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ARTICLE

Coastal Cutthroat Trout Redd Counts Impacted by Natural Water Supply Variations

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Abstract
During 2001–2003, we counted redds of Coastal Cutthroat Trout *Oncorhynchus clarkii clarkii* and measured microhabitat variables at fresh redds in Irely Creek upstream of Irely Lake in a largely undisturbed watershed within Olympic National Park, Washington. Redd numbers declined abruptly in 2003, the year after a dry summer caused the dewatering of Irely Lake; therefore, we continued the redd counts during 2004–2012 to determine whether pond dewatering was a factor in the decline and whether redd counts would track Irely Lake surface area. The estimated number of redds varied from a high of 51 (in 2002) to a low of 2 (in 2006, 2007, and 2010); increases in estimated redd number occurred after wetter summers, and decreases were observed after drier summers. This pattern was significant in chi-square tests for redd number and the change in redd number with Irely Lake condition in the preceding year (dry, semi-dry, or wet). Rather than indicating juvenile mortality, the lack of a lag in response suggests the mortality of adults that would otherwise have spawned during the subsequent spring. The clear impact of dry summers in one of the wettest regions of North America underscores the important influence of hydrology on fish, even in the absence of other disturbances.

Hydrology influences the production of many salmonid fishes, and habitat reductions from low flows are sometimes associated with reduced production (Hvidsten and Ugedal 1991; Jager et al. 1997; Smith 2000; Mitro et al. 2003; Lobon-Cerviá 2004; Ebersole et al. 2009; Beecher et al. 2010). Recognition of the impact of low flows on fish production has led to instream flow protection being authorized in some jurisdictions, including the state of Washington (Barwin and Slattery 1989; Reiser et al. 1989; Beecher 1990), although the ecological importance of natural hydrologic variation (Poff et al. 1997, 2003) receives less legal attention. Establishment of instream flows as protected water rights pits fishery and environmental interests against other potential water users (e.g., irrigators, hydropower developers, industrial water users, and municipal water suppliers) in competition for a finite resource—often with the other water users arguing for low instream flows (Barwin and Slattery 1989; Shupe 1989; Beecher 1995). A common proposal made by other water users is that the instream flow should be the lowest known flow; this proposal is based the rationale that the fish population has survived the lowest flow in the past.

Most studies of low-flow limitation on salmonid production are confounded by a variety of human impacts on the fish and their habitat. During a study of spawning habitat suitability for Coastal Cutthroat Trout *Oncorhynchus clarkii clarkii* in an unmodified watershed (the Irely Lake–Irely Creek system) within Olympic National Park (ONP), Washington, we observed an abrupt decline in redd numbers after a very low flow event that dewatered Irely Lake. Harvest in the Irely Lake watershed is prohibited, the habitat is unmodified, and the

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Coastal Cutthroat Trout population appears to be restricted to the watershed, thereby reducing some factors that confound studies of flow limitation. To assess whether the decline in redd numbers was related to water quantity, we monitored the redd counts and hydrologic variables during the spawning season in subsequent years. Our null hypothesis was that redd numbers varied independently of late-summer base flow in Irely Creek and the associated water level and wetted area of Irely Lake.

METHODS

Study site.—Irely Creek is a small, low- to mid-elevation stream that flows through Irely Lake to Big Creek, a tributary of the Quinault River in ONP (Table 1; Figure 1). The Quinault River receives glacial and snowmelt inputs, whereas Irely Creek is fed by rainfall and rain-on-snow events (Mobbs 1999). The Quinault River flows into Lake Quinault and on to the Pacific Ocean.

Situated on the southwest slope of the Olympic Mountains, the Quinault River basin consists of temperate rainforest and is subject to wet, mild winters and dry, cool summers (June 1981; Mobbs 1999; Smith and Caldwell 2001), making this montane region the wettest in the contiguous USA (Hyatt and Naiman 2001; NPS 2015). The Irely Creek watershed has few human impacts beyond one primitive trail that crosses the lower main stem once and tributary L1 once (Figure 1). The watershed's old growth forest contains Douglas-fir *Pseudotsuga menziesii*, western hemlock *Tsuga heterophylla*, firs *Abies* spp., Sitka spruce *Picea sitchensis*, western redcedar *Thuja plicata*, and bigleaf maple *Acer macrophyllum* in the overstory; dominant understory riparian plants include the red alder *Alnus rubra*, salmonberry *Rubus spectabilis*, devil's club *Oplopanax horridus*, and western sword fern *Polystichum munitum* (Mobbs 1999; Smith and Caldwell 2001; NPS 2015).

Irely Lake (47°33′58″N, 123′40′25″W; elevation ~170 m) is a shallow, marshy pond (sensu EPA 2009) with a maximum depth of approximately 3 m and an area of about 8 ha (Wolcott 1973:619–690). Much of Irely Lake is lined with emergent grass—notably an expanding, exotic population of reed canarygrass *Phalaris arundinacea*—whereas the open-water zone has much submerged aquatic vegetation. The lake contains at least one lodge constructed by North American beaver *Castor canadensis*. A log dam that may be beaver-formed (perhaps in conjunction with past landslide or treefall event[s]) constitutes the lake outlet. The outlet is intermittent, as it is often dry in summer and early fall (Phinney et al. 1975; Smith and Caldwell 2001; Vadas et al. 2008). The lake outlet's debris dam is passable by salmonids; we consistently observed juvenile and adult Coho Salmon *O. kisutch* in Irely Creek above the lake. Some years during prolonged summer low flows, Irely Lake dries and shrinks to a small size (~0.5–2.0 ha) or to a few small pools where the creek enters the lake (Wolcott 1973:619–690). Under those conditions, lake temperatures generally exceed the temperatures recorded in Irely Creek (our unpublished data). Irely Lake is always full during the winter months.

The spawning area for salmonids in Irely Creek above the lake encompassed a length of over 2.4 km, including both main-stem and tributary habitats (Figure 1). Most of the spawning area had a stream order of 3 based on an updated topographic (1:24,000-scale) map except that the stream order was 2 above a big bend where tributary U1 entered. The Coastal Cutthroat Trout run within the Irely Lake watershed is likely restricted to the lake and the inlet stream given the (1) seasonal intermittency downstream (through middle Big Creek) and (2) the smaller, diffuse, steep nature of the other lake tributary (where spot checks found no evidence of trout spawning).

The Coastal Cutthroat Trout population in the system is mostly to entirely adfluvial (Vadas et al. 2008). The fish likely out-migrate to the lake within 1–3 years of hatching, although some of the deeper, wood-rich pools may support a few adults year-round. Such restriction of Coastal Cutthroat Trout to small, cold headwater systems (stream order ≤ 3) is common (Sullivan et al. 1987; Harvey 1998; Blakley et al. 2000; Rosenfeld et al. 2000; Boss and Richardson 2002; Berger and Gresswell 2009; Buehrens 2011; Buehrens et al. 2013; Ptolemy 2013). Coastal Cutthroat Trout prefer mean annual flows (MAFs) of up to 0.63 m^3/s and summer flows below 0.31 m^3/s (especially 0.08–0.11 m^3/s; Trotter 1989; Ptolemy 2013), consistent with the estimated MAF of 0.40 m^3/s for Irely Creek (Table 1).

Irely Lake provides rearing habitat for larger trout (15.5–40.0 cm TL; J. H. Meyer, ONP [retired], unpublished data; H. A. Beecher and S. N. Boessow, personal observations), which are subject to catch-and-release angling. Fish fauna in Irely Creek consist of the Coastal Cutthroat Trout, Coho Salmon, Prickly Sculpin *Cottus asper*, and Western Brook Lamprey *Lampetra richardsoni*, with previous Irely Lake observations of steelhead/Rainbow Trout *O. mykiss*, native char (likely Bull Trout *Salvelinus confluentus*), and introduced Brook Trout *Salvelinus fontinalis* (Meyer, unpublished data; B. A. Caldwell, Washington Department of Ecology, personal communication). During those years when Irely Lake was reduced to a semi-dry state, the largest of the remnant pools had sufficient water to support fish provided that the conditions did not worsen. Juvenile Coho Salmon were sampled when Irely Lake was reduced in size to 0.4 ha and temperatures of 19°C were recorded (S. N. Boessow and J. H. Kohr, unpublished data).

Annual redd surveys.—We counted Coastal Cutthroat Trout redds along Irely Creek upstream of Irely Lake each year during the spawning season in 2001–2012 to estimate the total annual numbers of redds and spawners. The most complete redd surveys occurred in 2001–2002, during which time we (1) started in early spring (March) before spawning began and (2) sampled at 1–2-week intervals except for more intense work during the spawning peak (Tables 2, 3). The trout spawning season extended from mid–late March to mid-May

TABLE 1. Hydrology and watershed traits of the Quinault River basin and its subbasins, including Irely Creek (USGS 2013, 2014), and other Olympic Peninsula drainages. Streamflow data from other Olympic Peninsula gauges were used to classify Irely Lake level when field or aerial survey data did not extend into early fall (USGS 2013; WDOE 2015). Mean basin elevation is upgradient from the gauge. The presence of glacial, snowpack, and/or lacustrine influences was based on literature data (Nassar 1973; Phinney et al. 1975). Mean annual flow (MAF) was based on the period of record or was estimated (estimates are designated by asterisks).

Stream (river basin)	Gauge number	Drainage area (km^2)	Annual precipitation (cm)	Mean basin elevation (m)	MAF (m^3/s)	Unit runoff (m^3/s per km^2)	Dominant precipitation
Sol Duc (Quillayute)	20A070	561	262	570	43	0.077	Rainfall
Calawah River (Quillayute)	12043000	334	290	451	30	0.090	Rainfall
Hoh River (Hoh)	12041200	655	414	744	72	0.100	Snow/glacial
Queets River (Queets)	12040500	1,153	381	460	124	0.108	Snow/glacial
Quinault River (Quinault)	12039500	684	404	774	81	0.118	Snow/glacial, lacustrine
Big Creek at the confluence with the Quinault River (Quinault)	NA	51.5	455	561	6.7*	0.131	Rainfall
Irely Lake outlet (Quinault)	NA	5.15	457	411.5	0.7*	0.132	Rainfall
Irely Creek at the inlet to Irely Lake (Quinault)	NA	3.3	457	421	0.4*	0.132	Rainfall
Humptulips River (Grays Harbor)	12039005	342	394	344	41	0.120	Rainfall
Wishkah River (Chehalis)	22D110	149	312	157	11	0.074	Rainfall
Satsop River (Chehalis)	12035000	774	279	224	58	0.075	Rainfall
Bingham Creek (Chehalis)	22K070	70	284	180	4.2	0.060	Rainfall

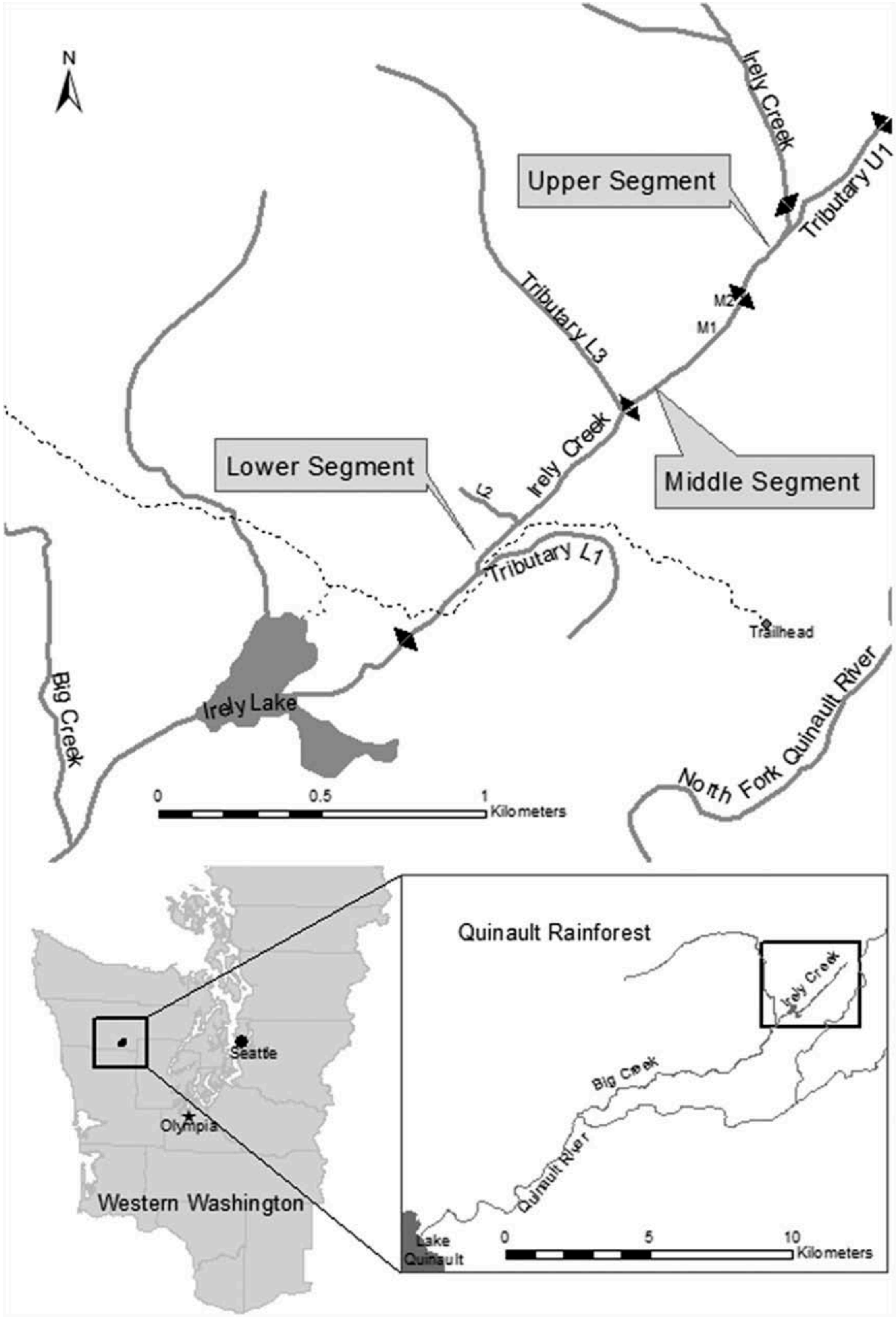

FIGURE 1. Map of the Irely Creek study area and its location in Washington. The big bend referenced in the text is at the confluence of Irely Creek and tributary U1. Boundaries of the survey segments (lower, middle, and upper) are indicated by dark diamonds.

TABLE 2. Spatiotemporal expansion factors that were used to estimate the number of Coastal Cutthroat Trout spawners and the total redd counts by year in the Irely Creek watershed, Washington (for spatial analysis, UBB = unsampled above the big bend in the upper segment of Irely Creek; ULS = unsampled in the turbid lower segment of Irely Creek on May 5, 2009). For temporal analysis, sampling dates when redds were found are shown in bold italics (peak spawning dates are presented in Table 3), the next "before" versus "after" site visit dates are shown in parentheses, and FT represents trips to the field during the known spawning season (across years).

Year	Spatial expansion factor	Basis for spatial expansion factor	Sample dates	Temporal expansion factor	Basis for temporal expansion factor
2001	1.128	UBB	***Mar 22, Apr 5–8, Apr 28*** (Mar 2, May 5)	1.000	NA
2002	1.128	UBB	***Apr 4–12, May 16*** (Mar 30, Jun 2)	1.000	NA
2003	1.000	NA	***Apr 18, May 2*** (Feb 10)	1.085	Only 2 FTs
2004	1.000	NA	***Apr 7, Apr 9*** (Feb 2)	1.076	Only 2 FTs
2005	1.000	NA	***Apr 13, May 2*** (Jan 25)	1.085	Only 2 FTs
2006	1.000	NA	***Apr 28*** (Apr 13, May 24)	1.042	Only 2 FTs
2007	1.000	NA	***Mar 28, Apr 12*** (Mar 15, Apr 26)	1.000	NA
2008	1.000	NA	***Apr 10, May 2*** (Jan 25, May 21)	1.085	Only 2 FTs
2009	1.221	ULS and UBB	***Apr 16, May 5*** (Jan 16)	1.042	Only 2 FTs
2010	1.000	NA	***Apr 13, Apr 30*** (Jan 20)	1.085	Only 2 FTs
2011	1.000	NA	***Apr 22*** (Feb 2)	1.268	Only 1 FT
2012	1.000	NA	***Apr 10, Apr 24*** (Feb 3)	1.175	Only 2 FTs

TABLE 3. Hydrologic condition in Irely Lake (2000–2011) and the number of Coastal Cutthroat Trout redds (2001–2012) in Irely Creek. Redd counts are actual counts; redd estimates include spatiotemporal expansion factors that accounted for incomplete sampling during 2002–2006 and 2008–2012 (Table 2). The driest month's percentage of long-term mean annual flow (%MAF) at the Quinault River gauge (12039500) served as an indicator of whether the summer prior to spawning was wet (>30%), semi-dry (20–26%), or dry (<17%; CPSF = critical period streamflow). For the year preceding redd counts, Irely Lake level was determined based on late-summer satellite images, direct observation, or both; gauge data were interpreted when satellite images and direct observation did not cover the probable time of the lowest lake level.

Spawning year	Redd count	Redd estimate	% change in redd estimate from previous year	Peak redd date(s)	Driest month's %MAF during year preceding spawning	Summer condition based on Quinault River gauge CPSF	Irely Lake condition in previous summer
2001	24	27	Unknown	Apr 5–8	24	Semi-dry	Semi-dry
2002	45	51	89	Apr 4–12	33	Wet	Wet
2003	8	9	–82	Apr 18	13	Dry	Dry
2004	8	8	–11	Apr 7	15	Dry	Dry
2005	15	16	100	Apr 13	34	Wet	Wet
2006	2	2	–87	Apr 28	13	Dry	Semi-dry
2007	2	2	0	Mar 28–Apr 12	14	Dry	Dry
2008	6	6	200	May 2	20	Semi-dry	Wet
2009	5	7	17	Apr 16	32	Wet	Wet
2010	2	2	–71	Apr 13–30	16	Dry	Dry
2011	4	4	100	Apr 22	31	Wet	Semi-dry
2012	7	8	100	Apr 10	47	Wet	Wet

across years in Irely Creek (Vadas et al. 2008). For the 3 years in which the most complete survey data were collected (i.e., 2001, 2002, and 2007; Table 3), the spawning season for a given year ranged from 0.5 to 1.5 months (median = 1 month).

During our study, we sampled most habitats that yielded Coho Salmon carcasses (Vadas et al. 2008; cf. McMillan et al. 2014) as well as sampling in the upper main stem above the big bend, where only trout spawning was evident (Figure 1); however, we did not sample tributary U1 or above the big bend in 2001 or 2002. Main-stem redd surveys were generally only conducted in the gravelly alluvial zone, which was upstream of Irely Lake's backwater (fine-bedded) area and most of the beaver activity and reed canarygrass. Sampling in 2001 and 2002 was primarily conducted below tributary U1, as main-stem habitat above this was steeper and dominated by step-pools and large rocks (boulder/bedrock; Mobbs 1999), with occasional trout redds but no salmon carcasses observed in this reach type. Sampling since 2003 included tributary U1 because Coho Salmon spawned in this alluvial channel and because trout fry inhabited the main stem near the mouth of U1 during summer 2002. No trout redds were found in the lower tributaries below U1. Hence, 2001 redd data were for the lower and middle main-stem segments, 2002 data also included most of the upper main-stem segment, and 2003–2012 data encompassed all three segments and often tributary U1. We did not sample unusually early or late spawning events during 2003–2004 and 2008–2012, when redd sampling was less intense (see below).

Two trained observers walked upstream on opposite shorelines or a single observer with polaroid glasses (R. L. Vadas) traversed both sides to view the bed from different angles while minimizing redd disturbance. To maximize visibility, we tried to avoid storm-induced high-turbidity periods, but correction was occasionally needed for reduced redd detection efficiency at higher flows. For consistency, a single observer identified and counted all completed redds of sufficient size that had definite pits and tailspills (Lowry 1971; Thurow and King 1994; Bennett et al. 2014). Trout redds typically showed "scalloping"—pit edges where digging reached fine substrata (including small gravel) for egg burial (Keenleyside and Dupuis 1988; Vadas 2006). We considered double redds with a single, joint tailspill to be a single redd unit. We rarely observed adult Coastal Cutthroat Trout near redds. All of the redds observed in 2001 and some of the redds observed in 2002 were confirmed by the nearby presence of at least one fry during late spring or early summer (June 1981; Buehrens 2011; Buehrens et al. 2013). We may have somewhat underestimated escapement by excluding possible redds that were discounted as "scour patches" or that never developed further.

During summer (August or September) and fall (late October or early November), we sampled young salmonids and other native fishes by using dip nets (in 2001) or a combination of dip nets and seines (in 2002–2011). Scale samples for age estimation were collected from most salmonids larger than 70 mm TL. This sampling revealed the presence of numerous trout fry during summer and some juveniles (age 1, age 2, and one age-3 fish seined during 2005–2011) across all seasons, consistent with the 1–3-year duration of stream rearing reported for adfluvial Coastal Cutthroat Trout in other streams (Trotter 1989; Blakley et al. 2000).

Estimation of the annual number of redds.—Given incomplete spatiotemporal sampling during 2001–2012, expansion factors (Table 2) were required to estimate the total number of redds (Table 3). Most data during 2003–2012 were collected over 2 d that strategically sampled the peak season (i.e., mid–early April to early May), which is a reasonable study design for assessing escapement given budget constraints (Bonar et al. 1997). For these later study years, sampling usually took place within a 21-d time frame to ensure that no redds were missed due to aging, as Rainbow Trout and Cutthroat Trout redds are nearly impossible to identify after that (Vadas 2006, and our unpublished data), but longer unsampled periods were assumed to potentially yield missing redds during the spawning season. The numbers of redds that were present during unsurveyed times and areas was estimated via instream indexing (sensu Johnston et al. 1987), which involved comparing the percentage of redds in those times and areas from complete surveys to those in incomplete surveys (Table 2) to yield potentially missed redds. Temporal expansions added one redd each during the years 2003, 2005, 2011, and 2012 but none during 2004, 2006, or 2008–2010, when redd counts were generally lower (Table 3). Three years (2001, 2002, and 2009) required spatial extrapolation because we did not sample the uppermost zone (Table 2). In 2002, we found many trout fry near the big bend (the limit of sampling). Hence, spawning likely occurred in upper habitats during 2002 and perhaps also during 2001 and 2009, so the main-stem and tributary redds that were missed above the big bend during all 3 years were estimated based on 2003–2008 and 2010–2012 data.

For 2009, we also could not discern redds in the lower main stem (below tributary L3) during the turbid flood of May 5. We estimated the number of lower main-stem redds that were missed during the second redd survey based on the relative distribution of actual and spatially extrapolated redds in the three stream segments during 2001–2008 and 2010–2012 (Tables 2, 3). Notably, the redd contribution of the lower segment remained at 26% even with the addition of extrapolated data for 2009.

Hydrologic indices.—We used direct observation, satellite imagery of Irely Lake, precipitation records, and streamflow gauge records from the Quinault River and other regional streams to assess the late-summer extent of Irely Lake in the year preceding each spawning survey; no one data source was consistent enough (given missing years or snow or glacial influence). This study was initially prompted by the observation that the dry condition of the Irely Lake bed in late summer 2002 was followed by a reduction in the number of trout redds in spring 2003.

We initially preferred direct observations, orthophotos from the U.S. Department of Agriculture's National Agriculture

Imagery Program (NAIP), and Landsat 5 and Landsat 7 satellite imagery (National Aeronautics and Space Administration) to determine the years when Irely Lake was dry in late summer, as the lake and its watershed constituted less than 1% of the watershed contributing to the Quinault River gauge. Flow at the gauge is influenced by glacial, snowpack, and large-lake factors that are absent in the Irely Lake watershed (Table 1). An independent review of the Quinault River gauge using the 30-d lowest flow (critical period streamflow [CPSF]) as a percentage of MAF used three similar categories: wet, semi-dry, and dry (R. Ptolemy, British Columbia Ministry of Environment, personal communication). The two categorizations were strongly correlated (r = 0.85, n = 12, df = 10, P < 0.01) and the Quinault River gauge was a more readily available data source, so we also compared redd numbers to CPSF at the Quinault River gauge (Tables 3, 4). However, we note that the use of Quinault River CPSF resulted in 2010 (2011 spawning year) being classified as "wet" in contrast to our "semi-dry" classification, which was supported by our August 2010 photograph that showed a largely dry pond.

For the aerial images to be useful in our study, two conditions were required: (1) satellite passes had to be available from August and September, when the likelihood of lake drying/dewatering was greatest; and (2) the weather had to be clear enough that cloud cover did not block the view of Irely Lake. Usable images ranged from 2 to 10 images/year, and we categorized years based on the driest state that was visible during the year (i.e., in the late summer or early fall). Satellite images were filtered to view in the near-infrared spectrum. Within the time frame of the study (2001–2011), we had fairly consistent visual observations and three NAIP orthophotos (2006, 2009, and 2011), which provided a very clear aerial view of the lake. On-site observations and NAIP orthophotos allowed us to compare the near-infrared satellite images with known conditions in order to validate and fine tune our assessment of the satellite images without direct observations. We assigned each year to one of four lake categories derived from ArcGIS imagery coloration: full (F); less than full (<F), with Irely Lake reduced in size but still connected to Irely Creek; semi-dry (>D), with isolated lake pools; and dry (D; Table 3). No year had F as the driest state, so we considered years in the < F category to be wet years, leaving three categories: wet, semi-dry, and dry.

Streamflow data from other Olympic Peninsula gauges (Table 1; USGS 2013; WDOE 2015) and precipitation records served as secondary sources of hydrologic data; when field or aerial survey data did not extend into early fall during 2000–2011, we used these secondary sources to confirm or complete our annual classification of Irely Lake's areal extent as wet, semi-dry, or dry (Table 3). Annual precipitation and annual unit runoff are highly correlated in the southern and western Olympic Peninsula (r = 0.86, n = 9, P < 0.01; Table 1). We examined daily and monthly rainfall records from the Quinault Ranger Station and full-year precipitation and air temperature records from Forks (located 68 km northwest of Irely Lake), which had more complete records than Lake Quinault (Western Regional Climate Center 2015); monthly precipitation at the two sites were well correlated (r = 0.96, n = 105; September 2006–May 2015).

Statistics.—We used a chi-square test (Chapman and Schaufele 1970) to compare the estimated number of Coastal Cutthroat Trout redds after years when Irely Lake condition was classified as dry, semi-dry, or wet (Table 4). Estimated redd numbers were compared with the number that would be expected if redds were equally likely in every year (i.e., mean estimated redds). Based on Quinault River gauge CPSF, we aggregated 5 years as dry, 2 years as semi-dry, and 5 years as wet years for analyzing the estimated number of redds. Using

TABLE 4. Chi-square (χ^2) comparisons of Coastal Cutthroat Trout redd estimates in Irely Creek relative to Irely Lake condition in the preceding year, as determined from a combination of direct observation, aerial and satellite imagery, and regional hydrology trends or from the critical period streamflow (CPSF) at the Quinault River gauge. Expected redd estimates were based on a uniform distribution of redds among years. The χ^2 tests had two degrees of freedom (df) and were significant (P < 0.01).

Irely Lake condition in previous summer	Number of years in category	Redd estimate	Expected redd estimate	Contribution to χ^2
Combination of data sources				
Wet	5	88	59.2	14.1
Semi-dry	3	33	35.5	0.2
Dry	4	21	47.3	14.7
χ^2 total (df = 2)				28.9
Quinault River CPSF				
Wet	5	82	59.2	8.8
Semi-dry	2	33	23.7	3.7
Dry	5	23	59.2	22.1
χ^2 total (df = 2)				34.6

the mixed strategy of direct observation, aerial and satellite imagery, and supplementary hydrologic data, we aggregated 4 years as dry, 3 years as semi-dry, and 5 years as wet (Tables 3, 4). We also calculated the correlation between the proportional change in estimated redd number and the Quinault River CPSF.

RESULTS

The distribution of estimated numbers of Coastal Cutthroat Trout redds during spring differed significantly among lake condition categories assigned to the late summer of the year preceding spawning ($P < 0.01$; Tables 3, 4; Figure 2). The estimated number of redds was significantly higher after a wet summer (<F) than after a drier summer (>D or D; Tables 3, 4; Figure 2). The highest two redd counts were estimated for the first 2 years of our study (2001 and 2002); smaller spikes in estimated redd number were evident during 2005, 2008, and 2011–2012 (Table 3; Figure 2). Increases in the estimated redd number relative to the previous year roughly corresponded with wet lake conditions in the previous year (i.e., spawning years 2001, 2004, 2007, 2008, and 2011; Figure 2b). In contrast, Irely Lake dewatering was complete during the summer–fall of 2002, 2003, and 2009, corresponding with Coastal Cutthroat Trout run declines and low abundances observed during 2003, 2004, 2006, 2007, and 2010 (Figure 2).

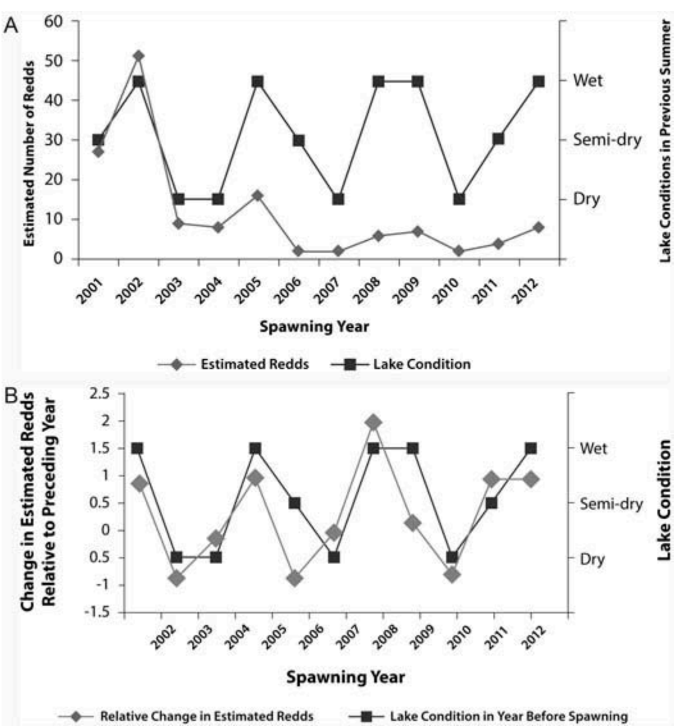

FIGURE 2. **(a)** Estimated number of Coastal Cutthroat Trout redds in Irely Creek, Washington; and **(b)** the change in estimated redd number relative to Irely Lake condition (wet, semi-dry, or dry) during the previous summer.

When the change in redd number was expressed as a percentage of the preceding year's redd number estimate (Table 3), there was a significant correlation ($r = 0.61$, $n = 11$, $P < 0.05$; Figure 3) between the change in redd number and Quinault River CPSF. The percent change in estimated redd number was somewhat more strongly correlated with lake area category (dry = 1, semi-dry = 2, wet = 3; $r = 0.73$, $n = 11$, $P < 0.05$) and slightly less correlated ($r = 0.71$, $n = 11$, $P < 0.05$) when the same three categories were based on Quinault River CPSF. Estimated redd numbers were not significantly correlated with the maximum, mean, or minimum air temperature at Forks or with the range mean ([maximum + minimum temperature]/2) in the water year preceding spawning ($r < 0.51$, $n = 12$, $P > 0.05$); the same was true for the percent change in estimated redd number ($-0.21 < r < 0.12$, $n = 11$, $P > 0.05$).

DISCUSSION

This study demonstrates a strong hydrologic influence—specifically that of dry conditions in a largely undisturbed watershed—on a resident population of Coastal Cutthroat Trout. The dewatering of Irely Lake led to a decline in the number of Coastal Cutthroat Trout that spawned during the subsequent spring. The strong linkage between dry conditions and a reduced number of spawners was likely attributable to poor adult survival during the previous summer, when habitat was greatly reduced. Specifically, low summer–fall flows and reduced Irely Lake area and volume appeared to limit adult survival to the next spawning season. A similar case of adult-oriented population regulation was reported for landlocked Brown Trout *Salmo trutta* in Europe (Baran et al. 1995; Elliott and Hurley 1998). These observations likely reflect declining pool (area and cover) conditions during droughts (Wesche 1976a, 1976b; Elliott 2000; Hakala and Hartman 2004). We cannot rule out that low water imposed

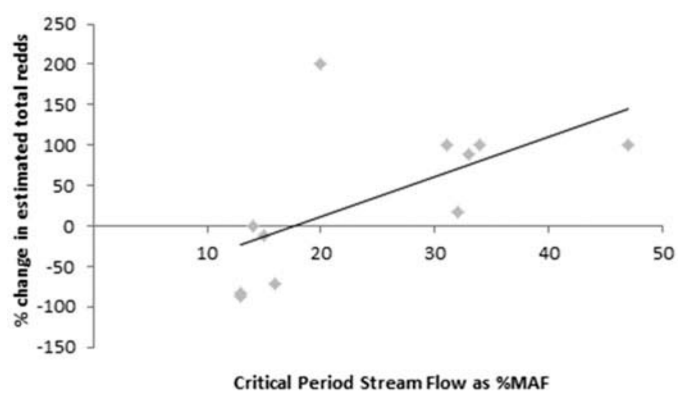

FIGURE 3. Percent change in the estimated number of Coastal Cutthroat Trout redds in Irely Creek, Washington, relative to the 30-d lowest flow (critical period streamflow; percentage of mean annual flow [MAF]) at the Quinault River gauge during the previous summer. The correlation was significant ($r = 0.61$, $n = 11$, $P < 0.05$).

additional mortality on younger fish, but any such impacts would not have been evident in redd numbers until the affected cohorts reached maturity, delaying for different lengths of time and thus masking the effect. Other possible causes of mortality that we considered were harvest, predation, and high temperature. We assumed that harvest mortality was low because only catch-and-release angling is permitted in this system, although some hooking mortality may occur, especially at higher temperatures. As pond area and depth decline, fish would be more crowded and thus more vulnerable to bird and mammal predation, particularly if they occupied the smaller of the disconnected pools. None of the Forks air temperature indices was significantly correlated with estimated redd number or with the percent change in estimated redd number; however, as water volume decreased and surface: volume ratio increased, the water temperature was closer to air temperature, potentially adding a hydrology-mediated stressor. The wet Irely Lake conditions during summer–fall in 5 of the 12 years likely favored Coastal Cutthroat Trout growth and survival to spawning, thus nearly doubling the number of redds and the spawning population in 2005 relative to the previous 2 years. Similarly, the 2008 and 2009 redd counts were at least triple the counts from the previous 2 years, and counts doubled between 2010 and 2011 and again during 2012. With partial to full dewatering of Irely Lake, run size expressed as a percentage of the previous year's run declined to approximately 17.6% in 2003, 12.5% in 2006, and 28.6% in 2010. Hence, recovery after wet years was weaker than the declines that occurred after dry years. Over 12 years, escapement varied over 25-fold from as few as two redds in each of 3 years (2006, 2007, and 2010) to about 51 redds in 2002. Such low numbers in the parental generations could cause a loss of genetic diversity, particularly if escapement is low for several years in a row. Our first 2 years of monitoring yielded the two highest redd counts; we then observed a sharp decline followed by fluctuating numbers (through 2012) that never reached the counts obtained in 2001 and 2002. Our long-term study in this undeveloped watershed yielded a strong ecohydrologic relationship for a largely to fully landlocked run of Coastal Cutthroat Trout (contra Railsback et al. 2002).

The Irely Creek watershed is largely undisturbed except for a trail, some catch-and-release fishing that we presume causes little mortality, and the presence of some nonnative reed canarygrass. Natural processes prevail in the watershed. Despite receiving some of the heaviest annual precipitation in North America, dry season conditions in the Irely Creek system appear to have a strong effect on the Coastal Cutthroat Trout population.

Hydrologic limitation during the dry season is most likely manifested as the drastic reduction in habitat volume for adult Coastal Cutthroat Trout in Irely Lake and Irely Creek. Although we have never observed complete cessation of Irely Creek's flow upstream of Irely Lake, we have measured flows as low as 0.015 m^3/s (~4% of MAF; September 8, 2003), which probably limits both living space and food transport. The month(s) of lowest flow is an important rearing constraint on the distribution and productivity (survival and abundance) of Coastal Cutthroat Trout (June 1981; Berger and Gresswell 2009; Buehrens 2011) and other Pacific salmonids (Erman et al. 1973; Zillges 1977; Beecher 1981; Scarnecchia 1981; Vadas 2000; Beecher et al. 2010). Berger and Gresswell (2009) found that low discharge and reduced invertivory during fall were the major seasonal environmental constraints affecting Coastal Cutthroat Trout survival; thus, perennial flow and intact riparian flora are important for this subspecies' viability in Pacific Northwest watersheds (Blakley et al. 2000). Summer–fall low flows in some creeks also constrain the upstream migrations of adult Coastal Cutthroat Trout to the winter–spring season (Blakley et al. 2000), although fall–winter spawning is occasionally seen (McMillan et al. 2014).

Hydrology has diverse influences on fish habitat (Poff and Allen 1995; Annear et al. 2004; Arthington 2012), and the response of the Coastal Cutthroat Trout run to dry conditions in Irely Creek demonstrates the net effect. Limitation of lotic fishes by low flows is often seen in arid regions or areas with major water withdrawals (Matthews 1988; Matthews and Marsh-Matthews 2003; Poff and Zimmerman 2010; Arthington 2012). However, Irely Creek is situated in one of the wettest areas of North America—a temperate rainforest (mean annual precipitation at Lake Quinault was over 450 cm; see Table 1)—and its location within ONP means that the watershed lacks significant human modification. Although our finding of hydrologic limitation for Coastal Cutthroat Trout in a temperate rainforest seems counterintuitive, it reflects the unusual sensitivity of the relatively small, shallow, unshaded Irely Lake, which provides crucial adult maturation habitat for this small, confined trout population. Indeed, Irely Lake's high surface : volume ratio makes it more vulnerable to evaporation and warming when inflow is low. Other studies have revealed the sensitivity of landlocked salmonids to summer low flows in Montana (Kraft 1972), Wyoming (Wolff et al. 1990), New Zealand (Jowett 1992), France (Baran et al. 1995), and Spain (Lobón-Cerviá 2003, 2004, 2005, 2014). Rainbow Trout fry in semi-natural channels showed growth declines when flow was reduced (Rimmer 1985). Droughts reduced Brook Trout growth and survival in headwater streams of West Virginia, including longer-term (winter and postdrought) food reduction and sedimentation impacts (Hakala and Hartman 2004) that may likewise apply to Pacific salmonids (McDonald 1960; Erman et al. 1973). Seasonal and interannual fluctuations in abundance of Redband Trout (inland Rainbow Trout) and resident Bull Trout both corresponded to whether normal or drought conditions prevailed in Idaho desert streams (Warren and Partridge 1993; Allen et al. 1995, 1997; Zoellick et al. 1996), similar to the interannual fluctuations of Brown Trout in a Wisconsin stream (Lowry 1971). Rainbow Trout and Cutthroat Trout often leave lotic rearing sites to enter main-stem habitats and associated lakes when streamflows decrease over the summer–fall (Benson 1960; Bulkey and Benson 1962; Erman and Hawthorne 1976; Berger and Gresswell 2009).

Besides being influenced by the great reduction in Irely Lake area and volume during dry-outs, the Coastal Cutthroat Trout run may also decline with creek habitat during summer–fall given that some reaches in the lower main stem are intermittent during dry years. However, even when surface flow was minimal, pools persisted to support abundant rearing Coho Salmon and some trout. Beaver ponds also retain water in lower Irely Creek, thereby providing some rearing habitat while reducing spawning habitat until natural breaching occurs (cf. Bennett et al. 2014; McMillan et al. 2014).

Detecting hydrological effects on a fish population is more difficult as life history becomes more complex, including repeat spawning or spawning at multiple ages. Migratory fish are affected in multiple locations and habitats by localized environmental, predation, and harvest factors. Despite repeat spawning and the ability to spawn at different ages, the Coastal Cutthroat Trout population in Irely Creek is confined to a small watershed—a common phenomenon for this subspecies (Ptolemy 2013).

Logistical challenges to measuring the hydrologic influence on Coastal Cutthroat Trout in Irely Creek required us to explore a variety of data sources (i.e., from the main-stem Quinault River gauge to remote sensing) and potentially correlated indicators. Although streamflow gauge records are the most continuous and most precise, the use of a categorical index based on remote sensing together with other sources showed a slightly stronger correlation with estimated redd numbers than the Quinault River CPSF index, which integrated a larger area with more diverse influences (e.g., glacial, snowpack, and lake) than the smaller subwatershed. This difference was illustrated for 2010, when our August photographs showed that the bed of Irely Lake was nearly dry (semi-dry), whereas the CPSF index suggested that 2010 was a wet year, despite agreement between the two indices for most years. Although the data for Irely Lake condition were imperfect, this trichotomous classification system provided a mechanistic basis for Coastal Cutthroat Trout demography.

If natural dry conditions in a temperate rainforest can have such a profound effect on a trout population, then the human use of water during the dry season would constitute an additional stress, potentially further reducing the run or impeding its recovery from the declines associated with severe dry spells. Allocation of surface water (or groundwater in hydraulic continuity with surface water) can lead to chronically low salmonid populations by reducing the amount of essential habitat. During water management planning that focuses on the demand for out-of-stream water use, we frequently hear the argument that salmonid populations have survived lower flows—indeed, the lowest flows on record—so protection of the lowest recorded flows is sufficient for salmonid conservation. However, our results strongly suggest that even in the absence of major, confounding human impacts on a watershed, maintenance of the driest naturally occurring hydrologic conditions will not protect the distribution and abundance (and, thus, persistence) of a trout population. Our finding of such a pronounced hydrologic effect on the Coastal Cutthroat Trout population in a mostly undisturbed watershed with no water diversion emphasizes the importance of managing water diversions in other watersheds to ensure that water levels and surface areas are not reduced to natural extreme-low levels or lower; such measures will help to avoid or minimize adverse impacts on fish populations.

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