USDA Forest Service
U.S. DEPARTMENT OF AGRICULTURE

Pacific Northwest Research Station | General Technical Report PNW-GTR-1009 | December 2022

Forest Legacies and Climate Realities: Spatial and Temporal Variation in Fish Populations and Habitat Characteristics on the Tongass National Forest, Alaska

Rebecca Flitcroft, Jay Munyon, Shannon Claeson,
Adelaide Johnson, Michael Moore, Emil Tucker,
Katherine Prussian, Sheila Jacobson, and Heidi Lombard

Authors

Rebecca Flitcroft is a research fish biologist, **Jay Munyon** is a biological scientist, and **Michael Moore** was an Oak Ridge Institute for Science and Education research fellow, USDA Forest Service, Pacific Northwest Research Station, 3200 SW Jefferson Way, Corvallis, OR 97331; **Shannon Claeson** is an aquatic ecologist, USDA Forest Service, Pacific Northwest Research Station, 1133 N Western Avenue, Wenatchee, WA 98801; **Adelaide Johnson** is a hydrologist (retired), USDA Forest Service, Pacific Northwest Research Station, 11175 Auke Lake Way, Juneau, AK 99801; **Emil Tucker** and **Katherine Prussian** are hydrologists and **Heidi Lombard** is a fisheries biologist, USDA Forest Service, Tongass National Forest, 19 Fram Street, Petersburg, AK 99833; **Sheila Jacobson** is a forest fish program manager, USDA Forest Service, Tongass National Forest, 504 9th Street, Craig, AK 99921.

Cover: Maybeso Creek, Alaska. Tributaries to Maybeso Creek were included as sample sites in the Management Indicator Species Study. USDA Forest Service photo.

Abstract

Flitcroft, Rebecca; Munyon, Jay; Claeson, Shannon; Johnson, Adelaide; Moore, Michael; Tucker, Emil; Prussian, Katherine; Jacobson, Sheila; Lombard, Heidi. 2022. Forest legacies and climate realities: spatial and temporal variation in fish populations and habitat characteristics on the Tongass National Forest, Alaska. Gen. Tech. Rep. PNW-GTR-1009. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 77 p. https://doi.org/10.2737/PNW-GTR-1009.

A new, dynamic reality is unfolding as climate change interacts with historical land management, causing changes in riverscape conditions that affect stream habitat and populations of native fishes. In Alaska, and elsewhere, land managers are facing new challenges as they seek to balance forest use with ecological resilience in rivers that support culturally and commercially important salmonids. In this context, data-driven forest management intended to maintain and restore landscapes relies on information that defines conditions over time. In this study, we analyzed 8 years of stream habitat and fish population data from a robust dataset developed to monitor aquatic conditions on the Tongass National Forest, Alaska. We found that patterns of fish population distribution, abundance (particularly anadromous salmonids), and instream habitat overlap with past forest-harvest site selection intended to maximize timber extraction. Historical riparian harvest disproportionately targeted easily accessible marine-connected subwatersheds that currently support anadromous salmonids such as coho salmon. Hydrologic type and forest stand age also influenced fish habitat. Further, we found that in rain-dominated watersheds with >42 percent old-growth cover, streams had wider channels and deeper pools that may provide some refuge for native fish from summer drought and low-flow conditions. However, as more watersheds transition from snow to rain, and winter storm intensities increase, even streams with wider channels and deeper pools that provide summer habitat may not provide winter refugia for native fish.

Keywords: Management Indicator Species study, climate change, legacy land management, biological and fish responses.

Executive Summary

Analysis and monitoring that links aquatic habitat with hydrologic regimes and land management over time is critical as climate drives unprecedented changes in riverscape conditions that have potential to affect different species of salmonids in different ways (Bryant 2009). This new, dynamic reality poses new challenges for land managers with jurisdiction over broad spatial extents. In this context, data-driven forest management intended to maintain and restore landscapes relies on information that defines conditions over time.

The Tongass National Forest prioritized long-term monitoring of fish and their habitats in a statistically rigorous sample design using consistent data collection methods as part of its work to support the Tongass National Forest Land and Resource Management Plan (USDA FS 2008). In this plan, coho salmon (*Oncorhynchus kisutch*), cutthroat trout (*Oncorhynchus clarkii*), and Dolly Varden trout (*Salvelinus malma*) were identified as management indicator species whose population status was interpreted to reflect ecological conditions of the watersheds in which they were found. Managers reasoned that tracking these populations in watersheds of the Tongass National Forest would provide information critical to the maintenance and improvement of instream conditions throughout the forest. The central goal of monitoring (the Management Indicator Species Study) was to determine if the standards and guidelines for timber harvest and all management activities prescribed by the Tongass National Forest Land and Resource Management Plan were effective in protecting habitat and subsequently maintaining salmonid populations.

Modern riverscapes reflect a combination of historic and current land uses in the overarching context of a changing climate that modifies thermal and hydrologic regimes in rivers. On the Tongass National Forest, several different types of hydrologic regimes are found (e.g., snow- and rain-dominated) that can directly affect sediment transport and seasonal patterns of water availability (Sergeant et al. 2019). A combination of field- and GIS (geographic information system)-based datasets were analyzed using multivariate and univariate statistical models and tests to better understand fish distribution, aquatic habitat, and geomorphic characteristics across different hydrologic regimes—as well as timber harvest history—on the Tongass National Forest. Four key questions were addressed:

- What are the species-specific relationships between fishes and aquatic habitat over space and time?
- What are the spatial and temporal influences of timber harvest history and hydrologic regime on resident and anadromous fish communities?
- What are the spatial and temporal influences of timber harvest history and hydrologic regime on physical stream characteristics?

- What are the spatial and temporal influences of hydrologic processes on stream geomorphic characteristics by hydrologic regime, percentage of old-growth forest, and drainage area?

We found that patterns of fish population distribution, abundance (particularly anadromous salmonids), and instream habitat overlap with past forest-harvest site selection intended to maximize timber extraction. Historical riparian harvest disproportionately targeted easily accessible marine-connected subwatersheds that also support anadromous salmonids such as coho salmon. These productive forests coincide with core population areas for coho salmon that were surveyed for the Management Indicator Species Study.

Hydrologic type influenced fish habitat that was also influenced by forest stand age. We found that in rain-dominated watersheds with >42 percent old-growth cover, streams had wider channels and deeper pools that may provide some refuge for native fish from summer drought and low-flow conditions. However, we observed linkages between intense winter storm events in rain-dominated systems and decreases in fish population sizes the following summer in both of the long-term, annually surveyed watersheds in this study, which represented both an actively managed watershed and an unmanaged watershed. As more watersheds transition from snow to rain, and winter storm intensities increase, even streams with wider channels and deeper pools that provide summer habitat may not provide winter refugia for native fish.

Our finding that core populations of salmon overlap with historically harvested forests in the Tongass National Forest has implications for future land management. These highly productive forests align with ideal fish habitat conditions of gradient, distance to the ocean, sediment size, and pool depth, attracting and supporting large populations of anadromous fish. These anadromous fish contribute a significant subsidy of marine-derived nutrients when they spawn and die in the streams that move through the landscape, thereby also supporting neighboring forests. As a result of their productivity, these forests are becoming viable for harvest in the near future. The productivity loop that connects fish and forests necessitates ongoing protection of riparian corridors and floodplains from negative effects of harvest that could compromise fish populations that contribute to long-term forest productivity. The function and condition of both streams with fish, as well as fishless headwater streams that supply sediments and nutrients downstream, indicate the potential benefit of continued protection measures that support fish persistence and resilience into the future.

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Introduction

Modern riverscapes reflect a combination of historical and current land use (Foster et al. 2003) in the overarching context of a changing climate that is modifying thermal and discharge regimes in rivers (Stocker et al. 2001). The vast landscapes of the northern latitudes, particularly in temperate regions that support forests, embody this complex mosaic of land management as it interacts with natural ecosystems. In North America, northern temperate forests contain some of the most extensive wilderness areas on Earth (Allan et al. 2017), supporting a host of rare and imperiled species (Stanturf and Madsen 2006). Streamflow in forests is a critical driver of biological community composition (Carlisle et al. 2011). Further, Alaska, identified as a possible Anthropocene refugium for biodiversity in a changing climate (Monsarrat et al. 2019), has thousands of watersheds that border the Gulf of Alaska and comprise a largely pristine and diverse range of streams (O'Neel et al. 2014). The Gulf of Alaska region discharges 25 percent more freshwater than the Mississippi River from a drainage area only one-seventh the size (Beamer et al. 2016, Dia et al. 2009), with watersheds having patterns of rain or snow as dominant runoff sources (>75 percent of watersheds). The remaining watersheds are driven by rain-snow, glacier, or low-elevation wetland runoff (Sergeant et al. 2019). Forest hydrology is influenced by timber harvest, slow growth of trees, and post-disturbance influences, such as changes in nutrient and carbon runoff into aquatic systems (Kreutzweiser et al. 2008, Maynard et al. 2014). Therefore, historical land use is the template upon which current climate change interacts with natural ecosystems.

The rate of climate change is high at northern latitudes, destabilizing the narrow balance point between rain and ice that, when tipped, reduces continental glaciation and permafrost, thus changing land and near-shore seascape processes and physical characteristics (Stocker et al. 2001). In the northern maritime temperate region of southeast Alaska, anticipated climate change effects of increased storm intensity, glacial retreat, and altered precipitation regimes from snow to rain are already occurring (Larsen et al. 2007, Thoman and Walsh 2019). Native species that occupy these areas represent survivors of similar changes associated with past ice ages (e.g., Pacific salmon [*Oncorhynchus* spp.]) (Waples et al. 2008). However, the current rate of environmental change exceeds historical rates of change, possibly reducing resilience for many biota (Hope et al. 2015, Pitman et al. 2020). For example, salmonids that spawn in higher gradient areas could be vulnerable to changing hydrologic regimes that may cause streambed scour resulting from higher intensity precipitation and storm events (Shanley and Albert 2014, Sloat et al. 2017). Additionally, forests may exhibit decreased growth in response to warming coupled with changes in precipitation regimes (e.g., in boreal forests of western Canada)

(Chen and Luo 2015). Migration of these forests into more suitable environments requires gradual changes in climate (Hope et al. 2013), but in southeast Alaska and across the northern forests, climate is changing even more rapidly than at more southerly latitudes (Malcolm et al. 2002).

As climate drives unprecedented changes in riverscape condition, managers of large-scale landscapes will likely encounter a new, dynamic reality. In this context, data-driven forest management intended to maintain and restore landscapes relies on information that defines conditions over time. The Tongass National Forest prioritized long-term monitoring of fishes and their habitats in a statistically rigorous sample design using consistent data collection methods to support the Tongass National Forest Land and Resource Management Forest Plan (USDA FS 2008). In this plan, coho salmon, cutthroat trout (*O. clarkii*), and Dolly Varden trout (*Salvelinus malma*) were identified as management indicator species whose population status was interpreted to reflect ecological conditions of the watersheds in which they were found. Tracking these populations in watersheds of the Tongass National Forest provides information critical to the maintenance and improvement of instream conditions throughout the forest. A key goal of the monitoring effort was to determine if the standards and guidelines for timber harvest and other management activities prescribed by the Tongass National Forest Land and Resource Management Plan were effective in protecting habitat and subsequently maintaining salmonid populations. Four key questions explored in this analysis of management indicator species and stream habitats pertain to Tongass National Forest management specifically, but broadly inform linkages between environmental conditions and ecosystems in temperate, high-latitude environments:

- What are the species-specific relationships between fishes and aquatic habitat over space and time?
- What are the spatial and temporal influences of timber harvest history and hydrologic regime on resident and anadromous fish communities?
- What are the spatial and temporal influences of timber harvest history and hydrologic regime on physical stream characteristics?
- What are the spatial and temporal influences of hydrologic processes on stream geomorphic characteristics by hydrologic regime, percentage of old-growth forest, and drainage area?

A combination of field- and GIS (geographic information system)-based datasets were combined for analysis using multivariate and univariate statistical models and tests to better understand the spatial and temporal effects currently evident in fish, aquatic habitat, and bedform characteristics across the broader context of time, hydrologic regime, and timber harvest history in the Tongass National Forest.

Methods

Study Area

The Tongass National Forest is the largest national forest managed by the U.S. Department of Agriculture Forest Service, encompassing 16.7 million ac (6.7 million ha, or 67 582 km^2) in southeast Alaska, supporting diverse ecosystems and native species in terrestrial and aquatic environments (USDA FS 2016). Southeast Alaska is an archipelago with small watersheds that drain into the Gulf of Alaska. This complex landscape is composed of a variety of vegetation communities, including temperate rain forests, muskegs, wetlands, and salt marshes, as well as rock and ice fields and glaciers. Underlying lithology is primarily metamorphic, carbonate, or volcanic (Wilson et al. 2015). Climate is temperate with cool summers and without a dry season (Peel et al. 2007). Areas of active timber harvest in the coastal portions of the Tongass National Forest are the focus for analysis in this study.

Survey Design and Sample Sizes

Fish and instream habitat metrics were collected using a rotating panel sample design to capture variation over time and space. Watersheds were selected from forested areas on the Tongass National Forest (fig. 1). Two to four sites were selected in each watershed. We identified sample sites using GIS analysis to isolate low-gradient, fish-bearing sites with alluvial channels across a range of management histories, including areas with no harvest, historical, and recent timber harvest, respectively. Waterfalls that isolate upstream watersheds from access to the marine environment were targeted in this study to compare resident and anadromous fish community responses to land management. Isolated resident fish communities were also of interest based on the assumption that these populations would be less influenced by the variable environmental conditions of marine environments. Therefore, half of selected subwatersheds are connected to the marine environment, and half contain waterfalls that restrict marine connection.

We identified 21 watersheds for sampling in the Management Indicator Species Study (fig. 1). In those 21 watersheds, a total of 114 sites (and their associated subwatersheds) were sampled at least twice between 2012 and 2019 (table 1). Sites were generally sampled every 4 years, but four of the watersheds were sampled more frequently than every 2 years (table 1). Each year, 6 to 9 watersheds and 38 to 51 subwatersheds were sampled (table 2), resulting in a total of 328 samples. A total of 58 subwatersheds with connection to marine environments were surveyed (containing fish with both resident and anadromous life histories), along with 56 subwatersheds that were isolated from the marine environment by waterfalls (only fish with resident life histories).

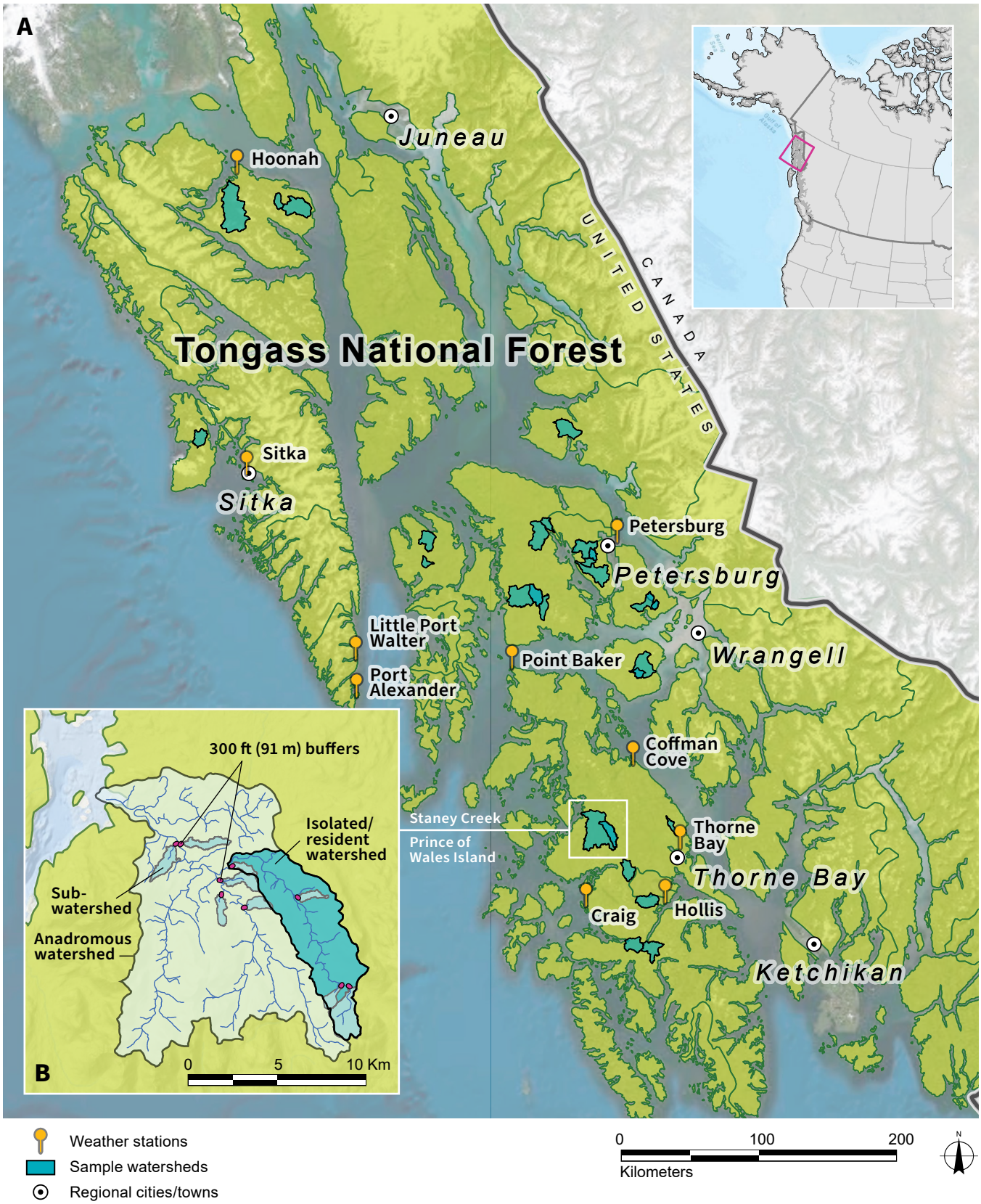

Figure 1—(A) Management Indicator Species Study area weather station locations and sampled watersheds, Tongass National Forest, southeast Alaska. (B) Watershed survey and sample design with an isolated/resident (I/R) watershed nested within a larger, connected/anadromous (C/A) watershed. Individual sampling sites are dots (here, represented with a 300-ft buffer), and the associated upstream subwatershed is outlined and shaded.

Table 1—Summary information for watersheds and subwatersheds sampled in the Management Indicator Species Study, Tongass National Forest, Alaska

Watershed	Hydroregime	Riparian buffer harvest time period	Subwatersheds			Returns (n)	Years surveyed
			n	Connected/ anadromous	Isolated/ resident		
Cable	Rain	1950–1969	4	4	0	1	2016
Duncan	Snow	1990–2019	8	4	4	2	2012, 2016
Farragut	Snow	Never	4	0	4	2	2015, 2019
Game	Snow	1990–2019	4	4	0	2	2014, 2018
House Rock	Snow	1970–1989	4	0	4	2	2013, 2017
Iyouktug	Snow	Never	4	4	0	2	2015, 2019
Maybeso	Rain	1950–1969	5	5	0	2	2015, 2019
Meterbight	Snow	1970–1989	8	4	4	2	2012, 2016
Mitchell	Snow	Never	4	4	0	2	2013, 2017
Ohmer	Snow	1950–1969	12	4	8	3	Multiple years
Rowan	Rain	1970–1989	4	0	4	2	2014, 2018
Saginaw	Rain	1950–1969	4	4	0	2	2014, 2018
Shelikof	Rain	1950–1969	4	4	0	2	2015, 2019
Slide	Rain	1950–1969	4	0	4	2	2013, 2017
Staney	Rain	1970–1989	9	5	4	8	2012–2019
Steelhead	Rain	1990–2019	4	0	4	2	2015, 2019
Suntaheen	Snow	1970–1989	4	0	4	2	2014, 2018
Towers	Rain	Never	8	4	4	8	2012–2019
Tunehean	Rain	Never	8	4	4	4	Multiple years
Twelvemile	Rain	1950–1969	4	4	0	2	2013, 2017
Zim	Rain	Never	4	0	4	2	2013, 2017

n = number.

Table 2—Number of watersheds and subwatersheds surveyed per year in the Management Indicator Species Study, Tongass National Forest, Alaska

Year	Number of watersheds	Number of subwatersheds
2012	6	38
2013	9	51
2014	7	41
2015	8	41
2016	6	41
2017	8	40
2018	8	41
2019	8	41

Datasets

Fish species—

We calculated fish population estimates at the site scale for coho salmon, Dolly Varden trout, steelhead/rainbow (*Oncorhynchus mykiss*), cutthroat trout, and sculpin (*Cottus* spp.). Sampled reaches were 262 to 703 ft (87.4 to 234.2 m) long, with an average length of 373 ft (124.5 m). Survey lengths represent about 20 times bankfull width and were intended to capture both fast- (i.e., riffle, glide) and slow-water (i.e., pool) habitats. We captured fish with three capture-pass removals using minnow traps and block nets. We calculated fish population estimates and confidence intervals using an algorithm from Capture software (Otis et al. 1978) and methods similar to those outlined in Bryant (2000) and Bryant et al. (2008).

The three fish species of interest to the Tongass National Forest include coho salmon, cutthroat trout, and Dolly Varden trout. Cutthroat and Dolly Varden trout have either an anadromous or resident life history, whereas coho salmon are only anadromous. In Alaska, coho salmon frequently exhibit a 2-year juvenile freshwater residency before they become smolts, migrate to the ocean and rear into adults that then return to freshwater to spawn and then die. We distinguished newly emerged age 0 fry from age 1 parr based on body length as measured in the field. Bryant et al. (2008) developed a length-frequency distribution that guided the differentiation between fry and parr. In analysis that included population estimates, we kept fry and parr separate because effects of habitat and environmental conditions are likely different between size cohorts (Bryant et al. 2008). In some analyses that explored spatial patterns of distribution, we combined fry and parr (whose spatial distribution is the same) as coho salmon.

Instream habitat variables—

Instream metrics were collected by Tongass National Forest survey crews at fish sample sites using USDA Forest Service Alaska Region aquatic habitat survey field methods (Nichols 2013) (table 3). Although rain may occur at all times of the year in southeast Alaska, crews conducted surveys during summer low-flow conditions in June, July, and August to control for interannual variability in water level, temperature, and fish size. Field data collection included classified wood counts; measurement of pool and riffle length; width and depth; and measurement of channel morphology, sediment, and length of undercut banks (table 3).

Using GIS, we calculated the stream network distance from the start of the survey site to the ocean. Because all sites occurred in watersheds with close connection to marine environments, this measure allowed for the spatial context of individual sites to be used as a co-variate in analyses. We measured distances in kilometers using the 1:100,000 National Hydrography Dataset (USDI GS) accessed in 2019.

Table 3—Variables used for analysis and modeling in the Management Indicator Species Study area

Category	Variable	Unit	Variable description	GLMM	PCA	PCA overlay	NMS	NMS overlay	LMM
			FIELD DATA						
Year	Year	Year	Year of field survey	✓		✓ (categorical)		✓ (categorical)	✓
	Survey period		Survey occurred from 2012–2015 (T1) or 2016–2019 (T2)			✓ (categorical)		✓ (categorical)	✓ (categorical)
Fish	CO (fry and parr)	Pop. est.	Coho salmon fry and parr population estimate						
	CO (fry)	Pop. est.	Coho salmon fry population estimate	✓		✓	✓		
	CO (parr)	Pop. est.	Coho salmon parr population estimate	✓		✓	✓		
	DV	Pop. est.	Dolly Varden trout population estimate	✓		✓	✓		
	SH	Pop. est.	Steelhead/rainbow trout population estimate	✓		✓	✓		
	CT	Pop. est.	Cutthroat trout population estimate	✓		✓	✓		
	SC	Pop. est.	Sculpin population estimate				✓		
	K condition coho young-of-year	Calculated	Physical condition young of year coho salmon						
	Biomass	Gram	All fish species combined biomass	✓				✓	
Large Wood	Key LWD	Count	Key pieces of large wood (description)	✓	✓			✓	
	LWD total	Count	Count of large wood pieces >1 m long and 0.1 m in diameter		✓			✓	✓
	LWD/m	Calculated	LWD pieces/meters surveyed					✓	
	Key LWD/m^2	Calculated	LWD key pieces/area surveyed					✓	
	LWD-pool	Percent	% large wood pools per unit total large woody debris		✓			✓	
	LWD-RF	Percent	% large wood riffles per unit total large woody debris					✓	
Sediment	D50	Percent	Median sediment particle size	✓	✓			✓	
	D84	Percent	84^{th} percentile sediment particle size					✓	
Bank	UB_m	Percent	Length of undercut/total bank length of undercut bank		✓			✓	
Geomorphology	Pools/km	Kilometer	Pools per kilometer	✓	✓			✓	
	Pool count	Count	Pools in reach					✓	
	Wetted pool area	$Meter^2$	Wetted pool area					✓	
	Wetted riffle area	$Meter^2$	Wetted riffle area	✓	✓			✓	

Table 3—Variables used for analysis and modeling in the Management Indicator Species Study area (continued)

Category	Variable	Unit	Variable description	GLMM	PCA	PCA overlay	NMS	NMS overlay	LMM
	Total wetted area	Meter^2	Total wetted area					✓	
	Average bankfull depth	Meter	Average bankfull depth	✓	✓			✓	✓
	Average bankfull width	Meter	Average bankfull width	✓	✓			✓	✓
	Bankfull width/ bankfull depth	Calculated	Average bankfull width/ average bankfull depth		✓			✓	✓
	Reach gradient	Percent	Gradient of reach		✓			✓	✓
	Riffle gradient	Percent	Gradient in riffle habitat		✓			✓	
	Residual pool depth	Meter	Residual pool depth	✓	✓			✓	✓
	Average channel bank with	Meter	Average channel bank width					✓	
	Reach/average channel bank width	Calculated	Reach length/average channel bank width	✓	✓			✓	
	Average relative pool depth/ average channel bank width	Calculated	Average residual pool depth/ average channel bank width		✓			✓	
	Relative pool area	Meter^2	Relative pool area	✓	✓			✓	
	Hydraulic radius (Rbf)	Calculated	Channel bankfull cross-sectional area/ channel bankfull perimeter		✓				✓
	Shields stress/ critical stress (τ^*bf / τ^*c)	Calculated	Theoretical relationship between sediment supply and channel morphology (see text)						✓
			SPACIAL DATA						
Reach scale	Watershed	ID number	Watershed identification	✓		✓ (categorical)		✓ (categorical)	✓
	Reach_m	Meter	Field survey length	✓	✓			✓	
	Network distance	Meter	Network distance from the start of the survey reach to the ocean	✓	✓			✓	
	Elevation	Meter			✓			✓	
	Boundaries	Polygon line	Watershed, subwatershed, and 91-m buffer boundaries						

Category	Variable	Unit	Variable description	GLMM	PCA	PCA overlay	NMS	NMS overlay	LMM
Watershed scale	Lithology	Raster	Dominant underlying geology			✓ (categorical)		✓ (categorical)	
	Cover type	Categorical	Dominant cover vegetation type						
	Hydrology	Categorical	Dominant hydroregime based on Sergeant et al. (2019)			✓ (categorical)		✓ (categorical)	
	Roads	Kilometer	Length of roads		✓			✓	
	Road crossings	Count	Number of road crossings					✓	
	Resident fish	Kilometer	Length of stream for resident fishes					✓	
	Anadromous fish	Kilometer	Length of stream for anadromous fishes					✓	
	Stream kilometer headwater/ high gradient	Calculated	Length of headwater streams/gradient					✓	
Pour-point scale	Area	Acre	Catchment area above the survey reach, starting at the beginning of the survey length						
	Canopy cover	Percent	Percentage of total pour point area with more than 50 percent canopy cover	✓	✓			✓	
	Old growth	Percent	Percentage of total pour point area with trees greater than 9 inches (23 cm) diameter at breast height and older than 150 years	✓	✓			✓	
	Old growth	Categorical	Major or minor classification of area of old grown based on median amount across subwatersheds (104 ac [0.42 km^2])						✓ (categorical)
	Small or large subwatershed	Categorical	Greater or less than median drainage area of 894 ac (3.62 km^2)						
	Disturbed area	Percent	Percentage of total pour point area with combination of harvest within the previous 10 years and windthrow	✓	✓			✓	
	Harvest history	Decade, acre	Decade and area of most recent harvest within 300-ft (91-m) buffer						
	Harvest group	Categorical	Decades with historical harvests that intersected riparian zones (1950–1969, 1970–1989, 1990–2019, never)			✓ (categorical)		✓ (categorical)	✓ (categorical)
	Landslides	Acre	Area of landslides within the 300-ft (91-m) buffer						

GLMM = generalized linear mixed-effects model; LMM = linear mixed model; LWD = large woody debris; NMS = nonmetric multidimensional scaling; PCA = principal components analysis.

To explore linkages between the sediment supply and channel configurations, we approximated bankfull shields stress (τ^*_{bf}) relative to the critical bankfull shields stress (τ^*_c) required to mobilize the median bed surface grain size (τ^*_{bf}/τ^*_c) (Pfeiffer et al. 2017) using available channel measurements and median pebble size, bankfull width and depth, and bed slope (additional methods in app. 4).

Upslope characteristics—

A variety of variables were intended to capture characteristics of the riparian and upslope environment in the subwatersheds and watersheds of interest to this study. We summarized variables including lithology, vegetative cover type (particularly percentage of area of old-growth forest), roads, culverts, harvest history, and landslides at three spatial extents for analysis (table 3). Spatial extents included a 300-ft (91-m) buffer on each side of the site, intended to capture riparian conditions directly adjacent to the sampled section of stream; the upstream subwatershed associated with the site; and the entire watershed within which multiple subwatersheds were nested (fig. 1). Buffers were generated on 1:100,000-scale National Hydrography Dataset linework. We did not summarize lithology at the buffer or subwatershed extent because of the coarseness of the lithology spatial dataset, and we summarized harvest history only at the 300-ft (91-m) buffer scale, reflecting direct influences of harvest on riparian habitat conditions.

We evaluated precipitation as rain or snow over the duration of the study (2011–2019). To accomplish this, we accessed and plotted rain and snow data from 10 weather stations within the study area (fig. 1). Data were acquired from the National Weather Service (NOAA NWS, n.d.) (additional methods in app. 2).

Storms lead to discharge events capable of moving sediment that can alter channel morphology over time. To capture the distribution of precipitation across the study area of specific storm events, we created a map of isohyets (equal precipitation contours) for a peak precipitation event that occurred during the study (using only available precipitation data at sea level) that occurred on 20–21 January 2015. Stage discharge measurements, where available, were added to the isohyet map.

Watershed classifications—

To explore broad-scale characteristics of watersheds that may influence patterns in the data, we investigated several watershed or subwatershed groups, including time period, connection to the ocean, hydroregime, and harvest history.

Survey time period—To compare resampled sites for the duration of this study, we established two time periods coincident with the rotating panel of the study design. For sites surveyed more than twice, we selected the first sample from 2012–2015 to represent time period 1 (T1), and the first sample from 2016–2019 to represent time period 2 (T2).

Connected/anadromous and isolated/resident—Based on their configuration and the presence of waterfalls that restrict upriver migration, different subwatersheds in the study area support resident or anadromous fish life histories. Resident-only fish are found in subwatersheds that are disconnected from marine environments, whereas a combination of resident or anadromous life histories are found in watersheds with open connection to the ocean. We designated connected/anadromous (C/A) or isolated/resident (I/R) subwatersheds to explore relationships between fish communities and physical habitat characteristics across the study area.

Hydraulic regime—Intensity and timing of precipitation and runoff varies between rain- and snow-dominated systems and directly influences phenology of aquatic biota (Campbell et al. 2018) and channel morphology (Harvey 1969, Pickup and Warner 1976). We identified watersheds with rain- or snow-dominated hydrology using classifications developed by Sergeant et al. (2019). These classifications of a rain- or snow-dominated hydrology were based on prior work by Beamer et al. (2016) and strongly reflect watershed elevation.

Harvest history group—Land use legacies can affect stream conditions for many years (White et al. 2017). Harvests in riparian areas are likely to result in long-term differences in wood and sediment recruitment to the adjacent stream (Richardson et al. 2012). In western Oregon, riparian-adjacent trees are a key source of instream wood (Gregory et al. 2003, Spies et al. 2013, Welty et al. 2002). Here, we identified timber harvests that intersected the 300-ft (91-m) buffer within the subwatershed of sampled stream segments. We acquired USDA Forest Service GIS datasets of harvest history from the Tongass National Forest to overlay harvest history on the 300-ft (91-m) stream buffer layer of sample sites. The year of the harvest and the area of the harvest contained within the 300-ft (91-m) stream buffer were quantified.

Timber harvest that included riparian trees and active work in stream channels has varied over time (Richardson et al. 2012). Historical harvests on the Tongass National Forest specifically targeted high productivity riparian areas, floodplains, and alluvial fans prior to the 1990 Tongass Timber Reform Act (H.R. 987 1990). To identify harvest periods with different types of forest practices that could affect instream conditions, we reviewed the records of harvest year and acres of harvest in the 300-ft (91-m) stream-buffer layer. We assigned sites to four groups based on year of harvest: 1950–1969 (harvest group 1), 1970–1989 (harvest group 2), 1990–2020 (harvest group 3), and never harvested (harvest group 4). Harvest group 3 is coincident with current forest management buffers established in the Tongass National Forest Land and Resource Management Plan (USDA FS 2016). Implementation of buffers began before 1997 at some sites, but after 1997 for sites that were sold before 1997 and harvested later; therefore, the transition between no buffers and the use of riparian buffers is captured by this harvest group. In each

watershed, we summed riparian harvest area for each year across all sites within a watershed, and over the years of the harvest interval. We identified the harvest interval with the largest area of harvest as the harvest group with greatest potential influence on current instream conditions at the watershed scale. These intervals were described as harvest groups for analysis of individual sites and at watershed scales. Sample sizes of watersheds and subwatersheds varied by harvest group, as did the number of subwatersheds with C/A or I/R classification (table 4).

Table 4—Acreage of riparian timber harvests during different periods across Management Indicator Species Study sites in the Tongass National Forest, Alaska

Harvest group	Watersheds | subwatersheds	Subwatersheds: C/A | I/R	Area harvested		
			C/A	I/R	Total
	(n | n)	*(n | n)*	----- *Acres (percentage of total)* ----		
1: 1950–1969	7 | 37	25 | 12	37 (71)	15 (29)	52 (100)
2: 1970–1989	5 | 29	9 | 20	12 (19)	50 (81)	62 (100)
3: 1990–2020	3 | 16	8 | 8	9 (30)	21 (70)	30 (100)
4: Never	6 | 32	16 | 16	N/A	N/A	N/A
Totals	21 | 114	58 | 56	58 (40)	86 (60)	144

C/A = connected/anadromous; I/R = isolated/resident.

Subwatershed size—Area of the drainage basin strongly influences rainfall-runoff patterns and channel geomorphology. For hydrologic analysis, we used median drainage area (894 ac [362 ha]) to classify subwatersheds as small (81–857 ac [33–347 ha]) or large (894–3657 ac [362–1480 ha]).

Area of old-growth forest—Influence of old-growth forest in the upland has been shown to influence hydrology, sediment supply, and wood inputs (Bilby and Ward 1989, Jones et al. 2000). We incorporated old-growth forest cover into the hydrologic analysis by identifying the median percentage of old-growth cover in the subwatershed (42 percent). This allowed us to categorize sites as having minor amounts of old-growth (0 to 42 percent) or major amounts of old-growth (>42 percent) (app. 1).

Analysis—

Question 1: What are the species-specific relationships between fishes and aquatic habitat over space and time? We undertook a preliminary exploration of patterns over time in fish populations grouped by watershed classifications (to compare T1 and T2 between isolated/resident and connected/anadromous subwatersheds) through graphs, boxplots, and dendrograms. We developed graphs

of fish population estimates and confidence intervals by site and sample year for the two watersheds that were sampled every year (Towers Creek, a watershed with no timber harvest, and Staney Creek, a watershed with a long history of timber harvest). To compare between T1 and T2, we generated dendrograms and histograms of fish population size.

To estimate the response of fish populations (coho salmon parr and fry, cutthroat trout, Dolly Varden trout, steelhead/rainbow trout, and sculpin) to selected instream habitat metrics at the site scale, we used log-linked generalized linear mixed-effects models (GLMMs). We completed separate population models for fish with resident or anadromous life histories in connected/anadromous or isolated/resident subwatersheds (a total of 10 sets of GLMM models). We based metrics selected for modeling on preliminary analysis that identified variables that were sensitive over time, as well as variables from the literature that have been identified as important in understanding fish use of habitat. We used 14 metrics in analysis (tables 3 and 5). Several variables were in different units and spatial scales, requiring transformation. We rescaled network distance relative to the longest distance among all sites. We left canopy cover and old-growth cover unmodified as percentages of total area. Prior to GLMM analysis, we standardized by centering around the median and dividing by the standard deviation for: reach length, average bankfull depth and width, reach length divided by channel bed width, sediment (D_{50}), wetted riffle area (wet-riffle area), pool area, residual pool depth, pools per kilometer, total key of large woody debris, and fish biomass.

GLMMs were designed based on the assumption that features that are close to one another in space are more related than features that are farther away (Tobler 1970). Based on this assumption, we allowed intercepts to vary among watersheds by including watershed as a random variable (Dormann et al. 2007). Additionally, sites were sampled at least twice, introducing temporal correlation through this repeat sample design. Therefore, we included year within watershed as a random variable. For each model, we used a randomly selected subset of 70 percent of the total data to determine the coefficients. This model was validated using the full dataset. Final models used the full dataset and an adjusted R^2 was calculated from a linear regression of the observed and predicted fish populations. These pseudo R^2 values do not represent the proportion of the total variability of the outcome that is accounted for by the model as in ordinary least-squares regression; instead, these values serve to compare models produced from the same data and predicting similar outcomes allowing an interpretation of model validation.

We ran individual models for each fish species using all combinations of selected metrics in statistical software R (v4.0.3) (R Core Team 2020). For each species or life stage model, we only included sites with counts >0. In the GLMM and elsewhere, we treated coho salmon fry and parr as separate species. Counts of

Table 5—Generalized linear mixed-effects model results for fish populations in the Tongass National Forest, Alaska

Parameters	Transformation for modeling	Coho salmon		Cutthroat trout			Dolly Varden trout			Steelhead/ rainbow	Sculpin
		Parr (C/A)	Fry (C/A)	I/R	C/A	All	I/R	C/A	All	C/A	C/A
Adjusted R^2		0.71	0.89	0.83	0.66	0.50	0.61	0.63	0.56	0.24	0.43
Number of samples		144	133	135	80	215	148	127	275	74	79
(Intercept)		208.51	252.14	12.06	3.35	12.43	5.37	2.01	4.66	1.35	8.85
Fixed effects:											
Network distance	Relative to longest	—	0.73	1.15	0.80	2.26	—	2.87	0.98	—	0.50
Canopy cover >50 percent	Percentage of area	-2.70	-0.39	-1.02	-0.3	-1.15	-0.59	1.20	-0.26	1.94	—
Old growth	Percentage of area	—	3.24	—	-1.57	—	-0.48	—	-1.56	—	-2.43
Average bankfull depth	Standardized	-0.07	-0.01	—	0.06	—	—	0.02	-0.02	—	0.05
Average bankfull width	Standardized	1.56	-1.04	—	—	—	0.18	-0.98	-1.06	-1.09	—
Wetted riffle area	Standardized	26.24	-38.29	47.29	—	1.85	71.59	15.87	39.86	193.20	151.90
Reach length	Standardized	-8.79	69.64	17.20	23.91	29.26	—	—	23.56	24.38	-67.85
Reach length/average channel bed width	Standardized	—	-8.43	—	0.31	—	0.12	—	-0.35	-13.29	—
Total key large wood	Standardized	1.23	-0.38	—	-3.50	-1.33	0.17	—	-0.16	—	0.70
Pools/km	Standardized	-15.32	4.78	-7.21	28.94	1.91	5.72	—	11.48	21.33	-28.16
Relative pool area	Standardized	28.82	-5.78	15.63	—	1.30	23.35	—	4.61	-26.81	83.23
Average residual pool depth	Standardized	—	-0.12	-0.05	—	-0.05	0.05	0.15	0.08	0.00	—
Biomass	Standardized	0.37	-0.77	0.59	—	-0.10	0.67	0.44	0.69	0.9	0.9
D_{50}	Standardized	-0.23	-8.95	-0.75	-0.73	—	-1.59	-3.46	-2.26	-19.31	-7.09
Random effects:											
Variance of watershed Intercept		0.28	1.15	0.17	0.67	0.29	0.00	0.36	0.37	1.09	0.80
Variance of year within watershed intercept		0.24	0.67	0.02	0.25	0.14	0.29	0.60	0.22	0.82	0.25

Fish populations were tested from connected-anadromous (C/A) subwatersheds, isolated-resident (I/R) subwatersheds, or both (all); thus the difference in sample sizes. The adjusted R^2 values were determined by comparing the model-predicted population estimates to all of the observed population estimates for each fish population.

— = not present.

coho salmon fry are large compared with coho salmon parr and other fishes, making the separation of these life stages mathematically necessary (to avoid fry dominating parr), as well as useful to understand habitat relationships for these important and different life stages of coho salmon. We used Akaike information criterion (AIC) for model selection (Burnham and Anderson 2002). Only sites where the species of interest were present were included in species-specific fish population models, making sample sizes different among species (table 5).

Question 2: What are the spatial and temporal influences of timber harvest history and hydrologic regime on resident and anadromous fish communities?

To provide spatial context for multivariate analyses, we developed boxplots of stream network distance and fish species as well as harvest group over time. We also developed boxplots of fish species population estimates in connected/anadromous subwatersheds for time periods 1 and 2. For these boxplots, we used a log10(x+1) transformation of fish population densities to keep zeros as zeros and to better visualize the distribution of values ranging over several orders of magnitude.

Multivariate analyses were implemented for questions 2 and 3. These multivariate analyses require complete data matrices; therefore, six sites with many missing data points were excluded. For cases in which missing habitat data were limiting (fewer than 5 missing data points for the site), and data were available for that site from another sample year, we copied the missing values from the most recent year with data. This was most often the case for habitat variables of sediment D_{50} and D_{84}, reach or riffle gradient, and undercut bank. The final dataset for multivariate analyses contained 322 samples from 114 subwatersheds among 21 watersheds. We completed all multivariate ordinations using statistical software PC-ORD Version 7 (PC-ORD V. 7 2016) and included nonmetric multidimensional scaling (NMS) for question 2 and principal components analysis (PCA) for question 3.

To understand the distribution of fish communities in connected/anadromous subwatersheds on the Tongass National Forest, we implemented NMS using Sorenson distance. We completed NMS ordination using only watersheds connected to marine environments (n = 160) where six fish species/size-classes could be included in the community matrix (coho salmon fry and parr, cutthroat trout, Dolly Varden trout, steelhead/rainbow trout, and sculpin). Isolated/resident watersheds contained only two fish species (Dolly Varden and cutthroat trout), making NMS ordination less meaningful. As with the GLMM analysis in question 1, in the NMS, we treated coho salmon fry and coho salmon parr as separate species to clarify habitat and community relationships for these life stages. To reduce the effect of extreme values, we used log10(x+1) transformed population estimates for each of the fish species. All fish and most habitat metrics were used as overlay variables in joint plots (table 3). With NMS, these secondary matrix variables may be correlated

with each other and are automatically centered and standardized during analysis. In addition, we included six classification metrics in the secondary matrix for analysis by group (table 3).

Multi-response permutation procedure (MRPP) is a multivariate, nonparametric, permutation significance test for comparing groups of samples based on within-group similarities (McCune and Grace 2002). Tests by MRPP provide both a likelihood p-value and an effect size (A) that measures the chance-corrected, within-group homogeneity: $-1 < A \leq 0$ when there is no difference between groups, and $0 < A < 1$ when groups differ. It is important to note that statistical significance may result between groups even when the effect size is small ($A < 0.1$) if the sample size is large (e.g., >100 samples). In these cases, the ecological significance of the result should be interpreted with caution. For question 2, MRPP analysis was linked to the NMS ordination that used Sorenson distance and focused on testing the fish community in connected/anadromous subwatersheds ($n = 160$) among groups of (1) the first and second time periods, (2) hydrologic regimes of rain or snow, and (3) harvest history groups.

Question 3: What are the spatial and temporal influences of timber harvest history and hydrologic regime on physical stream characteristics? Principal components analysis was used to explore relationships among instream habitat metrics and fish species abundance. We conducted PCA with Euclidean distance on 25 habitat metrics (table 3) with data prepared as described above for multivariate analyses. We completed four PCAs on different subsets of surveys for: (1) connected/anadromous subwatersheds, (2) isolated/resident subwatersheds, and (3) Staney Creek and (4) Towers Creek watersheds individually. Staney Creek and Towers Creek watersheds were selected for analysis because of the annual surveys conducted at these sites. Both watersheds have a rain-dominated hydrology, and Staney Creek experienced timber harvest, whereas Towers Creek did not. The 25 selected habitat metrics reflect variable reduction from the full suite of available variables. Correlated response variables in a PCA will have the effect of emphasizing that relationship or structure in the ordination. To avoid weight or emphasis on any one habitat metric over another, correlated (Pearson's $r > 0.7$) or redundant metrics were excluded. Remaining habitat metrics were log10 or square root transformed to approximate normality (skewness < 1). During the PCA analysis process, response variables are automatically centered and standardized. We overlaid population estimates for coho salmon fry and parr, cutthroat trout, Dolly Varden trout, steelhead/rainbow trout, and sculpin on the PCA to assess their association with habitat axes. Six categorical variables were overlaid on the PCA to explore grouping patterns (table 3).

We linked MRPP analyses to the PCA ordinations and used Euclidean distance to test for differences in habitat characteristics. We completed three MRPP analyses

using the connected/anadromous subwatersheds (n = 160) and isolated/resident subwatersheds (n = 162) to test for differences among groups of the (1) first and second time periods, (2) hydrologic regimes of rain or snow, and (3) harvest history groups. The MRPP analyses of Staney Creek (n = 70) and Towers Creek (n = 62) tested for differences in the first and second time periods and between isolated/resident or connected/anadromous subwatersheds.

Question 4: What are the spatial and temporal influences of hydrologic processes on stream geomorphic characteristics by subwatershed groupings of hydrologic regime, percentage of old-growth forest, and drainage area? Poststratification of landscape-scale categories relevant to hydrological process comparisons removed the nested spatial structure of the original dataset (app. 1; fig. A1-2). We generated boxplots of key stream geomorphic and hydrologic variables to compare subwatershed groupings (of hydrologic regime, percentage of old-growth forest, drainage area, harvest history, and connected/anadromous versus isolated/resident). Comparing rain- and snow-dominated hydrologic regimes involved generating scatter plots of hydrologic variables. Graphical plots of record peak storm events that occurred at the 10 weather stations with long-term records within the study area were used to explore precipitation patterns during the study period.

To evaluate whether stream geomorphic and hydrologic variables changed over time, and whether a detected change was linked to the hydrologic regime or percentage of old-growth forest in the subwatershed, we developed linear mixed models (LMMs). Models were fit using the lme4 package (Bates et al. 2015), coefficient tests were conducted using the lmerTest package (Kuznetsova et al. 2017), and estimated marginal means were calculated using the lsmeans package (Lenth 2016) in statistical program R (R Core Team 2020). Our response variable was the change in an individual habitat metric from the first to last survey for 103 sites with repeat surveys. As for the GLMM analysis of fish populations in question 1, we controlled for spatial nestedness of sites within watersheds by adding a random effect for watershed. The habitat metrics tested for change from T1 to T2 in separate models were D_{50}, bankfull depth, bankfull width, width-to-depth ratio, hydraulic radius, relative pool area (rpa), residual pool depth, count of large woody debris, and percentage of reach gradient (rch-gradient%). However, LMMs did not converge for D_{50} or rpa; therefore, these metrics were discarded from the analysis. We included main and interactive effects of the categorical variables for the two different hydrologic regime classifications, two levels of old-growth forest cover, and four harvest history groups. Because both old-growth cover and harvest history provide information on forest stand age and condition, we included these variables in separate models. We controlled for differences in total years surveyed for each site by adding a fixed effect for number of years between the first and

last survey at a site. Metric change from T1 to T2 was tested by assessing if the estimated marginal means of factor groups (n = 4 groups for hydrologic regime and old-growth cover in model one, and n = 6 groups for hydrologic regime and harvest category) were significantly different from 0 at $\alpha = 0.05$. We used likelihood ratio tests with Satterthwaite degrees of freedom to evaluate the null hypothesis that change was not affected by hydrologic regime, old-growth cover, or harvest group. When significant effects of grouping variables were detected, we conducted Tukey post-hoc multiple comparisons of estimated marginal means to determine how group means differed.

Results

Results for Question 1: What Are the Species-Specific Relationships Between Fish and Aquatic Habitat Over Time and Space?

Most of the physical habitat variables showed similarity over time and between isolated/resident or connected/anadromous subwatersheds (fig. 2). Annual fish population estimates in the Staney Creek and Towers Creek watersheds exhibited strong variability over time in coho salmon fry and parr, and Dolly Varden trout (fig. 3). In the Staney Creek watershed, coho salmon fry population sizes dropped in 2015 and 2019; coho salmon parr numbers dropped in 2015. At Towers Creek, coho salmon fry numbers dropped between 2015 and 2017 at most sites, whereas coho salmon parr numbers did not drop during this time period. Population numbers of cutthroat trout appeared to increase after 2015 to higher than pre-2015 levels in some Staney Creek sites, while cutthroat trout abundance at sites in Towers Creek watersheds remained relatively similar over time (fig. 3). Population numbers of Dolly Varden trout appear to have greater interannual variability in the Towers Creek watershed compared with the Staney Creek watershed. Steelhead/rainbow population estimates appear higher post-2016 in one subwatershed of Staney Creek (Orpheus Creek) and in one subwatershed in Towers Creek (Upper East Creek), before returning to pre-2015 population levels.

Dendrograms of population estimates at sites sampled in T1 and T2 display variation in abundance between these two time periods at many subwatersheds for several species (fig. 4). However, both higher and lower population estimates were observed between T1 and T2, depending on the site (fig. 4). Sites that were occupied in T1 were generally occupied in T2 (fig. 4).

Generalized linear mixed-effects model results—
In the GLMM analysis, many parameters were standardized, and therefore an increase of one standard deviation for a particular parameter results in a respective increase or decrease of the predicted population estimate (see table 6 for standard deviations for each parameter). For both cutthroat and Dolly Varden trout,

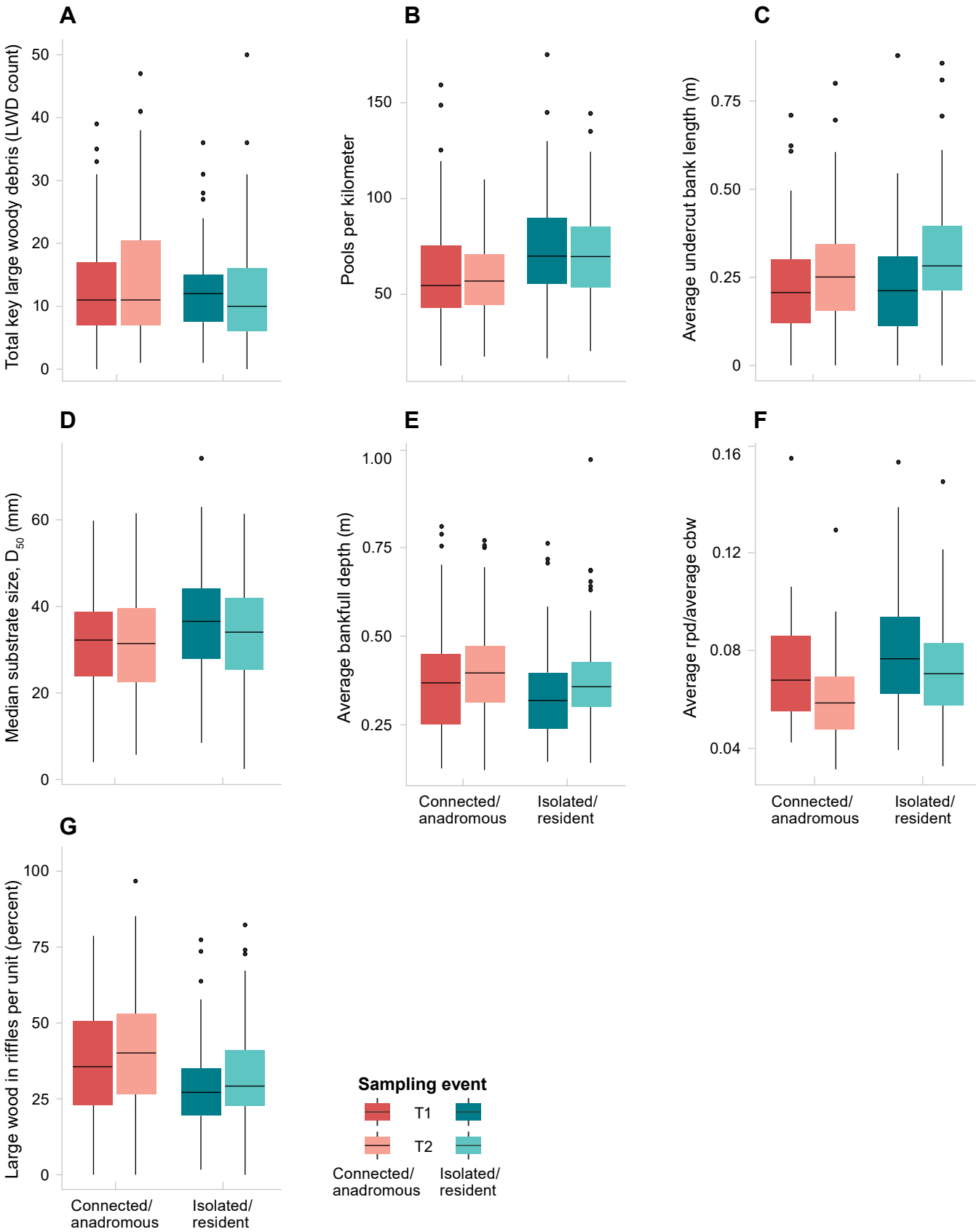

Figure 2—Instream variables for two time periods (T1 and T2) in subwatersheds connected to the ocean (connected/anadromous) and isolated from the ocean (isolated/resident). Rpd = residual pool depth, cbw = channel bed width.

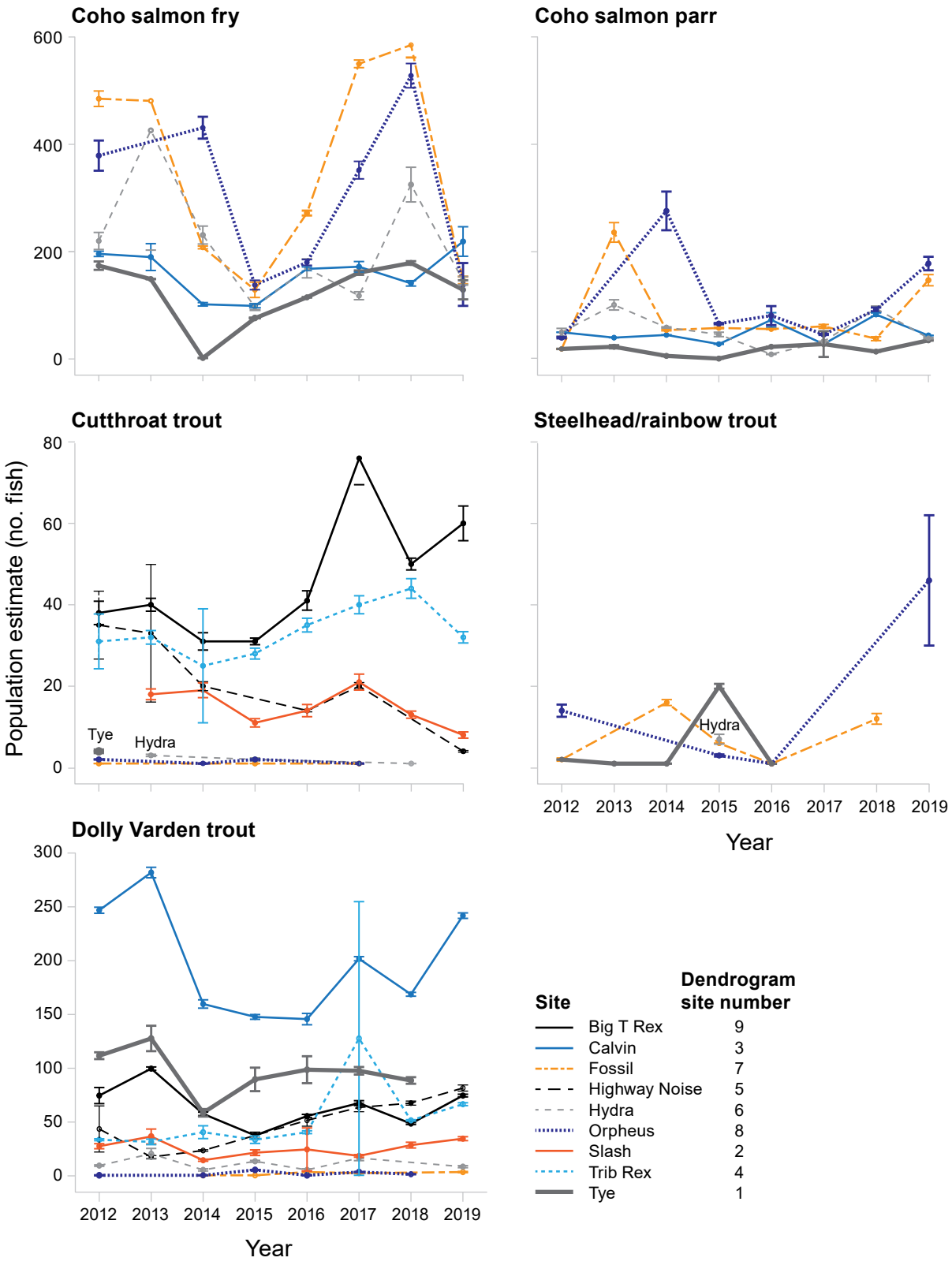

Figure 3—Population estimates and confidence intervals at annually sampled sites in (A) Staney Creek and (B) Towers Creek watersheds, excluding population estimate of 1370 at Upper East in 2012.

B (Towers Creek Watershed)

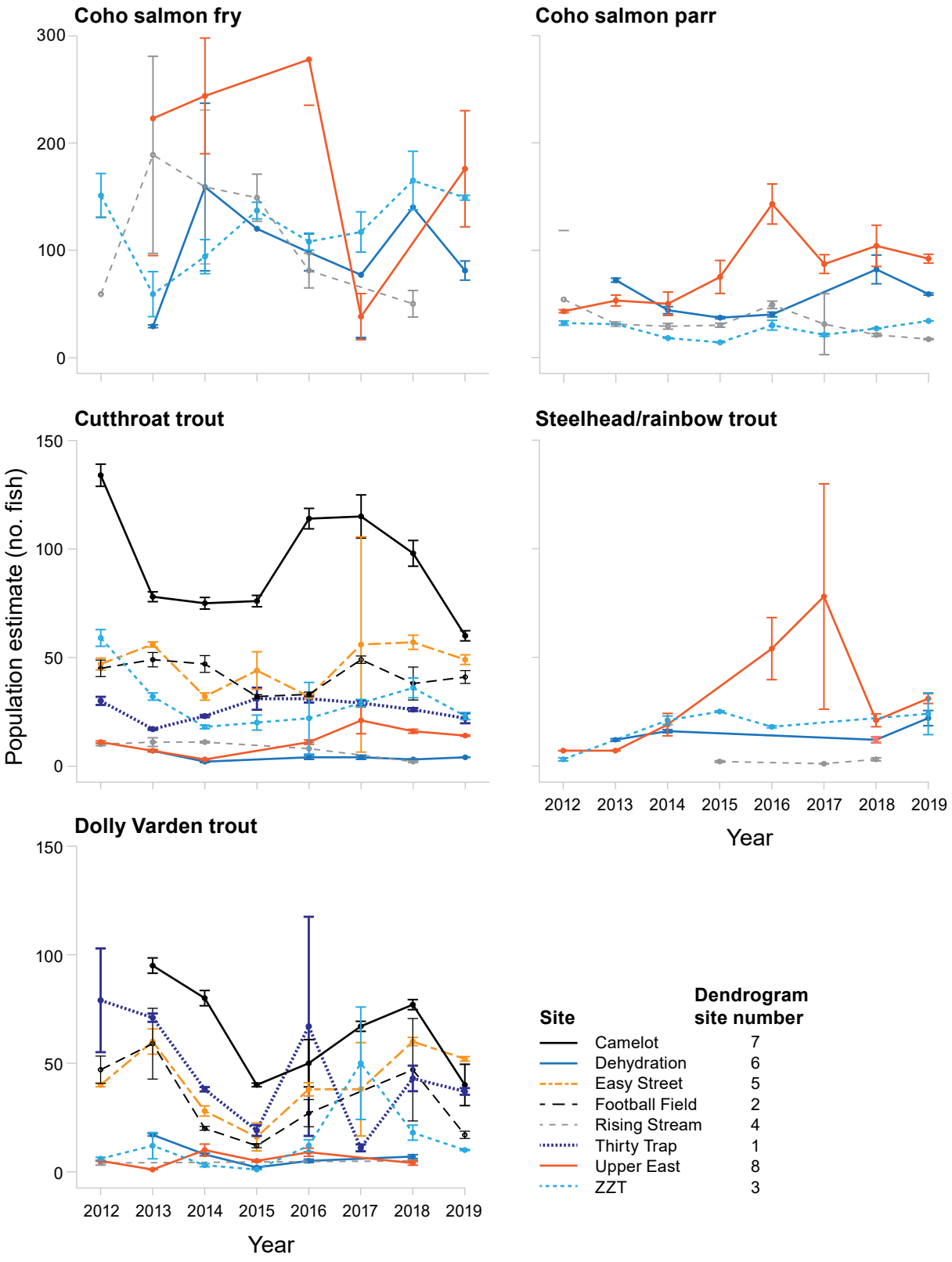

Figure 3 (continued)—Population estimates and confidence intervals at annually sampled sites in (A) Staney Creek and (B) Towers Creek watersheds, excluding population estimate of 1370 at Upper East in 2012.

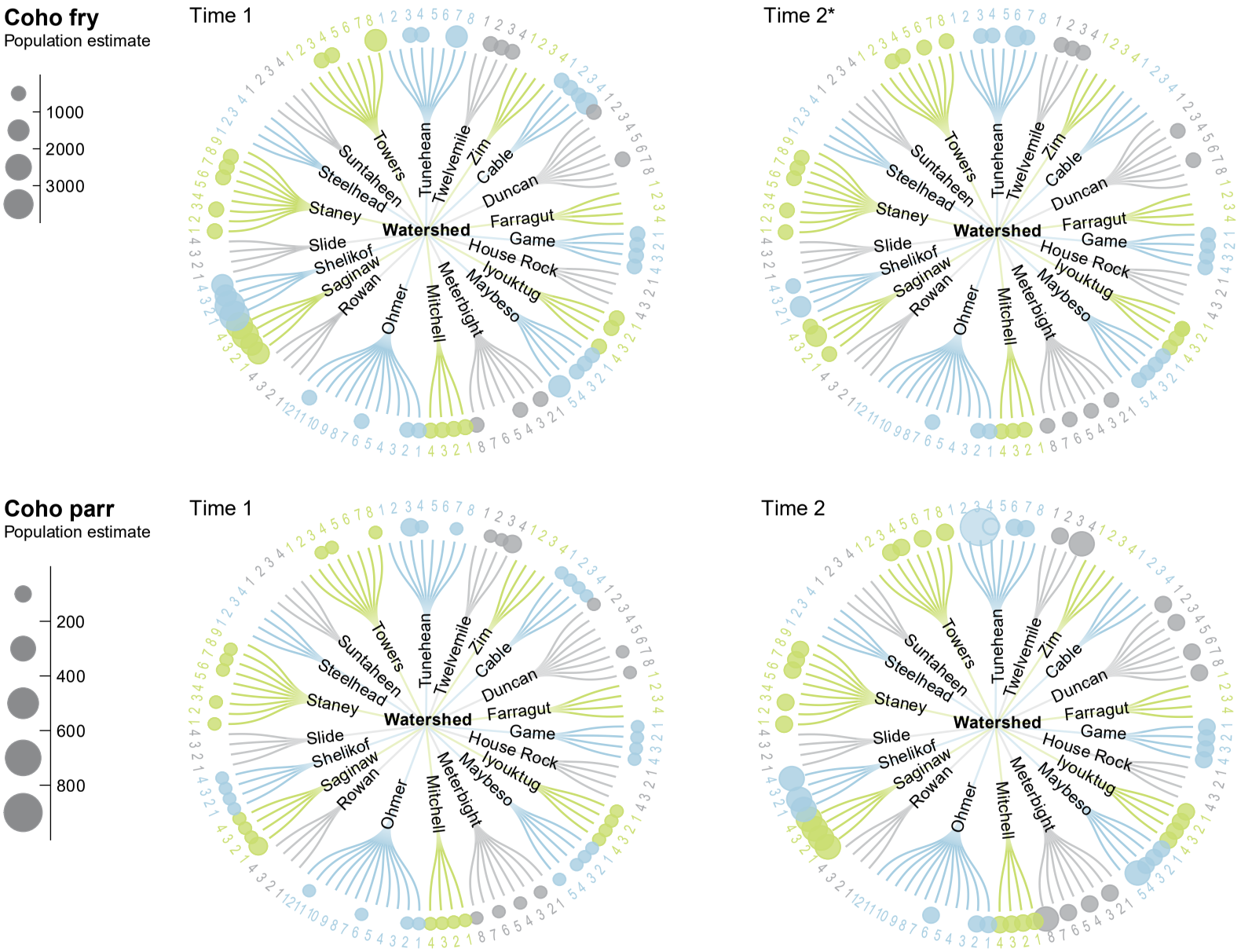

Figure 4—Dendrograms of individual fish species population estimates (size of dots) at sites nested within watersheds (different colors) for the first (left) and second (right) sample of sites between 2012 and 2019. See appendix 3 for a crosswalk between site numbers and names.

*Excludes Shelikof:Kaching with population estimate: 10,589.

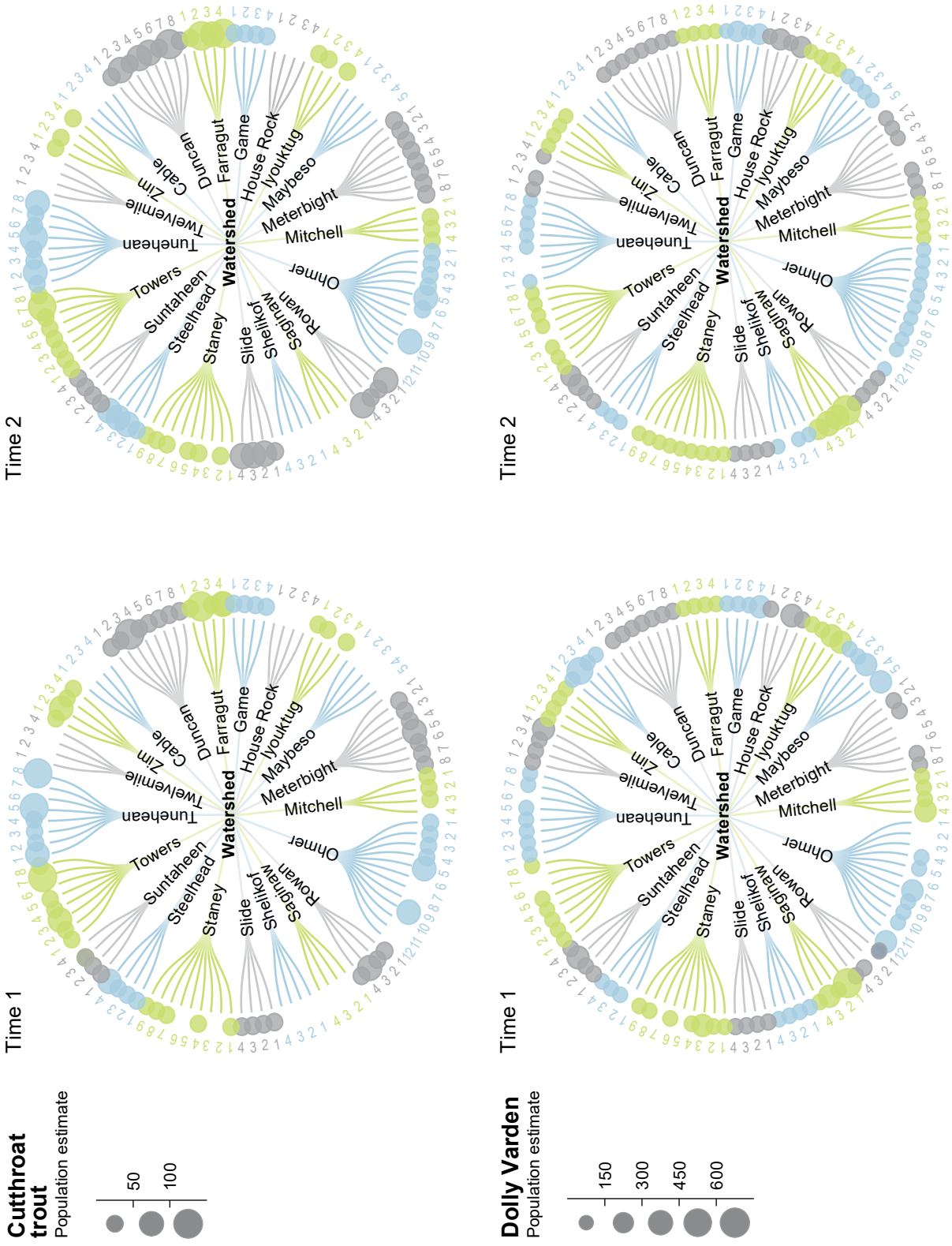

Figure 4 (continued)—Dendrograms of individual fish species population estimates (size of dots) at sites nested within watersheds (different colors) for the first (left) and second (right) sample of sites between 2012 and 2019. See appendix 3 for a crosswalk between site numbers and names.

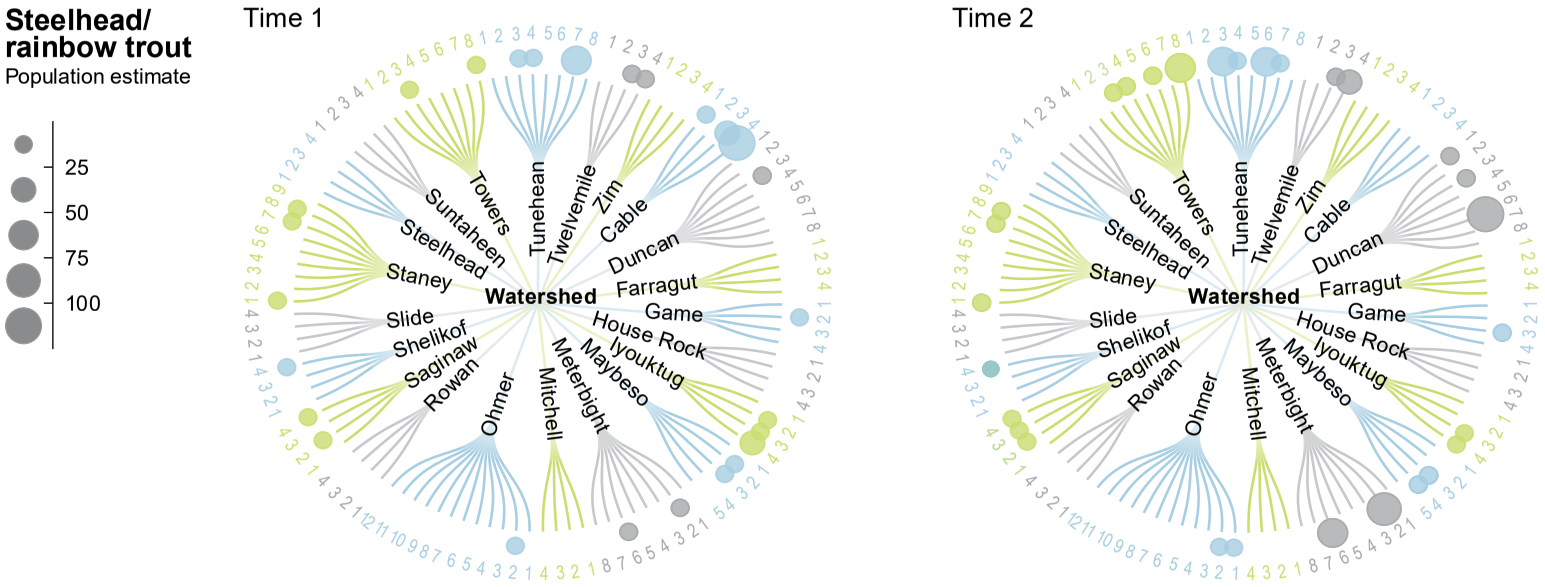

Figure 4 (continued)—Dendrograms of individual fish species population estimates (size of dots) at sites nested within watersheds (different colors) for the first (left) and second (right) sample of sites between 2012 and 2019. See appendix 3 for a crosswalk between site numbers and names.

Table 6—Standard deviations for the standardized habitat variables used in the generalized linear mixed-effect models of fish populations in watersheds of interest in the Tongass National Forest, Alaska

	Coho salmon		Cutthroat trout			Dolly Varden trout			Steelhead	Sculpin
	Parr (C/A)	Fry (C/A)	I/R	C/A	All	I/R	C/A	All	C/A	C/A
Average bankfull depth (m)	0.15	0.15	—	0.13	—	—	0.16	0.15	—	0.14
Average bankfull width (m)	3.49	3.29	—	—–	—	2.51	3.49	2.80	3.45	—
Wetted riffle area (m^2)	168.59	136.49	134.44	--	146.71	126.82	192.35	146.93	149	124.88
Reach length (m)	23.47	18.94	20.03	19.71	21.48	—	—	20.42	18.01	18.7
Reach length/average channel bed width	—	8.52	—	7.75	—	6.54	—	6.95	8.09	—
Total key large wood	10.14	10.05	—	8.47	8.11	8.26	—	8.67	—	9.99
Pools/km	24.26	23.7	26.92	20.75	28.56	27.64	—	28.13	17.58	24.24
Relative pool area	22.4	22.41	19.34	—	19.99	18.24	—	20.88	22.17	23.16
Average residual pool depth	—	0.15	0.1	—	0.12	0.11	0.16	0.12	0.16	—
Biomass	1.11	1.15	0.72	—	0.84	0.69	1.13	1.03	1.01	1.06
D_{50}	11.23	11.25	11.57	10.34	—	13.58	11.92	12.39	12.41	12.81

Fish populations were tested from connected/anadromous (C/A) watersheds, isolated/resident (I/R) subwatersheds, or both (All).

— = not present.

the models for the isolated/resident or connected/anadromous subsets had greater predictive capacity than the models derived using data from all sites (adjusted R^2) (table 5). Only steelhead/rainbow and sculpin had adjusted R^2 values for their predictive models that were <0.50, whereas predictive model adjusted R^2 values for coho salmon parr and fry and cutthroat (I) were >0.70 (table 5).

The GLMMs identified a negative relationship between total fish biomass and coho salmon fry and cutthroat (all), whereas a positive relationship was observed with other species, including coho salmon parr (table 5). Higher amounts of canopy cover had a negative relationship with abundance of coho salmon fry and parr, but greater area of old-growth cover had a positive relationship with coho salmon fry abundance (table 5). As D_{50} values increase (i.e., mean substrate particle size gets larger), population estimates decrease for all species (table 5). The model supports network location as an important factor in explaining relationships between physical habitat and different fish species, reflecting the observation of coho salmon fry and parr lower in the network, with cutthroat and Dolly Varden trout throughout the networks (table 5; fig. 5A). The wet-riffle area was strongly associated with steelhead/rainbow and sculpin and minimally associated with Dolly Varden and cutthroat trout. The wet-riffle area had a positive influence on coho salmon parr, but a negative influence was found for coho salmon fry (table 5).

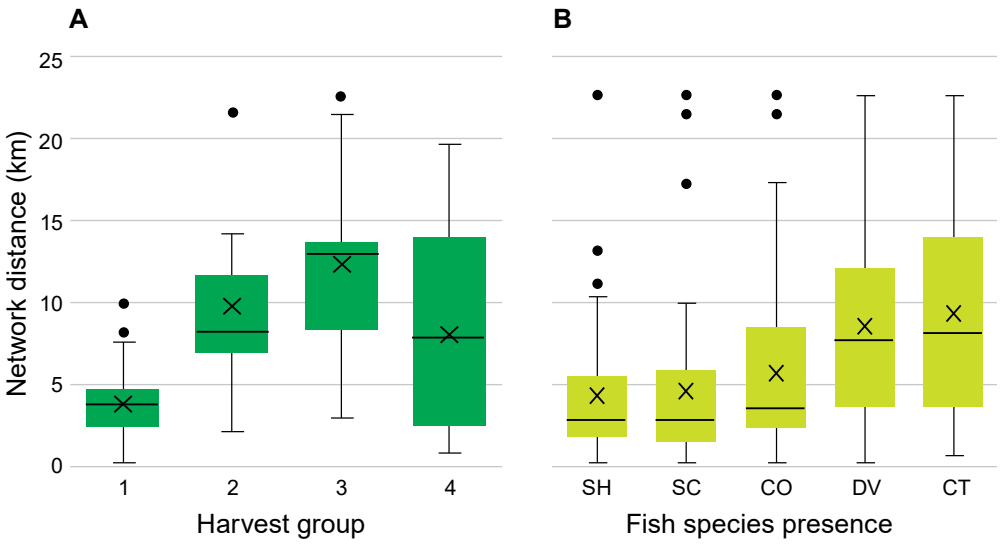

Figure 5—Distance along the river channel between sample sites and the marine environment by (A) harvest group and (B) fish species presence. SH = steelhead/rainbow trout; SC = sculpin; CO = coho salmon fry and parr; DV = Dolly Varden trout; CT = cutthroat trout.

Results for Question 2: What Are the Spatial and Temporal Influences of Timber Harvest History and Hydrologic Regime on Resident and Anadromous Fish Communities?

Since 1950, timber harvest occurred within the 300-ft (91-m) buffer of sampled sites at 82 of the 114 subwatersheds in the study area. Higher amounts of harvest adjacent to streams occurred in harvest group 1 (figs. 5A and 6; table 4). More connected/anadromous subwatersheds were present in harvest group 1, whereas more isolated/resident subwatersheds were present in harvest groups 2 and 3 (table 4). This is also reflected by network distance, which was shortest for harvest group 1 (fig. 5A). Further, boxplots of fish population density (log 10/m^2) by harvest group demonstrated that coho salmon fry and parr have higher estimates in group 1, and are also the most dominant species in harvest groups 1 and 2, compared with other species (fig. 7).

Relationships of stream network distance with the presence of different fish species as graphed in boxplots suggest that steelhead/rainbow and sculpin were predominantly found in sites closer to the ocean, and cutthroat occupied sites farthest from the ocean. Coho salmon tended to be found in the lower portions of river networks, and Dolly Varden trout could be found throughout river systems but tended to be found in river network locations overlapping both coho salmon and cutthroat trout (fig. 5B).

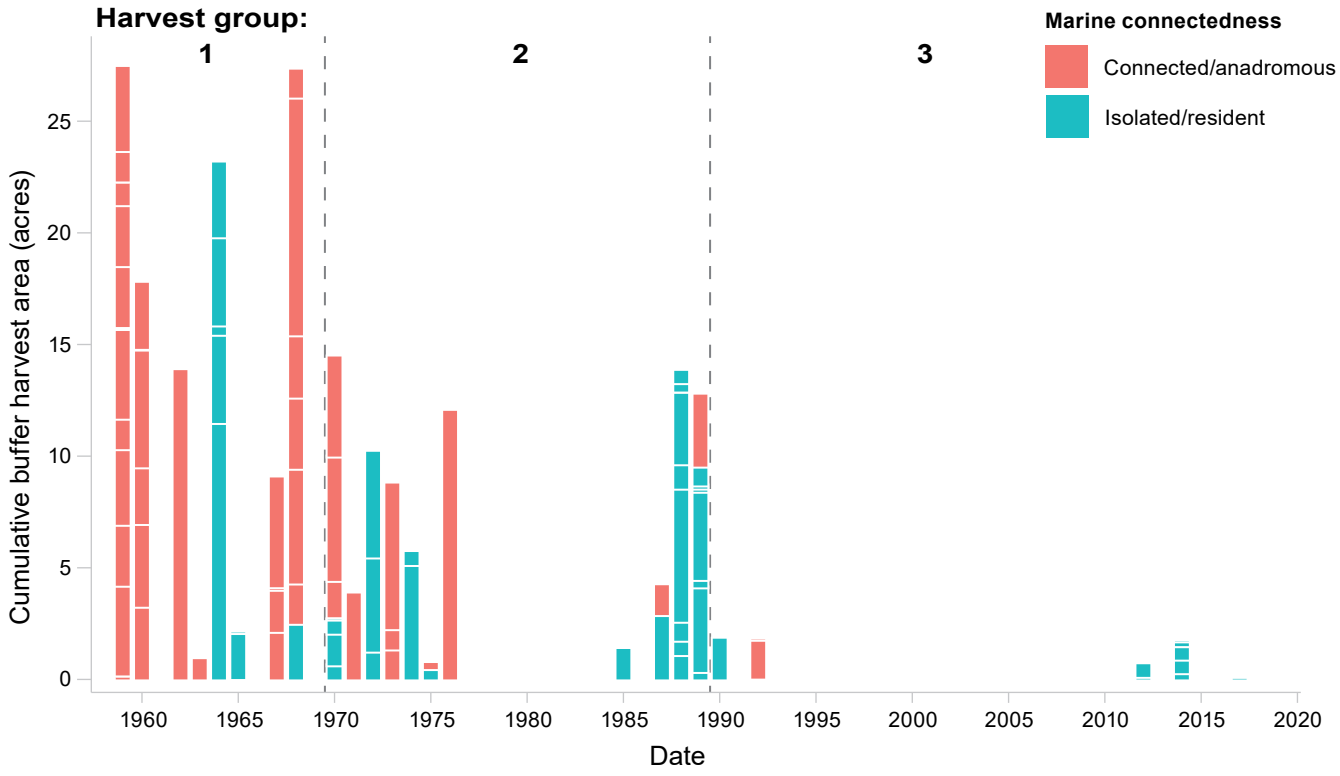

Figure 6—Cumulative riparian harvest history for all watersheds in the Management Indicator Species Study area. Riparian harvest was defined as harvest that occurred within a 91-m (300-ft) buffer on each side of the stream channel at sample locations.

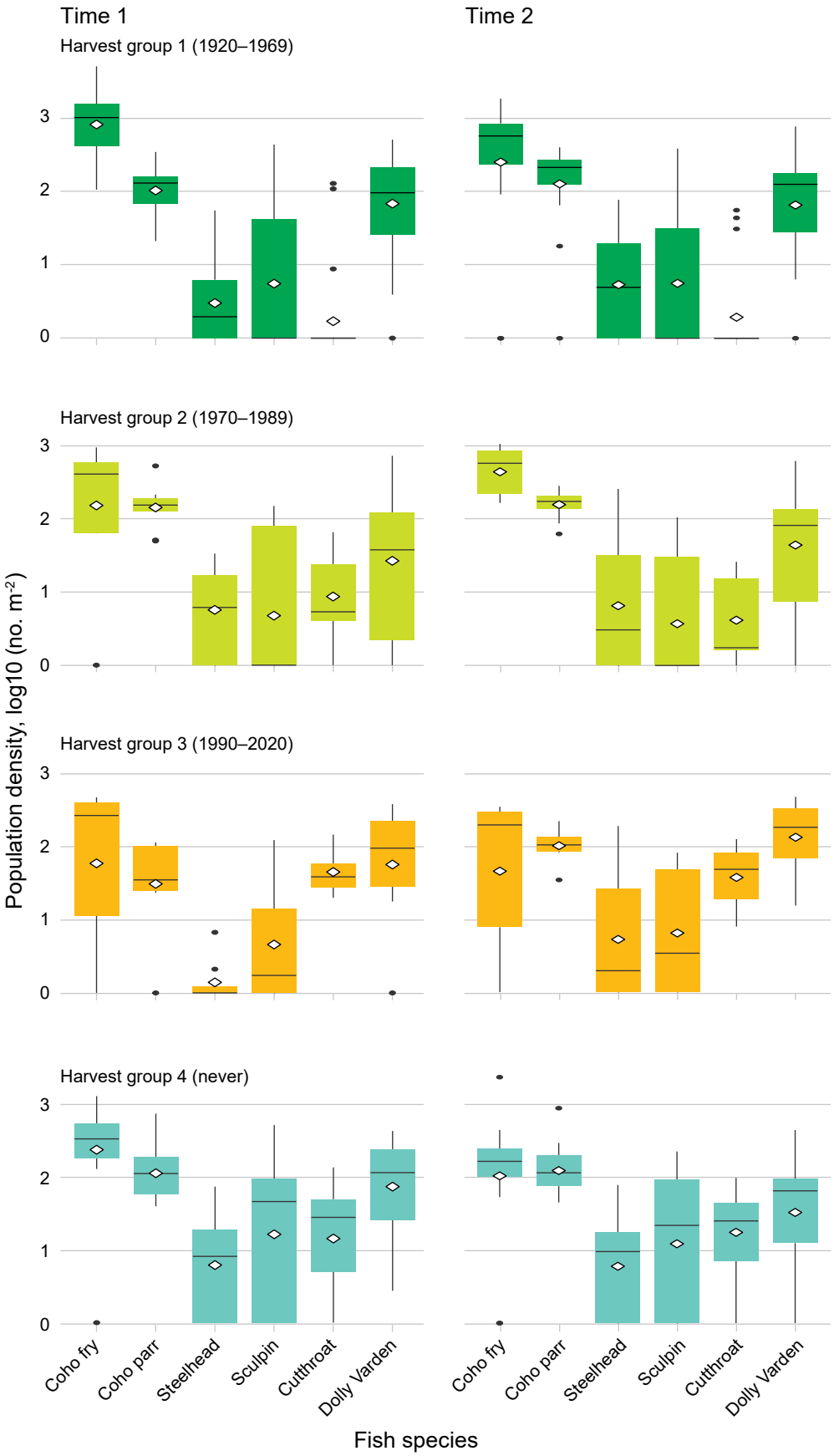

Figure 7—Fish population sizes by species and harvest group at sites sampled in time periods 1 (excluding coho salmon fry population estimates >10,000) and 2.

Nonmetric multidimensional scaling and multi-response permutation procedure results—

In NMS of fish communities in connected/anadromous subwatersheds, the first three axes of the ordination explained 93 percent of the variation. Fish species population estimates were contrasted along axis 1 (Dolly Varden trout vs. sculpin) and axis 2 (coho salmon fry vs. cutthroat) (fig. 8). Steelhead/rainbow did not

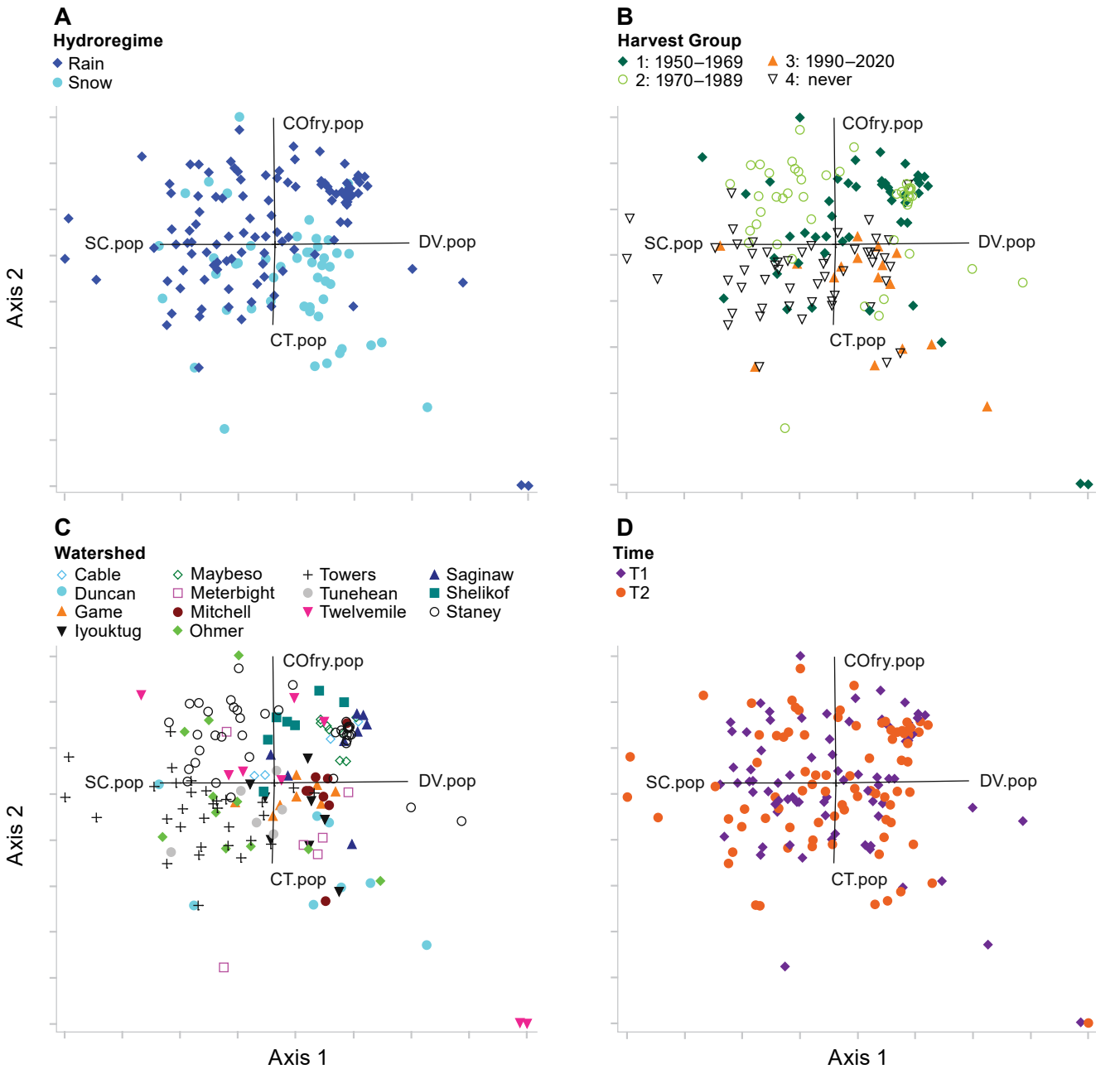

Figure 8—Nonmetric multidimensional scaling ordination plots of fish communities from connected/anadromous subwatershed surveys by (A) hydroregime, (B) riparian harvest history, (C) watershed, and (D) survey time periods (T1 and T2). The 3D ordination had a final stress of 0.11 and total R^2 of 0.93. Jointplots (black line vectors) denote relative strength and direction of fish species association with axes. Note that the two points in the far lower right corner are from Hanging Pipe and are outliers, as surveys detected only Dolly Varden trout (connected subwatershed, although they are often disconnected by stream drying). Fish species populations: CO = coho salmon; DV = Dolly Varden trout; CT = cutthroat trout; SC = sculpin.

align along any axis (i.e., they were generally distributed and found in the center of ordination space) and were relatively low in abundance. Coho salmon parr were also not correlated with a specific axis, likely reflecting their much lower abundance compared with coho salmon fry. Fish community differences between rain- or snow-dominated hydrologic regimes were detected by MRPP analyses, although the effect size was small (table 7). Cutthroat trout were more associated with snow-dominated hydrologic regimes, and coho salmon fry were more associated with rain-dominated hydrologic regimes, although not exclusively (fig. 8A). Watersheds with riparian harvests occurring from 1950 to 1989 (harvests groups 1 and 2) support different fish communities than watersheds with more recent riparian harvest or that were not harvested (harvest groups 3 and 4) (table 7). Coho salmon fry abundances were associated with older harvest (pre-1990), whereas cutthroat trout were associated with more recent or no harvest (fig. 8B). Fish communities also differed across some watersheds, although sample size differences among watersheds complicate the interpretation and reliability of results (table 7; fig. 8C). MRPP analyses found no differences in fish community composition between T1 and T2 (table 7; fig. 8D).

Table 7—Multi-response permutation procedure (MRPP) results on the differences between groups from the nonmetric multidimensional scaling (NMS) ordination of fish communities and the principal components analysis (PCA) ordinations of habitat metrics

				PCA	
Groups	**NMS (C)**	**PCA (C)**	**PCA (I)**	**Staney**	**Towers Creek**
Sample size	160	160	162	70	62
T1 vs. T2	0.00	0.00	0.00	-0.01	-0.01
Rain vs. snow	0.07***	0.06**	0.02**	Na (rain)	Na (rain)
Harvest group (H1, H2, H3, vs. H4)	0.09***	0.12***	0.11***	Na (H2)	Na (H4)
Watersheds	0.24***	0.25***	0.24***	Na	Na
Connected vs. isolated	Na (C)	Na (C)	Na (I)	0.32***	0.21***

Groups tested included differences between time-periods, hydro-regime, harvest history, watersheds, and marine connectedness (connected/anadromous vs. isolated/resident). The larger the group difference effect size (A), the greater the difference between groups (** $p < 0.001$, *** $p < 0.0001$). Note that values of $A < 0.10$ indicate small differences between groups, even though they may be statistically significant due to large sample sizes. Groups with "na" were not tested because there was only one group within the respective dataset (e.g., all data were from Connected "C" subwatersheds, or all data were from Isolated "I" subwatersheds).

Results for Question 3: What Are the Spatial and Temporal Influences of Timber Harvest History and Hydrologic Regime on Physical Stream Characteristics?

We found a larger particle size in D_{50} sediment to be associated with isolated/resident subwatersheds from harvest group 1 compared with connected/anadromous subwatersheds in the same harvest group, or across all other harvest groups (fig. 9A). D_{50} was not linearly correlated (Pearson r) with either rch-gradient% or network distance. Total key large wood per meter was higher in T2 for connected/anadromous subwatersheds in harvest groups 2 and 3, with lower amounts of key large wood in isolated/resident subwatersheds in harvest group 1 (fig. 9B). More roads were present in harvest group 1 compared with all others (fig. 9: C and E). However, the number of roads closed during the study period was also higher in harvest group 1 subwatersheds (fig. 9D).

Principal components analysis and multi-response permutation procedure results—

From the PCA analysis on habitat and watershed characteristics, we identified five significant axes (i.e., principal components) from the connected/anadromous subwatersheds (n = 160, 60 percent of variation explained) and four axes from the isolated/resident subwatersheds (n = 162, 52 percent of variation) (table 8). The PCA identified four axes from Staney Creek watersheds (n = 70, 66 percent of variation) (fig. 10G) and four axes from Towers Creek watersheds (n = 62, 72 percent of variation) (fig. 10H; table 9). Axes that captured more variation than would be expected by chance are identified as significant (broken-stick eigenvalues > 1.0). The PCA of the Staney Creek and Towers Creek watersheds explained more variation than the combined watershed analyses because some of the habitat metrics varied little or not at all within one watershed, so the Staney Creek and Towers Creek matrix of habitat data was less variable.

Riparian harvest history groups were found to have small habitat differences by MRPP analyses in both the connected/anadromous and isolated/resident subwatershed datasets (table 7); however, the effects vary between the datasets. Among connected/anadromous subwatersheds, those that have never been harvested were most similar to the oldest harvest group (1950–1969) and are correlated with large wood (lwd total), rpa and residual pool depth (rpd), average bankfull width (bf-width) and average bankfull depth (bf-depth), and percentage of old-growth cover (fig. 10C). Among isolated/resident subwatersheds, those that have never been harvested were most different from the two oldest harvest groups (1950–1989), and no individual habitat metric was clearly associated with any harvest history group (fig. 10D).

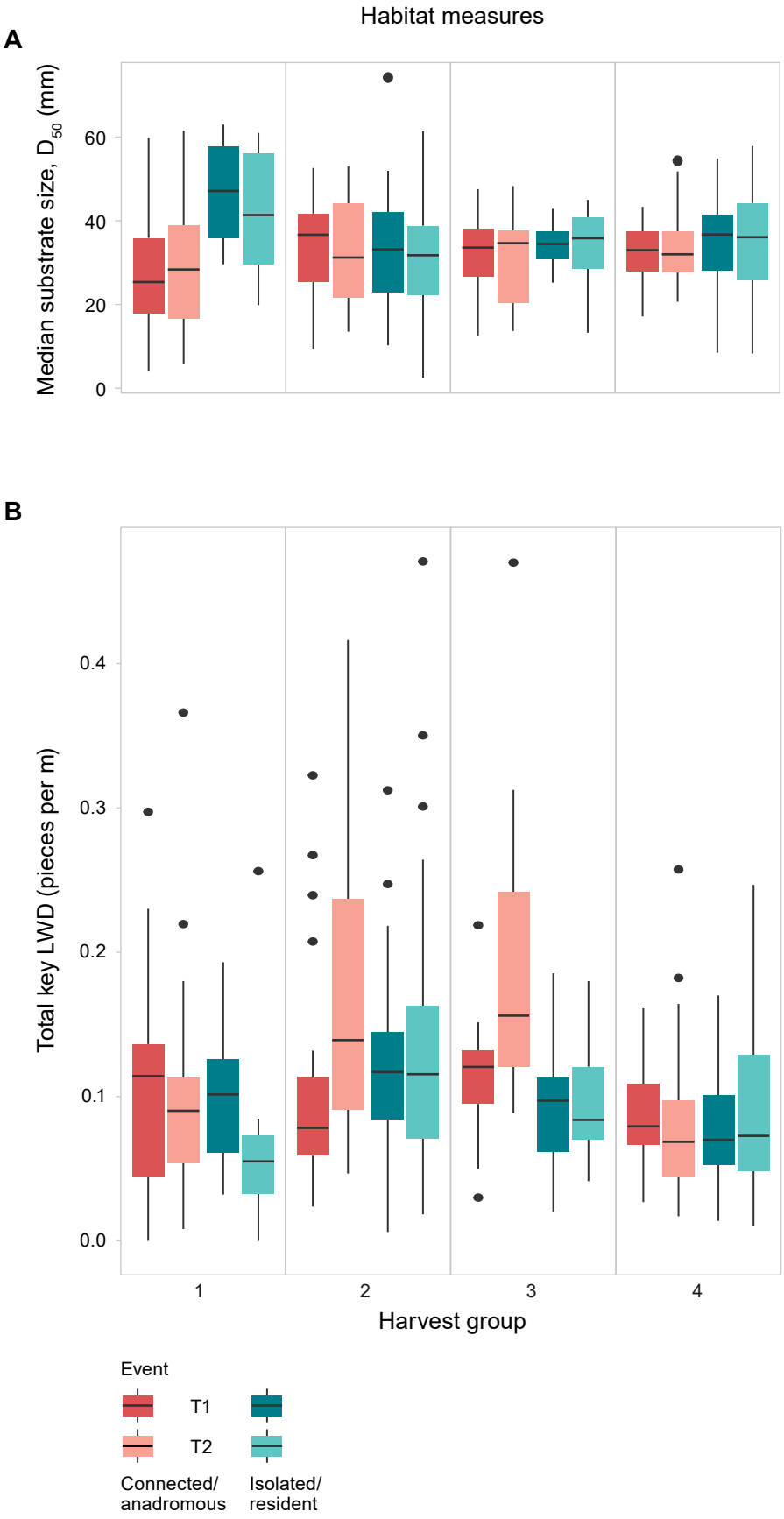

Figure 9—Habitat and subwatershed characteristics measured at survey sites in the Management Indicator Species Study area by harvest history, comparing connected/anadromous and isolated/resident subwatersheds.

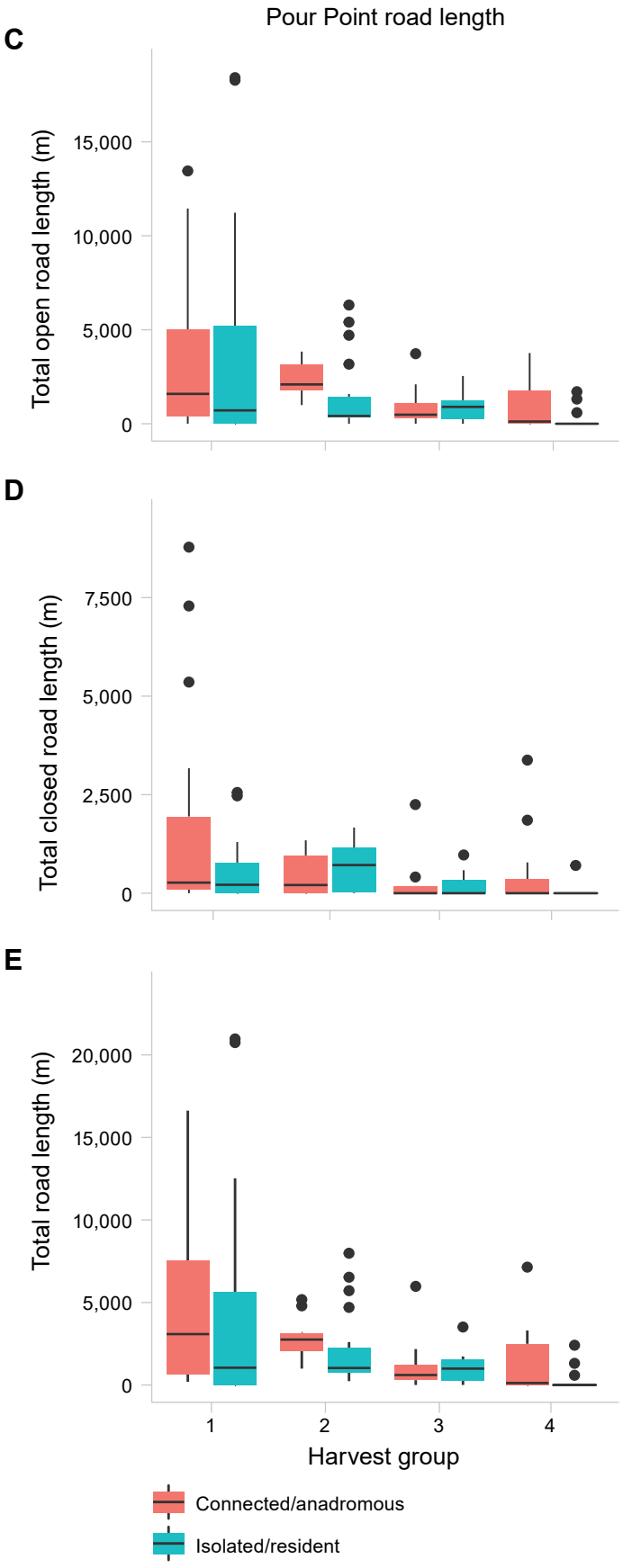

Figure 9 (continued)—Habitat and subwatershed characteristics measured at survey sites in the Management Indicator Species Study area by harvest history, comparing connected/anadromous and isolated/resident subwatersheds.

Table 8—Principal components from the datasets of connected/anadromous (n = 160) and isolated/resident subwatersheds (n = 162)

	Connected/anadromous subwatersheds			Isolated/resident subwatersheds		
Habitat	**1**	**2**	**3**	**1**	**2**	**3**
	Principal components, r					
Fish biomass	-0.08	0.20	-0.32	-0.15	-0.01	0.26
Headwater	**-0.68**	-0.30	-0.19	-0.43	-0.26	0.37
Roads	0.25	-0.45	-0.17	0.34	0.22	-0.07
Elevation	-0.24	0.32	**-0.71**	**0.55**	-0.36	0.29
Network distance	-0.47	0.21	**-0.67**	-0.01	-0.41	**0.54**
Canopy	0.45	0.21	0.48	-0.25	-0.15	0.24
Disturbed	-0.12	-0.43	-0.05	0.22	0.04	-0.26
Old growth	0.49	0.21	-0.34	0.07	-0.02	0.36
Bf-depth	**0.58**	0.04	0.27	0.16	0.49	-0.20
Bf-width/depth	0.39	-0.40	-0.48	**0.69**	-0.34	0.28
Bf-width	**0.77**	−0.34	-0.26	**0.90**	-0.03	0.09
D_{50}	-0.12	-0.29	0.05	0.27	-0.34	-0.44
Key-lwd total	-0.10	0.05	-0.37	-0.16	**-0.58**	0.25
Lwd-pool%	**0.65**	**0.56**	-0.09	0.08	**0.62**	0.37
Lwd total	**0.61**	-0.04	-0.27	0.11	-0.31	0.42
Pools/km	-0.23	**0.60**	-0.27	-0.49	-0.24	**0.60**
Reach-grad%	**-0.66**	-0.12	-0.08	-0.45	**-0.51**	-0.18
Riffle-grad%	**-0.52**	0.03	-0.06	-0.36	-0.33	-0.20
Reach/cbw	**-0.80**	0.15	0.21	**-0.77**	-0.07	-0.29
Reach length	**0.57**	-0.38	-0.06	**0.68**	-0.10	-0.12
Rpa	**0.75**	**0.53**	-0.02	0.03	**0.72**	**0.52**
Rpd.avg	**0.81**	0.03	-0.29	**0.64**	0.34	0.12
Rpd/cbw	-0.49	0.45	-0.03	**-0.64**	0.26	-0.12
Ucbank%.avg	0.07	0.12	0.18	-0.17	0.35	-0.12
Wet-riffle area	0.18	**-0.75**	-0.20	**0.58**	**-0.59**	-0.33

= negative correlation with axis = positive correlation with axis

Standardized regression coefficients are reported (i.e., correlations between the variable and axes) for each habitat variable. Coefficients in **bold** highlight the stronger correlations (r > |0.5|).

Avg = average; bf = bankfull; cbw = channel bank width; grad = gradient; lwd = large wood; rpa = relative pool area; rpd = residual pool depth; ucbank = undercut bank; rch-grad% = reach gradient percentage; rif-grad% = gradient in riffle habitat.

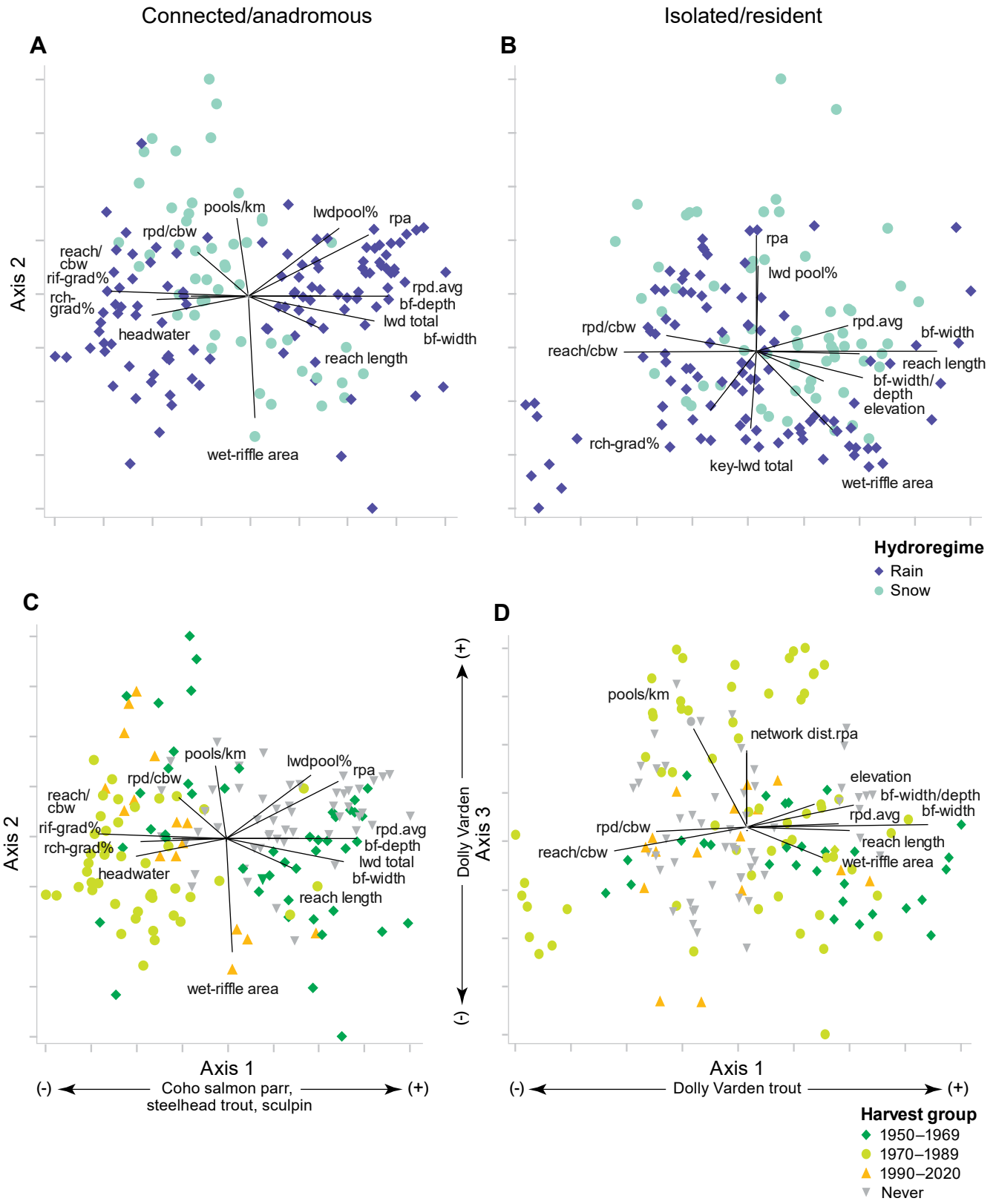

Figure 10—Principal components analysis ordination plots of physical habitat and watershed characteristics in connected/anadromous or isolated/resident subwatersheds by: (A–B) hydroregime, and (C–D) riparian harvest history. Jointplots (line vectors) denote relative strength and direction of habitat and watershed characteristics along axes. Fish species correlated with each axis are noted in parentheses along the axis of correlation. Continued on page 36.

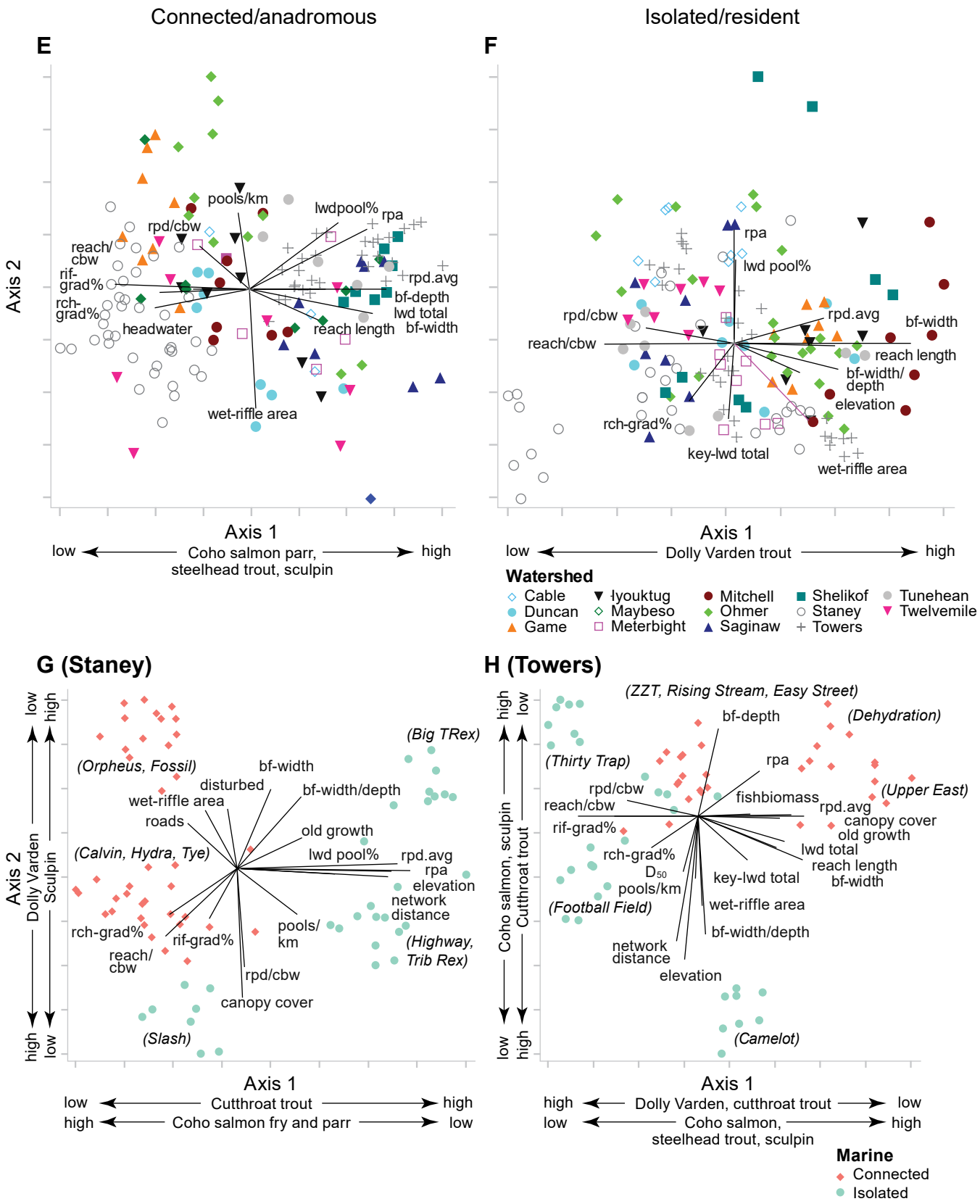

Figure 10 (continued)—Principal components analysis ordination plots of physical habitat and watershed characteristics in connected/anadromous or isolated/resident subwatersheds by subwatershed (E–F). Annual surveys at Staney Creek (G) and Towers Creek (H) watersheds were grouped by marine connection or isolation. Jointplots (line vectors) denote relative strength and direction of habitat and watershed characteristics along axes. Fish species correlated with each axis are noted. Bf = bankfull; cbw = channel bed width; rpd = residual pool depth; rpa = relative pool area; lwd = large wood; rch-grad% = reach gradient percentage; rif-grad% = gradient in riffle habitat.

Table 9—Principal components from the watershed datasets of Staney (n = 70) and Towers Creek (n = 62) watersheds

	Staney Creek watershed			Towers Creek watershed		
Habitat	**1**	**2**	**3**	**1**	**2**	**3**
	Principal components, r					
Fish biomass	-0.48	0.23	0.13	**0.54**	0.11	0.39
Headwater	NA	NA	NA	NA	NA	NA
Roads	**-0.50**	0.48	-0.18	Na	Na	Na
Elevation	**0.94**	-0.10	0.08	-0.27	**-0.88**	0.23
Network distance	**0.88**	-0.21	0.01	-0.35	**-0.82**	0.32
Canopy	0.16	**-0.81**	-0.20	**0.76**	0.00	**-0.59**
Disturbed	-0.22	**0.55**	-0.43	NA	NA	NA
Old growth	**0.58**	0.39	0.48	**0.67**	-0.11	**0.57**
Bf-depth	-0.13	0.22	0.46	0.33	**0.69**	-0.39
Bf-width/depth	**0.57**	**0.60**	-0.22	0.20	**-0.80**	0.30
Bf-width	0.41	**0.63**	0.03	**0.76**	-0.49	0.01
D_{50}	-0.46	-0.19	**0.63**	-0.29	**-0.55**	-0.18
Key-lwd total	0.03	-0.07	-0.13	**0.52**	-0.49	0.31
Lwd-pool%	**0.71**	-0.17	0.02	0.27	0.13	**0.52**
Lwd total	0.49	-0.16	-0.19	**0.69**	-0.37	-0.27
Pools/km	**0.55**	-0.48	0.18	-0.13	**-0.58**	-0.30
Reach-grad%	**-0.59**	-0.48	0.33	**-0.51**	-0.41	-0.12
Riffle-grad%	-0.38	**-0.50**	0.34	**-0.68**	-0.02	0.08
Reach/cbw	**-0.60**	**-0.58**	-0.40	**-0.81**	-0.03	-0.24
Reach length	-0.24	0.11	**-0.61**	**0.66**	-0.41	-0.40
Rpa	**0.89**	-0.12	0.07	**0.58**	0.49	0.08
Rpd.avg	**0.90**	0.15	-0.05	**0.72**	0.10	**0.50**
Rpd/cbw	0.19	**-0.70**	-0.38	**-0.62**	0.29	**0.50**
Ucbank%.avg	-0.11	0.20	0.49	-0.39	0.06	0.24
Wet-riffle area	-0.40	**0.54**	-0.10	0.14	**-0.70**	-0.36

= negative correlation with axis = positive correlation with axis

For each habitat variable, the standardized regression coefficients are reported (i.e., correlations between the variable and axes). Coefficients in bold highlight the stronger correlations ($r > |0.5|$). Habitat variables with "NA" were removed from the datasets because they did not vary among surveys.

Avg = average; bf = bankfull; cbw = channel bank width; grad = gradient; lwd = large wood; rpa = relative pool area; rpd = residual pool depth; Ucbank = undercut bank.

Small habitat differences were detected by MRPP analyses between rain- and snow-dominated hydrologies in both the connected/anadromous and isolated/resident subwatersheds (table 7). Rain-dominated hydrologies in the connected/anadromous subwatersheds were heavily split along PCA axis 1 (fig. 10A), but the habitat differences appear to be between a few watersheds and are not clearly associated with one hydrologic regime. Rain-dominated Staney surveys are on the left (negative axis 1) versus Towers, Saginaw, and Shelikof surveys on the right (positive axis 1), with surveys from Cable, Maybeso, and Twelvemile on both sides of axis 1 (fig. 10E). In the isolated/resident subwatersheds, rain- and snow-dominated hydrologies were weakly differentiated along PCA axis 2 (fig. 10B), where more rain-dominated hydrology surveys were associated with large wood (key-lwd total), wet-riffle area, and rch-gradient% (negative axis 2). An equal number of surveys from rain- and snow-dominated hydrologies were associated with rpa and large wood in pools (lwd-pool%) (positive axis 2). In the isolated/resident subwatersheds, variation in rain- or snow-dominated subwatersheds does not appear to be due to watershed differences (fig. 10F), as they are in the connected/anadromous subwatershed dataset.

Habitat differences among watersheds appear to be stronger in the connected/anadromous dataset than in the isolated/resident dataset (based on more stronger correlations with axis 1) (table 8), although sample size differences between watersheds complicate the interpretation and reliability of results. Values of $r > |0.5|$ indicate strong correlation (McCune and Grace 2002). Connected/anadromous subwatersheds within the Staney Creek watershed were correlated with reach length/average channel bed width (reach/ave cbw), reach and riffle gradient, and headwater stream length; whereas in the Towers Creek and Shelikof watersheds, C/A subwatersheds were correlated with rpa and depth (rpd.avg), bf-width and bf-depth, and lwd total (fig. 10E). Isolated/resident subwatersheds within the Staney and Towers Creek watersheds were not clearly associated with any habitat metric, but Slide was associated with greater bf-width and Farragut appears to be associated with rpa and lwd-pool%, similar to other subwatersheds (fig. 10F). When looking at the data from the watersheds of Staney or Towers Creek alone, strong differences were detectable in habitat metrics between isolated/resident and connected/anadromous subwatersheds (table 8; fig. 10: G and H); these differences are likely a result of differences between specific subwatersheds (note the clumping of surveys and subwatershed names in parentheses in fig. 10: G and H). The MRPP analyses found no habitat difference between T1 and T2 when timber harvest history or hydrologic regime were compared in multivariate space (table 7).

Results for Question 4: What Are the Spatial and Temporal Influences of Hydrologic Processes on Stream Geomorphic Characteristics by Subwatershed Groupings of Hydrologic Regime, Percentage of Old-Growth Forest, and Drainage Area?

Precipitation data from weather stations across the study area recorded decreasing quantities of snow from 2011 to 2019 ($p = 0.00002$, $r^2 = 0.19$), with similar amounts of total rain ($p = 0.26$, $r^2 = 0.0035$) (fig. A2-1). The years 2014 and 2015 experienced the highest number of peak precipitation events across the 10 weather stations compared, but 2016 experienced the fewest (fig. A2-2). The most extreme precipitation event across the period of record occurred on 20–21 January 2015, and was mapped to visualize rainfall patterns across the area of interest to this study (fig. 11).

Small subwatersheds—

Rain-dominated channels with major old-growth cover (>42 percent of subwatershed area) had wider bankfull channels than rain-dominated minor old-growth sites (0–42 percent of the subwatershed area) and snow-dominated major old-growth sites (fig. 12B). The rpa and rpd were greater for major old-growth rain-dominated subwatersheds (fig. 12: C and D).

Among connected/anadromous subwatersheds, rain-dominated major old-growth sites had the highest numbers of fish (compared with rain-dominated minor old-growth, snow-dominated major old-growth, and snow-dominated minor old-growth sites) (fig. 13: A and B). For isolated/resident subwatersheds, snow-dominated major old-growth sites had a greater proportion of sites in harvest group 4 (no harvest in riparian areas) compared with other groups (fig. 13A). Fish numbers in isolated/resident subwatersheds were greater for rain-dominated major old-growth sites (fig. 13C).

Large subwatersheds—

In the sites included in this analysis, large rain-dominated subwatersheds with major amounts of old-growth cover tended to have larger rpa and greater rpd compared with other categories (fig. 12: G, H, I, and J). These subwatersheds also tended to have lower D_{50} particle size and were located in lower elevation areas (fig. 12: K and J).

Among connected/anadromous large subwatersheds, snow-dominated major old-growth sites had the greatest proportion of harvest group 4 (uncut riparian zones). Anadromous fish numbers were greater for rain-dominated major old-growth sites than for snow-dominated major or minor old-growth sites (fig. 14B). Isolated/resident subwatersheds with rain-dominated minor old-growth characteristics had the largest proportion of area in harvest group 1 (harvested between 1950 and 1969) (fig. 14C).

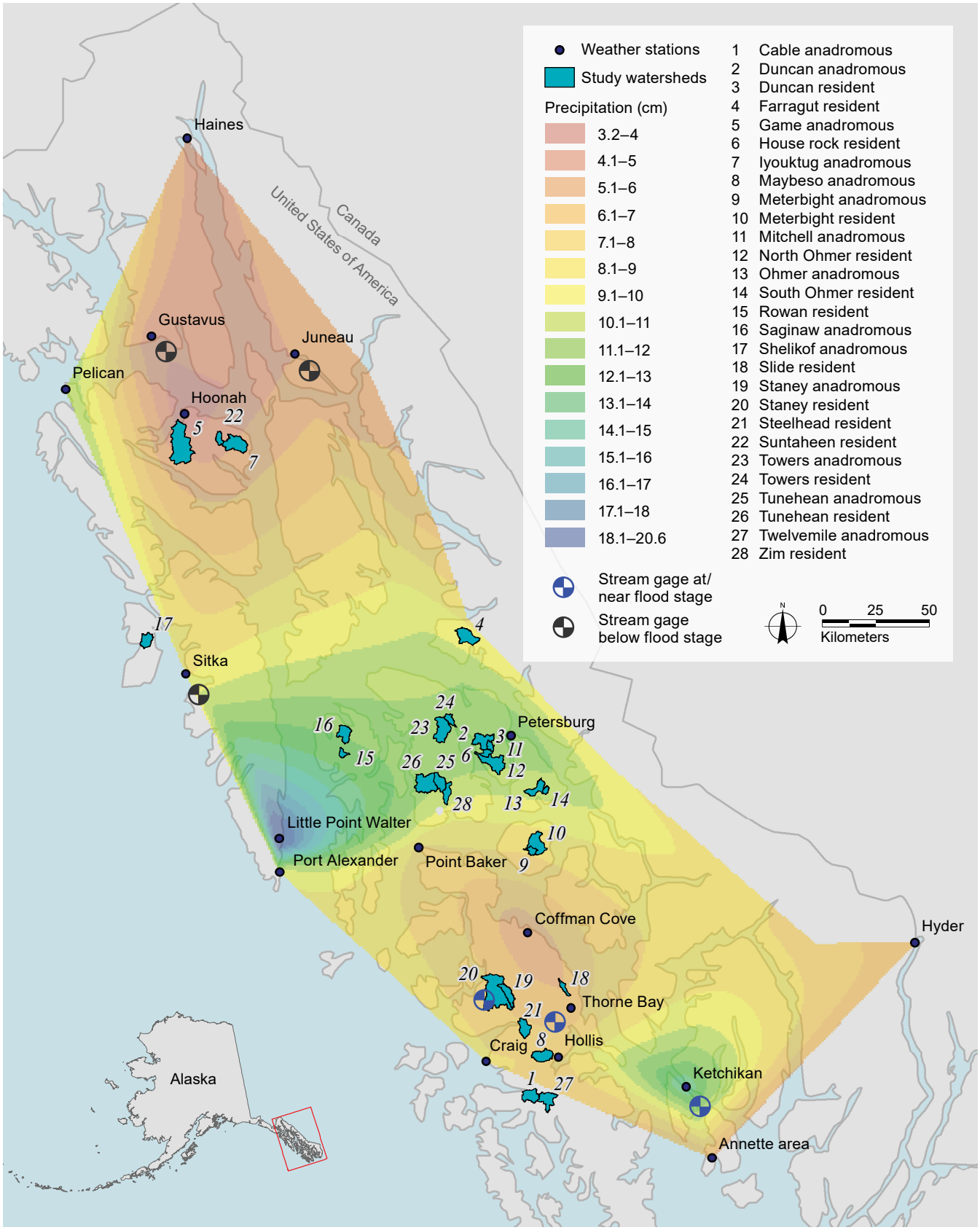

Figure 11—Precipitation isohyets (low elevation only) associated with a record-breaking storm event on 20–21 January 2015 during the Management Indicator Species Study (2012–2019) in the Tongass National Forest area of interest.

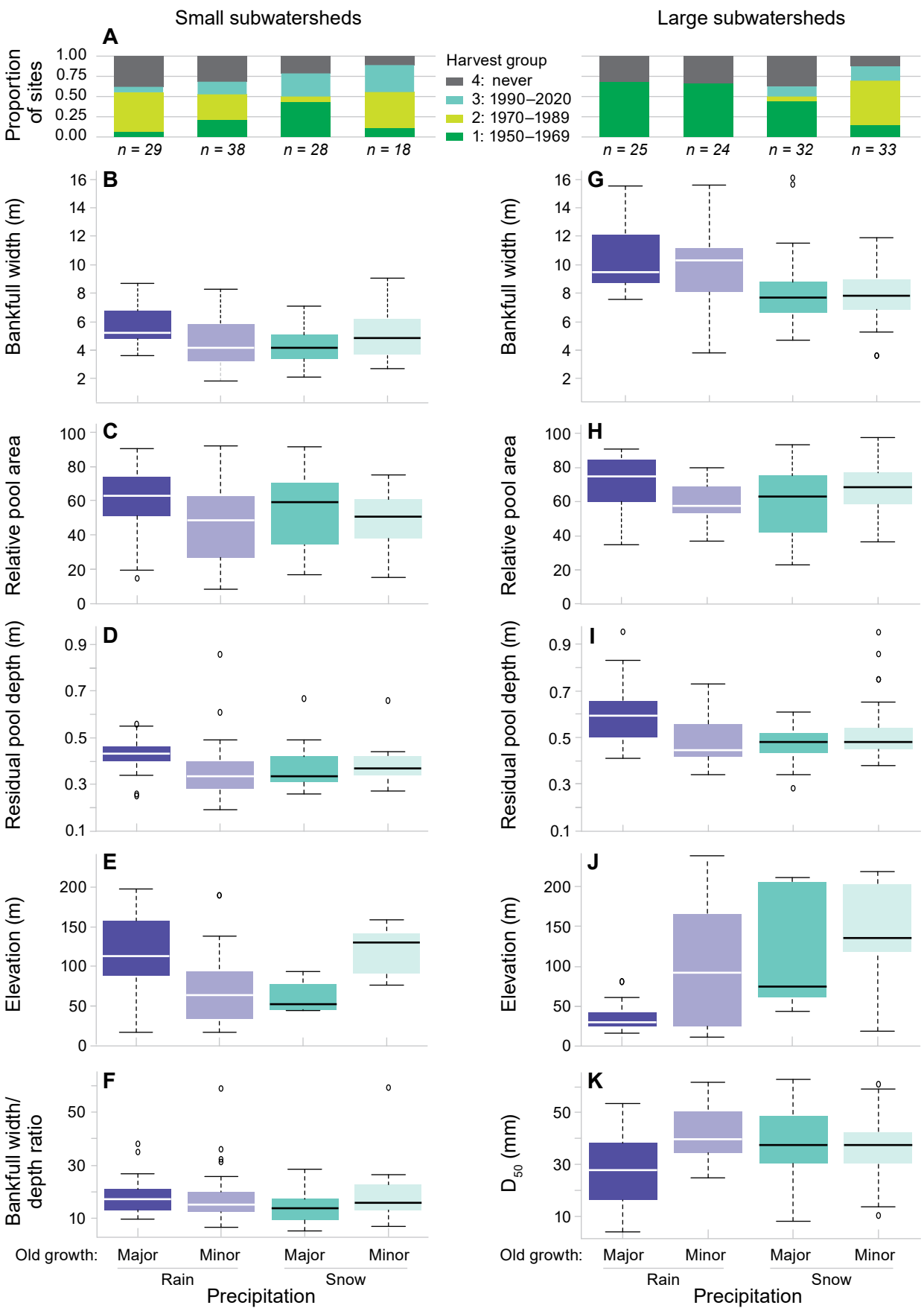

Figure 12—(A) Proportion of sites by harvest group in contributing areas of small and large subwatersheds as it relates to hydroregime and amount of old-growth forest in contributing areas for small (B–F) and large (G–K) subwatershed characteristics.

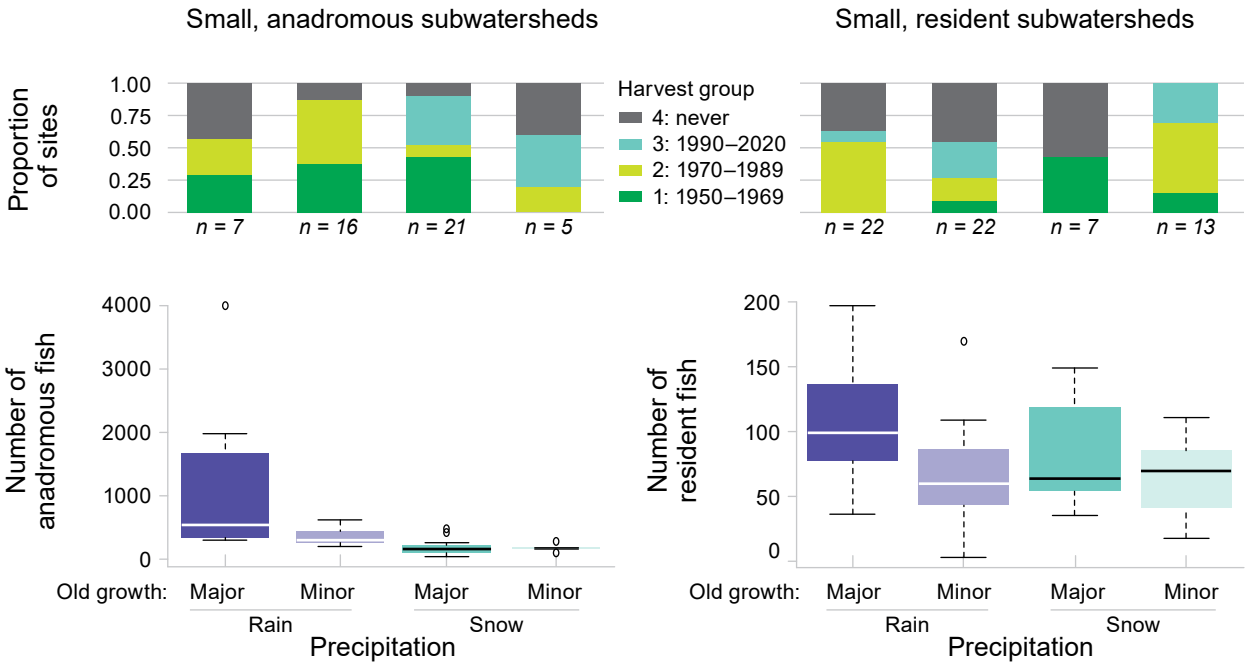

Figure 13—Summary of small subwatershed data by marine connectivity, hydroregime, and amount of old-growth forest in a catchment.

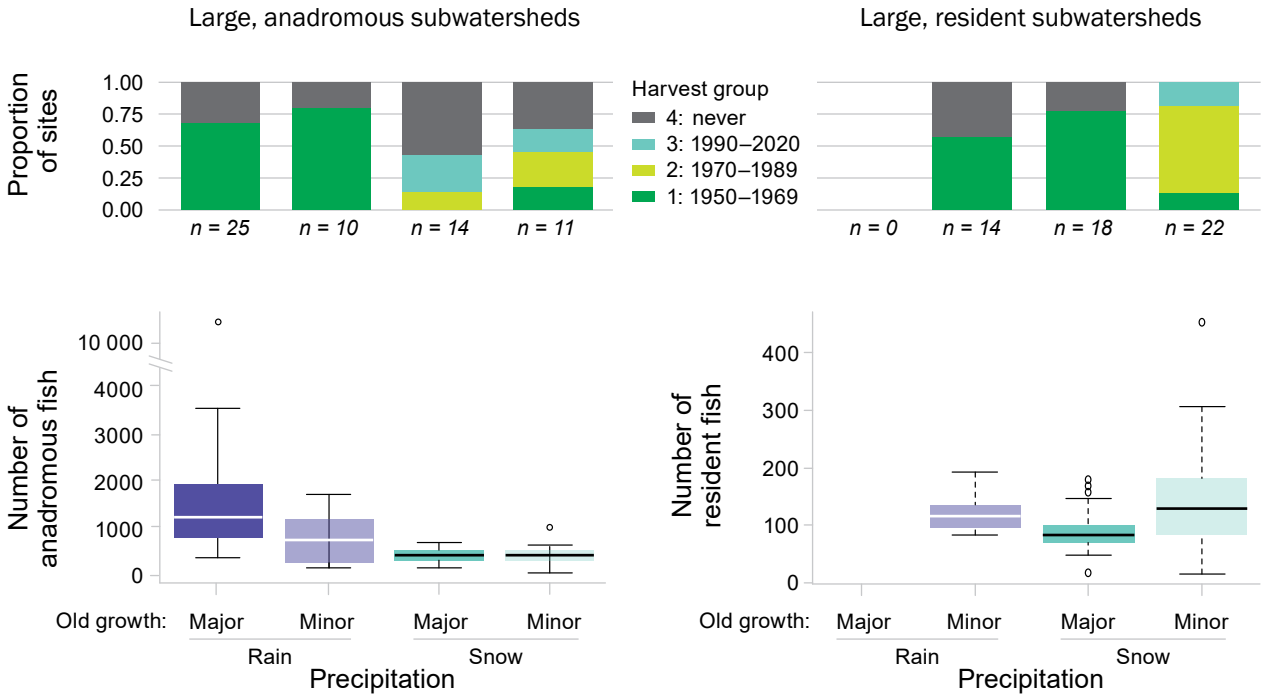

Figure 14—Summary information for large subwatersheds by marine connectivity, hydrologic regime, and amount of old-growth forest in the catchment.

Linear mixed model results—

The LMM results show that the estimated marginal mean change of bf-depth, bf-width, and hydraulic radius were significantly different than 0 for some groups (tables 10, 11). The bf-depth increased in major old-growth sites and rain-dominated sites when harvest groups were included in the model. The bf-width increased at minor old-growth sites. Hydraulic radius increased at major old-growth sites and for harvest groups 1 and 3. There was no significant change detected in estimated marginal means of width-to-depth ratio, rpa, large woody debris count, or rch-gradient% change for any of the factor level groups (e.g., hydrologic regime and old-growth cover, and hydrologic regime and harvest category).

Likelihood ratio tests on LMM output support the finding that only bankfull width-to-depth ratio changed during the study period, with a significantly greater increase in bankfull width-to-depth ratio detected for sites with ≤42 percent of their watershed in old-growth forest than sites with >42 percent of their watershed in old-growth forest (post-hoc Tukey pairwise comparison, $p = 0.04$).

Table 10—Marginal least-square mean estimates of change for individual habitat metrics between time periods T1 and T2 from linear mixed-effects models (LMMs) that included fixed main effects of hydroregime and old-growth forest coverage

	Precipitation		Old-growth proportion	
Metric	**Rain**	**Snow**	**Major**	**Minor**
	Group p-value (SE)			
Bf-depth	0.05 (0.07)	0.04 (0.15)	0.06 (0.02)*	0.03 (0.19)
Bf-width	0.46 (0.07)	0.38 (0.17)	0.26 (0.23)	0.58 (0.01)*
Bf-width/depth	-0.93 (0.66)	-1.15 (0.62)	-3.30 (0.09)	1.23 (0.51)
Hydraulic radius	0.03 (0.08)	0.03 (0.12)	0.05 (0.01)*	0.02 (0.28)
Rpa	0.17 (0.95)	-3.02 (0.29)	-2.20 (0.37)	-0.65 (0.79)
Lwd	-0.00 (0.91)	0.01 (0.23)	0.00 (0.87)	0.00 (0.24)
Reach-grad%	-0.00 (0.91)	0.01 (0.23)	0.00 (0.86)	0.00 (0.24)
Shear stress	0.61 (0.12)	0.16 (0.71)	0.38 (0.29)	0.38 (0.28)

Hydroregime classifications are rain or snow dominated. Major old-growth sites had >42 percent of their catchment in old-growth forest, whereas minor old-growth sites had <42 percent of their catchment area in old-growth forest. The p-values are in parentheses with an asterisk (*), indicating that changes within groups were significantly different than 0 at $\alpha = 0.05$.

Bf = bankfull; grad = gradient; lwd = large wood; rpa = relative pool area.

Table 11—Marginal least-square mean estimates of change for individual habitat metrics between T1 and T2 from linear mixed-effects models (LMMs) that included fixed main effects of hydroregime and harvest group treatment

	Hydroregime		Harvest group			
Metric	**Rain**	**Snow**	**1: 1950–1969**	**2: 1970–1989**	**3: 1991–2020**	**4: Never**
			Group p-value (SE)			
Bf-depth	0.06 (0.04)*	0.05 (0.09)	0.07 (0.06)	0.05 (0.15)	0.10 (0.03)*	-0.01 (0.65)
Bf-width	0.43 (0.14)	0.43 (0.16)	0.69 (0.08)	0.44 (0.24)	0.39 (0.42)	0.19 (0.56)
Bf-width/depth	-1.46 (0.54)	-1.07 (0.68)	-0.26 (0.94)	-3.10 (0.34)	-2.73 (0.52)	1.04 (0.73)
Hydraulic radius	0.04 (0.06)	0.04 (0.07)	0.06 (0.04)*	0.03 (0.21)	0.07 (0.05)*	-0.01 (0.66)
Rpa	0.68 (0.80)	-2.94 (0.32)	0.07 (0.98)	2.00 (0.59)	0.11 (0.98)	-6.71 (0.06)
Lwd	0.00 (0.52)	0.00 (0.25)	-0.00 (0.65)	0.01 (0.33)	0.01 (0.07)	-0.00 (0.81)
Reach-grad%	0.00 (0.53)	0.00 (0.26)	-0.00 (0.62)	0.01 (0.32)	0.01 (0.08)	-0.00 (0.83)
Shear stress	-1.27 (0.39)	0.58 (0.70)	1.77 (0.34)	-1.30 (0.50)	-1.49 (0.56)	-0.37 (0.84)

Hydroregime classifications are rain dominated or snow dominated. Harvest groups were associated with time periods when timber harvest occurred within a catchment with harvest occurring in group 1 from 1950–1969, group 2 from 1970–1989, group 3 from 1990–2020, and group 4 never harvested. The p-values are in parentheses with an asterisk (*), indicating that changes within groups were significantly different than 0 at $\alpha = 0.05$.

Bf = bankfull; grad = gradient; lwd = large wood; rpa = relative pool area; SE = standard error.

Discussion

Broad-scale processes of climate and land use history (riparian and watershed-scale) set the stage for existing habitat conditions and future resilience on the Tongass National Forest and elsewhere. On the Tongass National Forest, patterns of fish populations and associated habitat relate to the footprint of historical forest harvest-site selection that was intended to maximize timber extraction rather than protect fish habitat. Historical riparian harvest with the greatest potential to affect instream habitat quality tended to be focused on marine-connected subwatersheds that support populations of anadromous salmonids such as coho salmon. Likely owing to the long history of timber harvest in these subwatersheds, road networks and culverts are more extensive in these areas than elsewhere. This contrasts with recent harvest patterns in riparian areas that are linked to subwatersheds dominated by populations of cutthroat trout.

Wider channels and deeper pools occurred in rain-dominated watersheds with >42 percent area of old-growth trees in the drainage, regardless of watershed size. As climate changes, these pools have potential to provide water and thermal refugia to native fish. The importance of summer low-flow refugia in rain-dominated systems has been identified in the Oregon Coast Range (May and Lee 2004), where similar climate projections of more intense winter storms and longer, drier summers are predicted (NAS 2012). Restoration that enhances pool depth in main-channel habitats, and connects off-channel habitats in both rain-dominated and snow-to-rain transitional watersheds could enhance resilience to winter storm events among native fish.

Lack of randomization, particularly in poststratification of data, limited the statistical analyses that could be performed on the data, as well as the interpretation of results. Future studies that incorporate stratification in site selection would facilitate greater opportunities for data exploration to better understand patterns and processes that drive habitat and fish populations at small and large spatial and temporal scales.

The following sections specifically address the four interconnected questions of interest to this study. These questions reflect the multidimensional considerations necessary for broad-scale forest and riparian management in high-latitude forests generally, and in the Tongass National Forest specifically. In their simplest form, these questions allowed us to tease apart relationships between fish and aquatic habitat, broad-scale processes and fish, broad-scale processes and habitat, and hydrologic processes and geomorphic characteristics.

Question 1: What Are the Species-Specific Relationships Between Fishes and Aquatic Habitat Over Time and Space?

Key findings—

- Across all sites and subwatersheds, aquatic habitat and occupancy patterns were relatively stable throughout this study period. However, high interannual variability in fish population sizes was evident at sites surveyed annually.
- We observed highly variable coho salmon fry population estimates in the Staney Creek watershed, with a decrease in population possibly linked to high-flow events in 2015. Similar declines in fish population numbers were also observed in other fish species in the Towers Creek watershed in 2015, with variation in coho salmon fry population estimates throughout the study period.
- GLMM models found:
    - A negative relationship between biomass and coho salmon fry and cutthroat (all) population estimates, but a positive relationship was observed between biomass and population estimates for other species (including coho salmon parr).
    - Higher amounts of riparian canopy cover had a negative relationship with coho salmon fry and parr population estimates, whereas greater area of old-growth forest had a positive relationship with coho salmon fry population estimates.
    - As D_{50} sediment values increased, population estimates decreased for all species.
    - The wet-riffle area was strongly associated with steelhead/rainbow and sculpin, and minimally associated with Dolly Varden and cutthroat trout.
    - The wet-riffle area had a positive influence on coho salmon parr but a negative influence on coho salmon fry population estimates.

Aquatic habitat and patterns of fish occupancy appear generally stable during this study. However, some changes may be developing in channel configuration, as is evident in boxplots of undercut bank and bf-depth. Further, differences in fish population sizes was evident in the two sampling intervals present in this study: the 4-year return interval and annual sampling. Across the entire dataset, with a 4-year interval between sampling events, interannual variability in fish population size showed no overall trend. However, annual monitoring documented interannual variability highlighted by a drop in population sizes for multiple fish species in 2015.

The observed drop in fish populations at some annually monitored watersheds may be linked to intense storm events recorded in 2015. The high-magnitude rain of the 2015 season tracks climate change projections that include storms with increased intensity and greater potential to induce landslides (Jakob and Lambert 2009, Salathé et al. 2008). Staney Creek and Towers Creek watersheds, where fish population drops were observed in 2015, are rain dominated with a limited snowpack. Rain-dominated systems have limited capacity to store precipitation, resulting in immediate high-flow events in response to storm events. Staney Creek, where the most dramatic drop in fish population was observed, also saw stream gages registering at or near flood stage during the 20–21 January 2015 flood event. The coincident drop in fish populations may be evidence that intense storm events, should they occur annually, have the potential to negatively affect the community of fish that currently occupy streams on the Tongass National Forest. This finding is consistent with the modeled predictions of Sloat et al. (2017), who anticipated declines in spawning habitat for coho salmon coincident with high-flow scour events in Alaska. Managers may focus on maintenance and restoration of high-flow refugia, such as off-channel pools and multi-thread channels, as well as large wood placement in mainstem channels to facilitate deeper pool habitats that dissipate flow and reduce scour during high-discharge events.

Modeling results found that Dolly Varden and cutthroat trout may target slightly different habitats depending on whether they occurred in watersheds connected or disconnected from downstream habitats. Differences in habitat characteristics were not observed between connected and disconnected subwatersheds, suggesting that habitat selection may reflect a combination of physical stream characteristics and interactions with other fish species, particularly coho salmon. Because marine environments are necessary for coho salmon to complete their life cycle, they are found only in connected/anadromous watersheds that have access to the ocean. Coho salmon parr and fry, in particular, dominated fish population counts and biomass where they were present. Therefore, Dolly Varden and cutthroat trout may be selecting different habitat characteristics in areas that contain coho salmon, compared with areas that do not have coho salmon, so as to maximize their foraging success (i.e., ideal free distribution) (Avgar et al. 2020). Bisson et al. (1988)

found that coho salmon tend to dominate habitats in the presence of cutthroat trout, which is consistent with our findings here. Further, we found that coho salmon fry and cutthroat trout population estimates decline at higher amounts of biomass, evidence that these two species may be experiencing negative density-dependent conditions that could further influence habitat selection by all species in the fish community.

The life-stage analysis of coho salmon found some differences in habitat selection between fry and parr. Fry are positively associated with higher densities of smaller pools in areas with less riffle habitat and more old-growth forest conditions. This compares with parr, which are strongly associated with larger pools, riffle habitats in reaches, and large wood. These differences in habitat preferences for fry versus parr life stages likely reflect a combination of factors, including proximity to spawning habitats for fry and dominance of larger bodied and mobile parr in selection of complex foraging habitats. Larger parr may also be tracking salmon spawning locations to feed on eggs during the summer (Armstrong et al. 2010). Further, Flitcroft et al. (2012) found consistent occupancy by juvenile coho salmon in sites near spawning habitats, perhaps owing to limited mobility at this life stage, which could influence site selection for fry at the sites surveyed here. Density-dependent relationships with habitat that are linked to life stages of juvenile Atlantic salmon were described by Gibson et al. (2008) for whom fish distribution appeared to maximize foraging and refugia rather than growth. Likewise, in experimental work, Young (2004) found that large juvenile coho salmon strongly influence the distribution pattern of smaller fishes, including other salmonids, as a result of their territorial behavior for high-quality feeding locations and cover.

Question 2: What Are the Spatial and Temporal Influences of Timber Harvest History and Hydrologic Regime on Resident and Anadromous Fish Communities?

Key findings—

- Higher amounts of harvest adjacent to streams occurred in harvest group 1 (harvested between 1950 and 1969).
- More connected/anadromous subwatersheds were present in harvest group 1, whereas more isolated/resident subwatersheds were present in harvest groups 2 (harvested between 1970 and 1989) and 3 (harvested between 1991 and 2020).
- Harvest group 1 had higher numbers of coho salmon and other species compared to other harvest groups, indicating overlap between the location of productive forests and fishes. Coho salmon fry abundances were associated with older harvests, but cutthroat trout were associated with more recent or no harvest, reflecting changes in the spatial distribution of more recent harvest activity.

- MRPP analyses detected fish-community differences between rain and snow hydrologic regimes: cutthroat trout were more closely associated with snow-dominated hydrologic regimes, and coho salmon fry were more closely associated with rain-dominated hydrologic regimes.

In this analysis, we found that broad-scale processes of timber harvest and hydrologic regime align with distribution patterns of native fishes. Historical timber harvest occurred in the lower portions of watersheds that were connected to marine environments. This activity overlapped with the distribution of anadromous fishes in the system, particularly coho salmon. Our statistical analysis identified differences in fish population sizes among timber harvest groups, with the oldest harvested watersheds hosting higher fish population sizes compared with later harvest groups or the never harvested category. Cutthroat trout were associated with later harvest groups and with the never harvested watersheds, as might be expected given their distribution higher up in river systems and their occupancy of isolated/resident streams that are inaccessible to anadromous coho salmon.

The association between coho salmon and early harvest primarily reflects the habitat needs of these fish in ocean-connected and highly productive subwatersheds. The dominance of coho salmon fry numbers within the fish community and much lower numbers of parr may also reflect harvest history. At Carnation Creek, where effects of timber harvest have been studied for decades, high numbers of juvenile salmonids are followed by much lower over-winter survival, resulting in lower smolt survival than pre-harvest (Hartman et al. 1996). Over the long term, documented increases in solar radiation and growth period for juvenile coho salmon at Carnation Creek (Holtby 1988) did not translate into survival to the smolt stage because timber harvest treatments caused over-winter habitat simplification (Tschaplinski and Pike 2017). Similar relationships may be responsible for the patterns we are observing on the Tongass National Forest; more detailed investigation would likely be beneficial.

Our analyses found differences in fish species composition between rain- and snow-dominated hydrologic regimes, highlighting potential differences among species' vulnerability (or adaptation) to climate change. Cutthroat trout were associated with snow-dominated hydrologic regimes, sculpin and coho salmon associated with rain-dominated regimes, and Dolly Varden trout were found in both. This may partially reflect the higher gradient streams that cutthroat trout occupy compared to coho salmon, but suggests different sensitivities to changes in the hydroregime by species. Coho salmon in rain-dominated streams may already be experiencing effects related to high-flow conditions, as described previously. For fishes in snow-dominated watersheds, the transition from a snow- to rain-dominated hydrology may be occurring. Our analysis documented a decline in

snow for the duration of this study, while average total precipitation (both rain and snow) remained the same. This change could result in lower summer flow conditions in these streams as spring snowmelt declines, coupled with higher peak storm events. For cutthroat and Dolly Varden trout that were associated with snow-dominated systems in our analyses, these changes may influence both phenology and habitat characteristics. Life-stage linkages by native fishes to specific characteristics of discharge and temperature have been reported in the Pacific Northwest (Flitcroft et al. 2016, Lovellford et al. 2020) and vary depending on local watershed characteristics (Flitcroft et al. 2019). Further, phenological shifts in response to changes in thermal regime have been detected in spawn timing of wild Chinook salmon in Washington state (Austin et al. 2021) and in salmon in Alaska (e.g., pink salmon [Taylor 2007]; pink salmon and both coho and sockeye salmon adults and jacks [Kovach et al. 2013]). Monitoring fish populations in both rain- and snow-dominated systems, as well as river discharge and water temperature, would provide information about the effects of climate change and species-specific resilience.

Question 3: What Are the Spatial and Temporal Influence of Timber Harvest History and Hydrologic Regime on Physical Stream Characteristics?

Key findings—

- Total key large wood (key-lwd) per meter was higher in T2 for connected/anadromous subwatersheds in harvest groups 2 and 3, with lower amounts of key-lwd in isolated/resident subwatersheds in harvest group 1.
- Larger particle size in D_{50} sediment is associated with isolated/resident subwatersheds from harvest group 1 compared with connected/anadromous subwatersheds in this harvest group, or across all other harvest groups.
- More roads and associated stream crossings were present in harvest group 1.
- Riparian harvest history groups have small habitat differences in both the connected/anadromous and isolated/resident subwatershed datasets.
    - Connected/anadromous subwatersheds that have never been harvested were most similar to the oldest harvest group (1: 1950–1969) and are correlated with lwd total, relative pool area (rpa) and residual pool depth (rpd), bankfull width (bf-width) and bankfull depth (bf-depth), and old-growth forest cover.
- Small habitat differences were detected by MRPP analyses between rain- and snow-dominated hydrologies in both the connected/anadromous and isolated/resident subwatersheds.
    - Habitat in connected/anadromous subwatersheds with rain-dominated hydrology was associated with lwd total and pool characteristics (rpa, bf-depth).

    - Habitat in isolated/resident subwatersheds with rain-dominated hydrology consisted primarily of key-lwd total, wet-riffle area, and percentage of reach gradient (rch-gradient%).
- Temporal changes in aquatic habitat characteristics were not identified in multivariate analysis, likely because of the short duration of this study.

Significant differences were detected in aquatic habitat among harvest groups, between rain- or snow-dominated hydroregime, and between isolated/resident and connected/anadromous subwatersheds. Analysis showed that timber-harvest history is linked to differences in aquatic habitats in connected watersheds, but less so in isolated/resident watersheds. Connected/anadromous watersheds in harvest groups 1 and 4 (sites that were never harvested) are correlated with more lwd total, greater rpa and rpd, wider bf-width, and higher bf-depth compared with sites harvested since the 1970s (harvest groups 2 and 3). Some of these differences may be attributable to wider channels and wood accumulation associated with the lower portions of marine-connected watersheds, as well as a management focus on habitat restoration (principally wood additions) in coho salmon-bearing streams. However, Lisle (1986) found that wood in streams contributed to the development of pool habitats in harvested and unharvested streams on Prince of Wales Island, Alaska. The presence of deeper pools and greater residual pool depth may be legacies of past conditions when more wood was present in streams associated with harvest group 1. This would be consistent with the findings of Burton et al. (2016) who found that the majority of wood in streams with a history of forest thinning was legacy wood associated with historical stand conditions. More recent harvest is associated with headwater, higher gradient stream channels in isolated/resident streams that are linked to populations of cutthroat trout and Dolly Varden trout. These areas are also associated with a snow-dominated hydrology, which was shown to have lower key-lwd, wet-riffle area, and rch-gradient% compared with rain-dominated systems.

Temporal changes in aquatic habitat characteristics were not identified in multivariate analysis, likely because the duration of this study was short. Active land management or restoration can result in more immediate detection of changes in aquatic habitat condition, but limited riparian harvest and an absence of large-scale disturbance processes such as wildfire may make change difficult to detect. Aquatic monitoring by the Aquatic and Riparian Effectiveness Monitoring Program in Oregon, Washington, and northern California found detectable changes in aquatic habitats after 2 decades of passive riparian management (Hirsch 2022). However, emerging changes in river hydrographs associated with climate change could result in short-term detectable changes in channel configuration, making data collected as part of this study important in future analysis of geophysical changes.

Question 4: What Are the Spatial and Temporal Influences of Hydrologic Processes on Stream Geomorphic Characteristics by Subwatershed Groupings of Hydrologic Regime, Percentage of Old-Growth Forest, and Drainage Area?

Key findings—

- Precipitation data from weather stations across the study area recorded decreasing quantities of snow from 2011 to 2019, with similar amounts of total precipitation.
- The most extreme precipitation event across the period of record occurred on 20–21 January 2015.
- Large, rain-dominated subwatersheds with major amounts of old-growth cover tended to have wider bf-width, larger rpa, and greater rpd compared with all other categories (fig. 12: G, H, I, and J). These subwatersheds also tended to have lower D_{50} particle size and were located in lower elevation areas (fig. 12: K and J).
- In linear mixed models (LMMs), the estimated marginal mean change of bf-depth, bf-width, and hydraulic radius were significantly different from 0 for some groups.
  - The bf-depth increased in old-growth major and rain-dominated sites when harvest groups were included in the model.
  - The bf-width increased at minor old-growth sites.
  - Hydraulic radius increased at old-growth major sites and for harvest groups 1 and 3.
- In likelihood-ratio tests on LMM output, only bf-width-to-depth ratio changed during the study period, with a significantly greater increase in bf-width-to-depth ratio detected for sites with ≤42 percent of their watershed in old-growth cover.

The proportion of large standing trees in watershed-contributing areas and harvest groups was associated with channel geomorphic conditions. Wider channels with greater rpd and rpa were observed for both small and large rain-dominated subwatersheds having >42 percent old-growth cover. This result is consistent with Martin (2001), who also found a positive relationship between channel width and rpd. Because residual depths represent extreme low-flow conditions (Lisle 1987), this finding is evidence that when holding wood constant, increases in old-growth forest cover may be linked to more water in streams during summer, providing refugia for aquatic biota during periods of summer drought. May and Lee (2004) found that greater rpd was linked to the depth of alluvial deposits in gravel-bed streams in the Oregon Coast Range. Alluvial deposit depth was not part of our analysis, but is an additional factor that may be contributing to the greater rpd found for watersheds with greater old-growth forest assessed in this study. Further, drivers of the amount of old-growth trees include a combination of targeted harvest extraction, as well

as the presence of other vegetation types, including muskegs and wetlands. More detailed analysis of the drivers of old-growth area in upstream catchments could provide insights into some of the patterns that we detected.

Our univariate LMMs found that bf-depth, bf-width, and hydraulic radius changed over the duration of this study, and that the width-to-depth ratio was significantly greater at sites with ≤42 percent old-growth cover in their subwatersheds. The bf-width-to-depth ratios are strongly correlated with drainage area, as expected from considerations of hydraulic geometry (Leopold and Maddock 1953), and have shown promise as an indicator of land use effects (e.g., Lisle 1981); however, like Wood-Smith and Buffington (1996), our dataset was not large enough to isolate drainage-specific effects over time. Increases in bf-depth and hydraulic radius over time may be associated with increased channel incision, a common response of alluvial channels to isostatic rebound or channels that have been disturbed (e.g., Hogan and Church 1989, Lisle 1981, Lyons and Beschta 1983) when streams contain excess amounts of flow energy or stream power relative to the sediment load (Baldwin et al. 2003, Simon and Renaldi 2006, Zhang et al. 2014). Channel incision, however, represents one of a range of possible adjustment scenarios for disturbed streams that are free to adjust boundaries (Simon and Renaldi 2006). Hicks et al. (1991) found aggradation via landslides in streams with less forest cover resulted in channel widening. Investigations of sites having a range of old-growth cover quantities in subwatershed area, both with and without riparian zone harvest, are warranted. Such analyses will help to decipher the influence of standing trees on changes in channel morphology, factors that may influence fish habitat.

Management Considerations

Ongoing monitoring of aquatic ecosystem in the Tongass National Forest, along with research that supports emerging and long-term questions about resilience and change in these high-latitude river systems, can provide valuable information for management plans. A more robust understanding of how broad-scale climate and land-management processes affect local stream conditions over time could provide essential benefits. The questions and analyses presented in this report targeted instream fish habitat, fish populations, and river geomorphology in relation to land management history and hydrologic regime. We found that most habitat conditions and fish distributions appeared to be generally stable across broad scales for the duration of this study. However, evidence of the immediate and prolonged effect of extreme events that we hypothesize are related to climate variability were found in interannual variability of fish populations at annually surveyed sites. Additionally, some characteristics of river geomorphology appear to have changed, even during the short duration of this 8-year study.

An additional finding of this work with relevance to ongoing timber management on the Tongass National Forest was the overlap in distribution of high population juvenile anadromous salmon-rearing streams with areas that were historically harvested. The competing interests of timber harvest and salmon production in these locations highlight the need for effective protection measures and interdisciplinary land management planning. The colocation of productive forests that produce viable timber with high numbers of juvenile coho salmon reflects patterns in underlying geomorphology and landscape configuration. Salmon and forests are linked energetically. These highly productive forested ecosystems benefit from the significant subsidy of marine-derived nutrients provided to them from large numbers of adult salmon who spawn and then die in these locations (Quinn et al. 2018), and complex salmon habitat is derived from the large wood contributed to the stream from these forests. Complex stream systems are more likely to retain marine-derived nutrients from salmon carcasses (Levi et al. 2011). Timber harvest has been shown to modify stream complexity and alter the role of salmon carcasses in nutrient cycles of streams in southeast Alaska (Tiegs et al. 2008). Higher fine sediment levels and lower wood quantities that have been linked to timber harvest can increase the negative effect of the disturbance associated with intense salmon spawning on local macroinvertebrate communities (Campbell et al. 2011). Salmon and forests are, therefore, linked, with altered forests affecting stream habitat that can in turn affect aquatic ecosystems that support salmon production.

Low-lying floodplain forests contained high-quality timber that was readily accessible, factors that led to their original harvests. As a result of their productivity, these forests will become eligible for harvest in the near future. Riparian areas of these young forests provide considerable terrestrial food inputs for rearing salmon, contributing to the ongoing productivity of these forests for fish (Wipfli 1997). Continued protection of riparian corridors and floodplains from additional harvest effects will be critical for the long-term persistence of salmon populations. Red alder-conifer mixes, rather than uniform stands of conifer, are often found along these second-growth riparian corridors. Red alder presence does not inhibit the production of large-diameter conifers nor influence the type or size of dead trees (Deal et al. 2017). Stream restoration practices may include instream placement of large woody debris to mimic wood input patterns supported by old-growth forests. The connectivity and flux of sediment and nutrients from headwater streams should also be considered for protection measures.

Disturbance associated with climate change appears to have a potentially immediate effect on fish populations, while manifesting more slowly in changes to stream morphology. Likewise, change over time related to different land management legacies is not immediate at large spatial scales. Therefore, there are

different time steps at which disturbance processes of climate change and timber management might be expected to be detectable in fish and stream habitats at broad and local scales. Together, these observations and the results of this study suggest several additional research questions and monitoring objectives for management to consider.

Fish population monitoring—
Fish populations appeared highly responsive to extreme disturbance events in this study. Although interannual variability in fish populations is to be expected, an event that we hypothesize to be related to climate change (i.e., intense storm events) resulted in site-scale drops in fish population estimates at some annually monitored sites. Because this pattern was observed in populations of both resident and anadromous subwatersheds, it is likely related to an event that affected all freshwater sites, rather than a change in the marine environment (with potential to affect populations of anadromous more than resident fishes), hence the potential of an environmental climate-driven disturbance. Although this event was clearly evident at the two annually surveyed sites, no change in fish populations was discernable across the Tongass National Forest as a whole in our analysis of sites sampled every 4 years. This likely reflects high interannual variability in fish population sizes across the region. Therefore, we recommend ongoing annual monitoring at existing sites in the Staney Creek and Towers Creek watersheds where we know we can detect impacts from extreme climate events. Coupling this annual monitoring with temperature and discharge monitoring (links to process-based climate assessments discussed below) could improve understanding of the drivers of interannual population variability.

Stream habitat monitoring—
Generally, we found that (1) broad-scale changes in fish habitat do not occur on an annual time step and (2) the 4-year return interval used in this study was long enough to detect some changes in stream habitat and channel geomorphology. Therefore, the temporal scale for return sampling of stream habitat does not need to be annual, in contrast to what we recommend for detecting changes in fish populations. Decoupling fish and stream-habitat sample rotations may allow for the targeted allocation of resources to answer more specific research questions about both fish and stream habitat. A rotation interval of 4 or 5 years for return sampling of aquatic habitat may be required to balance the number of repeat surveys necessary to make comparisons over time, with time frames relevant for forest management. Longer resurvey intervals extend the amount of time necessary to fully survey all sites in the return sample rotation and may not be fast enough to provide timely information necessary for adaptive forest management.

Process-based research of harvest effects on fish and stream environments—
The pattern detection that is characteristic of broad-scale monitoring datasets, such as those we analyzed for this report, often points to additional fine-scale and specific questions that cannot be answered with data collected to detect pattern and trends across large spatial extents. Therefore, we recommend targeted research designed specifically to explore the effect of forest harvest practices on fish and stream habitat (such as paired watershed studies or before-after, control-impact (BACI) approaches). Topics of interest that emerged from this analysis include the following:

- The effect of timber harvest and forest landscape management on (1) sediment supply and transport dynamics, (2) large wood recruitment, (3) resident fish population size and biomass, and (4) anadromous fish population size and biomass.
- Whether subwatersheds with different hydrologic regimes have similar or different patterns in fish population over time in relation to habitat responses from timber harvest and land management.

Process-based research of climate change effects on fish and stream environments—
Climate change is an emerging topic of vital importance in the management of aquatic resources on the Tongass National Forest. This study found evidence of predicted changes in precipitation and thermal regimes. Research and monitoring that focus on changes in river discharge, temperature, scour, and life history phenology of fishes could provide additional information on how these factors are affecting fish and stream habitats. As with the process-based assessment of harvest and land management described above, this likely requires targeted studies that can better control variation in the dataset to detect signals of change over time. This could, for example, be accomplished by instrumenting specific basins for temperature and discharge monitoring (related to fish populations described above). Specific topics of interest to explore in more detail include the following:

- What are the effects of high-flow event intensity and occurrence on fish populations in subwatersheds with different hydrologic regimes (i.e., rain, snow, or transitional)?
- What are the effects of low-flow timing and extent on fish populations in subwatersheds with different hydrologic regimes (i.e., rain, snow, or transitional)?
- How do high-flow event intensity and occurrence affect sediment supply and transport dynamics in subwatersheds with different hydrologic regimes and underlying lithology?

Conclusions

Intensive data collection using an established sample design on the Tongass National Forest made possible our evaluation of the effects of broad-scale processes of timber harvest and hydrologic regime. Management of aquatic ecosystems on the Tongass National Forest will likely benefit from additional monitoring and research of patterns detected in this analysis, as well as by specifically targeting threats to forests and fish from changing climates. How climate change interacts with the effects of timber harvest is not clear, which enhances concerns about the future resilience of aquatic ecosystems and fisheries. Past experience and outcomes may not provide the guidance necessary in an uncertain future.

The questions and analyses presented in this report targeted instream fish habitat, fish populations, and river geomorphology in relation to land management history and hydrologic regime. We found that most habitat conditions and fish populations appear to be generally stable at broad scales for the duration of this study. However, we observed evidence in fish populations of the immediate and prolonged effect of extreme events that we hypothesize are related to climate variability. Additionally, some characteristics of river geomorphology appear to have changed, even in the brief 8 years of this study.

An additional finding of this work relevant to ongoing timber management on the Tongass National Forest was the overlap in distribution of high population juvenile anadromous salmon-rearing streams with areas that were historically harvested. This observation reflects the co-occurrence of the most productive and accessible forests with salmon in areas of similar geomorphology and landscape configuration. Historical riparian harvest with the greatest potential to affect instream habitat quality targeted the same marine-connected subwatersheds that support anadromous salmonids such as coho salmon. Thus, productive forests coincide with anadromous fish population areas surveyed by the Management Indicator Species Study. Further, the legacy of forest harvest affects fish populations at broader watershed scales in terms of intact old-growth forest in stream catchments. We found that in rain-dominated watersheds with >42 percent old-growth forest, streams had wider channels and deeper pools, regardless of watershed size. These channels may provide refugia for native fish from summer drought and low-flow conditions. However, rain-fed systems may experience lower and warmer flows relative to snow-fed systems, which can negatively impact salmon (e.g., Sergeant et al. 2017). Moreover, we observed linkages between intense winter storm events in rain-dominated systems and drops in fish population size the following summer in both of the annually surveyed watersheds in this study, which represented both an actively managed and an unmanaged watershed. As more watersheds transition from snow to rain, and as predicted winter storm intensities

increase, even streams with wider channels and deeper pools that provide summer habitat may not provide adequate winter refugia for native fish. Emphasizing protection of off-channel refugia habitats will support efforts to ensure that productive forests and salmon populations can continue to coexist on the Tongass National Forest, even under changing conditions.

Acknowledgments

The authors acknowledge the contributions to this work from the many field survey leads and team members who completed data collection in the often logistically and physically challenging environment of the Tongass National Forest, particularly Alexander "Alex" Rodriguez-Smith for his key role as field supervisor for 4 years. We thank Kathryn Ronnenberg for editorial revisions and figure development, and Kelly Christiansen for data compilation assistance and map design. We also thank Alex Rodriguez-Smith and Dean Anderson for data compilation, GIS, and calculation assistance. And we thank Robin Welling, Ryan Bellmore, Carlos Polivka, Gordon Reeves, and Marcía Snyder for their instructive peer reviews of the manuscript. We further acknowledge the contribution of John McDonell, who was key to the development of the Management Indicator Species Study design, site selection, and field surveys.

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Appendix 1: Subwatershed Designation—Old-Growth Cover and Post Stratification

Old-Growth Cover in Subwatershed Area

Presence of old-growth forest in the upland has been shown to influence hydrology, sediment supply, and wood inputs (Bilby and Ward 1989, Jones et al. 2000). Old-growth forest cover was incorporated into the hydrologic analysis by identifying median percentage of old-growth cover in the subwatershed (42 percent) (fig. A1-1). This allowed for sites to be categorized as having minor amounts of old-growth forest (≤ 42 percent) or major amounts of old-growth forest (> 42 percent).

Many subwatersheds with >42 percent old-growth cover experienced some form of riparian harvest (see fig. 12A). Over 60 percent of sites in large or small, rain-dominated subwatersheds that still have >42 percent old-growth cover in the subwatershed area experienced riparian harvest associated with harvest group 1 (fig. 12A). Similarly, at least half of the sample sites in all other categories of rain- or snow-dominated hydrologies with major or minor amounts of old-growth cover in large or small subwatersheds fell into harvest groups 1–3 (fig. 12A). These patterns suggest that the interval since riparian harvest is not directly translatable to the amount of old-growth forest remaining in subwatershed catchments.

Organization of Sites into Large and Small Subwatersheds for Hydrologic Analysis

Drainage basin area strongly influences rainfall-runoff patterns and channel geomorphology. For hydrologic analysis, median drainage area (894 ac [362 ha]) was used to classify subwatersheds as small (81 to 857 ac [33–347 ha]) or large (894 to 3657 ac [362–148 ha]). The number of subwatersheds with old-growth major or minor designations or rain- or snow-dominated hydrology varied within watersheds, and by large or small subwatersheds (fig. A1-2).

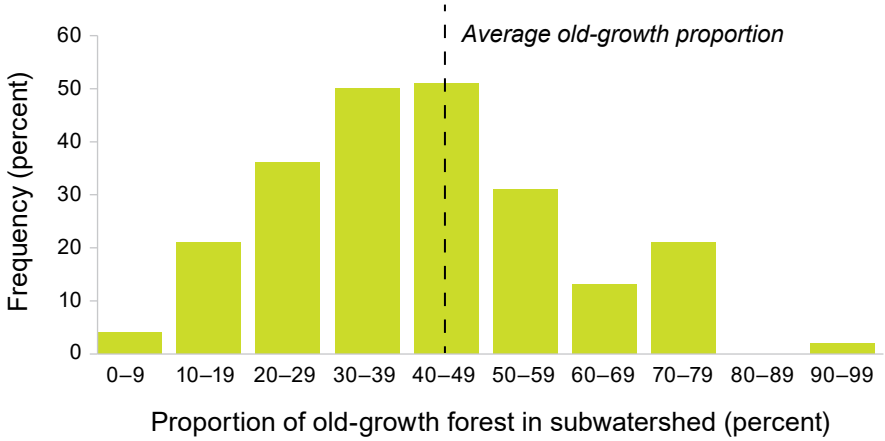


Figure A1-1—Percentage of old-growth forest in upstream subwatershed catchments for survey sites. Dashed line shows a median 42 percent of old-growth forest draining to sites.

Figure A1-2—Number of large- or small-classified subwatersheds per site by hydroregime and amount of old-growth forest (both represented by differing colors) that were sampled for the Management Indicator Species Study on the Tongass National Forest. The *n* value is the total number of sites (or subwatersheds) in a watershed.

Appendix 2: Precipitation Records Over Time

To evaluate precipitation as rain or snow for the duration of the Management Indicator Species Study (2011–2019), we acquired data from the National Weather Service (NOAA NWS) collected from 10 weather stations in the study area (see fig. 1). If rain or snow data were missing for a single month, we calculated the arithmetic average of the data from the nearest two weather stations, following methods from Sattari et al. (2017) and using the equation:

$$V_0 = \frac{\sum_{i=1}^{n} V_i}{N}$$

Where V_0 is the estimate of the missing monthly precipitation data, V_i is the value of the same metric at the *i*th nearest weather station, and N is the number of the nearest stations. Rain and snow were plotted separately by weather station (fig. A2-1). Trends in rain and snow precipitation were evaluated (separately) using linear regression in the software package R.

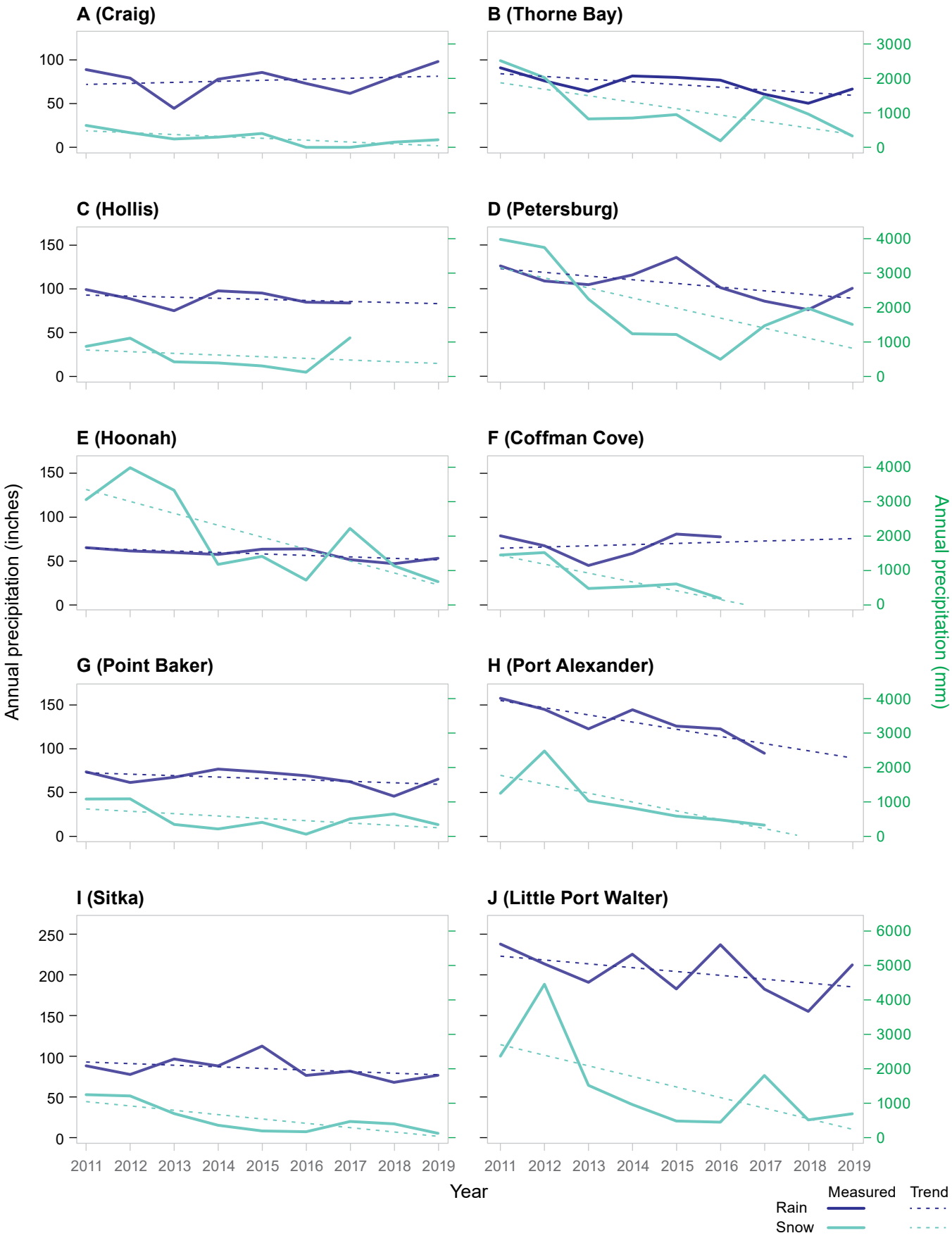
Storms may generate competent streamflows, thus altering channel morphology over time. To capture storm trajectory, we created a map of isohyets (equal precipitation contours), using only available precipitation data at sea level, for a peak precipitation event that occurred on 20–21 January 2015. Stage discharge measurements, where available, were added to the isohyet map (see fig. 11).

For each of the 10 weather stations, the top 10 precipitation events over the 9-year period were identified, summed, and plotted per year (fig. A2-2). For example, in 2015, all weather stations had between one to four 24-hour precipitation events surpassing all others in the 9-year record.

Plotting the subwatershed contributing area by site rain or snow hydroregime highlights five notable patterns (figs. A2-3: A–E and A2-4: A–E):

- Bankfull width widens as contributing area increases.
- Parameters, including bankfull depth and sediment (D^{50}) have considerable variation with increasing contributing area.
- Snow-dominated hydroregime sites have less old-growth cover with increasing contributing area than rain-dominated hydroregime sites.
- Key large wood per area appears to decrease with increasing contributing area.
- Relative pool area appears to increase with increasing contributing area.

Figure A2-1 (next page)—Precipitation in the form of rain or snow recorded at weather stations in the Tongass National Forest for the Management Indicator Species Study, 2011–2019.


A (Craig)
B (Thorne Bay)
C (Hollis)
D (Petersburg)
E (Hoonah)
F (Coffman Cove)
G (Point Baker)
H (Port Alexander)
I (Sitka)
J (Little Port Walter)
Annual precipitation (inches)
Annual precipitation (mm)
Year
2011 2012 2013 2014 2015 2016 2017 2018 2019
Measured
Trend
Rain
Snow

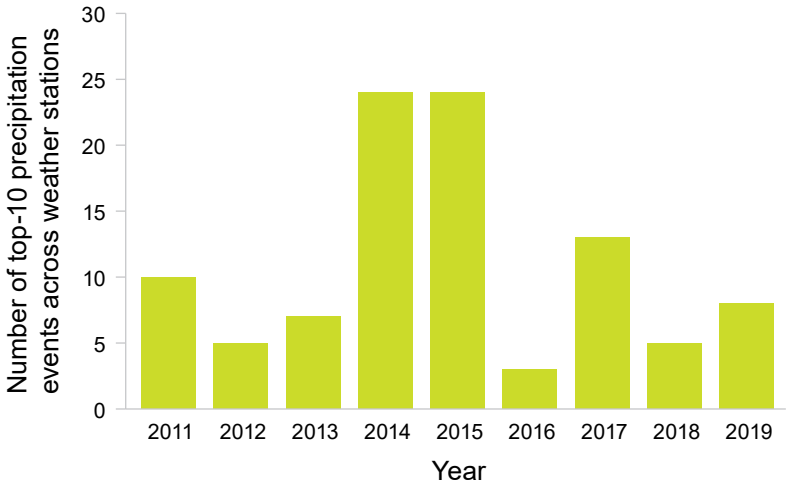


Figure A2-2—Number of top-10 peak precipitation events at the 10 weather stations in the Management Indicator Species Study area over a 9-year period. For example, in 2015, all weather stations had one to four 24-hour precipitation events that surpassed all others in the 9-year period.

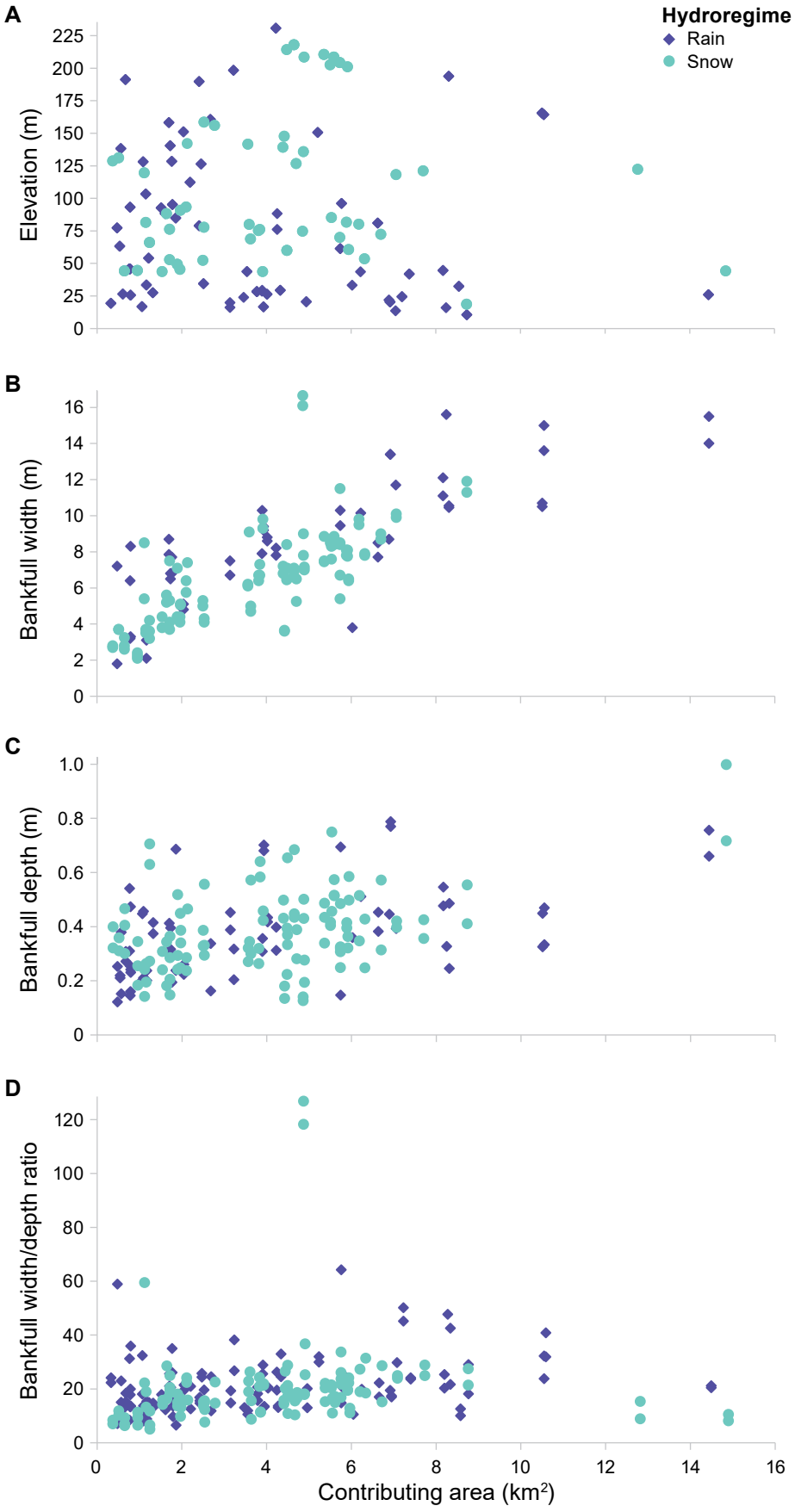


Figure A2-3—Relationships among subwatershed contributing areas with hydroregimes (rain or snow) and watershed conditions (A–D).

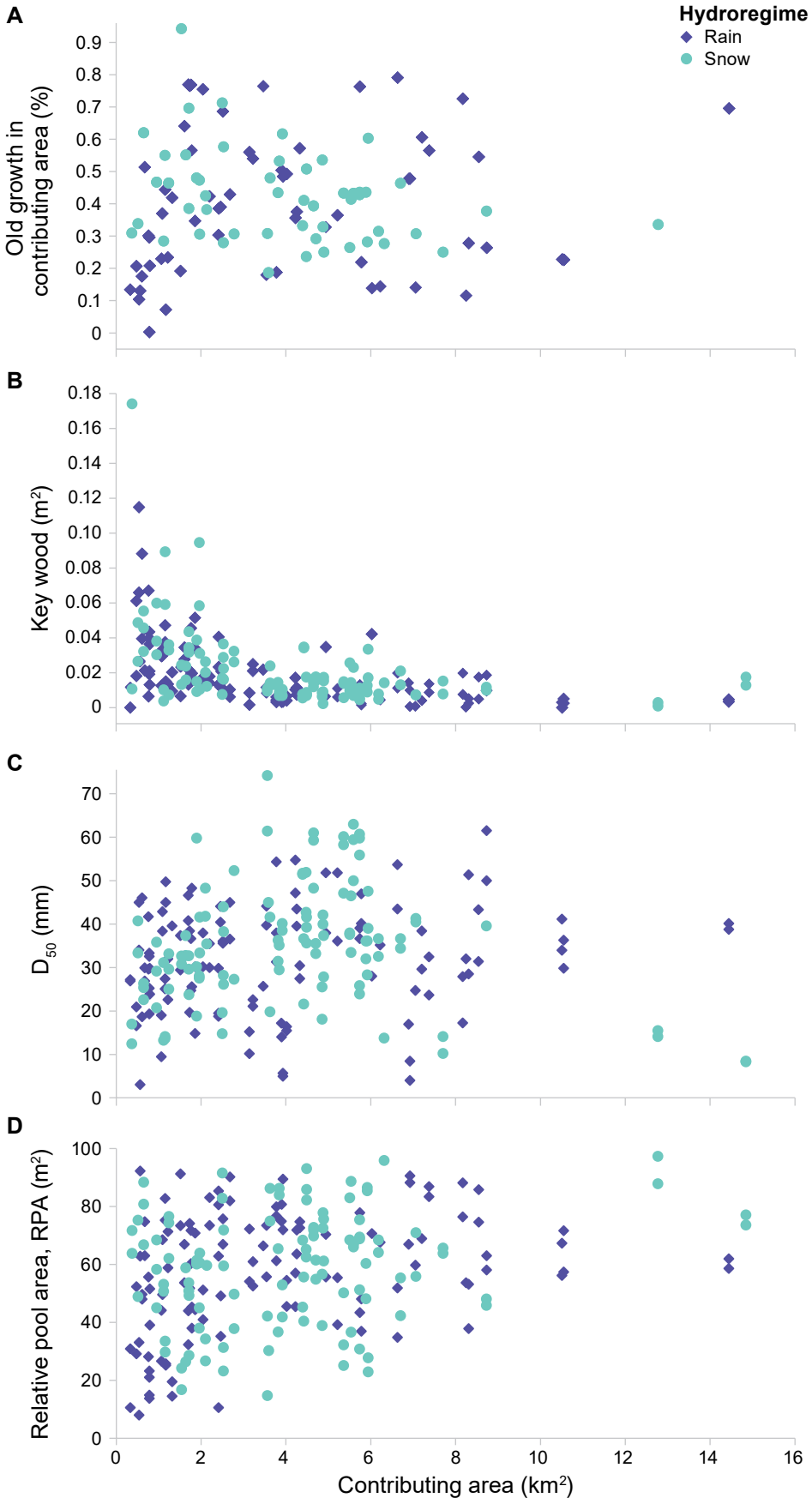


Figure A2-4—Relationships among subwatershed contributing areas to hydroregimes (rain or snow) and subwatershed conditions (A–D).

Appendix 3: Reference of Site Name to Index Number for Figure 4

Table A3-1—Site names and numbers by watershed in figure 4 dendrograms (p. 22–24)

Watershed	Site name	Site name number
Cable	Cable1	1
	Walder	2
	Daves Bacon	3
	Big Tiny	4
Duncan	MooseSkull	1
	Gunshow	2
	Skunker	3
	Rockslide	4
	Uno	5
	Inbetween	6
	Headwall	7
	Bridge	8
Farragut	JohnsFinale	1
	NineOnePapa	2
	Lamprey	3
	Play	4
Game	Ancient	1
	BearBait	2
	Sean	3
	DoubleParr	4
House Rock	AxMen	1
	Chainsaw	2
	TreeThunder	3
	TheSpill	4
Iyouktug	Woodrun	1
	BodyGuard	2
	Turnabout	3
	Snack	4
Maybeso	WT	1
	CedarCreek	2
	SeedsAnyone	3
	DeadBeaver	4
	BeaverMeadow	5
Meterbright	LastChance	1
	Decapitation	2
	R2D2	3
Meterbright	HighWater	4
	Campfire	5
	LostTrap	6
	TenSecondsofSun	7
	DansDemise	8
Mitchell	CCForest	1
	BeaverPond	2
	Fabulous	3
	Admin	4
Ohmer	Alder	1
	Sprinkle	2
	CindySaturday	3
	ChumDogMillionaire	4
	CoffeeBreak	5
	NoRibs	6
	SuperTrap	7
	BitofBedrock	8
	Sushi	9
	Porcupine	10
	SkinnedBear	11
	OlderOhmer	12
Rowan	Rage	1
	WhatADay	2
	Office	3
	BustedTripod	4
Saginaw	LilDipper	1
	SouthSag	2
	Change	3
	BigUg	4
Shelikof	Kaching	1
	HumpDay	2
	BreakIn	3
	Nameless	4
Slide	SwimmingHole	1
	CatsRule	2
	Ham	3
Slide	GreenEggs	4
Staney	Tye	1
	Slash	2
	Calvin	3
	TribRex	4
	HighwayNoise	5
	Hydra	6
	Fossil	7

Table A3-1—Site names and numbers by watershed in figure 4 dendrograms (continued)

Watershed	Site name	Site name number
	Orpheus	8
	BigTRex	9
Steelhead	Spillage	1
	WetFork	2
	BearSounds	3
	MyLittlePony	4
Suntaheen	Glazed	1
	ManDown	2
	Glide	3
	Odin	4
Towers Creek	ThirtyTrap	1
	FootballField	2
	ZZT	3
	RisingStream	4
	EasyStreet	5
	Dehydration	6
	Camelot	7
	UpperEast	8
Tunehean	Toadstool	1
	Bear	2
	Homestretch	3
	SlowCole	4
	TuneheanLegacy	5
	TheBlob	6
	TGIF	7
	SixPack	8
Twelvemile	HangingPipe	1
	Azalea	2
	Bramble	3
Twelvemile	CaveCreek	4
Zim	SouthZim	1
	Thimbleberry	2
	Huckleberry	3
	NorthZim	4

Appendix 4: Calculating Bankfull Shields Stress

Bankfull Shields stress was calculated as:

$$\tau^*_{bf} = \rho R_{bf} S/(\rho_s-\rho)D_{50}$$

Where ρ is the density of water (1000 kg/m^3), ρs is the density of sediment (2650 kg/m^3), R_{bf} is the bankfull hydraulic radius, and S is the channel bed slope. Bankfull Shields stresses referred to herein apply to D_{50}, the median diameter of gravel and cobble substrate.

We computed hydraulic radius, R_{bf}, from average reach bankfull height (H_{bf}) and bankfull width (W_{bf}) with:

$$R_{bf} = A/P$$

Where A is the bankfull channel cross-sectional area (H_{bf}*D_{bf}) and P is the average bankfull wetted perimeter (2*H_{bf}+W_{bf}). Given steep channel side slopes, we assumed that channel shape was rectangular.

We assumed that sediment supply drives the magnitude of bankfull Shields shear stress relative to the critical stress required to mobilize the median bed-surface grain size (τ^*_{bf}/τ^*_c) (Pfeiffer et al. 2017). We used a reach-averaged slope for computing the critical Shields stress, τ^*_c, (Goode et al. 2013, Lamb et al. 2008, Sloat et al. 2017) with:

$$\tau^*_c = 0.15\ S^{0.25}$$

Slope (empirically measured in the field), if presented in the database as 0, was assumed to be 0.001 percent.

Pacific Northwest Research Station

Website	https://www.fs.usda.gov/pnw
Telephone	(503) 808-2100
Publication requests	(503) 808-2138
FAX	(503) 808-2130
E-mail	sm.fs.pnw_pnwpubs@usda.gov
Mailing address	Publications Distribution Pacific Northwest Research Station USDA Forest Service 1220 SW 3rd Avenue Portland, OR 97204