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ARTICLE

Is Marine Survival for Puget Sound's Wild Steelhead Really That Bad? A Nisqually River Case Study Evaluating Estimates of Productivity and Survival of *Oncorhynchus mykiss*

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Abstract
We highlight the uncertainty that exists around estimating productivity and survival for one population of threatened steelhead *Oncorhynchus mykiss* (anadromous Rainbow Trout) with the goal of strengthening our understanding of the well-documented poor marine survival of Puget Sound steelhead. We evaluated how sensitive estimates of productivity and survival were to the uncertainty associated with smolt trap enumerations, redd survey methodology, estimates of fish per redd, and estimates of smolt production by resident Rainbow Trout in order to clarify causes of poor steelhead survival in this area. We show that from 2004 to 2014, estimates of both freshwater productivity and marine survival were highly sensitive to estimates of fish per redd used to expand redd counts, as well as error around smolt abundance estimates. Regardless, uncertainty associated with these inputs did not explain the low survival and high productivity observed for Nisqually River steelhead relative to other populations. In addition, we identified progeny from anadromous mothers upstream of what was previously considered a barrier, and we also documented that a proportion of steelhead smolts ($N = 4/43$) originated from resident mothers (Rainbow Trout). While these results indicated an underestimation in the total number of steelhead redds counted each year and an overestimation of steelhead progeny enumerated at smolt traps, they had little impact on estimates of survival and productivity. Results from the current study support previous work reporting poor marine survival for populations of Puget Sound steelhead and highlight the sympatric relationship between resident and anadromous life histories of *O. mykiss*. Overall, our study supports a management strategy that protects both the anadromous and fluvial forms of *O. mykiss*, prioritizes habitat improvements that promote freshwater productivity, and increases research focused on identifying causes of poor marine survival.

The adult abundance of steelhead *Oncorhynchus mykiss* (anadromous form of Rainbow Trout) has declined across their range since the late 1900s (Gayeski et al. 2011), with some of the largest declines occurring in Puget Sound (Kendall et al. 2017). Despite decreased harvest and improved ocean conditions in the early 2000s, the majority of steelhead populations in Puget Sound remain below historic levels (Kendall et al. 2017; Losee et al. 2019). A lack of recovery for Puget Sound steelhead and the recent listing as threatened under the Endangered Species Act (ESA; NMFS 2006) has resulted in large-scale research projects (Long Live the Kings 2014; Moore et al. 2015; Berejikian et al. 2016) and recovery plans (Blanton et al. 2011; NMFS 2019) for those populations most at risk.

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Leading hypotheses explaining chronic low abundances and survival rates for steelhead populations in Puget Sound are diverse and include habitat degradation, increased abundance of predators (Berejikian et al. 2016; Nelson et al. 2019), disease (Jacobson et al. 2008), and toxins (O'Neill and West 2009). Together, these factors have been attributed to causing poor marine survival of Puget Sound steelhead (Sobocinski et al. 2018).

Marine survival rates are lowest in the southernmost populations in Puget Sound (Kendall et al. 2017), and this may be related to the distance individuals must migrate to reach the Pacific Ocean (Moore et al. 2015). Because of this, the Nisqually River, the southernmost steelhead population in Puget Sound, has received increased attention and monitoring in recent years. The majority of monitoring work is conducted by the Nisqually Indian Tribe and the Washington Department of Fish and Wildlife (WDFW) and comprises two parts: spawning ground surveys to enumerate redds (Madel and Losee 2016) and juvenile trapping in the lower river to estimate smolt abundance (Klungle et al. 2018). Results from steelhead monitoring in the Nisqually River support previous conclusions that marine survival is low relative to other steelhead populations; on average, less than 2% of steelhead smolts leaving the Nisqually River return to the river as adults (Klungle et al. 2018). However, unlike other systems in Puget Sound, the Nisqually River also may have high freshwater productivity, where a large number of smolts are produced by a few adult spawners, which has raised questions associated with the accuracy of the estimates of juvenile and adult abundance, as well as factors limiting the marine survival of Nisqually River steelhead. For example, while an average of only 1,000 adult steelhead returned to the Nisqually River annually between 2002 and 2015, production of steelhead smolts ranged from 20,178 in 2012 to 133,597 in 2018 (mean = 77,178 smolts), resulting in an estimated 153 smolts per spawner. If smolts-per-spawner estimates are accurate, the Nisqually River steelhead population may rank as one of the most productive populations among those with available production estimates while also having one of the lowest marine survival rates.

The life cycle of the anadromous form of Pacific salmon *Oncorhynchus* spp. lends itself to monitoring during two time points: (1) when juvenile fish emigrate from their freshwater rearing grounds, and (2) when mature adults return to spawn in natal streams from remote, offshore environments. By monitoring the abundance of out-migrating smolts and returning adults, managers can estimate the marine survival for a given out-migration year and the freshwater productivity of a given spawning cohort. In addition, long-term, annual estimates of survival and production allow managers to identify factors limiting the recovery of populations that are threatened.

While juvenile and adult abundance serve as the foundation for steelhead management, estimates that rely on redd surveys and smolt trapping are subject to a variety of sources of error and include numerous assumptions. Common sources of error include surveyor observation efficiency, juvenile trapping efficiency and assumptions regarding habitat use, the influence of hatchery fish, in-river harvest of adults, and expansions of redd counts to estimate adults. If estimates of adult returns are biased low due to missed redds and combined with an overestimate of smolt production, they could lead to a dramatic overestimation of production and underestimate of survival. For example, the rotary screw trap in the Nisqually River, like other rotary screw traps, samples a relatively small portion of out-migrating steelhead smolts, often fishing through variable environmental conditions (e.g., flow). Trap catch, a subsample of the population, may not be representative of the smolt population, and changes in trap efficiency may be difficult to detect, biasing any estimates or inferences made about smolt abundance, and can result in imprecise estimates of production (wide confidence intervals). This is important because redd-based estimates of spawning adults represent a conservative estimate of spawner abundance (Al-Chokhachy and Budy 2005; Gallagher et al. 2007). Further, redd surveys may be confounded by nontarget life histories influencing redd counts and ultimate spawner abundance estimates (Al-Chokhachy and Budy 2005). An additional variable that may influence estimates of steelhead production and survival but that is rarely considered is the contribution resident Rainbow Trout make to the production of out-migrating smolts. For instance, Berejikian et al. (2013) demonstrated that up to 67% of parr from Hood Canal, a large fjord of Puget Sound, were the product of resident mothers, but the ultimate life history of those juvenile fish (freshwater resident versus anadromous) was unknown. In the Nisqually River, the resident form of *O. mykiss* is known to be abundant in some years and may contribute to smolt production. Smolts derived from resident Rainbow Trout may have lower marine survival than those originating from anadromous mothers (Kostow et al. 2003; Thrower and Joyce 2004; Pearse et al. 2009). If smolt trap estimates are inaccurate, redds are missed, and estimates of anadromous smolts are comprised of a large proportion of fish originating from resident Rainbow Trout, the compounded sources of error could result in underestimates of marine survival and inflated estimates of production.

Our study sought to improve estimates of steelhead abundance, survival, and productivity in the Nisqually River to better understand the anomalously low survival of Puget Sound steelhead. To achieve this, we explored the following inputs: (1) uncertainty around estimates of smolt abundance, (2) the contribution freshwater residents make in the production of anadromous individuals, (3) spatial coverage of spawning ground surveys, (4) survey method, and (5) variability in estimates of fish per redd. The effect that changes to these inputs have on estimates of survival and productivity will be evaluated. This insight will be used to help identify the factors leading to continued low abundance of steelhead in Puget Sound.

METHODS

Study Overview

The most accurate estimates of adult and smolt abundance, freshwater productivity, and marine survival were calculated, and the degree to which common sources of uncertainty in estimates of juvenile and adult steelhead abundance can influence estimates of survival and productivity was evaluated. Specifically, we designed studies to investigate the juvenile trapping efficiency, the estimate of smolt production from resident mothers, the redd-accounting error, and the range of estimates of fish per redd. Information gleaned from these studies was used to recalculate estimates of survival and productivity to investigate the degree to which data manipulations can result in an estimate of survival and productivity within the range observed in other steelhead populations.

Study Area

The Nisqually River originates from the Nisqually Glacier on the slopes of Mount Rainier and drains 1,890 km^2 of the west slope of the Cascade Range, flowing west-northwesterly for approximately 125 km before draining into south Puget Sound northeast of Olympia, Washington. Rainfall, snowmelt, and glacial melt all contribute flow to the Nisqually River. The LaGrande (river kilometer [rkm] 68.0 on the Nisqually River, measuring from its mouth) and Alder (rkm 71.0) hydroelectric projects both influence the flow regime, and LaGrande Dam is the upstream boundary for anadromous salmonids. Downstream of LaGrande Dam, the Nisqually River flows through a mix of forested, rural, and agricultural land before bordering the Fort Lewis Military Reservation (rkm 31.0 downstream to rkm 4.0) and the Nisqually Indian Reservation (rkm 17.6 to 8.6). Below LaGrande Dam, the Nisqually river is comprised of four main tributaries (Mashel River and Muck, Ohop, and Yelm creeks) that have the potential to support fall and winter spawning populations of all five species of Pacific salmon (Quinn 2018) as well as steelhead and Cutthroat Trout *Oncorhynchus clarkii*, which spawn in the spring (Kendall et al. 2015; Losee et al. 2016).

Trap Operation

A 2.4-m rotary screw trap located at rkm 20.5 was typically installed in mid-January and operated with the intent to fish continuously through mid-August to sample the entire steelhead smolt out-migration period. However, missed catch did occur during planned and unplanned trap outages over the course of a trapping season due to a variety of reasons, such as environmental (e.g., high river flows and high debris loads), mechanical (e.g., worn out bearings), and to avoid recreational river traffic. Outages can bias abundance estimates, and therefore any missed catch was accounted for by interpolating hours not fished by the average catch rates (catch per hour) before and after the outage (Volkhardt et al. 2007).

Smolt abundance.— A stratified mark–recapture study design was used to estimate the abundance of steelhead smolts out-migrating annually. Maiden-captured fish were marked and released back into the river above the trap, some portion of which were recaptured in subsequent days.

Because smolt out-migration lasts several weeks, marking schemes were stratified weekly to minimize bias in trap efficiency by accounting for temporal changes in capture rates caused by variable environmental conditions (e.g., flow, debris loads) that may occur over the course of the out-migration. A *G*-test (Sokal and Rohlf 1995) was used to test for homogeneous capture rates between adjacent weeks and guide decisions regarding how to combine continuous homogeneous mark–recapture trials to increase sample size and thus increase estimate precision. Stratified abundance estimates were made using the Baily modification of the Lincoln–Petersen estimator (Seber 1992). Stratum estimates were summed to estimate total abundance.

Smolt Age Composition

Age composition estimates were used to partition annual abundance estimates into production by brood year. Nisqually River smolts were sampled for scales at a target rate of 10% to estimate age composition of the migrating smolts. Scales were taken from the preferred area for salmonids, about three rows above the lateral line between the posterior dorsal fin ray and the anterior anal fin ray (Clutter and Whitesel 1956; Scarnecchia 1979). Scales were mounted in the field on gummed scale cards, and acetate impressions were made using a heated press in the laboratory. All scales were read on a rear-projecting microfiche reader (48×). Ages were assigned based on formation of annuli given a birthday of January 1. An annulus is defined as a period of tighter scale circuli spacing (winter) followed by a period of wider circuli spacing (summer). Using annuli to estimate age has been validated for naturally produced juvenile O. *mykiss* smolts, where ages were approximately 95% accurate (Dauer et al. 2009). Scales were not sampled in 2009 and 2010; thus, we used the following 5-year average for ages 1 through 4 to fill these gaps.

Adult Abundance

In the absence of an adult fish trap or counting device, salmonid managers rely on the enumeration of spawning nests to estimate the abundance of spawning steelhead. Steelhead redds were enumerated in the Nisqually River through a combination of float and foot surveys conducted by the WDFW, the Nisqually Indian Tribe, and staff from Joint Base Lewis–McChord across known steelhead spawning grounds in the Nisqually River basin, including the Nisqually River, Mashel River, Little Mashel River, Ohop Creek, Muck Creek, and Yelm Creek, during the winter and the spring. During float and foot surveys, index areas were surveyed from February 1 to June 1 using standardized salmonid redd survey methodology (Gallagher et al. 2007). Surveyors wore polarized sunglasses and brimmed caps to reduce glare. The same crew lead was assigned to train individuals to survey redds in the Nisqually River for the life of the study with few changes to the survey team, thus reducing interobserver error and allowing for a comparison of relative abundance across various timescales (i.e., days, months, and years). The locations of redds were marked with fluorescent flagging and recorded electronically in the field with a targeted survey frequency of 7 d.

Since 1990, the WDFW has relied on an estimate of fish per redd calculated from Snow Creek, an independent tributary draining into the Strait of Juan de Fuca. While Snow Creek is greater than 150 km from the mouth of the Nisqually River and is different than the Nisqually River in many ways, the estimate acquired there is robust and represents the only of its kind in the Salish Sea. The Snow Creek estimate is based on sampling and enumerating all upstream adults at a weir with 100% efficiency while also enumerating all redds during the spawning season (January through June) using standard redd survey methodology (Gallagher et al. 2007). The known number of female steelhead passed above a trap and associated redds counted above the trap were used to estimate females per redd in the Snow Creek watershed across 11 years from 1977 to 1989 (Table 1). The average number of females per redd (0.81) was multiplied by two (1:1 sex ratio) and the product (1.62) was then multiplied by the number of redds observed to estimate total escapement.

TABLE 1. Number of steelhead females, redds, and females per redd upstream of the trapping operations in Snow Creek, Washington, during 11 brood years from 1977 to 1989.

Return year and average	Females	Redds	Females per redd
1977	39	46	0.85
1978	43	59	0.73
1979	20	22	0.91
1980	52	63	0.83
1981	43	53	0.81
1982	30	43	0.70
1984	11	17	0.65
1985	34	43	0.79
1986	21	36	0.58
1987	29	25	1.16
1989	11	13	0.85
Average			0.81

Smolt Survival

Smolt-to-adult return rates for steelhead smolts leaving the Nisqually River were estimated for ocean entry years 2009 to 2014. Smolt-to-adult return rates describe the percentage of smolts that survive their period of ocean residence and return as adults, so are commonly thought of as “marine survival.” However, the Nisqually River smolt trapping operation is not at the stream mouth (it is at rkm 22.5), so some freshwater effects are included in estimates. Therefore, these estimates are referred to as “smolt survival” consistent with Kendall et al. (2017). Cohort run reconstruction was completed consistent with Allen et al. (2017) by using estimates of age for returning adults to assign the adults to a cohort (i) in a given ocean entry year. The number of total adults in a given cohort (A_i) were compared with the number of smolts from that ocean entry year cohort (S_i) to estimate the smolt-to-adult return (SAR) rate for that cohort:

$$\mathrm{SAR}_i = \frac{A_i}{S_i}.$$

No fishery or adult trap currently exists in the Nisqually River targeting steelhead; therefore, age-at-return data were not available for the study period. To estimate age at return and assign adults to the appropriate ocean entry year cohort, annual age data collected from the White River, a tributary of the Puyallup River, was applied to adult returns in the Nisqually River. Estimates of age for steelhead returning to the White River represent the best source of age data in southern Puget Sound given that 100% of steelhead passing upstream are sampled at the Buckley Trap, limiting bias associated with size or gear type. Additionally, the White River is a neighboring system to the Nisqually River with similar geology (glacial, rain dominated) and geographic location (southern Puget Sound) and has been sampled for scales from 1985 to 2019 with the exception of a 5-year period of no sampling between 1993 and 1998. Applying age data from a neighboring system assumes that the age composition of returning adults is similar between the White River and Nisqually River. If this assumption is false it would be expected to have little effect on long-term survival trends because estimates of adults and smolts during the time series are independent of estimates of age. Rather, inaccurate estimates of age would have an effect on how the total number of individuals are assigned to brood year, with the potential to effect patterns of interannual variability in survival and productivity.

To understand how smolt survival rates of wild Nisqually River steelhead relate to those of other systems, annual estimates of smolt survival were compared with estimates of wild smolt survival in other systems reported in Kendall et al. (2017) and in unpublished estimates from the WDFW during the same time period (2009–2014; Table 2).

Productivity

The number of smolts per spawner (productivity) was calculated for brood years 2008 through 2014 using adult abundance, smolt abundance, and smolt age composition. Age-specific estimates of smolt production allowed for the assignment of out-migrating smolts from a given ocean entry year to a particular spawning cohort (brood year). For example, adults spawning in brood year 2008 produced smolts out-migrating in ocean entry years 2009 (age 1), 2010 (age 2), 2011 (age 3), and 2012 (age 4). Smolts attributed to a given brood year were summed and then divided by the spawner abundance of that brood year for an estimate of productivity for a given cohort.

To understand how rates of productivity for Nisqually River steelhead relate to those of other systems, annual estimates of productivity were compared to estimates in other systems during the same time period (2009–2014) reported in Kendall et al. (2017) and in unpublished WDFW data (Table 2).

Factors Influencing Estimates of Adult and Juvenile Abundance

Aerial redd surveys.— In many areas within the range of steelhead, managers rely solely on data acquired from visual counts of redds via aircraft. While aerial surveys have been shown to provide consistent estimates of relative abundance for steelhead, limited information is available to describe the magnitude and direction of bias of data acquired through ground versus flight data. To understand the potential error associated with flight and ground methods, floats and flights of index reaches were conducted throughout the watershed between 2004 and 2013. Index areas were selected for paired float and flight surveys across two different habitat types existing in the main stem of the Nisqually River: Puget Sound Prairie and Puget Lowland (Nisqually River Steelhead Recovery Team 2014). Ground surveys of index areas took place every 7 d (weather permitting) and were followed by biweekly aerial surveys when weather allowed. The number of redds observed from the air was compared with those observed on the ground within index reaches for all years where floats were conducted consistently prior to flights. The percent difference between flight and float surveys was calculated by dividing the difference in the number of redds observed in flights and floats by the number of redds observed on floats. Calculations were performed for each year of the study for the two habitat types that were previously defined on the main-stem Nisqually River (Puget Sound Prairies and Cascade Lowland), as well as all index areas combined.

Fish per redd.— To evaluate the sensitivity of estimates of survival and productivity to changes in the estimate of fish per redd, estimates of fish per redd in Snow Creek (described above) were compared with estimates of fish

TABLE 2. Survival (smolt-to-adult return [SAR] rate) and productivity (smolts per spawner) of naturally produced *Oncorhynchus mykiss* from a variety of streams in Washington State (Kendall et al. 2017; WDFW, unpublished data).

			Survival (% SAR)			Productivity		
Population	Region	Run type	Ocean entry years	Mean	Range	Brood years	Mean	Range
Nisqually River	Puget Sound	Winter	2009–2014	1.7	0.2–3.7	2008–2014	153	28.5–271.8
Big Beef Creek	Puget Sound	Winter	2009–2014	4.2	0.7–4.2	2008–2010	43.8	14.8–85.2
Snow Creek	Puget Sound	Winter	2009–2011	4.9	2.9–6.8	2008–2011	60.2	25.4–88.4
Bingham Creek	Chehalis River	Winter	2009	5.6		2008–2013	19.8	6.3–32.7
Coweeman River	Lower Columbia River	Winter	2010	1.3		2009–2013	57.3	26.9–106.8
Kalama River	Lower Columbia River	Winter + summer	2009	6.2		2008–2013	19.5	8.4–30.9
Wind River	Lower Columbia River	Summer	2009–2011	2.3	2.2–2.4	2008–2012	29.3	21.6–40.6
Touchet River	Mid Columbia River	Summer	2009–2010	4.9	2.9–6.8	2008–2012	40.3	15.5–95.2
Methow River	Upper Columbia River	Summer	2009–2010	0.8	0.8–0.8	2008	4.9	
Tucannon River	Snake River	Summer	2009–2010	0.5	0.5–0.6			

per redd reported in the literature (Table 3). Comparisons included five winter steelhead populations and one summer steelhead population where counts of total steelhead and redds allowed for estimation of fish per redd.

Expansion of survey area.— Since 2003, survey methodologies on the Nisqually River were designed to include the majority of spawning habitat (census); however, survey frequency and coverage is based in large part on environmental conditions, which affect safety and visibility, particularly in tributary reaches. In addition, results from otolith microchemistry of juvenile *O. mykiss* (methods below) sampled above a previously identified anadromous barrier revealed additional spawning by anadromous *O. mykiss* (steelhead) in the Mashel River that had not been accounted for historically. To expand traditional estimates for uncounted redds, all available spawning habitat was surveyed intensively for 3 years (2016, 2017, and 2018). The areas of the river that had been surveyed consistently in the past (index areas; Figure 1) were used to calculate the proportional contribution these index areas made to the total number of redds counted in years of intensive monitoring. Historic index areas included the main-stem Nisqually River from rkm 0.0 upstream to rkm 68.4 (La Grande Dam) and the Mashel River from rkm 0.0 (measuring from its confluence with the Nisqually River) upstream to rkm 5.1. To evaluate the potential for expanded survey reaches to influence estimates of steelhead abundance, smolt survival, and productivity rates, historical estimates of redd counts in index areas were expanded by the mean proportional contribution calculated in years of intensive monitoring to estimate a total watershed redd count for years 2004–2018 that includes previously unsurveyed areas and could be compared with historical estimates.

Otolith microchemistry.— Otolith microchemistry has been shown to be a useful tool in determining the maternal origin (resident or anadromous) of *Oncorhynchus* spp. because the progeny of anadromous females incorporate marine-derived strontium in their otolith core (Rieman et al., 1994; Zimmerman et al. 2009). In 2014, otolith microchemistry was used to both confirm the presence of anadromous *O. mykiss* above what was previously considered an anadromous barrier and estimate the contribution resident mothers make to the out-migrating *O. mykiss* smolts.

This microchemistry analysis was supplemented with otolith samples obtained from *O. mykiss* collected in various parts of the Nisqually River at various life stages to support findings from the smolt trap and "above barrier" location. Samples were collected using seining and hook-and-line techniques (David et al. 2014; Madel and Losee 2016; Winkowski and Zimmerman 2017).

For each fish, one otolith was mounted on a glass slide with thermoplastic resin. Otoliths were ground first on the distal side to provide a flat surface then flipped and ground on the proximal side to expose the primordia with a Buehler Meta Serv 250 using successive grits of sanding discs (P800, P1200; Buehler) and polished using an aluminum oxide slurry (1 μm; Buehler). To

TABLE 3. Observed number of fish per spawning nest (redd) for naturally produced *Oncorhynchus mykiss*.

Watershed and mean	Region	Run type	Study years	Adult per redd	Minimum	Maximum	Reference
Snow Creek	Puget Sound	Winter	1977–1982, 1984–1987, 1989	1.61	1.17	1.61	WDFW, unpublished
Asotin Creek	Snake River	Summer	2004	1.65			Mayer et al. 2005
Fishhawk Creek, Nehalem River	Oregon coast	Winter	1998–2000	1.96	1.44	2.50	Jacobs et al. 2002
Mill Creek, Yaquina River	Oregon coast	Winter	1998–2000	2.08	1.04	3.13	Jacobs et al. 2002
Mill Creek, Siletz River	Oregon coast	Winter	1998, 1999	2.08	2.33	1.83	Jacobs et al. 2002
Smith River, Umpqua River	Oregon coast	Winter	2000–2002	1.08	0.97	1.17	Jacobs et al. 2002
West Fork Smith River, Umpqua River	Oregon coast	Winter	2000–2003	1.64	1.27	2.25	Jacobs et al. 2002
Noyo River	Northern California	Winter	2000–2003, 2006–2008	0.84			Gallagher and Wright 2008
Pudding Creek	Northern California	Winter	2004–2008	1.61			Gallagher and Wright 2008
Caspar Creek	Northern California	Winter	2006–2008	0.99			Gallagher and Wright 2008
Mean				1.55	0.97	3.13	

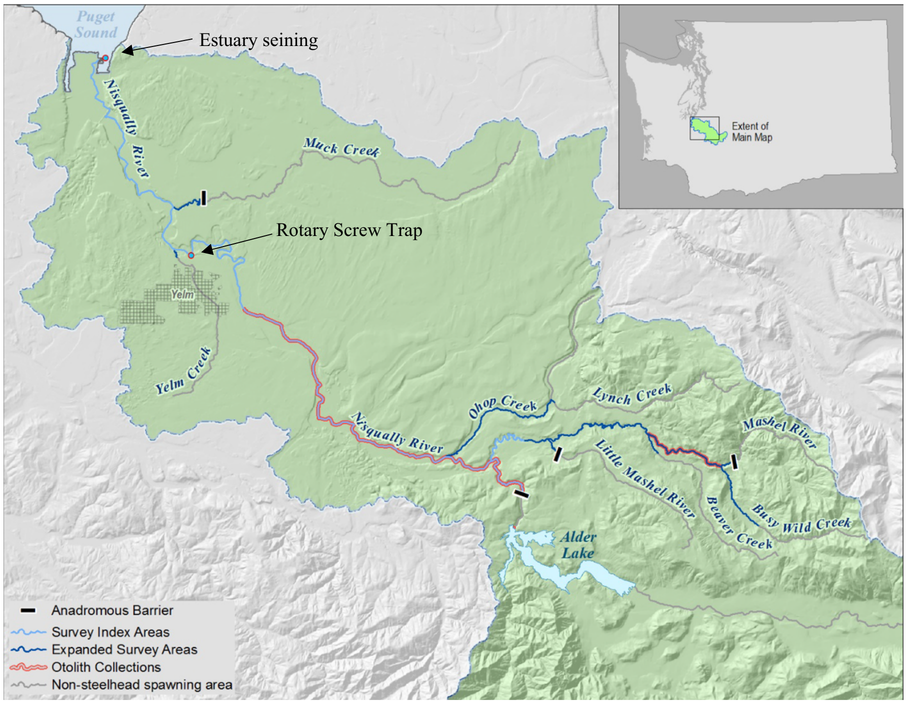

FIGURE 1. Map of the study area, showing the Nisqually River and its tributaries in Washington State.

determine the maternal origin of each sample, we measured otolith strontium (Sr) and calcium (Ca) using a Thermo X series II inductively coupled plasma mass spectrometer coupled with a Photon Machines G2 193 nm excimer laser (laser ablation inductively coupled plasma mass spectrometry) at the Keck Collaboratory for Plasma Mass Spectrometry at Oregon State University. Partial-diameter laser ablation scans were completed from the ventral side of each otolith through the primordia to the dorsal edge. The laser was set at a pulse rate of 8 Hz traveling across the sample at 5 μm/s with a spot size of 30 μm. Normalized ion ratios were converted to elemental concentration using a glass standard from the National Institute of Standards and Technology (NIST 612) and finally converted to molar ratios for analysis. Fish were classified as having either a resident or an anadromous mother based on mean Sr:Ca within the otolith core and otolith edge. A fish was determined to be progeny of a resident mother if core Sr:Ca was within two standard deviations of the mean Sr:Ca edge ratios and were progeny of an anadromous mother if the ratio was greater than two standard deviations above the mean, consistent with previously published work (Berejikian et al. 2013; Claiborne et al., in press). In total, 170 otoliths were collected from various locations and life stages for Nisqually River *O. mykiss* (Table 4) and examined for elemental chemistry.

Recalculated Estimates of Productivity and Survival

Calculations used to estimate rates of productivity and survival incorporate data from a variety of sources (Figure 2) that each carry with them sources of uncertainty. The additive effect of this variability can lead to false conclusions when comparing central tendency between groups or across time series (Feingold 1995). Estimates of smolt and adult abundance were recalculated under a variety of modeling scenarios with the goal of understanding if inputs incorporated in efforts to model productivity and survival estimates could account for the low survival and high productivity rates observed in the Nisqually River relative to other watersheds. Rather than using point estimates that represent central tendency for inputs to estimates of survival or productivity, values on the edge of the range were used to force the output in the direction of state averages. This is referred to as the “worst-case scenario” approach later. For survival, estimates that were the highest and lowest within the range of values calculated were compared with traditional estimates. Specifically, this work explored the range of smolt survival estimates and productivity that could be calculated when considering uncertainty associated with estimates of smolt abundance, redd accounting, and the contribution resident *O. mykiss* made to smolt production.

This was done by incorporating each source of variability into estimates of productivity and survival

TABLE 4. Results from otolith microchemistry estimating the contribution of anadromous and resident mothers to juvenile *Oncorhynchus mykiss* captured at four locations in the Nisqually River in 2014.

					Maternal life history	
Site	Life history	*N*	Mean FL (mm)	SD	Anadromous	Resident
Upper Mashel River	Parr	12	119.2	44.4	12	0
Screw trap	Smolt	43	188.8	19.9	39	4
Main stem[a]	Parr	89	146.6	56.9	88	1
Main stem[a]	Adult Rainbow Trout	4	265.8	44.8	4	0
Estuary seining[a]	Smolt	22	194.8	17.0	22	0

[a]Supplementary collections.

independently, resulting in multiple iterative estimates. The percent change was then compared across these estimates. For smolt trap estimates, the lower bound of 95% confidence intervals was utilized and it was assumed that smolts produced from resident females do not contribute to the production of returning adults. In other words, the total smolt estimate in all years was reduced by the percent of sampled smolts that originated from resident mothers. Uncertainty associated with adult surveys was then included by using an estimate of redds that included redds unseen in historical estimates and applying the maximum reported number of fish per redd for winter steelhead (Table 3) to calculations.

Other well-documented sources of error include the influence of hatchery-origin fish and removals from fisheries. During the life of the study there were no hatchery-produced steelhead released or targeted fisheries for steelhead; therefore, these factors were not explored.

Finally, a stepwise approach was used to better understand the cumulative effect that sources of uncertainty described above could have when combined. Survival and productivity were calculated through multiple iterations, as described above, each with one additional source of uncertainty included.

RESULTS

Smolt Abundance

From 2009 to 2018, the estimated number of steelhead smolts out-migrating from the Nisqually River ranged from a low of 20,178 in 2012 to a high of 133,597 in 2018, with coefficients of variation ranging from 9.5% (2011) to 26.7% (2012). Using the *G*-test (Sokal and Rohlf 1995) to combine stratified estimates for increased precision tended to pool estimates into a single stratum for 6

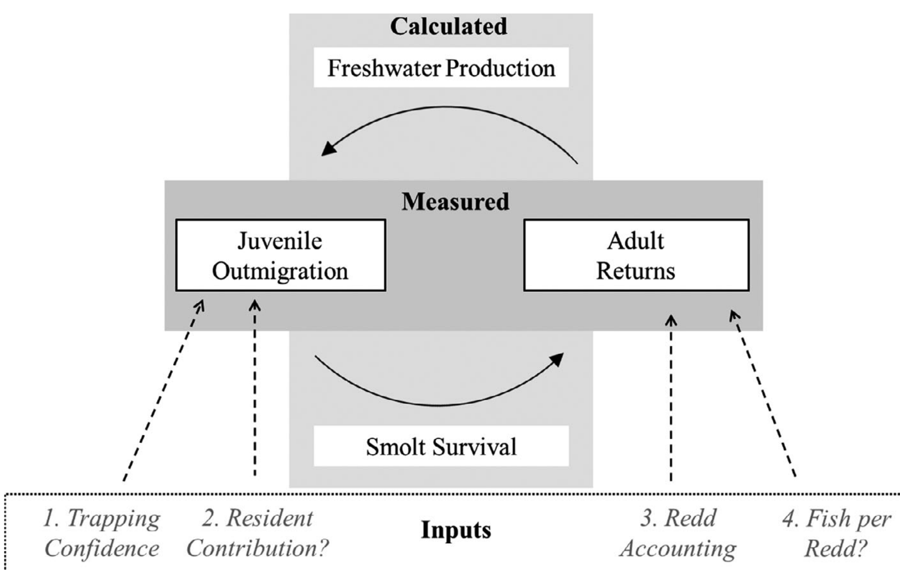

FIGURE 2. Conceptual diagram highlighting four sources of error associated with estimates of juvenile out-migration and adult returns of steelhead and the corresponding effect this error would have on estimates of productivity and survival.

of the 10 years available (2012, 2012–2018), into two strata for 3 years (2009, 2011, 2013), and into three strata for 1 year (2010).

The age of out-migrating smolts was dominated by age-2 fish in all years (mean ± SD = 61.1 ± 0.11%); however, age-1 and age-3 smolts were also common (mean = 27.6% and 10.5%, respectively).

Adult Abundance

Between 2004 and 2018, we counted a total of 6,190 redds in historical index reaches, including the entire mainstem Nisqually River and lower 5.1 km of the Mashel River, using the traditional methodology described above. Redd counts in the index reaches averaged 413 (SD = 254.5) annually (range = 133 in 2005 to 1,037 in 2016).

Smolt Survival

Steelhead smolt survival was variable during the study period, ranging from a low of 0.002 in ocean entry year 2009 to a high of 0.037 in ocean entry year 2012 (mean ± SD = 0.017 ± 0.013). Smolt survival was consistently lower for Nisqually River smolts than for other Washington streams and lower than all streams analyzed in all years (Figure 3C). Specifically, average rates of smolt-to-adult return for Nisqually River steelhead were 16.0% (0.006 versus 0.036) of those estimated from other streams in overlapping years of ocean entry (2009–2011; Figure 3C).

Productivity

Productivity (smolts per female) ranged from 28 for steelhead spawning in 2010 to 272 in 2011 and averaged 165 (SD = 87.3) across the study period. Nisqually River was the most productive system in all years of the study when compared to other Washington streams, with the exception of 2010 when productivity reported from Big Beef Creek was higher (85.2 versus 28.44; Figure 3D). On average, rates of productivity for steelhead spawning in the Nisqually River were 4.6 times higher than those estimates from streams in overlapping brood years (2008–2013; Figure 3D).

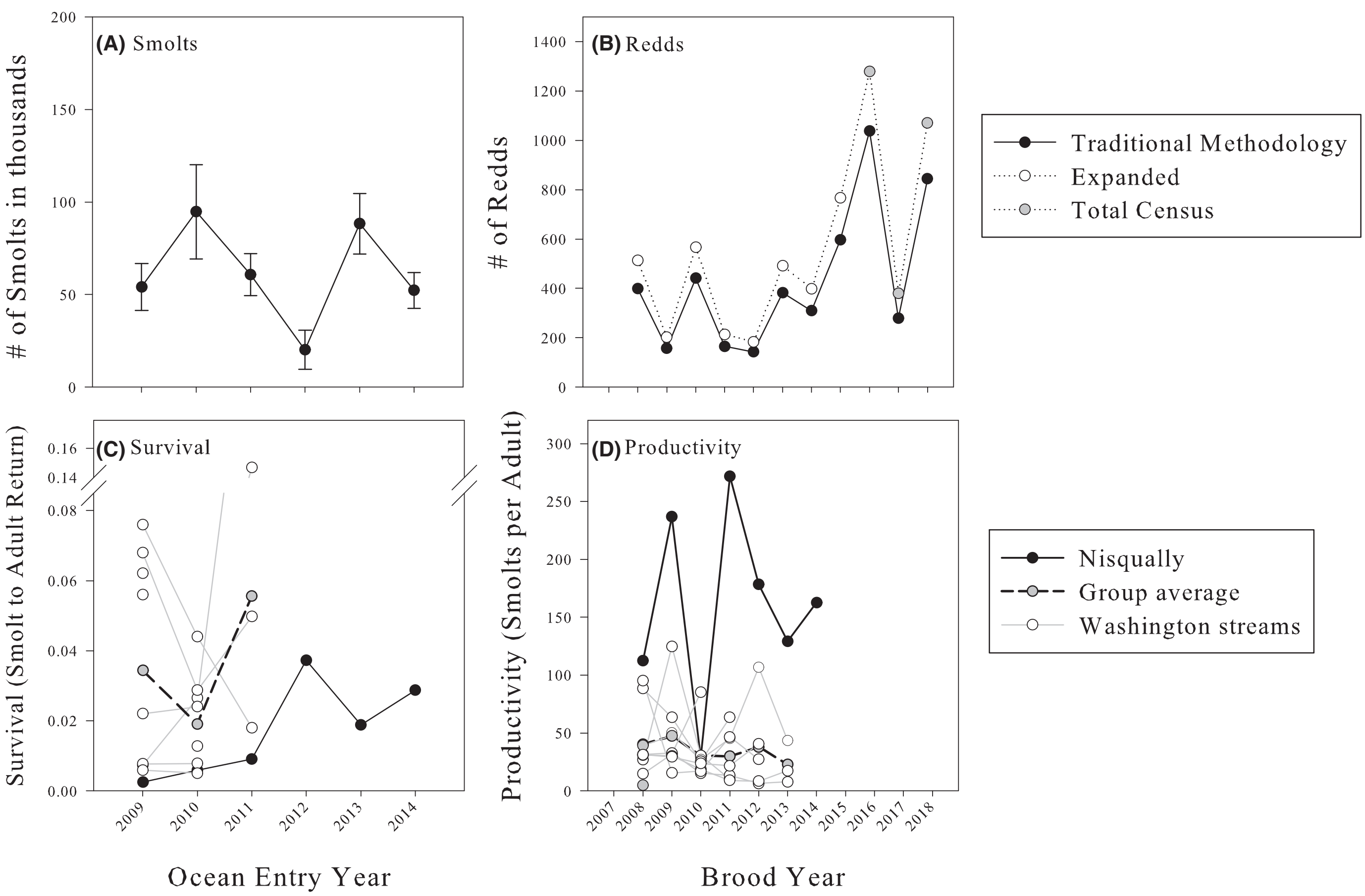

FIGURE 3. Estimates of the **(A)** number of smolts, **(B)** number of redds, **(C)** survival, and **(D)** productivity for steelhead from 2007 to 2018 in the Nisqually River, Washington. Error bars show SD.

Factors Influencing Estimates of Adult and Juvenile Abundance

Aerial redd surveys.— Aerial survey methodology consistently underestimated total redd counts in the Nisqually River, with only two exceptions in Puget Sound Prairie habitats in 2004 and 2008. On average, estimates of total redd counts from aerial surveys underestimated redds by 16.1% during the study period (Figure 4A). When index areas were organized by habitat type, aerial surveys underestimated total redd counts by 11.9% in Puget Sound Prairie habitats and 27.9% in Cascade Lowland on average (Figure 4B, C).

Fish per redd.— Estimates of fish per redd across study streams averaged 1.73 (SD = 0.33) and ranged from 1.08 for winter steelhead in the Smith River, a tributary to the Umpqua River, to a high of 2.08 in both Mill Creek of the Yaquina River and Mill Creek of the Siletz River. The estimate derived from sampling of steelhead in Snow Creek that is used to expand redd counts in the Nisqually River and other

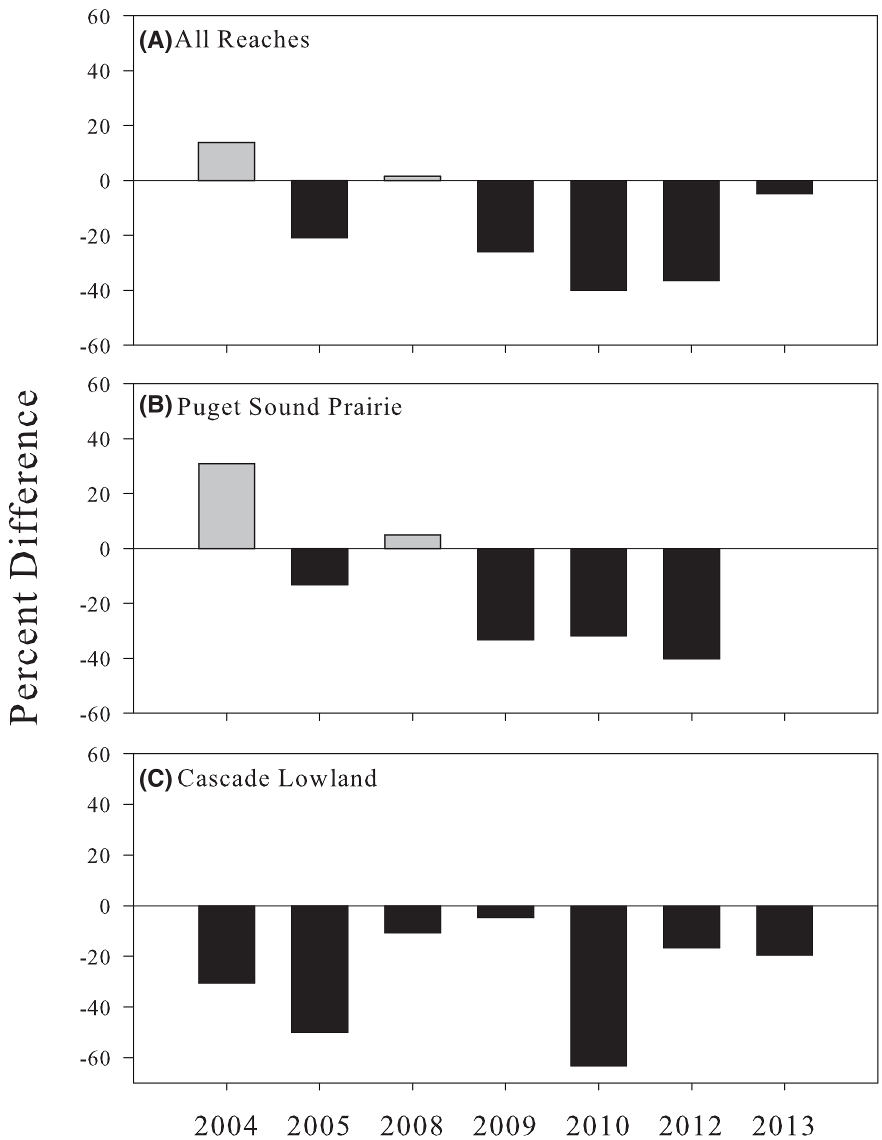

FIGURE 4. The percent that total redd counts differed using flights versus floats on **(A)** all index reaches of the main-stem Nisqually River, **(B)** reaches defined as Puget Sound Prairie, and **(C)** reaches classified as Cascade Lowland. The colors of the bars represent years where redd counts from flights were greater than those from floats (gray) or were less than those from floats (black).

rivers in Puget Sound averaged 1.61 fish/redd (SD = 0.29).

Expansion of survey area.— In 2016 through 2018, redd surveys were expanded spatially to account for survey reaches outside core index areas. Expansions included an additional 19 km of survey area of the Mashel River, as well as reaches in Yelm, Muck, Ohop, Busywild, and Beaver creeks (Figure 1), which were surveyed intermittently during the study period but not included in calculations consistently. Including the redds counted in expanded survey areas resulted in an increased total redd count by an average of 22.2% (range = 18.9% in 2016 to 26.6% in 2017; Figure 3B). Expanding redd counts by 22.2% across other years in the study period (2008–2015) resulted in a mean redd count of 527 (SD = 316.0) compared with 413 (254.5) prior to applying expansion.

Otolith microchemistry.— All *O. mykiss* sampled in 2014 above what was previously thought to be an anadromous barrier ($N = 12$; Table 4) originated from anadromous mothers based on otolith microchemistry. Results from otolith analysis were the impetus for expanding spawning ground surveys in the Mashel River above rkm 19, informing spawning ground survey methodology in years 2016–2018.

Otolith microchemistry analysis of steelhead smolts revealed a high proportion of individuals originating from resident mothers. Specifically, 9.3% ($N = 4/43$; Table 4) of otoliths sampled from smolts had levels of Sr:Ca at the core, consistent with a resident maternal signal. In contrast, supplementary sampling of *O. mykiss* throughout the Nisqually River and estuary revealed a low frequency of individuals produced from resident mothers. Specifically 1.1% ($N = 1/88$; Table 4) of parr sampled in the main stem of the Nisqually River were the product of resident mothers, and less than 1% of both resident adults (freshwater residents determined from scales) and smolts captured in the estuary (0/4 and 0/22, respectively) were the product of resident mothers.

Recalculated Estimates of Productivity and Survival

When evaluated independently, inputs incorporated in estimates of juvenile and adult steelhead abundance had a strong influence on estimates of survival and productivity, with estimates of fish per redd having the strongest influence (Tables 5 and 6). Calculating survival and productivity using the maximum reported estimate of fish per redd altered final estimates of productivity and survival by 52% and 48%, respectively, when compared with the traditional estimate. Uncertainty around smolt trap estimates (95% confidence intervals) also had a strong effect on survival and productivity. When assuming that the lower bound of the 95% confidence interval for smolt production represented the actual abundance, freshwater productivity decreased by 23% and survival increased by 54%.

Under all scenarios, Nisqually River steelhead demonstrated anomalously low survival and high productivity

TABLE 5. Five estimates of productivity (smolts per spawner) of Nisqually River steelhead, each adjusted to incorporate one type of error.

	Brood year								
Source of error	2008	2009	2010	2011	2012	2013	2014	Mean	Mean change (%)
Traditional estimate	237	28	272	178	129	163	62	153	
Smolt trapping, lower bound of 95% CI	181	19	212	145	100	117	46	117	–23
Resident contribution	215	26	246	162	117	148	56	138	–9
Redd surveys, spatial distribution	218	25	244	166	118	156	58	141	–8
Fish per redd, maximum reported	113	13	127	86	61	81	30	73	–52
Aerial redd counts, mean error	150	305	29	302	198	143	180	187	22

TABLE 6. Estimates of survival (smolts per adult return) of Nisqually River steelhead, each adjusted to incorporate one type of error.

	Ocean entry year								
Source of error	2009	2010	2011	2012	2013	2014	2015	Mean	Mean change (%)
Traditional estimate	0.002	0.006	0.009	0.037	0.019	0.029	0.005	0.015	
Smolt trapping, lower bound of 95% CI	0.003	0.008	0.011	0.078	0.023	0.035	0.006	0.024	54
Resident contribution	0.003	0.007	0.010	0.041	0.021	0.032	0.005	0.017	10
Redd surveys, spatial distribution	0.003	0.007	0.010	0.041	0.020	0.029	0.005	0.016	7
Fish per redd, maximum reported	0.004	0.010	0.015	0.060	0.030	0.039	0.000	0.023	48
Aerial redd counts, mean error	0.002	0.005	0.008	0.033	0.017	0.026	0.004	0.014	–10

compared with the statewide average. When uncertainty was compounded, in a "worst-case scenario" analysis, survival for wild Nisqually River steelhead smolts remained low and productivity remained high relative to estimates for other wild steelhead populations (Table 2). Specifically, average survival during the study period was 50.5% lower than and productivity was 52.4% higher than other Washington streams (Figure 5).

DISCUSSION

We concluded that variability in estimates of adult and smolt abundance had a strong effect on estimates of smolt survival and freshwater productivity in the Nisqually River. However, estimate measurement error did not account for the anomalously high productivity and low smolt survival relative to steelhead populations outside Puget Sound. Results reported here add overwhelming support for conclusions others have made (Nisqually River Steelhead Recovery Team 2014; Moore et al. 2015; Klungle et al. 2018) reporting poor marine survival for Nisqually steelhead. Our inability to rectify the high productivity and low smolt survival aligns with a number of studies regarding the conditions in marine waters and associated ecosystem dynamics that apparently have created a critical bottleneck for Puget Sound steelhead as they migrate to offshore feeding areas. For instance, recent work using acoustic telemetry has identified mortality hotspots for steelhead within Puget Sound prior to entering the nearshore marine waters of the Pacific Ocean (Moore et al. 2010, 2015). While increased marine mammal predation (Berejikian et al. 2016) and anthropogenic impacts (Sobocinski et al. 2018) have been identified as primary causes, the relationship between mortality incurred in the Salish Sea versus the Pacific Ocean for steelhead has not been well studied. Additionally, the early marine period has been identified as a critical period for all anadromous salmonids (Smith and Ward 2000; Beamish and Mahnken 2001; Quinn 2018) and basin-scale ocean process in the northern Pacific Ocean have been shown to influence the condition of early ocean-migrating steelhead (Thalmann et al. 2020); therefore, it is important to understand how mortality incurred in Puget Sound compares with that in the Pacific Ocean. It is possible that ocean survival rates among fish that have survived Puget Sound are high relative to coastal stocks. By investigating the relationship between the abundance of juvenile and adult steelhead, the current study strengthens our understanding of poor marine survival for Puget Sound steelhead and suggests that the cumulative mortality associated with various phases of the marine period is high for Puget Sound steelhead. Future research should be focused on identifying and quantifying phases of marine mortality for Puget Sound steelhead to aid in the forecasting of adult returns and guide recovery efforts.

The majority of steelhead escapement estimates throughout the range rely on enumerating redds on the

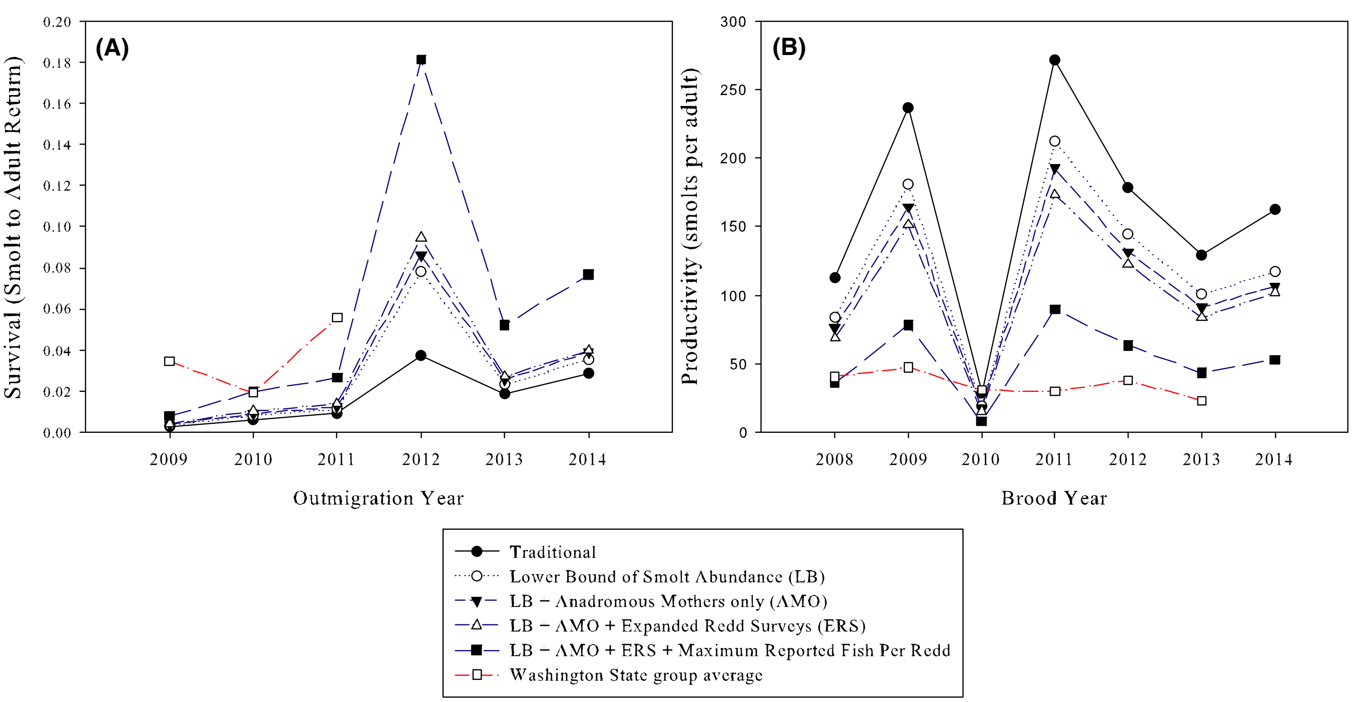

FIGURE 5. Comparison of estimates of **(A)** survival and **(B)** productivity utilizing increasingly conservative estimates of inputs for steelhead in the Nisqually River, Washington.

spawning grounds and expanding those counts by an estimate of fish per redd. Ideally, an estimate of fish per redd originates from the stream of interest, thus controlling for spatial and temporal variability in spawning of locally adapted populations. However, our review of the literature revealed that estimates of fish per redd are lacking and highly variable. More importantly, results from the current study indicate that estimates of fish per redd have a strong influence on the estimated abundance of the spawning stock, with the potential for a 2.5-fold difference in estimated spawner abundance. For the Nisqually River, a large watershed comprising a diversity of habitat types, managers and biologists rely on an estimate of fish per redd acquired from Snow Creek, a small independent tributary approximately 300 km from the Nisqually River. Given the federal mandate to recover Puget Sound steelhead under the ESA, we suggest incorporating new technologies (e.g., sonar, tagging, and tracking) to aid in accurate accounting of escapement, survival, and productivity or prioritizing stream-specific estimates of fish per redd. In addition, protecting long-term time series such as that produced in Snow Creek (longest running juvenile and adult steelhead trapping dataset in the world) will allow for comparisons with new and improved estimates and methodologies.

It is well known that *O. mykiss* exhibit a diversity of life histories, including resident, anadromous, and partial migrations (Kendall et al. 2015). Numerous studies have explored the genetic differentiation between concurring steelhead and Rainbow Trout and demonstrated exchange of genetic material between multiple life histories across the range (Docker and Heath 2003; McPhee et al. 2007). Furthermore, recovery plans, management plans, and technical reports have highlighted the importance of protecting all life histories to promote long-term stability and diversity (Marshall et al. 2006; Scott and Gill 2008; Blanton et al. 2011; McPhee et al. 2014; Madel and Losee 2016; NMFS 2019). Regardless, rules designed to protect ESA-listed steelhead rarely consider or protect resident life histories (Rainbow Trout). At the time the current study was published, Washington State fishing rules required the release of wild steelhead statewide. In contrast, the statewide rule for Rainbow Trout allows for a daily harvest limit of two wild Rainbow Trout over 8 inches (~20 cm) unless special, stream-specific rules differ. By analyzing otoliths of out-migrating steelhead smolts we show that ~10% of smolts out-migrating in the Nisqually River were the product of mothers that had never entered the marine environment. While the finding that the spawning of resident mothers can result in the production of anadromous offspring is not novel (Hayes et al. 2012), the current study is the first, to our knowledge, that has quantified the proportion of smolt production attributed to resident life histories (Rainbow Trout). Despite conservative management practices for Puget Sound's anadromous *O. mykiss* and extensive work focused on recovery, steelhead in Puget Sound remain threatened under the ESA. A better understanding of the relative survival of steelhead smolts produced from resident versus anadromous parents would help to prioritize recovery efforts across multiple life history strategies. Until then, the understanding that resident life histories produce anadromous offspring as demonstrated in the Nisqually River supports a management strategy that protects all life histories contributing to steelhead production.

Given the elusive nature of steelhead and the remote spawning areas utilized, managers frequently rely on aerial surveys to enumerate redds of steelhead. Aerial redd counts are considered a conservative estimate of relative abundance given the potential for redds to go undetected from the air due to obstructions in visibility. Additionally, it is possible that observations from the air could overestimate the number of steelhead redds present when features in the river produced by other species (Cutthroat Trout, Pacific Lamprey *Entosphenus tridentatus*) or associated with human activity (boats) or hydraulics are misidentified as steelhead redds. For these reasons, error associated with aerial surveys has the potential to skew estimates of productivity and survival but has not been fully evaluated. Overall, we found that aerial surveys in the Nisqually River have the potential to underestimate redds by up to 63%, suggesting that a large proportion of steelhead redds present were not observed from the air. While biologists and managers may view redd-based estimates of abundance as conservative, their use as input in calculations of performance metrics introduces a risk to accuracy. For example, if aerial surveys were relied on in the Nisqually River to enumerate redds, an underestimate of adults (generated from biased-low redd counts) has the potential to lead to a significant underestimate of productivity and overestimate of survival, obscuring the understanding of key recovery benchmarks. In areas where steelhead are listed as threatened under the ESA, foot surveys conducted by trained, experienced surveyors will generate the most accurate estimates (Susac and Jacobs 1999) and should be prioritized.

Conclusion

Results reported here reveal numerous findings that are important for consideration by fish managers. Foremost, our results support previous conclusions that Puget Sound steelhead are faced with exceptionally poor marine survival. While research focused on steelhead in Puget Sound has only recently accelerated in effort, evidence is overwhelming that marine survival is the most important factor limiting the recovery of ESA-listed steelhead. For that reason, short-term actions must be taken to maximize the number of smolts out-migrating to Puget Sound to continue to promote the high productivity observed in recent decades. Given our observation of smolts produced by resident *O. mykiss* mothers, additional support for research focused on understudied, resident life histories and creative management actions predicted to lead to an increase in production of wild adult steelhead should be prioritized, especially in watersheds where both survival and productivity is low. Finally, our results support the continued attention on the marine phase of the steelhead life history. With survival rates for steelhead originating from Puget Sound ranking among the lowest in the world, a collaborative effort to improve ecosystem dynamics and habitat for steelhead during their early ocean migration should remain a high priority. Marine habitat work should also be coupled with research comparing Puget Sound survival with ultimate spawner abundance to fine tune recovery efforts and improve forecasting efforts.

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