and sediment wedges (Abbe and Montgomery 1996; Montgomery et al. 2003). As riparian forests are often a dominant source of wood to streams, their removal can have a substantial and long-lasting effect on in-stream wood loads (Murphy and Koski 1989; Stout et al. 2018). The loss of wood could also explain why a slight increase in Hv was observed, as a reduction in channel roughness could lead to elevated velocities at a given flow level (Davidson et al. 2015).

A number of debris flows occurring on previously harvested hillslopes delivered sediment and logging slash to the channel in the mid-1980s. Previous work focussing on the watershed (Hartman and Scrivener 1990; Reid et al. 2019) suggests that sediment delivered from these debris flows had an effect on sediment storage in certain locations along the channel, and at least one major logjam was formed from slash and debris near SA-8 (see Fig. 1). The sediment supplied from these events and evidence of channel widening was also found to propagate downstream over time (Reid et al. 2019). Numerous studies have documented the role of legacy forest practices on slope destabilization and delivery of sediment to streams and resulting consequences for channel morphology (e.g., Roberts and Church 1986; Gomi and Sidle 2003; Jordan 2006). It is likely that some of the temporal variability in habitat observed in Carnation Creek is also related to variation in sediment supply, which is often tied to morphological change (e.g., Hoffman and Gabet 2007). Given the association among channel morphology, in-stream wood, and diverse habitat for a variety of aquatic organisms (e.g., Cederholm et al. 1997; Hafs et al. 2014), this legacy harvesting effect may be a helpful factor for assessing whether a disturbed watershed is likely to have a reduction in habitat area at a given flow level.

While legacy harvest-related disturbances appear to be associated with a reduction in habitat availability, it may be possible to partially compensate by increasing streamflow at the lowest flow levels, should water supplies exist. However, given the downward shift in model asymptotes during postharvest conditions (Fig. 8), additional streamflow will not be able to compensate for the harvest effect at higher flows (generally >40% MAD). This issue of compensatory flows is, however, further complicated by potential trade-offs between low-velocity pool area and higher-velocity regions that would naturally be observed as streamflow increases.

In Carnation Creek, historical riparian and hillslope harvesting has likely led to changes in the supply of wood and sediment to the channel, affecting channel morphology and flow hydraulics. However, the habitat response to disturbance in other channels will strongly depend on the nature of the disturbance, the background process rates in the channel, and the mechanisms through which the disturbance can lead to changes. Given that specific channel morphology has bearing on the relationship between habitat availability and discharge, it is therefore not only important to understand the likelihood of morphological change occurring from watershed and riparian disturbance, but also the mechanisms behind the change.

Summary and conclusions

Using a 2D hydrodynamic modelling approach incorporating a 45-year dataset of channel morphology and in-stream wood, this paper has characterized the variability in habitat–discharge relationships in Carnation Creek, a small salmon-bearing gravel bed stream in coastal British Columbia. This study demonstrates the magnitude of variability through time in five flow-based habitat variables. This variability is driven both by changes to channel morphology and wood loads in the system. Collectively, these findings highlight the importance of channel morphology as co-control on the provision of aquatic habitat along with discharge and have implications worthy of consideration when estimating and setting presumptive flow standards for a variety of management purposes.

When flow level is held constant, changes in channel morphology appear to have a smaller influence on modelled habitat at the lowest of flow levels (<3% MAD and less) than for higher flows with four of five studied variables, though low flow variability is still apparent. Trade-offs were observed between pool-based and high-velocity habitat metrics as flow level increases, where low-velocity channel areas are replaced with greater areas of higher flow velocities. The habitat–discharge relationships are strongly nonlinear, with rapid gains in habitat at low and intermediate flow levels but diminishing returns at higher flows.

In four of the five habitat variables studied (total pool area, pool area with wood cover, shallow wetted area, and mean wetted width), a reduction was found after widespread watershed disturbance (including riparian area harvesting) occurred in the watershed during the mid- to late 1970s. The exception was for high-velocity (>0.6 $\mathrm{m \cdot s^{-1}}$) flow areas, which increased slightly in the postharvest channel state, with the likely change mechanism being a reduction in wood delivered to the stream channel.

These findings support the notion that adding more water to the channel can potentially compensate for variability in habitat or habitat losses through disturbance at very low flows (<10% MAD), but less so at higher flows (≥40% MAD). However, it is not feasible in many cases, especially for flows ≥ 20% MAD, to rely on water conservation to overcome losses in disturbance-driven habitat availability, particularly in regions with seasonally dry conditions. A combination of careful flow allocation, habitat management, or channel restoration may be required to recover predisturbance habitat production of the channel.

This paper has focussed on hydraulic components of aquatic habitat for juvenile coho salmon. It is important to note that other variables such as stream temperature, nutrient and food availability, rates of predation, and water quality could also be affected by watershed and riparian disturbance. These factors have bearing on the availability and quality of habitat over time and across space, and future work should aim to incorporate other variables into consideration of streamflow allocations in regions affected by disturbances.

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