

Effects of stream-adjacent logging in fishless headwaters on downstream coastal cutthroat trout

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> Abstract: To investigate effects of headwater logging on downstream coastal cutthroat trout (Oncorhynchus clarkii clarkii) populations, we monitored stream habitat and biotic indicators including biomass, abundance, growth, movement, and survival over 8 years using a paired-watershed approach. Reference and logged catchments were located on private industrial forestland on \sim 60-year harvest rotation. Five clearcuts (14% of the logged catchment area) were adjacent to fishless portions of the headwater streams, and contemporary regulations did not require riparian forest buffers in the treatment catchment. Logging did not have significant negative effects on downstream coastal cutthroat trout populations for the duration of the sample period. Indeed, the only statistically significant response of fish populations following logging in fishless headwaters was an increase in late-summer biomass $(g \cdot m^{-2})$ of age-1+ coastal cutthroat trout in tributaries. Ultimately, the ability to make broad generalizations concerning effects of timber harvest is difficult because response to disturbance (anthropogenically influenced or not) in aquatic systems is complex and context-dependent, but our findings provide one example of environmentally compatible commercial logging in a regenerated forest setting.

> Résumé : Pour étudier les effets de la coupe forestière dans les eaux d'amont sur les populations côtières de truites fardées (Oncorhynchus clarkii) en aval, nous avons suivi des indicateurs biotiques et de l'habitat de cours d'eau, dont la biomasse, l'abondance, la croissance, les déplacements et la survie, sur une période de huit années, en utilisant une approche de bassins versants jumelés. Les bassins versants de référence et exploité étaient situés dans une zone forestière industrielle non publique où la période de rotation des récoltes est d'environ 60 ans. Cinq coupes à blanc (14 % de la superficie exploitée du bassin versant) étaient attenantes à des portions de cours d'eau d'amont exemptes de poissons, et la réglementation en vigueur n'exigeait pas de zones tampons riveraines dans le bassin versant exploité. L'exploitation forestière n'a pas eu d'effets négatifs significatifs sur les populations de truites fardées côtières en aval pendant la période d'échantillonnage. De fait, la seule réaction statistiquement significative des populations de poissons après la coupe forestière dans les cours d'eau d'amont sans poisson était une augmentation de la biomasse (g·m⁻²) de truites fardées côtières d'un an et plus à la fin de l'été dans les affluents. Ultimement, il est difficile de tirer de grandes conclusions sur les effets de l'exploitation forestière parce que les réactions aux perturbations (influencées par les humains ou non) dans les systèmes aquatiques sont complexes et dépendent du contexte. Nos résultats fournissent toutefois un exemple d'exploitation forestière commerciale compatible sur le plan environnemental dans un contexte de forêt régénérée. [Traduit par la Rédaction]

Introduction

Headwater streams propagate water, materials, and organisms downstream, and the characteristics of headwaters are expected to influence downstream biological communities (Vannote et al. 1980; Gomi et al. 2002; Richardson and Danehy 2007). Furthermore, disturbance, such as forest harvest, adjacent to fishless headwaters can influence downstream fish populations by altering the quality, quantity, or timing of resource subsidies provided by headwater streams (Wipfli 2005; Piccolo and Wipfli 2002; Cummins and Wilzbach 2005). For example, drift of aquatic invertebrates from headwaters can elevate prey densities for downstream fish populations (Wipfli and Gregovich 2002; Wipfli et al. 2007). Altered headwater hydrologic and temperature regimes can also propagate downstream and influence fish growth and survival (Hicks et al. 1991). Because 60% to 90% of heavily dissected mountain catchments may be drained by fishless headwater streams (Benda et al. 1992; May and Gresswell 2003; Richardson and Danehy 2007), land use adjacent to these headwaters can exert considerable cumulative effects on downstream abiotic and biotic conditions.

The fish-bearing segments in the upper portions of many catchments that drain into the Pacific Ocean are inhabited by vertebrate assemblages dominated by coastal cutthroat trout (Oncorhynchus clarkii clarkii), and populations exhibiting a fluvial life history (movements limited within an individual river or stream; Varley and Gresswell 1988; Northcote 1997) often predominate in the high-gradient (>4%) extremities of these systems (Richardson and Danehy 2007; De Groot et al. 2007). Although coastal cutthroat trout populations have been negatively affected by timber harvest (Reeves et al. 1997), in some cases, harvest of riparian forests can result in increased growth and biomass of coastal cutthroat trout populations, at least during the first decade following harvest

Received 25 September 2015. Accepted 19 April 2016

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(Connolly and Hall 1999; Wilzbach et al. 2005). Indeed, the highgradient systems inhabited by coastal cutthroat trout are often resilient to disturbances associated with timber harvest (e.g., increases in water temperature and fine sediments and loss of large woody debris; Mellina and Hinch 2009).

Over the last 60 years, increased recognition of the strong linkages between terrestrial and aquatic ecosystems has led to an evolving series of state and federal forest harvest regulations designed to protect aquatic resources, principally salmonids (Hall et al. 2004; Ice et al. 2010). These regulatory changes, in conjunction with changing wood product markets, social attitudes, and technological advances have resulted in a de facto adaptive management approach to forest harvest that has left a complex legacy of harvest treatments across the landscape over time. Long-term monitoring associated with pioneering studies such as the Alsea Watershed Study, Oregon, USA (Stednick 2008), and the Carnation Creek and Queen Charlotte Islands studies, British Columbia, Canada (Tschaplinski et al. 2004), provided valuable information on the effects of historical forest harvest practices to streams. However, these studies were carried out during an era when naturally regenerated old-growth or late-seral forests were converted to forestry plantations. Logging equipment and practices used during that period have since been replaced. Contemporary forest harvest is typically carried out on previously harvested stands. Harvested trees tend to be smaller, requiring smaller harvest equipment. Road systems are present and usually require only refurbishing with minor additions of newly constructed roadway, and forest management activities are guided by a complex array of current best management practices.

Retention of riparian forest buffers is one of the primary best management practices currently used to reduce negative effects of logging to streams (Blinn and Kilgore 2001; Lee et al. 2004). Riparian buffer prescriptions vary across jurisdictional boundaries and according to a variety of reach-level environmental characteristics, one of which is the presence or absence of fish in adjacent streams (Lee et al. 2004). Fishless headwaters are usually subject to less stringent riparian forest protection than is required adjacent to fish-bearing streams (Cummins and Wilzbach 2005). In Oregon, for example, state regulations require retention of standing live trees in riparian buffers adjacent to fish-bearing stream reaches, but typically require no such protection along fishless reaches (Oregon Department of Forestry 2006). In practice, the timber harvesting method of clearcutting stands with no residual riparian forest protection can occur along fishless reaches that are immediately above fish-bearing reaches of the same stream.

Although numerous studies have been conducted to evaluate the effects of timber harvest on salmonid populations, few have focused specifically on the downstream effects of stream-adjacent logging in fishless headwater streams on stream salmonids (Mellina and Hinch 2009). Furthermore, the majority of earlier studies occurred in previously unlogged watersheds, and the effects of contemporary logging practices have received much less attention (De Groot et al. 2007). To this end, we examined the effects of headwater logging on downstream salmonid populations and habitat in a second-growth forest (with associated road network) of the Cascade Mountain foothills (Oregon, USA). Specifically, we sought to evaluate the effects of contemporary forestry practices in fishless headwater streams on temporal variation in downstream salmonid density, biomass, length, condition, growth, survival, and movement. The before-after control-impact (BACI) study design included a 5-year prelogging background period and a 3-year postharvest assessment of an experimental catchment that received multiple headwater clearcuts and an adjacent reference catchment. All logging activities were conducted according to current forestry standards and practices sanctioned in the state of Oregon (Oregon Department of Forestry 2001). We assumed that following forest harvest, mean stream discharge, water temperature, and sediment loads would increase; however, we hypothesized that biological responses would be muted because the watershed had been previously logged (e.g., there was an existing road network) and because contemporary forest harvest practices were implemented to reduce negative consequences. Given that the potential effects of forest harvest could be pronounced in fish-bearing tributaries downstream of harvested areas, we examined fish responses in portions of the stream network directly below harvested areas and in downstream mainstem reaches (Fig. 1), including an assessment of movement throughout the study area.

Whole-catchment studies of aquatic responses to forest harvest are uncommon because of their cost and logistical complexity (Gresswell et al. 2006). However, demographic processes that influence fish abundance (e.g., spawning and dispersal) commonly operate over the entire stream network (Frissell et al. 1986; Northcote 1997; Torgersen et al. 2008), which emphasizes the importance of catchment-scale analyses for understanding fish population responses to human disturbances such as forest harvest (Gresswell et al. 2006). Our paired-catchment approach allowed us to evaluate the effects of headwater harvest on temporal variation in downstream coastal cutthroat trout populations.

Materials and methods

Study location

This study was conducted in Hinkle Creek, Oregon, USA (43°25'20"N, 123°02′10″W) located in the Umpqua River basin in the foothills of the Cascade Mountain Range at the southern end of the Western Cascades Province (Franklin and Dyrness 1988). The catchment is situated on private industrial forestland owned by Roseburg Forest Products and managed for timber production. The landscape is vegetated by Douglas fir (Pseudotsuga menziesii) in plantation forests that are harvested on 55- to 60-year rotations (Skaugset et al. 2007). Western hemlock (Tsuga heterophylla), western red cedar (Thuja plicata), red alder (Alnus rubra), bigleaf maple (Acer macrophyllum), vine maple (Acer circinatum), and salmonberry (Rubus spectabilis) occur along riparian corridors. Bedrock geology of the study catchment is primarily basalt (Walker and McLeod 1991), and elevation ranges from 424 to 1275 m. Precipitation occurs mostly as rainfall (152-203 cm·year-1; http://www.wrcc.dri.edu/pcpn/or.gif) from November through May, but snow can fall intermittently throughout winter. Highest discharge events occur when large rain storms follow snow.

The portion of Hinkle Creek included in the study area consists of high-gradient (≥4%), cobble-bedded reaches with step-pool, bedrock, and cascade morphologies. The stream channel tends to be constrained alternately by terraces and hillslopes. Hinkle Creek supports an unexploited and naturally reproducing fish community of coastal cutthroat trout, steelhead trout (Oncorhynchus mykiss irideus), and reticulate sculpin (Cottus perplexus). Coastal cutthroat trout are the most abundant fish species and are distributed throughout the stream network upstream into low-order headwater tributaries. Coastal cutthroat trout in Hinkle Creek express fluvial (movement limited to the Hinkle Creek stream network) and fluvial-adfluvial (mature individuals migrate from downstream mainstem rivers into Hinkle Creek for spawning and rearing) migratory populations (Varley and Gresswell 1988; Northcote 1997), but the fluvial migration patterns predominate in the study area. Anadromous steelhead and stream-resident (limited local movement) reticulate sculpin distributions overlap with coastal cutthroat trout in the lower portion of the study area, but they do not extend into the headwaters as far as coastal cutthroat trout. Pacific giant salamanders (Dicamptodon tenebrosus) complete the aquatic vertebrate assemblage and are present throughout all fish-bearing portions of the stream network.

Roads were generally not close to streams in the study area. A road crossed main stems once in both catchments, over a bridge at the junction of South Fork Hinkle Creek (SFHC) and SFHC tributary 1 (hereinafter ST1), and over a culvert on North Fork Hinkle

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Fig. 1. Study catchments in the Hinkle Creek stream network, Douglas County, Oregon. USA, showing locations of nutrient sampling sites and weirs, temperature loggers, fixed antenna, stream gauges, and the fish-bearing tributaries in each catchment, including the distributional extent of steelhead (*Oncorhynchus mykiss irideus*), reticulate sculpin (*Cottus perplexus*), and coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) in North Fork and South Fork Hinkle Creek (NFHC and SFHC, respectively). NT1 = NFHC tributary 1, NT2 = NFHC tributary 2, NT3 = NFHC tributary 3, ST1 = SFHC tributary 1, ST2 = SFHC tributary 2, and ST3 = SFHC tributary 3. [Colour online.]



 Table 1. Stream channel characteristics of stream segments in North Fork Hinkle Creek (NFHC) and

 South Fork Hinkle Creek (SFHC).

	Drainage area (ha)	Gradient (%)	Active channel width (m)	Valley floor width (m)	Fish-bearing channel length (m)	Logged (%)		
Segment						2001	2005	Total
NFHC	858	8	3.8	31.0	4635	_	_	
NT1	112	11	2.7	38.0	687	—	—	_
NT2	203	9	2.7	23.7	832	—	—	_
NT3	366	15	3.1	33.9	544	—	—	_
SFHC	1083	8	4.0	32.4	7045	10	14	24
ST1	111	8	1.9	37.1	1488	4	24	28
ST2	362	10	3.4	29.4	1366	10	24	37
ST3	129	13	3.3	18.6	596	24	33	56

Note: Drainage area is calculated from the downstream pour point of each segment; NFHC and SFHC represent the entire catchment for each system. The total percent logged is the combined area of clearcuts installed prior to the start of the study (2001) and those installed during the fall and winter of 2005–2006.

Creek (NFHC), just upstream of the confluence NFHC and NFHC tributary 2 (NT2; Fig. 1). Fish passage was documented at the NFHC mainstem culvert. Roads crossed SFHC tributaries 2.1 (ST2.1) and 2 (ST2) and NFHC tributaries 1 (NT1) and 2 (NT2) (Fig. 1). All tributary culverts except the one on NT2 were impassable to fish, and there were no fish above the culvert in ST2.1.

Study design and harvest treatment

The effects of timber harvest in fishless headwaters on downstream aquatic biota in the SFHC were evaluated with a systems approach combining watershed-scale and instream physical and biological variables with the distribution and abundance of fish. Within-basin variation in physiography was assessed by examining the entire stream network at various levels in a spatial hierarchy (e.g., network, stream, segment, reach, and channel unit). We examined biological responses within this hierarchy of scales by focusing on distribution, movement, and growth of coastal cutthroat trout and anadromous steelhead through mark–recapture and tracking studies.

We used a BACI study design (Stewart-Oaten et al. 1986; Stewart-Oaten and Bence 2001) to determine downstream fish population responses to logging in fishless headwaters of Hinkle Creek. NFHC served as the "control" or reference catchment, and SFHC served as the "impact" or experimental catchment where logging occurred. These fourthorder catchments are similar in area and perennial stream length (Table 1), and each catchment contains fishless headwaters above three fish-bearing tributaries to their respective main stems (Fig. 1).

From August 2001 to September 2005, we collected data to characterize stream habitat and fish populations prior to logging. Logging planned as part of this study occurred between August 2005 and May 2006. Postlogging data was collected from May 2006 through September 2008. We considered 2001 to 2005 to be the prelogging period, but three clearcuts totaling 103 ha (approximately 10% of SFHC catchment area) had already been completed in SFHC in 2001, just prior to the initiation of our study (Table 1; Fig. 1). These clearcuts were adjacent to fishless streams and were logged in accordance with Oregon Forest Practice Rules (Oregon Department of Forestry 2001). Although this logging activity could have affected conditions observed in SFHC during the 5-year prelogging monitoring period, ultimately it became part of the baseline for our study. Forest harvest in 2005-2006 consisted of five clearcuts ranging from 17 to 45 ha and totaling 154 ha (approximately 14% of the SFHC catchment area and 24%-34% of SFHC tributaries; Table 1). Clearcuts were located adjacent to fishless headwaters of three SFHC tributaries (Fig. 1), and no riparian forest buffers were retained adjacent to fishless reaches within the clearcuts. Four of the clearcuts were upstream of the fish-bearing reaches, and weirs located at the downstream edges of those clearcuts were 293-913 m (mean = 551 m) above those boundaries. The clearcut adjacent to SFHC tributary 3 (ST3) extended downstream and was adjacent to the upper 261 m of fish-bearing channel (Fig. 1). In accordance with Oregon Forest Practice Rules, no logging occurred within a 15 m riparian buffer on each side of the fish-bearing reaches of ST3 (Oregon Department of Forestry 2006).

Trees were felled by hand and yarded to landings with a slacklineskyline cable system that enabled trees to be lifted into the air and transported fully suspended to the landings. All shrubs were left behind, and large wood was left in streams. A total of 3.2 km of new road was constructed, and an additional 6.4 km of existing road was restored to facilitate harvest and transport of trees. Postharvest activities included piling and burning of logging slash near the landings, but logging slash that fell into or over the streams was not removed. The two catchments were fertilized with urea (46% N) CO(NH₂)₂ in October 2004 at the rate of 493 kg·ha⁻¹. Aerial application of herbicides was applied to harvested areas during autumn 2006, and clearcuts were replanted with Douglas-fir seedlings during the winter of 2006-2007. In general, logging practices used in the South Fork Hinkle Creek catchment during this study are similar to those currently being broadly applied in western Oregon and Washington, USA.

Data collection

Stream habitat

Stream habitat surveys were conducted annually (2001-2008) throughout the fish-bearing portions of each catchment during late-summer, low-discharge periods. A hierarchical approach was used to classify habitat features at the stream-segment, geomorphic channel reach, and channel-unit scales (Frissell et al. 1986). Each catchment was divided into stream segments based on the location of major fish-bearing tributary junctions (Fig. 1; Gresswell et al. 2006). Stream segments were classified according to channel confinement and were considered narrow and confined when the ratio of active channel to valley floor width was <2.5. When this ratio was \geq 2.5, the valley floor was consider broad and could be either constrained or unconfined based on the presence of terraces, alternating terraces with hill slopes, or anthropogenic structures such as roads (Moore et al. 1997). Within stream segments, geomorphic reach types (cascade, step-pool, bedrock) were identified based on substrate, gradient, bed morphology, and pool spacing (Montgomery and Buffington 1997). Minimum reach length was 10 active channel widths. Channel-unit types (pool, riffle, cascade, and vertical step) were subsequently classified within each geomorphic reach according to criteria developed by Bisson et al. (1982)

For each channel unit, length and wetted width, streambed composition (i.e., percentage of surface area in bedrock, boulder, cobble, gravel, sand, and silt), active channel width, and valley floor width were visually estimated. The species, number, and volume of large wood (LW: ≥ 10 cm in diameter 2 m in from the largest diameter end, estimated visually) were tallied in zones 1-3 (zone 1 = wetted cross-section during summer low flow; zone 2 = between summer and bankfull flow; zone 3 = above active channel, i.e., above zones 1 and 2; Robison and Beschta 1990) for each 15 m distance interval denoted by fixed distance makers (see section on PIT-tagged fish detection, below). Diameter and length of every tenth piece were measured and compared with visual estimates to develop correction factors for each surveyor. Wetted width, length, and active channel and valley floor widths were also measured with a metre tape at every tenth habitat unit and compared with visual estimates to develop correction factors for each surveyor. Maximum depth of all pool and riffle-rapid habitats was measured to the nearest 1 cm with a metre stick. Habitat characteristics could not be measured in the uppermost 261 m of fish-bearing channel in ST3 during 2006 and 2007 because tree blowdown and slash from upslope logging prevented access to that portion of the stream.

Stream discharge and temperature were measured at the mouths of NFHC and SFHC and in six tributaries at or near the transition from a fish-bearing to fishless designation (Fig. 1). In the SFHC catchment, this transition coincided with the downstream boundary of clearcut harvest units (except as noted for ST3). Stream discharge in the tributaries was estimated by installing gauging stations with Montana flumes (Tracom, Alpharetta, Georgia, USA). Stream discharge at the mouths of NFHC and SFCH was obtained from US Geological Survey (USGS) gauging stations (USGS stations 14319830 and 14319835; http://water.usgs.gov/waterwatch/). Summer stream temperatures were measured at 10-30 min intervals using Vemco 12 bit Minlog and Onset HOBO data loggers (±0.2 °C). Detailed accounts of stream discharge, sediment yield, and temperature monitoring associated with the Hinkle Creek paired watershed study were documented by Zégre (2008), Zégre et al. (2010), Kibler et al. (2013), and Surfleet and Skaugset (2013).

Water samples for chemical analysis were collected monthly from 1 October 2002 through 30 September 2003; beginning in October 2003, sampling occurred seasonally (Meininger 2011). During 2002, water samples were only collected at the gauged sites located in the NFHC and SFHC upstream of the confluence and in the headwaters above the flumes. Three additional water sampling sites were added in January 2003 at ungauged locations below the 2001 clearcuts (Fig. 1). George (2006) and Meininger (2011) provide detailed methods, results, and discussion concerning nutrient monitoring for the Hinkle Creek paired watershed study.

Fish capture

Single-pass electrofishing was conducted annually (2001–2008) during late-summer, low-discharge periods (15 August – 15 September) to capture salmonids in all pools in the fish-bearing portion of the stream network. The only exception to this census of pool habitats occurred in ST3 in 2006 and 2007, when tree blowdown prevented access to the upper 261 m of fish-bearing channel. In each year, both catchments were surveyed by the same electrofishing crew to avoid potential sampling bias associated with multiple crews.

Single-pass electrofishing was assumed to provide an unbiased index of age-1+ salmonid abundance during our study because the number of age-1+ fish captured with single-pass electrofishing is strongly correlated with multiple-depletion population estimates in streams similar to NFHC and SFHC (e.g., Pearson's r > 0.8; Bateman et al. 2005; Foley et al. 2015). We focused the electrofishing effort on pools because these channel units provide the primary rearing habitat in the study streams during summer when sampling occurred, and age-1+ salmonids were rarely encountered in other habitat types. Moreover, sampling in 2004 yielded pool: riffle-rapid ratios of age-1+ coastal cutthroat trout biomass (g·m⁻²) of 19.8:1 and 15.1:1 for NFHC and SFHC, respectively.

Upon capture, all salmonids were anesthetized, and fork length (FL) to the nearest millimetre and wet mass to the nearest 0.1 g were recorded. Fish were anesthetized with either clove oil (study years 2001–2006; 10:1 mixture of 100% ethanol and clove oil, diluted to 12.5 mg·L⁻¹ with stream water; Anderson et al. 1997; Keene et al. 1998) or a solution of buffered MS-222 (study years 2007–2008; 40 mg·L⁻¹). Salmonids \geq 80 mm were categorized as either coastal cutthroat trout or steelhead, but differentiating these species based on external characteristics was not possible for smaller individuals. Therefore, salmonids <80 mm were classified only as "trout." The 80 mm length threshold corresponds closely with the length used to differentiate age-0 from age-1+ salmonids in the Hinkle Creek catchment (based on examination of length frequency distributions; Jearld 1983).

Beginning in 2002, a 23 mm half-duplex (HDX) passive integrated transponder (PIT) tag (Texas Instruments, Inc., Dallas, Texas, USA) was surgically implanted in all salmonids \geq 100 mm following procedures described by Bateman and Gresswell (2006). In addition, the adipose fin was removed from all coastal cutthroat trout receiving a PIT tag to estimate tag retention rates (Bateman et al. 2009). Subsequently, all captured salmonids \geq 100 mm were scanned with an Allflex (Allflex USA, Inc., Dallas, Texas, USA) handheld PIT-tag scanner and examined for the presence of an adipose fin. All untagged salmonids \geq 100 mm were implanted with PIT tags, including fish that were previously marked but subsequently expelled (shed) the tag. After handling, all fish were allowed to recover (defined by upright swimming) in an aerated bucket of stream water and then returned to their location of capture.

PIT-tagged fish detection

Fixed and portable antennas were used to detect PIT-tagged fish within the study area. Fixed PIT-tag antennas (Barbin Zydlewski et al. 2001) were installed in the autumn and winter of 2002 immediately above the confluence of NFHC and SFHC and in tributaries and the mainstem NFHC and SFHC immediately above each fish-bearing tributary confluence (Fig. 1). Initially, a single antenna was installed at each location, but in 2003, a second antenna was added at each site to determine movement direction of individual fish.

Stationary antennas were operated continuously year-round. Fish detection data were uploaded, and antennas were tuned at weekly intervals to maintain a minimum read range of 25 cm in any direction. A minimum read range of 25 cm generally resulted in 100% detection of test PIT tags floated through antennas.

Antenna failure from either equipment malfunction or damage caused during storms resulted in temporary gaps in tagged fish detection. We attempted to account for the effect of antenna failure on tag detection efficiency by estimating the number of fish movements known to have been missed during these gaps. A fish movement was designated as "missed" if a fish was not detected at fixed antennas but subsequently was recaptured or detected at other locations in the stream network that would have necessitated movement through an antenna. Tag detection efficiency was defined as the proportion of the total movement events (antenna detections plus known missed movement events) that were actually detected by the antenna.

In 2003, we began to use portable PIT-tag antennas (Barbin Zydlewski et al. 2001) three times annually (December, March, and June) to detect PIT-tagged fish. During these sampling periods, stream discharge was higher than during late-summer electro-fishing sampling and age-1+ fish were less likely to be restricted to pool habitats. Therefore, the entire wetted area of the fish-bearing portion of the stream network (with the exception of the uppermost 261 m of ST3 in 2006 and 2007) was sampled. Because portable PIT-tag antennas have a maximum detection range of about 1 m, one to three antennas (depending on the active stream chan-

nel width) were employed simultaneously to increase relocation efficiency.

For each fish detection, the tag number, time, location, and habitat unit characteristics were recorded. Fish location was determined by referencing a fixed set of distance markers attached approximately every 15 m (measured along the thalweg using a hip chain) to riparian trees throughout the stream network. Detection of a PIT tag with a portable antenna does not always indicate detection of a live fish because it is possible to detect dead tagged fish or tags that have been shed (Hill et al. 2006; Bateman et al. 2009). Therefore, a qualitative categorization of tag status was developed to differentiate between live fish and potentially spurious detections (Bateman et al. 2009). Categories included live trout (tag location varying), possible live trout (tag detected in habitat likely to accommodate trout), possible shed tag (tag detected in habitat unlikely to accommodate trout), and shed tag (tag detected in habitat that would not accommodate trout, i.e., dry channel or shallow water with very fine substrate). All tags detected in redds were categorized as shed tags (Bateman et al. 2009). The same methods and surveyors were used in each catchment during each sampling event.

Data analysis

We hypothesized that the potential effects of logging would be more apparent in fish-bearing tributaries immediately below harvested areas than in mainstem habitats further downstream. Therefore, we conducted two separate sets of analyses: one that examined stream habitat and fish population response variables for the entire catchments (i.e., main stem and tributaries combined) and a second that only considered data from tributaries in each catchment (hereinafter referred to as "catchment-level" and "tributary-level" analyses, respectively).

We analyzed channel-unit substrate composition (e.g., percent fines), channel unit composition (e.g., percent pool habitat), and channel unit (i.e., pool and riffle–run) maximum depth as stream habitat response variables. Fish population response variables included fish density, biomass, size-at-age, body condition, growth, movement, and survival. For catchment-level analyses, we separately calculated fish density (fish·m⁻²) and biomass (g·m⁻²) of age-1+ coastal cutthroat trout and age-1+ steelhead captured in pools during late summer by dividing the total number or biomass of fish captured by the total area of pool habitat sampled in each catchment. For tributary-level analyses, age-1+ coastal cutthroat trout and age-1+ steelhead density and biomass in pools were first determined for each tributary and then averaged across tributaries within their respective catchments.

We focused our analyses of age-1+ fish population responses on coastal cutthroat trout because age-1+ steelhead trout were not present in all fish-bearing portions of the stream network in all years. Coastal cutthroat trout were distributed throughout the entire fish-bearing stream network and therefore provided a better indication of potential effects of headwater logging within the study catchments (Reeves et al. 1997; Hall 2008). However, biological interactions between age-1+ steelhead and coastal cutthroat trout could potentially confound the response of the latter to logging, especially in mainstem habitats where age-1+ steelhead were locally abundant in some study years. Consequently, we first considered only coastal cutthroat trout in analyses of age-1+ fish population response variables and then performed identical analyses that combined both age-1+ coastal cutthroat trout and age-1+ steelhead trout to determine whether the addition of the latter influenced the outcome.

To characterize fish size, we calculated the mean and 90th percentile of fish length separately for age-1+ coastal cutthroat trout and age-1+ steelhead in each tributary and each catchment. We examined late-summer fish body condition (i.e., body mass for a given length) by regressing log-transformed fish mass on logtransformed fish length for all combinations of species and study years, separately for each tributary and each catchment. Information on fish growth was obtained from PIT-tagged coastal cutthroat trout and steelhead trout \geq 100 mm that were captured during annual electrofishing. Because annual growth was highly variable for individuals among years, and because we recaptured some individuals more than once in a single sampling event, fish growth analysis was restricted to individuals that had been at liberty for 330–402 days between capture. Annual relative growth rate (mm·mm⁻¹·year⁻¹) was calculated as follows: RGR = [($L_2 - L_1$)/ L_1]·[365/($t_2 - t_1$)], where L_2 is the final length, L_1 is the initial length, t_1 is the day of initial capture, and t_2 is the day of recapture (Busacker et al. 1990). Relative growth rates were not analyzed for tributaries because of a low number of PIT-tagged fish recaptures.

Although movement of coastal cutthroat trout among habitat patches within headwater tributaries is common (Novick 2005), we hypothesized that changes in catchment-level movement patterns would ultimately be more indicative of effects associated with logging disturbance in the fishless upstream portions of the stream network. Indeed, coastal cutthroat trout display a broad range of movement patterns, but by limiting analysis to singleyear time steps, we were able to classify movements of PIT-tagged fish into one of four movement categories based on their capture and recapture histories within each study year: (i) upstream movement only; (ii) downstream movement only; (iii) both upstream and downstream movement within a main stem or tributary; or (iv) complex, if fish moved between main stems and tributaries or between catchments (after Young 2011). Although a simple analysis of immigration and emigration from the tributaries (represented here by the categories upstream only and downstream only) would probably be sufficient if the effects of logging were consistent among seasons and years, we hypothesized that logging could alter both the temporal and spatial distribution of resources or perhaps just the ability of fish to access existing resources because of changes in hydrologic parameters such as flow and temperature. Hence, we included the complex and the both upstream and downstream categories.

The proportion of fish in each movement category was estimated by dividing the number of fish in each category by the total number of tagged fish at large during each year for the entire catchment. The number of tagged fish at large in a given year was determined by summing the number of fish tagged during late summer and the number of tags detected during the three mobile antenna surveys and the annual electrofishing survey. Mobile antenna detections classified as shed tags were excluded. Both mobile antenna and electrofishing surveys were corrected for sampling efficiency. We assumed 70% and 50% sampling efficiency for mobile antenna and electrofishing surveys, respectively (Berger and Gresswell 2009).

The influence of logging on each response variable except fish survival (see below) was analyzed by first calculating the annual difference between the logged catchment (SFHC) and the reference catchment (NFHC) in the response variable mean and then using t tests to test for a change in this difference from the prelogging to the postlogging period (i.e., a BACI-type analysis; Stewart-Oaten et al. 1986; Stewart-Oaten and Bence 2001). With this approach, differences between SFHC and NFHC for each year are used as replicates to compare the prelogging period to the postlogging period (Stewart-Oaten et al. 1986). This approach is common in large-scale field manipulations where spatial replication is not feasible (e.g., Taylor et al. 2006; Greenwood et al. 2007; Tiegs et al. 2011). Prior to performing statistical tests, we examined data from the prelogging period for temporal trends and additivity (i.e., parallel trajectories between the manipulated and reference catchments; Stewart-Oaten et al. 1986; Stewart-Oaten 2003). Additionally, we visually assessed the data for symmetry of distribution (normality) and nonconstant variance. We used twosample Student's t tests when variances during prelogging and postlogging periods were approximately equal and used Welch's *t* tests when these variances were unequal. All statistical analyses were conducted using the software program NCSS (Hintz 2007). Statistically significant changes in the difference between catchments for a response variable were interpreted as a potential response to logging in SFHC fishless headwaters. In addition to the detection of statistical significance, we inspected graphs of the response variable time series to aid our inference about the potential effects of headwater logging on downstream fish populations and stream habitat (Conquest 2000).

Survival

Estimates of apparent annual survival (hereinafter referred to as survival) of PIT-tagged fish in mainstem and tributary streams were obtained from fish capture and "recapture" (including both capture via electrofishing and detection from PIT-tag antenna) data as described in Berger and Gresswell (2009). In short, program MARK (White and Burnham 1999) was used to estimate recapture and survival probabilities from individual capture and recapture histories using Cormack-Jolly-Seber (CJS) models. Following Lebreton et al. (1992), we identified the best model of recapture probability, assuming constant survival. Alternative candidate models of fish survival were then evaluated using the best recapture probability submodel (cf. Berger and Gresswell 2009). Model fit was examined by evaluating the ratio of the chisquared statistic (χ^2) to the degrees of freedom (df) for the fully parameterized model (Lebreton et al. 1992). The full model included parameters for each year, spatial unit (catchment and tributary), and all space-time interactions. Candidate models with reduced sets of explanatory variables were compared to evaluate evidence for an effect of logging on fish survival, as indicated by differences between catchments before and after logging (i.e., the selection of "catchment" and "treatment" variables in plausible models). The treatment variable was defined as differences in survival between before and after logging time blocks and thus was a reduced version of the complete time-variation model.

Model selection was performed using AIC adjusted for small sample sizes and overdispersion (evaluated using the fully parameterized model) related to lack of complete independence among recapture observations (QAIC_c). Model averaging was used to account for model uncertainty when more than one model was deemed plausible as indicated by a QAIC_c within 7 units of the best-fitting model. In such cases, estimates were calculated using a weighted average of each individual model estimate, where weighting factors were based on the relative likelihood of each plausible model (Burnham and Anderson 2002). Survival estimates resulting from CJS models were then adjusted to account for PIT-tag loss by double marking each fish (PIT tag and adipose fin clip; Berger and Gresswell 2009). Tagged fish that emigrated from the study area (defined as fish detected moving past and staying below the downstream boundary fixed antennas) were removed from the analysis. Estimated emigration rates were low (2% and 1% from NFHC and SFHC, respectively, after adjusting the number of detected emigrants by mean antenna efficiency), and therefore, any bias resulting from the removal of emigrants was likely negligible.

Results

Habitat

Cobble was the most abundant substrate type at the catchment scale (mean = 33% of the wetted streambed in both the NFHC and SFHC). Mean gravel and boulder substrates were 29% and 20% of the streambed in NFHC and 26% and 23% in SFHC, respectively. Fines were not abundant in either catchment (4% and 5% for NFHC and SFHC, respectively), but streambed proportions of fine substrate were about twice as high at the tributary level (13% and 10% for NFHC and SFHC tributaries, respectively). The proportion of the streambed occupied by each sediment size-class varied in a

synchronous pattern from prelogging to postlogging in both NFHC and SFHC and their tributaries (Table 2). Substrate conditions were highly variable across years in both catchments; there were no significant changes in the difference between catchments between prelogging and postlogging ($|t| \le 2.261$, $P \ge 0.073$; Table 2).

Mean LW abundance was greater in NFHC (8.5 m³ per 100 m) than in SFHC (5.0 m³ per 100 m). In both catchments, LW was more abundant in the tributaries (NFHC tributaries: 9.2 m³ per 100 m; SFHC tributaries: 9.9 m³ per 100 m) than in the main stems. Among the three zones describing LW location, zone 1 (wetted cross-section during low flow) contained the lowest proportion of LW in both catchments, ranging from 24% in the NFHC to 10% in the SFHC. The most common pool-forming agent was boulders. Boulders formed 48% and 61% of pools in NFHC and SFHC, respectively, but it formed a higher portion of pools in NFHC and SFHC, respectively, but it formed a higher portion of pools in the tributaries of each catchment (50% and 31% for NFHC and SFHC tributaries, respectively). Boulders formed a lower proportion of the pools in NFHC tributaries (31%) than in SFHC tributaries (49%).

Both catchments were dominated by fast water habitats with approximately 60% of the wetted area in riffle–rapid habitat in NFHC and SFHC. The proportion of wetted channel in pool habitat, pool maximum depth, and riffle–rapid maximum depth all followed a synchronous pattern of decline from prelogging to postlogging periods in both NFHC and SFHC and their tributaries (Table 2). Differences between prelogging and postlogging estimates were not statistically significant at the catchment or the tributary level for pool area (|t| < 0.847, P > 0.429; Table 2), pool maximum depth (|t| < 0.495, P > 0.639; Table 2), or riffle–rapid maximum depth (|t| < 0.323, P > 0.758; Table 2).

Surfleet and Skaugset (2013) estimated a mean increase of August discharge (summer low flow) for SFHC of 1.9 mm·year⁻¹ (45%) during the three years following forest harvest in fishless headwaters. Mean August discharge of the four treatment catchments was 1.7–4.4 mm above preharvest estimates during the first summer postharvest. During the initial 5 years following harvest, however, differences in August discharge from preharvest values were only statistically significant (increased) in one tributary catchment (the one with greatest proportion of area harvested; Surfleet and Skaugset 2013).

Downstream effects of forest harvest in the four fishless tributary segments included statistically significant increases in sediment yield at the tributary and catchment scales (Zégre 2008). More specifically, Zégre (2008) reported mean annual suspended sediment yield increased 1484 to 8954 kg·km⁻² (23%–42% above predicted) at the tributary scale; at the catchment scale, mean annual sediment yield increased 64 696 kg·km⁻² in SFHC (275% above predicted; Zégre 2008). Zégre (2008) assumed that the increased sediment yield at the catchment scale reflected combined effects of historical and current management activities, including timber harvest and the associated road network.

Water temperature changes varied among the four treatment catchments during the summer following harvest (Kibler et al. 2013). When compared with preharvest values, Kibler et al. (2013) found that mean maximum daily stream temperatures varied from 1.5 °C cooler to 1.0 °C warmer. No statistically significant cumulative effects of stream temperature were observed at the catchment scale, and differences in maximum, mean, and minimum daily stream temperatures between preharvest and postharvest values were not statistically significant (Kibler et al. 2013).

Postharvest increases in $NO_3 + NO_2$ concentrations from three of the SFHC tributaries were statistically significant, and reported values were 2–17 times greater than during the pretreatment period (Meininger 2011). Mean concentrations of $NO_3 + NO_2$ declined in the fourth tributary following harvest (Meininger 2011). Although the mean concentration of $NO_3 + NO_2$ in the South Fork during the preharvest calibration period was 6.6 times greater **Table 2.** Mean annual values for the prelogging and postlogging periods and the mean of the prelogging and postlogging difference with associated standard deviation (in parentheses) and lower (LCL) and upper (UCL) 95% confidence limits for SFHC and NFHC at the catchment and the tributary levels.

		Mean prelogging (SD)		Mean postlogging (SD)				
Variable	Level	SFHC	NFHC	SFHC	NFHC	Change in prelogging and postlogging difference (SD)	LCL	UCL
Bedrock (%)	Catchment	3.2 (0.2)	3.0 (0.5)	3.5 (0.8)	3.6 (0.5)	0.4 (0.5)	-0.7	1.4
	Tributary	3.1 (0.4)	2.6 (0.1)	3.7 (1.5	3.9 (1.9)	0.7 (0.5)	-0.2	1.6
Boulder (%)	Catchment	26.6 (7.9)	21.9 (8.5)	20.9 (3.4)	19.5 (1.9)	3.3 (1.9)	-0.4	7.0
	Tributary	19.7 (4.2)	14.2 (3.6)	15.4 (2.5)	12.8 (1.4)	2.8 (2.5)	-2.1	7.7
Cobble (%)	Catchment	36.5 (4.1)	35.2 (5.2)	33.1 (7.3)	32.0 (9.1)	0.2 (6.3)	-12.1	12.6
	Tributary	29.6 (3.7)	28.7 (2.4)	25.1 (6.3)	25.7 (7.0)	1.5 (8.6)	-15.4	18.3
Gravel (%)	Catchment	22.4 (8.1)	28.0 (12.8)	33.4 (8.7)	35.1 (9.0)	-3.9 (5.6)	-14.9	7.2
	Tributary	26.1 (8.1)	33.9 (10.0)	32.8 (9.7)	37.3 (4.2)	-3.4 (12.6)	-32.8	2.6
Fines (%)	Catchment	5.4 (1.5)	4.2 (2.5)	8.7 (2.1)	8.1 (2.9)	0.7 (3.0)	-5.2	6.6
	Tributary	13.3 (1.8)	9.6 (5.4)	18.9 (4.0)	16.5 (2.2)	1.4 (5.0)	-8.4	11.2
Pool area (%)	Catchment	31.3 (3.1)	30.3 (3.5)	26.7 (5.9)	27.6 (1.8)	0.9 (4.1)	-6.4	8.1
	Tributary	23.8 (3.6)	30.3 (4.0)	21.7 (4.8)	27.1 (3.0)	-1.0 (4.9)	-9.8	7.7
Pool maximum depth (cm)	Catchment	29.1 (1.8)	28.8 (1.5)	28.2 (2.2)	27.4 (2.7)	-0.5 (1.6)	-3.3	2.2
	Tributary	25.8 (2.1)	26.7 (1.6)	24.4 (2.1)	24.7 (2.9)	-0.6 (1.7)	-3.7	2.4
Riffle–rapid maximum depth (cm)	Catchment	14.8 (2.2)	13.5 (1.9)	13.8 (1.9)	11.6 (1.9)	-0.2 (0.8)	-1.7	1.3
	Tributary	12.4 (10.8)	11.5 (2.7)	10.8 (1.7)	8.7 (1.0)	-0.4 (1.6)	-3.3	2.5

Note: Values for substrate categories and pool area represent the percentage of the late-summer wetted stream channel occupied by that size class or unit type. The category "fines" includes both sand and silt-sized particles. Pool and riffle–rapid depths are the maximum depths measured (cm).

than in the North Fork, Meininger (2011) reported that it actually decreased 0.021 mg N·L⁻¹ following treatments in the fishless tributaries. Results for other nutrient characteristics varied. Ammonia concentrations were low (\sim 0.007 mg NH₃·L⁻¹) for all streams, and in many samples, they were below the limit of detection (Meininger 2011). Although ammonia concentrations increased in some treatment catchments following harvest, none of the changes were statistically significant. Similarly, dissolved organic nitrogen concentrations increased in all six tributaries following logging, but changes were not statistically significant (Meininger 2011). Statistically significant increases in the concentrations of dissolved phosphorus and PO₄ following timber harvest were only recorded in one treatment catchment (Meininger 2011).

Fish density and biomass

Mean late-summer densities of age-1+ coastal cutthroat trout in pools ranged from 0.04 to 0.36 fish·m⁻² during the study. At the tributary level, the difference between catchments in late-summer density of age-1+ coastal cutthroat trout (SFHC tributary means -NFHC tributary means) was -0.02 fish·m⁻² prior to logging and 0.09 fish·m⁻² after logging; however, the change in density after logging of age-1+ coastal cutthroat trout in SFHC tributaries relative to NFHC tributaries (~0.11 fish·m⁻²) was not statistically significant (t = -2.011, P = 0.091; Figs. 2a, 2b; also see online Supplementary Material Table S11). At the catchment level, there was not a statistically significant change in the difference between SFHC and NFHC in late-summer density of age-1+ coastal cutthroat trout in pools following logging (t = -0.973, P = 0.368; Figs. 2e, 2f). Similarly, when counts of age-1+ steelhead trout and age-1+ coastal cutthroat trout were combined to calculate latesummer fish density in pools, there was not a statistically significant change in the difference between catchments in density of age-1+ salmonids following logging (catchment level: t = 0.181, *P* = 0.863; tributary level: *t* = 2.070, *P* = 0.084).

Mean late-summer biomass of age-1+ coastal cutthroat trout in pools ranged from 0.69 to 5.19 g·m⁻² during the study. At the tributary level, the difference between catchments in mean late-

summer biomass of age-1+ coastal cutthroat trout in pools (SFHC tributary means – NFHC tributary means) was –0.06 g·m⁻² prior to logging and +1.48 g·m⁻² after logging (Figs. 2*c*, 2*d*; Table S2¹). This net increase of +1.54 g·m⁻² was statistically significant (t = -2.834, P = 0.047). At the catchment level, there was no statistically significant change in the difference between SFHC and NFHC in late-summer biomass of age-1+ coastal cutthroat trout in pools following logging (t = -0.841, P = 0.433; Figs. 2g, 2h).

Combining the catch of age-1+ coastal cutthroat trout and age-1+ steelhead trout to estimate the biomass of age-1+ salmonids did not qualitatively alter the outcome of comparisons between catchments. The increase in biomass of age-1+ salmonids in pools in SFHC tributaries relative to NFHC tributaries after logging was statistically significant (t = -2.90, P = 0.044), but there was no statistically significant change in the difference between SFHC and NFHC in biomass of age-1+ salmonid in pools at the catchment level (t = 0.172, P = 0.869).

Fish size

Mean late-summer lengths of age-1+ coastal cutthroat trout ranged from 105 to 130 mm for both catchment and tributary levels and across all years (Fig. 3; Table S3¹). Changes in differences between SFHC and NFHC in late-summer mean length of age-1+ coastal cutthroat trout were not statistically significant (catchment: t = 0.013, P = 0.990; tributary: t = 2.155, P = 0.075; Fig. 3) nor were changes in the 90th percentile of length (catchment: t =-0.628, P = 0.553; tributary: t = -0.666, P = 0.565). These results did not change when age-1+ steelhead were included with age-1+ coastal cutthroat trout to compare differences in late-summer mean lengths (catchment: t = -0.101, P = 0.923; tributary: t = 2.094, P = 0.081) or the 90th percentile of length (catchment: t = -1.147, P = 0.295; tributary: t = -0.875, P = 0.415).

Fish condition

Regressions of log(fish mass) on log(fish length) suggested no significant changes in age-1+ coastal cutthroat trout condition (the expected mass for a given fish length) following logging

¹Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2015-0455.

Fig. 2. Catchment- and tributary-level age-1+ coastal cutthroat trout biomass $(g \cdot m^{-2})$ and density (fish·m⁻²) in Hinkle Creek, Douglas County, Oregon, USA. (A, C, E, G) Estimates in the treatment (South Fork Hinkle Creek; open circles) and reference (North Fork Hinkle Creek; solid circles) catchments of Hinkle Creek, before and after logging in South Fork Hinkle Creek. (B, D, F, H) Differences between measured values of the treatment and reference catchment, before and after logging in South Fork Hinkle Creek. Logging occurred during the winter spanning 2005 and 2006 (indicated by vertical grey dashed line).



(Table S4¹). We found no change in the difference between SFHC and NFHC tributaries in either the regression slope (mean difference \pm 95% CI = -0.00967 \pm 0.137; *t* = -0.172, *P* = 0.869) or intercept estimates (mean difference \pm 95% CI = 0.0178 \pm 0.282; *t* = 0.154, *P* = 0.882) from regressions following logging. Similarly, changes in differences between SFHC and NFHC for slope (mean difference \pm 95% CI = -0.0082 \pm 0.0717; *t* = -0.280, *P* = 0.789) and intercept estimates

(mean difference \pm 95% CI = 0.0234 \pm 0.1396; *t* = 0.410, *P* = 0.696) were not statistically significant at the catchment level.

Fish growth

A total of 584 recaptured PIT-tagged coastal cutthroat trout and 56 PIT-tagged steelhead trout were sampled to estimate relative growth rate. Relative growth rates of PIT-tagged coastal cutthroat

Fig. 3. Mean fork length (mm) for age-1+ coastal cutthroat trout at the catchment and tributary level, Hinkle Creek, Douglas County, Oregon, USA. (A, C) Estimates in the treatment (South Fork Hinkle Creek; open circles) and reference (North Fork Hinkle Creek; solid circles) catchments of Hinkle Creek before and after logging in South Fork Hinkle Creek. (B, D) Differences between estimates from the treatment and the reference catchments. Logging occurred during the winter spanning 2005 and 2006 (indicated by vertical grey dashed line).



ences between catchments in growth were generally consistent over time (Fig. 4). At the catchment level, there was no significant change in the difference between SFHC and NFHC in relative growth rate for PIT-tagged coastal cutthroat trout following logging (t = -0.371, P = 0.745). This result did not change when the analysis included PIT-tagged steelhead trout in addition to PIT-tagged coastal cutthroat trout (t = 0.132, P = 0.901). Fish growth was not analyzed at the tributary level because of the low number of PIT-tagged fish recaptures.

trout were lower in SFHC than NFHC in most years, but differ-

Fish survival

The full CJS model of mean annual survival fit the data well (χ^2 /df = 1.19; Table 3). Mean annual survival probabilities of PIT-tagged coastal cutthroat trout ranged from 0.19 to 0.50 (Fig. 5; Table S5¹). Survival rates were consistently higher in SFHC relative to NFHC and were typically higher at the catchment level than the

tributary level (Fig. 5). Survival rates in both catchments were highly variable over time, but temporal trends were similar between catchments throughout the study (Fig. 5). A "treatment" effect of logging was included in the set of plausible reduced models of mean annual fish survival in both the catchment and tributary level analyses (Table 3), providing some evidence that survival changed from the prelogging to postlogging periods. At the catchment level, this effect resulted in a small (<1%) increase in model-averaged survival estimates in SFHC relative to NFHC after logging (Fig. 5). However, the 95% confidence interval for the effect of logging overlapped zero. At the tributary level, the treatment effect of logging resulted in a <1% increase in the difference between SFHC and NFHC survival estimates. Confidence in the inclusion of a treatment effect in models of survival was also low at the tributary level, and 95% confidence intervals overlapped zero. Consequently, statistical evidence for an effect of logging on mean annual fish survival did occur, but the strength of this effect does not appear to be biologically significant.

Fig. 4. Mean annual relative growth (mm·mm⁻¹·year⁻¹) of PIT-tagged coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) >100 mm in Hinkle Creek, Douglas County, Oregon, USA. (A) Estimates from the treatment (South Fork Hinkle Creek; open circles) and reference (North Fork Hinkle Creek; solid circles) catchments of Hinkle Creek, before and after logging in South Fork Hinkle Creek. (B) Differences between measured values of the treatment and the reference catchments, before and after logging in South Fork Hinkle Creek. Logging occurred during the winter spanning 2005 and 2006 (indicated by vertical grey dashed line).



Table 3. Primary models used in the analysis of survival of coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) in North Fork Hinkle Creek and South Fork Hinkle Creek at the catchment and tributary spatial scales.

Survival model	$\Delta QAIC_c$	Wt	Κ
Catchment scale			
Catchment + year	0.00	0.56	7
Catchment + treatment + year	0.53	0.43	8
Catchment × year	7.11	0.02	12
Catchment × segment × year*	41.25	0.00	105
Tributary-only scale			
Year	0.00	0.58	6
Tributary + year	1.93	0.22	7
Tributary × year	3.15	0.12	12
Tributary + treatment + year	3.91	0.08	8
Tributary × segment × year*	20.12	0.00	65

Note: Model averaging (by model weight; Wt) across the top models (Δ QAIC_c < 7) was implemented to account for model uncertainty when calculating final estimates and making inferences. The "full" model is shown for reference only; K denotes the number of estimable survival parameters.

*Denotes the full survival model.

Fish movement

Movement of PIT-tagged coastal cutthroat trout was substantial in the study catchments, and 43% of tagged fish were observed away from their original tagging location. Within a given year, the overall proportion of tagged fish that moved ranged from 20% to 36% (Fig. 6; Table S6¹). The mean annual proportion of coastal cutthroat trout that moved declined 8% in NFHC and 1% in SFHC from the prelogging to postlogging periods (Fig. 6), but the change in the difference between SFHC and NFHC in the annual proportion of PIT-tagged coastal cutthroat trout movers was not statistically significant (t = -1.205, P = 0.295; Fig. 6).

Among movement categories, fish that moved both upstream and downstream solely within their respective mainstem or tributary habitats were relatively rare. Among the other movement categories (downstream-only, upstream-only, and complex), com-



Year

plex movement patterns were typically the most prevalent. Complex movements increased slightly in SFHC following logging, but the change in the difference between catchments in the proportion of fish with complex movement was not statistically significant (t = -2.449, P = 0.071). Downstream-only and upstream-only movements declined in both catchments following logging (Table S4¹), and changes in the difference between catchments in these movement categories were not statistically significant (downstream only: t = -0.791, P = 0.473; upstream only: t = -0.756, P = 0.492).

Discussion

The spatial and temporal extent and sampling intensity incorporated in this study provided an uncommon opportunity to evaluate the effects of timber harvest with contemporary techniques in the fishless headwaters of a second-growth forest on downstream fish populations. Our sampling strategy yielded inference at the catchment scale, and the fact that responses did not differ statistically from controls for all but one of the biological variables being evaluated suggests that in this particular study, logging did not have significant effects on the coastal cutthroat trout population for the duration of the sample period. The only statistically significant response of the fish populations was an increase in late-summer biomass (g·m⁻²) of age-1+ coastal cutthroat trout in SFHC tributaries following logging in fishless headwaters.

On the other hand, it is important to recognize that inference of these results is limited. Despite the sampling extent and intensity, results are applicable only to the SFHC during the study period. Although the paired-watershed design can facilitate the exploration of causal mechanisms associated with observed effects of contemporary logging practices on second-growth forests, this type of experiment must be replicated across the landscape to gain a broader interpretation (e.g., De Groot et al. 2007; Gravelle and Link 2007; Leach et al. 2012). In recent years, multi-catchment regional studies focused on logging in second-growth forests have become more common (e.g., Groom et al. 2011; Janisch et al. 2012), and although this approach has limited potential to rigorously explore cause and effect, it will undoubtedly expand the ability to generalize at the landscape scale. For example, evidence from a **Fig. 5.** Estimated annual survival probabilities for PIT-tagged coastal cutthroat trout (*Oncorhynchus clarkii*) ≥100 mm at catchment (black circles with dashed trend line) and tributary (grey circles with solid trend line) levels in treated (South Fork Hinkle Creek) and reference (North Fork Hinkle Creek) catchments in Hinkle Creek, Douglas County, Oregon, USA. Data symbols are labeled by year. Logging occurred during the winter spanning 2005 and 2006.



Fig. 6. Annual proportion of PIT-tagged coastal cutthroat trout (*Oncorhynchus clarkii* clarkii) \geq 100 mm that moved among tributaries and the main stem, Hinkle Creek, Douglas County, Oregon, USA. (A) Estimates from the treatment (South Fork Hinkle Creek; open circles) and reference (North Fork Hinkle Creek; solid circles) catchments of Hinkle Creek before and after logging in South Fork Hinkle Creek. (B) Differences between estimates from treatment and reference catchments before and after logging in South Fork Hinkle Creek. Logging occurred during the winter spanning 2005 and 2006 (indicated by vertical grey dashed line).





study of six headwater catchments in the Kootenay River (USA and Canada) suggested a strong negative correlation between logging in non-fish-bearing streams and downstream population density of westslope cutthroat trout (*Oncorhynchus clarkii lewisi*; Valdal and Quinn 2010), but such results do not necessarily indicate causation.

Our study encompassed 8 years of field sampling, including a 5-year prelogging period and a 3-year postharvest evaluation period, but in the context of the physical and biological processes that shape the terrestrial and aquatic landscapes, the response period was brief. Variation in the magnitude of response to timber harvest has been documented in long-term studies of timber harvest in old-growth forests (e.g., Hicks et al. 1991; Hartman et al. 1996; Hall 2008); however, temporally extended studies from second-growth forests are uncommon. Alternative study designs, including "space-for-time" substitutions (Pickett 1989) based on a sample of catchments with varying time since timber harvest, provide opportunities for examining changes associated with logging in second-growth forests over extended time periods (e.g., Connolly and Hall 1999). On the other hand, if such studies are focused on evaluating the effects of contemporary forest practices in second-growth forests, the population of sample catchments is limited to periods following the implementation of the altered methods.

Ultimately, the ability to make broad generalizations concerning the effects of timber harvest is difficult because response to disturbance (anthropogenically influenced or not) in aquatic systems is complex and context-dependent (Gresswell 1999). The geological and geomorphological characteristics of the catchment, biological assemblage of both the terrestrial and aquatic systems, and the disturbance history of the catchment influence the response to new perturbations, in terms of both intensity and temporal extent (Frissell et al. 1997). Although effects of logging per se are generally direct and immediate (i.e., pulsed disturbance; Yount and Niemi 1990), effects associated with the ancillary infrastructure associated with timber harvest (e.g., logging roads and landings) can be sustained over extended periods (i.e., press disturbance; Yount and Niemi 1990). Furthermore, effects are modified by the size of the harvest, yarding techniques, and intensity, amount, and timing of postharvest precipitation events (Hartman et al. 1987; Gresswell 2005). Implementation of best management practices arising from results of research on logging systems, reforestation, and riparian management are intended to reduce production and transport of materials and energy into the stream channel (Ice 2004; Ice et al. 2010), and the application of contemporary timber harvest techniques and emerging alternatives requires continued evaluation.

Perhaps the most important result from the current study was the lack of response noted for all but one of the biological characteristics being monitored; however, this result is not unique for timber harvest in second-growth forests under contemporary forest practices. For example, De Groot et al. (2007) did not find any statistically significant effects of second-growth logging on summer or winter relative abundance or condition of coastal cutthroat trout. Their paired watershed study of headwater streams also failed to identify any significant changes in instream physical habitat associated with logging. Although both of these studies had limited postlogging monitoring (≤4 years), results are strikingly similar. In a meta-analysis of 37 studies on the effects of logging on summertime salmonid density, biomass, and habitat (large wood and pool size and number), Mellina and Hinch (2009) reported that within the time frame of the studies included in their analysis (1-100 years), salmonid populations were generally not affected (or affected positively) if stream cleaning did not occur. This practice of removing wood from stream channels was common in the Pacific Northwest portion of North America from the 1950s through the 1970s, but rarely occurred after 1985 (Mellina and Hinch 2009; Roni et al. 2015).

The increase in late-summer biomass (g·m⁻²) of age-1+ coastal cutthroat trout in SFHC tributaries following logging in fishless headwaters of SFHC occurred as both an absolute increase in biomass from pretreatment values in SFHC tributaries and an increase relative to biomass in tributaries in the unharvested NFHC catchment (Fig. 2). The lack of other biological responses, however, confounds efforts to determine causal mechanisms. Moreover, production is directly linked to density, mean size, condition, and survival, but none of these variables changed significantly following the logging treatment.

Increases in salmonid production have been reported for headwater populations of coastal cutthroat trout and rainbow trout following the removal of riparian vegetation in other secondgrowth systems (Murphy and Hall 1981; Wilzbach et al. 1986; Wilzbach et al. 2005). In these cases, removal of the riparian forest canopy can stimulate primary and secondary production and subsequent increases in salmonid biomass if increased light does not result in excessive water temperatures and if other detrimental effects of logging (e.g., wood removal, increased sedimentation, and loss of pools) are avoided (Murphy and Hall 1981; Mellina and Hinch 2009). It appears that in many cases light limitation may be more important than nutrient constraints in small headwater streams (Wilzbach et al. 2005).

Unfortunately, changes in growth of coastal cutthroat trout in tributaries could not be assessed in the current study because sample sizes were insufficient; however, growth is directly related to production, and statistically significant changes in $NO_3 + NO_2$ in all but one of the treated tributaries (Meininger 2011) suggest that increase nutrients may have been a factor in the observed change. Furthermore, higher base discharge may have also interacted with increased light and nutrient availability to increase secondary production in fishless headwaters and subsequently increase production of downstream salmonids (Fuchs et al. 2003; Danehy et al. 2007; Richardson and Danehy 2007). Fishless headwaters transport invertebrate prey into downstream fish-bearing reaches (Wipfli et al. 2007) and boost fish growth and abundance in food-limited streams (Boss and Richardson 2002; Wipfli and Gregovich 2002). Following logging, benthic invertebrate density, and chironomid density in particular, increased in fishless SFHC tributaries when compared with unharvested NFHC headwaters (J.L. Li and W.J. Gerth, Oregon State University, Corvallis, Oregon, USA, unpublished data). On the other hand, changes in mean condition and mean and 90th percentile of fish size of age-1+ coastal cutthroat trout in SFHC tributaries were not statistically significant, and therefore, it is difficult to infer that changes in growth alone could have resulted in statistically significant increases in production. In addition, increases in base flow may not have positively affected growth because periods of fastest growth of coastal cutthroat trout are in late winter and early spring prior to occurrence leaf-out of deciduous trees and shrubs (Connolly 1996)

Survival of coastal cutthroat trout was commonly higher at the catchment level than at the tributary level in preharvest and postharvest periods, and slight increases in survival during postharvest periods were not statistically significant at either spatial scale. Previous research in Hinkle Creek suggested that survival of coastal cutthroat trout was spatially and temporally dynamic, but variation was greater temporally (i.e., seasons and years) than spatially (i.e., within and among catchments; Berger and Gresswell 2009). In fact, survival was lowest and least variable in late autumn (mid-September - mid-December) when stream discharge was typically low, and low discharge appeared to be the most important constraint to survival (Berger and Gresswell 2009). These observations may partially explain somewhat higher survival at the catchment scale in the current study, because latesummer flows are generally greater in the mainstem reaches than in tributaries. Slightly, but not statistically significant, increased survival following timber harvest in the fishless headwaters could be related to increased base flow documented in SFHC during the postharvest period (Surfleet and Skaugset 2013). Indeed, it is possible that minor changes in survival, combined with small, but nonsignificant, increases in density, length, and (or) condition of age-1+ trout cumulatively produced the observed significant response in biomass.

Implications for forest management

The Hinkle Creek paired catchment study was designed to evaluate acute effects of contemporary forest management practices on fish in headwater streams. The first phase of the study, described here, evaluated the effects of stream-adjacent logging in fishless headwaters on downstream fish populations. The only substantive response of the fish populations to forest harvest in the fishless headwaters of Hinkle Creek in the 3-year period immediately after logging was a statistically significant increase in late-summer biomass (g·m⁻²) of age-1+ coastal cutthroat trout in SFHC tributaries. Concomitantly, unique aspects of the harvest treatment and spatial and temporal settings are important for understanding the short-term salmonid population response, or lack thereof, that we observed. For example, forest harvest in Hinkle Creek was accompanied by the significant increases in sedimentation, but changes did not cause declines in population characteristics of salmonids that have been reported in other studies (Holtby 1988; Scrivener and Brownlee 1989; Hartman et al. 1996). Apparently moderate to high channel gradients and confined stream channels of the Hinkle Creek stream network decrease the probability that substantial amounts of sediment produced from logging would be stored in the study area (Mellina and Hinch 2009). Furthermore, none of the changes in the other physical habitat characteristics that we measured (i.e., substrate, large wood, wetted channel in pool habitat, pool maximum depth, and riffle–rapid maximum depth) were statistically significant.

Here we have attempted to provide substantial detail concerning the specific logging treatment used to harvest timber in SFHC. Indeed, these details are rarely included in ecological studies evaluating the effects of timber harvest on aquatic systems. The assumption implicit in this more common approach is that all timber harvests are the same, and results have broad application. In fact, this lack of detail is common in many studies focused on effects of disturbance (e.g., wildfire, floods, and debris flows). In contrast, it has become increasingly apparent that specific details (context) concerning intensity, severity, and duration substantially influence the outcome of such events, both in the short term and over time (Gresswell 1999). Contemporary timber harvest of second-growth forests is much different than initial entries into old-growth stands (De Groot et al. 2007); not only is the biological context different, but the infrastructure necessary for timber harvest (e.g., roads) that is often the primary cause of ecological change in streams, especially in the long term, has already been established. Furthermore, research over the past 40 years has provided new approaches to, and technology for, timber harvest that are less invasive (Hairston-Strang et al. 2008).

Timber harvest of second-growth forests <100 years old is much different from the initial harvest of old-growth forests >300 years old, especially using modern technology under contemporary management constraints. Overall, very few changes in habitat or biological parameters were detected in conjunction with streamadjacent logging in the headwaters of Hinkle Creek. Apparently, contemporary forest practices rules provided adequate shortterm protection from acute negative effects to the downstream fish community in this experimental setting. In fact, there was an increase in biomass of age-1+ coastal cutthroat trout at the tributary scale during the 3-year postharvest evaluation. Although these findings are probably not applicable to logging in oldgrowth forests (De Groot et al. 2007), they provide one example of environmentally compatible commercial logging in a regenerated forest setting.

Acknowledgements

We thank J. Dunham, A. Simmons, A. Muldoon, and more than 30 seasonal research technicians for their valuable field assistance. Funding was provided by the Watershed Research Cooperative; US Geological Survey, Forest and Rangeland Ecosystem Science Center; Roseburg Forest Products; and the Douglas County (Oregon) Commission. Fish collections were authorized by Oregon Department of Fish and Wildlife taking permits (OR2001-127, OR2002-041, OR2003-814, OR2004-1579, OR2005-2198, OR2006-2923, OR2007-3578, and OR2008-4371) and by Oregon State University Institutional Animal Care and Use Committee (ACUP 2552, ACUP 3048, and ACUP 3504). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

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