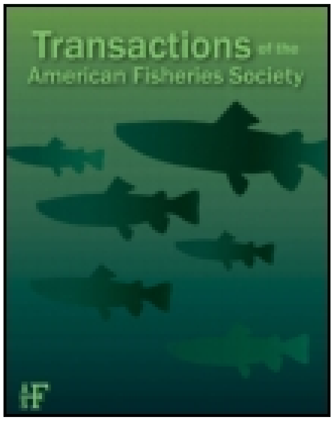

Transactions of the American Fisheries Society
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/utaf20

Documentation of Unusual, Fall Spawning by Coastal Cutthroat Trout in the Elwha River System, Washington

John R. McMillan[a], George R. Pess[a], Michael L. McHenry[b], Raymond Moses[b] & Thomas P. Quinn[c]

[a] National Oceanic and Atmospheric Administration, Northwest Fisheries Science Center, 2725 Montlake Boulevard East, Seattle, Washington 98112, USA

[b] Lower Elwha Klallam Tribe, Fisheries Department, 51 Hatchery Road, Port Angeles, Washington 98363, USA

[c] School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, Washington 98195, USA

Published online: 30 Oct 2014.

To cite this article: John R. McMillan, George R. Pess, Michael L. McHenry, Raymond Moses & Thomas P. Quinn (2014) Documentation of Unusual, Fall Spawning by Coastal Cutthroat Trout in the Elwha River System, Washington, Transactions of the American Fisheries Society, 143:6, 1605-1611, DOI: 10.1080/00028487.2014.963255

To link to this article: http://dx.doi.org/10.1080/00028487.2014.963255

Transactions of the American Fisheries Society 143:1605–1611, 2014

ISSN: 0002-8487 print / 1548-8659 online
DOI: 10.1080/00028487.2014.963255

NOTE

Documentation of Unusual, Fall Spawning by Coastal Cutthroat Trout in the Elwha River System, Washington

John R. McMillan* and George R. Pess
National Oceanic and Atmospheric Administration, Northwest Fisheries Science Center, 2725 Montlake Boulevard East, Seattle, Washington 98112, USA

Michael L. McHenry and Raymond Moses
Lower Elwha Klallam Tribe, Fisheries Department, 51 Hatchery Road, Port Angeles, Washington 98363, USA

Thomas P. Quinn
School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, Washington 98195, USA

Abstract
The timing of breeding is a key trait, reflecting selective forces acting on the adults and offspring in the population, contributing to reproductive isolation, and affecting the population's success during rapid environmental change. Salmon and trout populations vary greatly in the peak and range of breeding dates, and timing is a defining trait for salmonid populations. This study reports the occurrence and details of spawning by Coastal Cutthroat Trout *Oncorhynchus clarkii clarkii* in Indian Creek in the Elwha River, Washington, in October and November. This is unusually early in the season for this characteristically spring-spawning species and is much earlier than conspecifics elsewhere in the river system and the region. We hypothesize that the stream's low gradient and lake-dampened hydrologic regime reduced the depth of gravel scouring in the fall, and thus permitted the evolution of such an early breeding date by these small-bodied (ca. 20–35 cm) fish. The exclusion of otherwise sympatric, fall-spawning Coho Salmon *O. kisutch* for the past century from the habitat by Elwha Dam may also have contributed to this adaptation, and the recolonization by the larger and later-spawning Coho Salmon may have affected the Coastal Cutthroat Trout through redd disturbance.

The timing of breeding by animals is a very important feature of their biology, as it reflects ecological pressures on both parents and offspring (Krebs and Davies 1997). The great majority of freshwater fishes in the Northern Hemisphere breed in spring. A short larval period follows, allowing juveniles to feed when temperatures and food availability favor growth (Wootton 1984). Salmonids are among the few fishes in this region that breed in the fall, and they compensate for this with large eggs and protracted embryonic development so that juveniles emerge to feed in spring (Wootton 1984). Fall spawning is characteristic of the genera *Salmo* (Jonsson and Jonsson 2011) and *Salvelinus* (Balon 1980), and the semelparous Pacific salmon of the genus *Oncorhynchus* (Quinn 2005). In this case, fall is somewhat loosely defined, because Sockeye Salmon *O. nerka* begin spawning in mid to late July in southwestern Alaska (Burgner 1991), Coho Salmon *O. kisutch* can spawn as early as October and as late as March (Sandercock 1991), and Chum Salmon *O. keta* can spawn from July to March (Salo 1991). Unlike other salmonids, Pacific trout of the genus *Oncorhynchus*, including Cutthroat Trout *O. clarkii* and Rainbow Trout *O. mykiss* typically spawn in spring on the descending limb of the hydrograph as water temperatures increase (Behnke 1992). However, there are exceptions among native Rainbow Trout populations (Shapovalov and Taft 1954; Buchanan et al. 1990; Hemmingsen and Buchanan 1993) and introduced populations (e.g., Van Velson 1974). These exceptions are often associated with unusual physical features, such as the Rainbow Trout spawning in late November and early December

*Corresponding author: john.mcmillan@noaa.gov
Received April 24, 2014; accepted August 27, 2014

in the geothermally heated waters of the Firehole River in Yellowstone National Park, Wyoming (Kaya 1977).

In Oregon, Washington, and southern British Columbia, Coastal Cutthroat Trout *O. clarkii clarkii* generally spawn from mid-December through June with a peak occurring typically in February, and emerge as fry in spring (Trotter 1989). Spawning occurs later (April and May) in colder streams in Alaska (e.g., Armstrong 1971; Saiget et al. 2007). Given these general patterns, preliminary observations (M. L. McHenry, unpublished data) of what appeared to be spawning Coastal Cutthroat Trout (hereafter, Cutthroat Trout, as no other subspecies is found in this basin) from mid-October through November in the upper reaches of Indian Creek, a tributary of the Elwha River in the Olympic Peninsula of Washington, seemed sufficiently unusual to merit further investigation. Montgomery et al. (1999) hypothesized that high flows select against fall spawning in such small-bodied salmonids, so we assessed aspects of the habitat, flow, and thermal regimes that might permit or select for fall spawning. Moreover, the habitat where these trout spawn had been inaccessible to anadromous fishes since the construction of the Elwha Dam without fish passage facilities in 1913 (Duda et al. 2008). The dam was removed in fall 2011 and anadromous fishes are colonizing the habitat, including larger-bodied Coho Salmon that may compete with the Cutthroat Trout for spawning habitat as adults and compete for food and space as juveniles.

The selective advantage of early spawning by Cutthroat Trout may be altered by colonizing Coho Salmon through redd superimposition (Hayes 1987; Essington et al. 1998). Hence, it seemed particularly important to document the spawning timing of the trout and salmon before the anticipated numerical and spatial expansion of salmon. Accordingly, the purposes of this investigation were to (1) document the spawning by Cutthroat Trout in this system, including the dates of redd construction and redd site characteristics, (2) determine whether stream flow and temperature in the spawning reach differ from the lower part of the creek where Cutthroat Trout do not spawn in the fall, and (3) document the spatial and temporal extent of spawning by Coho Salmon. Such information may identify factors that influence the timing of breeding by Cutthroat Trout in this system, provide insights into future interactions with colonizing Coho Salmon, and guide investigation of Cutthroat Trout reproductive timing elsewhere.

METHODS

Study site.—Indian Creek is a second-order stream (wetted width, 5–13 m) originating at the outlet of Lake Sutherland (elevation, 160 m), and flowing 9.1 km west into the

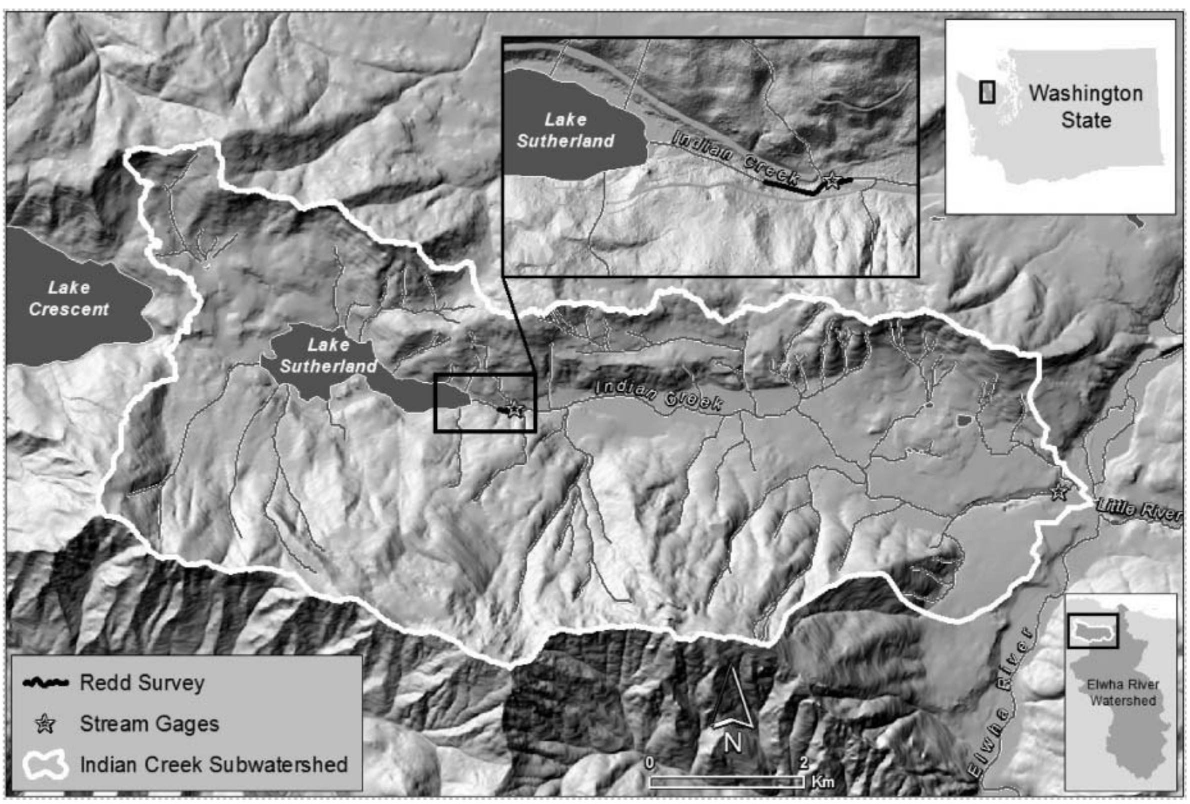

FIGURE 1. Indian Creek within the Elwha River drainage, Olympic Peninsula, Washington, and the location of the survey reach where the Coastal Cutthroat Trout redds were observed.

TABLE 1. The locations of upper and lower Indian Creek and physical attributes relevant to spawning Coastal Cutthroat Trout, including channel gradient and mean width, depth, water temperature, and stream flow for the entire year and, in parentheses, during the fall spawning period, and CV of flow during the fall spawning period.

Attribute	Upper Indian Creek	Lower Indian Creek
Location (rkm)	7.1–9.1	0.0–7.1
Channel gradient (%) (SD)	0.4 (0.01)	1.7 (1.1)
Mean wetted width (m) (SD)	6.1 (1.6)	10.4 (3.1)
Mean depth (m) (SD)	0.70 (0.22)	0.40 (0.13)
Mean water temperature (°C) for entire year (October–November)	12.3 (10.3)	9.0 (8.0)
Mean stream flow (m^3/s) for entire year (October–November)	0.56 (0.36)	1.61 (1.56)
CV of stream flow in October–November	0.18	0.72

Elwha River at river kilometer (rkm) 12.7 (elevation 65 m) (Figure 1). Lake Sutherland is a small (area, 146 ha; mean depth, 17.4 m) lake that drains 21 km^2 (Hiss and Wunderlich 1994). Groundwater inputs are the dominant source of water for Lake Sutherland, and Fall's Creek, the principle source of surface water, is very small. Consequently, Indian Creek has a slow and rather steady flow regime.

Indian Creek is unusual in that the upper 2.0 km below the lake are very different from the lower 7.1 km (Table 1), and it is the only stream in the Elwha River drainage known to support an abundant population of Cutthroat Trout, which is otherwise dominated by Rainbow Trout (Brenkman et al. 2008). Indian Creek has a very low gradient below the lake for 2.0 km (Table 1) as evidenced by its small substrate and lack of pool and riffle formations. In this reach there is dense instream and overhead cover from standing and fallen trees that protects rearing and spawning salmonids, but also greatly hinders surveying. Moving downstream, the creek gradually steepens, becoming more representative of typical mountain streams with alternating pools, riffles, and rapids. The fish population in the upper 2.0 km of Indian Creek is dominated by Cutthroat Trout, although within 400 m of the lake there are also a few Redside Shiners *Richardsonius balteatus* and spawning kokanee (lacustrine Sockeye Salmon). The latter species are absent in the lower 7.0 km of the creek, where the population is a mixture of Cutthroat Trout and resident Rainbow Trout. During and following the removal of the former Elwha Dam in 2011–2013, anadromous Coho Salmon, Chinook Salmon *O. tshawytscha*, and steelhead (anadromous Rainbow Trout) were reintroduced by comanagers to Indian Creek, but Chinook Salmon and steelhead have so far only been observed spawning in the lower 4.5 km of the creek (J. R. McMillan, unpublished data). Given the differences in habitat features and salmonid populations, we delineated the stream into two sections: upper (rkm 7.1–9.1) and lower (rkm 0.0–7.1) Indian Creek (Figure 1; Table 1).

Redd counts, particle size sampling, and observations of spawning Cutthroat Trout.—We conducted weekly surveys by foot and snorkeling in 2012 and 2013 to determine the temporal and spatial extent of Cutthroat Trout spawning. Weekly redd surveys were conducted on 14 dates in 2012 and 13 dates in 2013, from October through early January, and monthly surveys thereafter in 2012. We surveyed from rkm 7.1–8.9, the bottom of which is 7.1 km upstream from its confluence with the Elwha River and the upper part of which is 225 m downstream from the lake's outlet (Figure 1). After several initial surveys it was clear that nearly all Cutthroat Trout spawning occurred from rkm 8.2 to rkm 8.9, so we selected a representative 300-m reach to avoid damaging the ubiquitous but small redds. Redds, identified as disturbed areas in the stream bed where gravels were overturned to form the oval depression and tail spill characteristic of salmonids, were counted, and the locations were recorded on a hand-held GPS to prevent double counting in subsequent surveys. In 2012 we measured the surface area of 30 redds (length and width to nearest centimeter) and quantified the substrate size in the redd pit and the surrounding disturbed area by measuring the median axis on 100 randomly selected pebbles to the nearest millimeter (Wolman 1954). Substrate size was summarized as D50 (size of the 50th percentile). We tested for linear correlation between redd surface area and D50 substrate size using a Pearson product-moment correlation.

We also conducted weekly snorkel surveys to estimate the abundance and body length of male and female Cutthroat Trout and to record any reproductive behaviors (e.g., females digging redds, males courting and competing for access to females). We also counted Coho Salmon redds in 2012 and 2013 from rkm 7.1 to rkm 8.9 and in lower Indian Creek from rkm 0.0 to rkm 7.1. In the latter section we also counted Cutthroat Trout and smaller-sized Cutthroat Trout redds if they were present.

Stream flow, temperature, and habitat.—We obtained daily discharge (m^3/s) and water temperature data in upper and lower Indian Creek to test the hypothesis that fall spawning is associated with a more moderate flow regime and to allow estimation of embryo incubation rates. The upper Indian Creek gauge (Washington State Department of Ecology Gauge ID 18Q240) was at rkm 8.6, within the reach where the Cutthroat Trout spawned in the fall, and the lower Indian Creek gauge (Washington State Department of Ecology Gauge ID 18C070) was at rkm 1.4, where they have not been observed spawning in the fall. Continuous stream flow and water temperature data were not available, so we used the most recent data (water year 2009–2010 for stream flow and 2011–2012 for water temperature). Only weekly discharge measurements were available for the upper Indian Creek gauge, whereas daily measurements of mean discharge were obtained at the lower Indian Creek gauge.

RESULTS

Timing of Redd Excavation and Spawning Activity

We counted 104 Cutthroat Trout redds in 2012 and 138 in 2013, all of which were in upper Indian Creek. We did not enumerate any Cutthroat Trout redds in lower Indian Creek while conducting Coho Salmon redd surveys. The spawning period in upper Indian Creek was restricted to the fall, lasting approximately 7 weeks in 2012 (October 20–December 5) and 8 weeks in 2013 (October 4–December 2; Figure 2a). In 2012 most redds were constructed within a 2-week period in mid-November, but spawning was even earlier in 2013, occurring primarily in mid-October (Figure 2a). No redds were counted during winter–spring of 2012 or 2013. The downstream extent of spawning by Cutthroat Trout mostly ended at the head of a large beaver pond at rkm 8.2 but continued sporadically downstream to rkm 7.3.

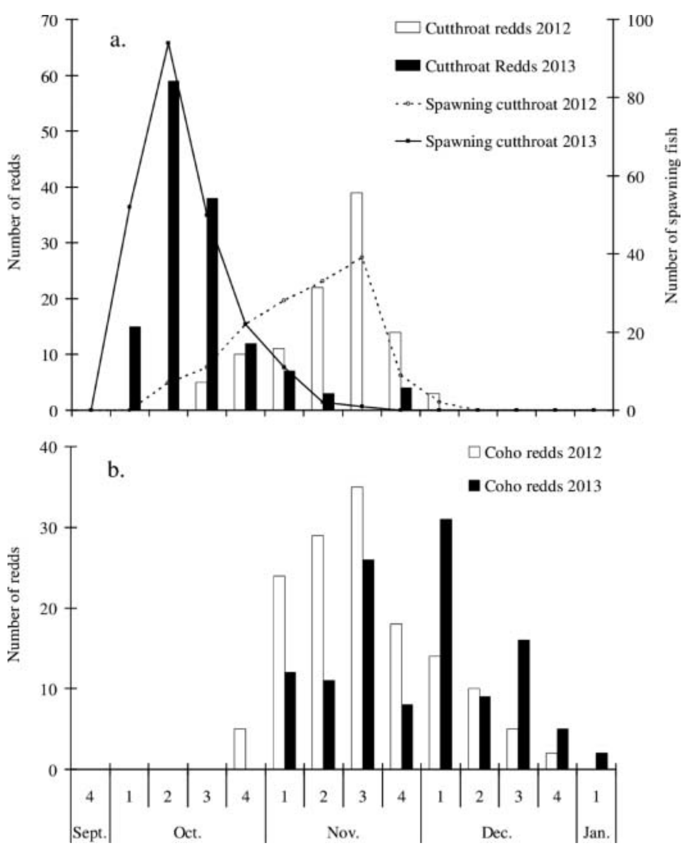

FIGURE 2. Timing of redd excavation and spawning activity by week (1–4) and month for (**a**) Coastal Cutthroat Trout in 300 m of upper Indian Creek by week (1–4) and month for 2012 and 2013, and (**b**) the number of Coho Salmon redds counted in Indian Creek throughout the entire drainage in 2012 and 2013.

Cutthroat Trout displaying reproductive activity were abundant (141 in 2012 and 232 in 2013). The peak counts tended to match the timing of redd counts (Figure 2a). In most cases, a single female occupied a redd and was flanked by several (up to 12) males. Total length of spawners was estimated visually as 100–375 mm. Of those, 58 (41%) in 2012 and 85 (37%) in 2013 were apparently females based on their spawning behavior, body morphology (e.g., short blunt nose and head), and other features (e.g., worn edges on the tails, distended ovipositors). The largest fish were apparently females (200–375 mm); males were mostly between 100 and 250 mm with a few larger than 300 mm.

We counted 142 Coho Salmon redds in Indian Creek in 2012 and another 120 redds in 2013. Only three redds were enumerated in an area that directly overlapped with the dense congregation of spawning Cutthroat Trout, but 29 redds were in the reach immediately downstream from the beaver pond at rkm 8.2 where a few Cutthroat Trout spawned. Coho Salmon spawning ranged from November to January and overlapped with Cutthroat Trout, though the trout began spawning before the salmon (Figure 2b). Peak Coho Salmon spawning occurred during the first 3 weeks of November in 2012, and during late November and early December in 2013 (Figure 2b).

Redd Size and Redd Particle Size

The mean surface area of 30 measured Cutthroat Trout redds was 664 cm^2 (SD = 419; range, 225–1,560 cm^2). Particle size distributions within the redd pits and surrounding disturbed areas also varied but were generally small (D50 range, 8–19 mm; mean = 11.5, SD = 2.8; maximum particle size range, 27–55 mm). The minimum particle size was less than 2 mm in all but two redds, where it was 3 mm. There was a strong positive correlation between redd substrate D50 and redd size (Pearson's correlation coefficient = 0.88, df = 29, $P < 0.0001$).

Stream Flow and Water Temperature

The upper and lower sections of Indian Creek differed in water temperature and flow regimes (Figure 3a, b). Upper Indian Creek was warmer than lower Indian Creek (and sometimes substantially so) in the spring, summer, and fall but was similar or colder in winter (Figure 3a; Table 1). During the fall Cutthroat Trout spawning period, upper Indian Creek ranged from 8.0°C to 13.0°C, compared with 6.5–9.0°C in lower Indian Creek (Figure 3a; Table 1). Peak flows were greatly reduced and occurred later in the year in upper Indian Creek compared with lower Indian Creek, particularly during

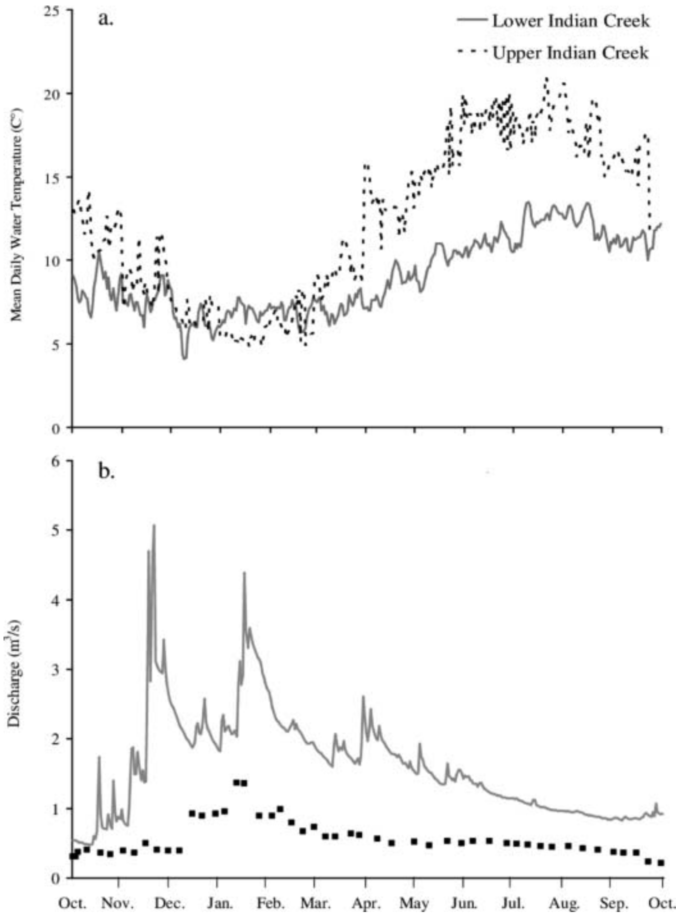

FIGURE 3. Annual patterns in daily mean (**a**) water temperature (°C) in 2011–2012 and (**b**) stream flow (m^3/s) in lower (gray line) and upper (black squares) Indian Creek in 2009–2010. Stream flow measurements were taken weekly in upper Indian Creek and hourly in lower Indian Creek.

the spawning season (Figure 3b; Table 1). For example, flows in upper Indian Creek ranged only from 0.34 to 0.40 m^3/s during the spawning season and peaked at only 1.39 m^3/s in January (Figure 3b); the CV (SD/mean) in flow was 0.18 (Table 1). In comparison, flows ranged from 0.68 to 5.09 m^3/s during the same period in lower Indian Creek (Figure 3b) and the CV in flow was 0.72 (Table 1).

DISCUSSION

Our major finding was the documentation of an unusually early and brief spawning period by Coastal Cutthroat Trout in Indian Creek, which contrasts with the more protracted spring spawning of most Pacific trout species (Behnke 1992). The timing of Cutthroat Trout spawning in Indian Creek is several months prior to the average of February through May in most Pacific Northwest populations (Trotter 1989), though Cutthroat Trout in nearby Lake Crescent also begin spawning early but over a much more protracted period (Samuel Brenkman, U.S. National Park Service, personal communication). Breeding date can evolve quickly under natural (Quinn et al. 2000) and artificial selection (Siitonen and Gall 1989; Sato et al. 2000; Quinn et al. 2002), and some streams have early and late spawning runs of salmon, sometimes spatially separated (Tallman and Healey 1991) and sometimes sympatric (Gharrett et al. 2013). In Indian Creek, the fall spawning is restricted to the upper section near the lake, as only spring spawning has been seen in the lower section during steelhead redd counts (McMillan, unpublished data). Such divergence in timing over a small spatial scale is especially remarkable because the shift is not merely earlier within the spring season but from spring to fall, reversing the normal trout cues for reproduction with increasing temperature and day length.

The Cutthroat Trout in Indian Creek fell within the range of body sizes previously reported (Trotter 2008). However, the range of substrate particle sizes (2–55 mm) and median particle size in our study were smaller or at the lower end of substrate size ranges reported previously for Coastal Cutthroat Trout redds (16–64 mm: Hooper 1973; 6–102 mm: Hunter 1973; 20–50 mm: June 1981) and for larger-bodied subspecies of interior Cutthroat Trout (60–100 mm: Cope 1957; Hickman and Raleigh 1982; Varley and Gresswell 1988; Thurow and King 1994). The substrate size in redds in our study reflects the smaller substrates present in upper Indian Creek compared with those in lower Indian Creek and other tributaries in the Elwha River basin (G. R. Pess, unpublished data).

The number of small-bodied Cutthroat Trout spawning early in the season in the same reach in multiple years suggests that this is a viable, discrete population. We hypothesize the fall spawning may occur here for several reasons. First, the flow regime and gravel scour that typically preclude fall spawning by small-bodied salmonids (Montgomery et al. 1999) must be relaxed; it is unlikely that the small females in Indian Creek could dig redds deep enough to avoid scour during the higher flows of fall and winter that characterize many coastal streams. For example, Kennedy Creek, in southern Puget Sound, is dominated by fall rains and commonly scours to depths of 10–20 cm (Montgomery et al. 1996; Schuett-Hames et al. 2000). Given the general relationship between female length and egg burial depth (Quinn 2005), a 300-mm female trout would bury her eggs only 8–10 cm deep, exposing embryos to scouring flow events, but large-bodied Chum Salmon successfully spawn in November. In upper Indian Creek, however, the peak stream flows were delayed and dramatically reduced, which presumably also reduced scour, compared with lower Indian Creek. We cannot be sure why this happens in upper Indian Creek, but the extensive groundwater and the lake may combine to flatten the fall and winter hydrograph.

The moderate temperature regime in upper Indian Creek likely also reflects proximity to the lake, and it too may affect spawning timing in this system. Temperatures were warmer during the fall spawning period in upper Indian Creek and also became warmer earlier in the spring than in lower Indian Creek, and warmer water accelerates embryonic development. Based on a temperature (8.0°C), which is similar to that of upper Indian Creek after spawning in early October, we predicted Cutthroat Trout fry would emerge after 79 d, in mid-December (estimated from data in Merriman 1935; Murray and McPhail 1988).

In addition to the mild regimes of flow and temperature, we hypothesize that the unusually early timing of spawning by Cutthroat Trout in upper Indian Creek reflects, in part, the absence of competition with larger, anadromous Coho Salmon. Coho Salmon have been excluded from the stream for almost 100 years by the Elwha Dam (Brenkman et al. 2008), but since the dam has been removed they are now present and likely to become increasingly abundant. Their spawning timing overlapped with, but was generally later than, that of the Cutthroat Trout. Competition for redd sites and redd superimposition by the larger-bodied salmon may select against early spawning by Cutthroat Trout in the reach studied here, as the spawning trout used much of the suitable stream bottom. Such interspecific competition affected the survival and dynamics of Brown Trout *Salmo trutta* and Rainbow Trout in New Zealand (Hayes 1987), and nonnative Chinook Salmon seem to have had a negative effect on native Atlantic Salmon *S. salar* in Lake Ontario tributaries (Scott et al. 2003). The effects of Coho Salmon on Cutthroat Trout could be magnified if the salmon selectively re-used trout redd sites, as was reported for Brook Trout *Salvelinus fontinalis* and Brown Trout in Minnesota (Essington et al. 1998).

Increased overlap in spawning locations could also increase interactions among juveniles, and larger Coho Salmon tend to dominate Cutthroat Trout (Sabo and Pauley 1997). However, the earlier spawning by trout in upper Indian Creek could reverse the normal pattern in which salmon emerge earlier and achieve a larger size at age. At an average incubation temperature of 8.0°C, Coho Salmon would require 109 d to emerge after spawning (Murray and McPhail 1988). Combined with the later spawning date, the Coho Salmon fry would emerge in mid-March compared with mid-December for the trout, reversing the normal pattern in these species. Earlier emergence by the Cutthroat Trout may allow them to grow and establish territories (Rhodes and Quinn 1998) before Coho Salmon emerge and thus compensate somewhat for their smaller initial size, though growth opportunities during winter are likely limited.

In conclusion, we documented unusually early spawning by Coastal Cutthroat Trout in one small reach of a tributary to the Elwha River. We were not able to determine the specific causes, but a strong candidate is the local hydrology that delays and truncates the fall peak flow events. The evolution of this unusual timing of reproduction could also be related to the absence of competition with fall-spawning Coho Salmon. It is difficult to predict whether the breeding time of Cutthroat Trout will persist as Coho Salmon abundance increases following dam removal, but the outcome will likely depend on the extent of spatial and temporal overlap during breeding and rearing. In this context, understanding dam removal is as much about documenting changes in upstream populations as it is about documenting the recolonization of anadromous salmonids from below the dam. Finally, the physical environment of upper Indian Creek is unusual but probably not unique, and other Coastal Cutthroat Trout populations spawn in small streams below beaver dams or have other features to moderate the thermal and flow regimes. If these populations spawn above barriers to anadromous salmon, they might also exhibit early spawning. Information on such populations might provide a useful test of the hypotheses underlying the present study.

ACKNOWLEDGMENTS

We thank Wilson Wells, Lower Elwha Klallam Tribe (LEKT), for his assistance in field work, Randall McCoy, LEKT, for his GIS expertise in drafting the Indian Creek map, Sam Brenkman, Olympic National Park, for sharing his knowledge of Cutthroat Trout, and Polly Hicks, NOAA, Northwest Fisheries Science Center (NWFSC), for support. Funding was partly provided through a grant to Thomas Quinn from Washington Sea Grant, University of Washington, pursuant to NOAA Award NA10OAR4170075, Project R/LME-7. We also thank Sarah Morley, Todd Bennett, and Phil Roni at NOAA–NWFSC and the anonymous reviewers and the journal's editorial staff for reviews and suggestions that improved the manuscript. The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its subagencies.

REFERENCES

Armstrong, R. H. 1971. Age, food, and migration of sea-run Cutthroat Trout, *Salmo clarki*, at Eva Lake, southeastern Alaska. Transactions of the American Fisheries Society 100:302–306.

Balon, E. K. 1980. Charrs: salmonid fishes of the genus *Salvelinus*. Dr W. Junk, The Hague, The Netherlands.

Behnke, R. J. 1992. Native trout of western North America. American Fisheries Society, Bethesda, Maryland.

Brenkman, S. J., G. R. Pess, C. E. Torgersen, K. K. Kloehn, and J. J. Duda. 2008. Predicting recolonization patterns and interactions between potamodromous and anadromous salmonids in response to dam removal in the Elwha River, Washington State, USA. Northwest Science 82(Special Issue):91–106.

Buchanan, D. V., A. R. Hemmingsen, D. L. Bottom, P. J. Howell, R. A. French, and K. P. Currents. 1990. Native trout project. Oregon Department of Fish and Wildlife, Fish Research Project F-136-R, Portland.

Burgner, R. L. 1991. Life history of Sockeye Salmon (*Oncorhynchus nerka*). Pages 1–117 *in* C. Groot and L. Margolis, editors. Pacific salmon life histories. University of British Columbia Press, Vancouver.

Cope, O. B. 1957. The choices of spawning sites by Cutthroat Trout. Proceedings of the Utah Academy of Sciences, Arts, and Letters 34:73–79.

Duda, J. J., J. E. Freilich, and E. G. Schreiner. 2008. Baseline studies in the Elwha River ecosystem prior to dam removal: introduction to the special issue. Northwest Science 82(Special Issue):1–12.

Essington, T. E., P. W. Sorensen, and D. G. Paron. 1998. High rate of redd superimposition by Brook Trout (*Salvelinus fontinalis*) and Brown Trout (*Salmo trutta*) in a Minnesota stream cannot be explained by habitat availability alone. Canadian Journal of Fisheries and Aquatic Sciences 55:2310–2316.

Gharrett, A. J., J. Joyce, and W. W. Smoker. 2013. Fine-scale temporal adaptation within a salmonid population: mechanism and consequences. Molecular Ecology 22:4457–4469.

Hayes, J. W. 1987. Competition for spawning space between Brown (*Salmo trutta*) and Rainbow trout (*S. gairdneri*) in a lake inlet tributary, New Zealand. Canadian Journal of Fisheries and Aquatic Sciences 44:40–47.

Hemmingsen, A. R., and D. V. Buchanan. 1993. Native trout project. Oregon Department of Fish and Wildlife, Fish Research Project F-136-R-6, Portland.

Hickman, T., and R. F. Raleigh. 1982. Habitat suitability index models: Cutthroat Trout. U.S. Fish and Wildlife Service, Habitat Evaluation Procedures Group, Western Energy and Land Use Team, Fort Collins, Colorado.

Hiss, J. M., and R. C. Wunderlich. 1994. Status of kokanee salmon (*Oncorhynchus nerka*) in the Lake Sutherland basin and prospects for Sockeye Salmon restoration. U.S. Fish and Wildlife Service, Olympia, Washington.

Hooper, D. R. 1973. Evaluation of the effects of flows on trout stream ecology. California Department of Engineering Research, Emeryville.

Hunter, J. W. 1973. A discussion of game fish in the State of Washington as related to water requirements. Prepared for Washington State Department of Ecology by the Washington State Game Department, Fishery Management Division, Olympia.

Jonsson, B., and N. Jonsson. 2011. Ecology of Atlantic Salmon and Brown Trout: habitat as a template for life histories. Springer, New York.

June, J. A. 1981. Life history and habitat utilization of Cutthroat Trout (*Salmo clarki*) in a headwater stream in the Olympic Peninsula, Washington. Master's thesis. University of Washington, Seattle.

Kaya, C. 1977. Reproductive biology of Rainbow and Brown trout in a geothermally heated stream: the Firehole River of Yellowstone National Park. Transactions of the American Fisheries Society 106:354–361.

Krebs, J. R., and N. B. Davies. 1997. Behavioural ecology: an evolutionary approach, 4th edition. Blackwell Scientific Publications Scientific Press, Oxford, UK.

Merriman, D. 1935. The effect of temperature on the development of the eggs and larvae of the Cut-throat Trout (*Salmo clarkii clarkii* Richardson). Journal of Experimental Biology 12:297–305.

Montgomery, D. R., E. M. Beamer, G. R. Pess, and T. P. Quinn. 1999. Channel type and salmon spawning distribution and abundance. Canadian Journal of Fisheries and Aquatic Sciences 56:377–387.

Montgomery, D. R., J. M. Buffington, N. P. Peterson, D. Schuett-Hames, and T. P. Quinn. 1996. Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. Canadian Journal of Fisheries and Aquatic Sciences 53:1061–1070.

Murray, C. B., and J. D. McPhail. 1988. Effect of incubation temperature on the development of five species of Pacific salmon (*Oncorhynchus*) embryos and alevins. Canadian Journal of Zoology 66:266–273.

Quinn, T. P. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press, Seattle.

Quinn, T. P., J. A. Peterson, V. Gallucci, W. K. Hershberger, and E. L. Brannon. 2002. Artificial selection and environmental change: countervailing factors affecting the timing of spawning by Coho and Chinook salmon. Transactions of the American Fisheries Society 131:591–598.

Quinn, T. P., M. J. Unwin, and M. T. Kinnison. 2000. Evolution of temporal isolation in the wild: genetic divergence in timing of migration and breeding by introduced Chinook Salmon populations. Evolution 54:1372–1385.

Rhodes, J. S., and T. P. Quinn. 1998. Factors affecting the outcome of territorial contests between hatchery and naturally reared Coho Salmon parr in the laboratory. Journal of Fish Biology 53:1220–1230.

Sabo, J. L., and G. B. Pauley. 1997. Competition between stream-dwelling Cutthroat Trout (*Oncorhynchus clarki*) and Coho Salmon (*Oncorhynchus kisutch*): effects of relative size and population origin. Canadian Journal of Fisheries and Aquatic Sciences 54:2609–2617.

Saiget, D. A., M. R. Sloat, and G. H. Reeves. 2007. Spawning and movement behavior of migratory coastal Cutthroat Trout on the western Copper River delta, Alaska. North American Journal of Fisheries Management 27:1029–1040.

Salo, E. O. 1991. Life history of Chum Salmon (*Oncorhynchus keta*). Pages 231–309 *in* C. Groot and L. Margolis, editors. Pacific salmon life histories. University of British Columbia Press, Vancouver.

Sandercock, F. K. 1991. Life history of Coho Salmon (*Oncorhynchus kisutch*). Pages 395–445 *in* C. Groot and L. Margolis, editors. Pacific salmon life histories. University of British Columbia Press, Vancouver.

Sato, H., A. Amagaya, M. Ube, N. Ono, and H. Kudo. 2000. Manipulating the timing of a Chum Salmon (*Oncorhynchus keta*) run using preserved sperm. North Pacific Anadromous Fish Commission Bulletin 2:353–357.

Schuett-Hames, D. E., N. P. Peterson, R. Conrad, and T. P. Quinn. 2000. Patterns of gravel scour and fill after spawning by Chum Salmon in a western Washington stream. North American Journal of Fisheries Management 20:610–617.

Scott, R. J., D. L. G. Noakes, F. W. H. Beamish, and L. M. Carl. 2003. Chinook Salmon impede Atlantic Salmon conservation in Lake Ontario. Ecology of Freshwater Fish 12:66–73.

Shapovalov, L., and A. C. Taft. 1954. The life histories of the steelhead Rainbow Trout (*Salmo gairdneri gairdneri*) and Silver Salmon (*Oncorhynchus kisutch*) with special reference to Waddell Creek, California, and recommendations regarding their management. California Department of Fish and Game Fish Bulletin 98.

Siitonen, L., and G. A. E. Gall. 1989. Response to selection for early spawn date in Rainbow Trout, *Salmo gairdneri*. Aquaculture 78:153–161.

Tallman, R. F., and M. C. Healey. 1991. Phenotypic differentiation in seasonal ecotypes of Chum Salmon, *Oncorhynchus keta*. Canadian Journal of Fisheries and Aquatic Sciences 48:661–671.

Thurow, R. F., and J. G. King. 1994. Attributes of Yellowstone Cutthroat Trout redds in a tributary of the Snake River, Idaho. Transactions of the American Fisheries Society 123:37–50.

Trotter, P. C. 1989. Coastal Cutthroat Trout: a life history compendium. Transactions of the American Fisheries Society 118:463–473.

Trotter, P. C. 2008. Cutthroat: native trout of the west. University of California Press, Berkeley.

Van Velson, R. C. 1974. Self-sustaining Rainbow Trout (*Salmo gairdneri*) population in McConaughy Reservoir, Nebraska. Transactions of the American Fisheries Society 103:59–64.

Varley, J. D., and R. E. Gresswell. 1988. Ecology, status, and management of the Yellowstone Cutthroat Trout. Pages 13–24 *in* R. E. Gresswell, editor. Status and management of interior stocks of Cutthroat Trout. American Fisheries Society, Symposium 4, Bethesda, Maryland.

Wolman, M. G. 1954. A method of sampling coarse river-bed material. American Geophysical Union Transactions 35:951–956.

Wootton, R. J. 1984. Introduction: strategies and tactics in fish reproduction. Pages 1–12 *in* G. W. Potts and R. J. Wootton, editors. Fish reproduction—strategies and tactics. Academic Press, London.