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FEATURED PAPER

Historical Records Reveal Changes to the Migration Timing and Abundance of Winter Steelhead in Olympic Peninsula Rivers, Washington State, USA

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Abstract
We analyzed multiple historical data sources (circa 1948–1960) to estimate migration timing and abundance of Olympic Peninsula winter steelhead *Oncorhynchus mykiss* in the Quillayute, Hoh, Queets, and Quinault rivers, Washington, to provide context for contemporary (circa 1980–2017) population trends. Contemporary wild winter steelhead migrations peak 1–2 months later than historical migrations, and migration timing breadth has contracted by up to 26 d (a 37% reduction of the interquartile range of the migration timing distribution). Migration timing changes coincide with an era of peak industrial forestry and introductions of early migrating hatchery winter steelhead stocks. We estimate that contemporary mean wild winter steelhead abundance has declined by 55% across populations compared to circa 1948–1960 historical means, with 1920s records suggesting declines of up to 77% in the Queets River. Migration timing shifts and the magnitude of population declines are not evident in modern fisheries monitoring records, which began around 1980. Our results demonstrate how modest extensions of the period of record (e.g., 30 years) increase the power to identify population changes that are not readily apparent from contemporary fisheries monitoring programs. Historical fisheries data can help managers to avoid the shifting baseline syndrome and provide important reference points for rebuilding population diversity and abundance.

Assessing the status and trends of exploited fish populations is fundamental to their sustainable management and conservation. However, identifying reliable baselines from which to evaluate recent trends is challenging because many stocks were not monitored before being depleted (Pauly 1995; Lenders et al. 2016). This is common in anadromous Pacific salmon *Oncorhynchus* spp., for which commercial fisheries have occurred for over 150 years, but methodical collection of data on harvest, escapement, and migration timing typically did not begin until the late 20th century.

A historical baseline could improve benchmarks for population attributes that are important for contemporary fishery management, such as migration timing and abundance

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(Ricker 1946; Hilborn 1985). For example, the timing of adult migration is highly heritable and sensitive to the timing and intensity of fisheries (Tillotson and Quinn 2018), but contemporary data spanning just a few decades may miss shifts in migration timing over longer time scales or that occurred prior to the onset of modern fisheries monitoring programs (Robards and Quinn 2002; Yoshiyama and Moyle 2010; Austin et al. 2020). Changes in population abundance are also difficult to detect over relatively short time frames because trends can be obscured by estimate errors and high natural variability in ecological processes underlying fisheries data (Porszt et al. 2012). Thus, with short time series, managers are less likely to detect contemporary population changes as they are happening (d'Eon-Eggertson et al. 2015). Further, without a longer-term context, there is a risk that contemporary population assessments will suffer from the "shifting baseline syndrome" wherein reduced population abundance and diversity are increasingly accepted as the natural baseline (sensu Pauly 1995; Lotze and Worm 2008).

In many cases, historical data for exploited fish populations precede the onset of modern monitoring programs, and when analyzed, such data can provide important historical context for contemporary status and trends (e.g., Lutz 2014; Price et al. 2019). For example, multiple approaches have been used to estimate historical population baselines, including but not limited to historical fisheries and cannery records (e.g., Chapman 1986; Meengs and Lackey 2005; Gayeski et al. 2011; Chaput 2012), observations and traditional ecological knowledge (Pauly 1995; McClenachan et al. 2012; Thurstan et al. 2015), stable isotopes (Rogers et al. 2013), and genetic analysis of archived biological samples (Price et al. 2019). The historical baselines resulting from those analyses have improved knowledge about the magnitude of change in abundance as well as how long-term changes are related to climatic variation, population exploitation, habitat loss and degradation, and other factors (Beechie et al. 1994; Lenders et al. 2016).

Here, we use historical fisheries data to extend the period of record for winter steelhead *O. mykiss* migration timing and abundance on the Olympic Peninsula (OP), Washington, USA. Olympic Peninsula winter steelhead have long supported regionally important in-river fisheries, but consistent monitoring of total winter steelhead abundance, including both harvest and escapement data, began only as recently as 1980 (Cooper and Johnson 1992; Johnson et al. 1997). Previous status assessments based on these contemporary fisheries data characterized OP winter steelhead populations as healthy until very recently (Table 1). However, contemporary monitoring efforts began after an era of fish canneries, peak industrial forestry activity, and the initiation of major hatchery programs, among other potential stressors. Thus, previous characterizations of population status may have been biased by a degraded reference baseline as well as a short time series length, both of which are factors that can delay awareness of the need for conservation action (Soga and Gaston 2018). Historical data from the early to mid-20th century that predate major habitat and hatchery impacts could therefore provide an important reference baseline from which to assess contemporary populations and inform recovery goals. This is timely because abundance declines in OP winter steelhead populations have recently reached a level that has prompted emergency changes in fishery rules, including reduced season length and restrictions on recreational sportfishing methods (WDFW 2021).

Our objective was to characterize historical winter steelhead migration timing and abundance in the Quillayute, Hoh, Queets, and Quinault rivers as a basis for comparison with their contemporary winter steelhead runs. Historical data, described in detail below, spanned the period of circa 1948–1960, with occasional earlier records. Although several previous investigations have estimated historical abundances of Pacific salmon, changes in migration timing have received considerably less attention (Robards and Quinn 2002; Austin et al. 2020). Filling this knowledge gap can be important for understanding abundance trends since reduced diversity in migration timing can negatively impact population resilience (Tillotson and Quinn 2018). The availability of some historical data sources reported in weekly time intervals provided the rare opportunity to characterize both the historical timing and abundance of OP winter steelhead migrations. We analyzed historical winter steelhead data (i.e., circa 1948–1960) with contemporary data (circa 1980–2017) to address the following questions: (1)

TABLE 1. Reports that have reviewed the status and trends of wild winter steelhead populations in the Quillayute, Hoh, Queets, and Quinault rivers, Olympic Peninsula, Washington (ESA = Endangered Species Act).

Reference	Status
Nehlsen et al. (1991)	Healthy, stable to increasing trend
Busby et al. (1996)	Stable to increasing, status review determined that ESA listing was not warranted
McHenry et al. (1996)	Healthy, stable to increasing trend
Johnson et al. (1997)	Healthy, stable to increasing trend
WDFW and Western Washington Treaty Tribes (2002)	Healthy, stable to increasing trend
Kendall et al. (2017)	Declining trend in the Hoh and Queets rivers
Cram et al. (2018)	Declining trend in the Hoh, Queets, and Quinault rivers

"How does the historical migration timing of wild winter steelhead compare to that of contemporary wild and hatchery winter steelhead?"; (2) "What was the historical abundance of wild winter steelhead populations?"; and (3) "How has contemporary wild winter steelhead abundance changed relative to historical abundance, and are there wild winter steelhead abundance trends within the contemporary period?" Answers to these questions will help to clarify the value of a historical reference baseline from which to assess contemporary salmonid populations.

METHODS

Study Area and Species

The Quillayute (1,629 km^2), Hoh (770 km^2), Queets (530 km^2), and Quinault (490 km^2) River basins are the largest watersheds draining the west side of the OP (Figure 1). The basins have relatively high amounts of protected habitat, with approximately 20% of the Quillayute River, 35% of the Quinault River, 40% of the Queets River, and 65% of the Hoh River watersheds located within Olympic National Park, where the habitat is considered relatively pristine. These rivers support the largest populations of wild winter steelhead in the OP distinct population segment (Cram et al. 2018). Wild winter steelhead enter rivers from November through May just prior to spawning and after most of the maturation process has already occurred in the ocean (Quinn et al. 2016). Spawning occurs from January through June (Cederholm 1984; McMillan et al. 2007). Hatchery winter steelhead are also released in each river basin, with most hatchery stocks having a river entry timing of November to early January (Crawford 1979; Cram et al. 2018; Duda et al. 2018). Wild and hatchery winter steelhead support in-river commercial and subsistence fisheries for the Hoh, Quileute, and Quinault tribal nations and popular recreational fisheries for anglers. Fisheries are co-managed by the Washington Coast Treaty Tribes and the Washington Department of Fish and Wildlife (WDFW; United States v. Washington 1975). Unlike many West Coast winter steelhead distinct population segments, OP winter steelhead are not currently protected under the U.S. Endangered Species Act (ESA; Busby et al. 1996) and they have generally been considered healthy in previous status assessments until very recently (Table 1).

Data Sources

Historical fisheries data.— The history of Pacific salmon and winter steelhead fisheries on the west side of the OP is similar to that of many other major salmon-producing regions on the West Coast (e.g., McEvoy 1986). Following an era of Indigenous management, colonial commercial

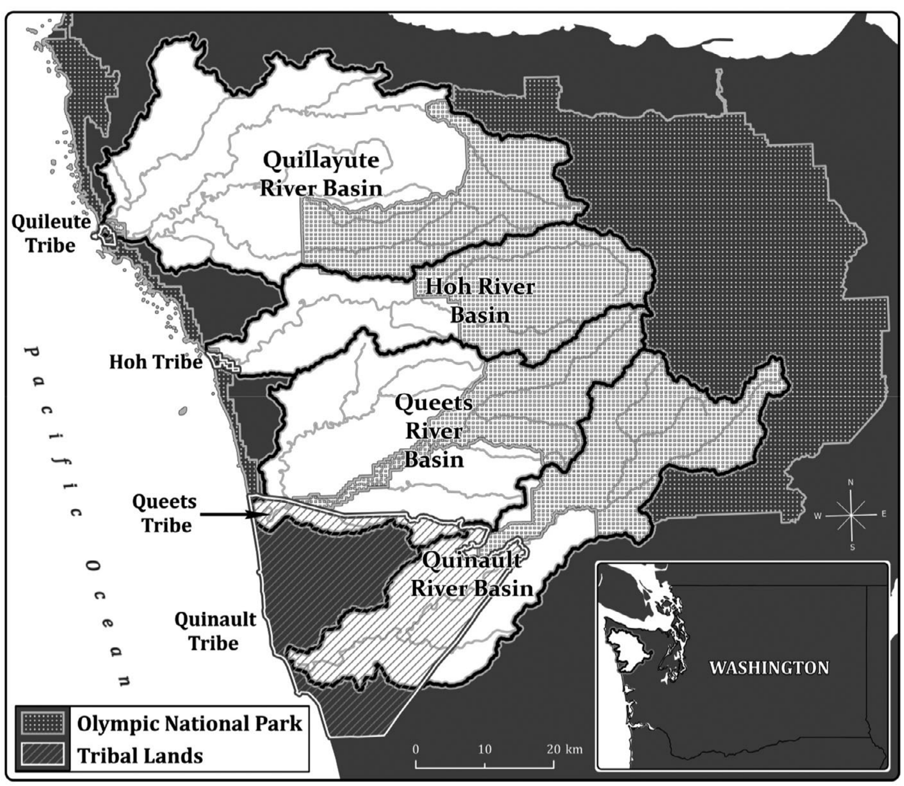

FIGURE 1. Olympic Peninsula, Washington, study watersheds for which migration timing and abundance of winter steelhead were estimated.

fisheries began in the late 1800s, with canneries operating at the mouths of most major OP rivers until their closure in the late 1920s (Cobb 1930). Canneries often recorded the catch of Chinook Salmon *O. tshawytscha* and Coho Salmon *O. kisutch* in terms of cases of processed fish, but records for winter steelhead are less common. We found only a single year for the Queets River in 1923, when more than nominal numbers of cases of winter steelhead were reported, and this represents the earliest data source we analyzed (Cobb 1930; Table 2).

Following cannery closures, Indigenous commercial and subsistence fisheries continued and recreational fisheries emerged. Information on both commercial and recreational harvest of winter steelhead was available for all populations from 1948 through 1960. Indigenous commercial and subsistence fisheries were—and generally still are—conducted in the lower portions of rivers, where gill nets are used to intercept migrating adults (Pettit 1950; Clark 1985; Wray 1997). Recreational anglers did, and still do, fish almost the entire length of many rivers and are sometimes allowed longer fishing seasons (McLeod 1944; Frear 1956). Although spawner escapement was not monitored during the historical period and thus harvest rate and run size are not known, three types of catch data were reported during this time period. First, commercial CPUE (fish caught per fisher-day) was reported for 5-d intervals from November through mid-March, averaged across multiple years from the mid-1950s to the early 1960s (Washington Department of Fisheries et al. 1973; Table 2). Second, from 1948 to 1960, commercial catch was reported as the total number of winter steelhead harvested per month from November through February, with sporadic records in March (Washington Department of Fisheries et al. 1973; Table 2). Third, recreational winter steelhead harvest was reported by month (November–April) and year from 1948 to 1960, as provided by WDFW based on sport catch record cards (Table 2).

Historical winter steelhead catch was almost entirely comprised of wild fish because this period predates the initiation of the large hatchery programs that currently operate in the study rivers (described in more detail below). We are not aware of hatchery winter steelhead releases in the Queets and Quinault rivers prior to the 1970s. However, the Quillayute River received relatively small releases of unmarked hatchery winter steelhead in 1954 (39,000 juveniles) and 1956 (22,000 juveniles), before receiving annual releases of hatchery winter steelhead beginning in 1960 (Duda et al. 2018). In the Hoh River, relatively small releases of hatchery winter steelhead first occurred in 1959 (25,982 juveniles), with annual releases of hatchery winter steelhead beginning in 1962 (Duda et al. 2018). Consequently, the Quillayute and Hoh River catch data may include a small number of unmarked adult hatchery fish in some of the latter years of the historical period, though they are unlikely to have been numerous enough to influence overall patterns of migration timing and abundance. Summer steelhead are also present in OP study rivers but at relatively low abundances compared to winter steelhead (Busby et al. 1996). Because migration timing for summer steelhead peaks in July and adults move to holding areas that are well upstream of winter steelhead fisheries (WDFW, unpublished data; J. R. McMillan, unpublished data), it is also highly unlikely that our data sources include significant numbers of summer steelhead.

Contemporary fisheries data.— We refer to circa 1980–2017 as the contemporary period for our analyses. We focus on this period because wild winter steelhead catch data from the years 1960–1980 are only intermittently available and they are confounded by the onset of consistent and increasingly large annual releases of unmarked hatchery winter steelhead (Cram et al. 2018; Duda et al. 2018). Beginning in 1980 (with some exceptions described in the Data Analysis section), monthly recreational harvest, weekly commercial harvest and effort, and spawning ground surveys were available from which to estimate winter steelhead escapement, harvest rates, and

TABLE 2. Date ranges for data sources used in analyses of historical and contemporary Olympic Peninsula, Washington, winter steelhead populations, including fisheries catch, CPUE (fish caught per fisher-day), and contemporary escapement records.

Population	Historical period		Contemporary period	
	Commercial and recreational catch	Commercial CPUE	Commercial and recreational catch and escapement	Commercial CPUE
Quillayute River	1948–1960	1958–1963	1978–2017	2000–2017
Hoh River	1948–1960	1956–1959; 1961–1963	1980–2017	2000–2017
Queets River	1923[a]; 1948–1960	1956–1963	1980–2017	2000–2017
Quinault River	1948–1960	1956–1959; 1961–1963	1980–2013	NA

[a]Data from Queets River cannery records.

total run size and migration timing (Table 2). However, while contemporary fisheries data are more complete than data from the historical period, they are complicated by the release of unmarked hatchery winter steelhead. By 1981, hatchery winter steelhead were being released in substantial numbers in each watershed (Duda et al. 2018), and they were not outwardly marked with an adipose fin clip in the Quillayute and Hoh rivers until adults returned in 1986 (Cram et al. 2018). Hatchery winter steelhead remain unmarked in the Queets and Quinault rivers, where determination of origin (hatchery or wild) is made via scale analysis after the fish are harvested. Detailed summaries of OP hatchery winter steelhead programs are provided by Cram et al. (2018) and Duda et al. (2018). Briefly, since 1980, the annual releases of hatchery winter steelhead have averaged 192,823 smolts in the Quillayute River, 109,327 smolts in the Hoh River, 147,291 smolts in the Queets River, and 598,385 smolts in the Quinault River. To eliminate possible confusion between hatchery and wild winter steelhead in the contemporary catch data, we relied on harvest and CPUE data from a subset of the contemporary period for some analyses, as described in greater detail in the Data Analysis section below.

Data Analysis

Question 1: What was the historical migration timing of wild winter steelhead, and how does it compare to the contemporary migration timing of wild and hatchery winter steelhead?.—We used commercial fishery CPUE data (number of fish captured per fisher-day; Table 2) to estimate the historical migration timing of wild winter steelhead and the contemporary migration timing of wild and hatchery winter steelhead. Winter steelhead enter rivers in an advanced state of maturation and move relatively quickly to spawning grounds, which are almost exclusively above the areas where commercial fishing occurs. Thus, we assumed that the number of fish entering the river (N_i) during each 5-d period i (nominally "week$_i$") was proportional to weekly CPUE$_i$. This follows when describing catch during week$_i$ as the product of N_i, weekly fishing effort (E_i), and weekly capture efficiency (q_i):

$$C_i = N_i E_i q_i. \tag{1}$$

For this analysis, in the absence of weekly catch efficiency values, we made the simplifying assumption that capture efficiency was approximately equal across the winter steelhead run. Although catch efficiency likely varies through the fishing season, a sensitivity analysis revealed that our results are robust to deviations from this assumption (see the Supplemental Material available in the online version of this article). Assuming that capture efficiency is approximately equal across the run ($q_i = q$), then

$$N_i = \frac{1}{q}\frac{C_i}{E_i} = \frac{\mathrm{CPUE}_i}{q}. \tag{2}$$

For the historical period, CPUE$_i$ was reported as weekly averages across a 6–9-year period (Table 2). For the contemporary period, we calculated average weekly CPUE$_i$ estimates for all populations except the Quinault River, as contemporary fisheries effort data were not available for that population. We calculated contemporary weekly CPUE$_i$ separately for hatchery and wild winter steelhead over a period common to all populations when fishing effort appeared to be relatively consistent (i.e., 2000–2017).

Because CPUE$_i$ data were typically not available at the very beginning and end of when fish entered the rivers, we fitted beta distributions to the historical and contemporary CPUE$_i$ values to estimate the tails of the migration period. We constrained these distributions to start no earlier than October 15 and to end no later than June 1 based on visual inspection of the data and knowledge of winter steelhead migration timing from the study area (McHenry et al. 1996; McMillan et al. 2007) and from other coastal winter steelhead populations (Shapovalov and Taft 1954; Withler 1966; Busby et al. 1996; Cram et al. 2018).

Lastly, during the contemporary period, there were some years with gaps in CPUE$_i$ data during weeks toward the end of the migration. To account for those gaps while still taking advantage of the available data, we first fitted a simple two-way ANOVA model (main effects for week and year) to the log-transformed CPUE$_i$ data and used predictions based on this model to impute missing CPUE$_i$ values. To match the historical CPUE$_i$ data, the complete contemporary CPUE$_i$ series was then averaged across years to produce a single value for each week and each river.

To compare migration timing between historical wild winter steelhead, contemporary wild winter steelhead, and contemporary hatchery winter steelhead, we used the following metrics derived from the beta distributions that were fitted to the CPUE$_i$ data: (1) the Julian dates at which 25% ($q25$) and 50% ($q50$) of the run had passed; (2) the number of days that elapsed between when 25% and 75% of the run had passed (interquartile range [IQR]); and (3) the percentage of the run that had passed by January 1 (*pJan1*). We identified the latter metric as a useful migration timing benchmark after visual inspection of the data suggested large differences between historical and contemporary periods in the frequency of migration prior to January 1. For each metric and population, we calculated the difference in migration timing (1) between the contemporary wild and historical wild winter steelhead and (2) between the contemporary wild and contemporary hatchery winter steelhead.

To account for uncertainty in the beta function fit to the $CPUE_i$ data, we used a parametric bootstrap procedure to construct 95% confidence intervals (CIs). The bootstrap procedure accounted for potential autocorrelation in $CPUE_i$ residuals around the beta function fit by drawing simulated residuals from an autoregressive time series model fitted to the observed residuals. Bootstrap CIs should be viewed as approximate because sample sizes were relatively small, capture efficiency may have changed during the fishing season, and start and stop dates for winter steelhead migration were presumed.

Question 2: What was the historical abundance of winter steelhead?.— We used multiple approaches to estimate historical winter steelhead run sizes under the assumption that congruence in results from different methods would increase confidence in our analyses. The approaches were based on the following data: (1) Queets River cannery records from 1923; (2) commercial and recreational fisheries catch from all four study rivers during 1948–1960; (3) CPUE data from commercial fisheries during the mid-1950s to early 1960s; and (4) relationships between watershed size and historical winter steelhead abundance from U.S. West Coast watersheds.

As described in more detail below, each approach included a different set of assumptions and we therefore chose not to consider any single approach to produce a "best estimate." Instead, we averaged results across analysis approaches because this can reduce bias associated with individual approaches (Dormann et al. 2018). Consequently, after producing point estimates of abundance from each approach, we generated ensemble abundance estimates for the historical period based on the average of the central tendencies from each individual analysis. We excluded Queets River cannery records from the ensemble estimates because similar data were not available for the other populations.

Approach 1: 1923 winter steelhead abundance estimate from Queets River cannery records.— Our first approach was to expand the 1923 catch records for winter steelhead from the Queets River cannery (Cobb 1930) to estimate total abundance by using the reported number of winter steelhead cases, estimates of cannery packing wastage rates, and a range of assumed harvest rates (e.g., Craig and Hacker 1940; Myers et al. 1998; Yoshiyama and Moyle 2010).

The formula we used to expand the cannery records into total run size (N) is

$$N = \frac{Cwt}{[(1 - Wa) \times STw \times R]}, \tag{3}$$

where Cwt represents the total weight of fish in all of the cases combined, Wa is the wastage rate, STw is the average weight of Queets River winter steelhead, and R is the harvest rate.

For all calculations, we used the original values reported in English units (lb) to be consistent with historical data sources. We first converted the number of cases of canned winter steelhead into the total canned fish weight (Cwt). Each case contained 48 cans at 1 lb (0.45 kg) per can, or 48 lb (22 kg) per case (Cobb 1930). Canned fish weight is a fraction of the total fish weight at capture because nonessential fish parts (e.g., head, tail, and internal organs) were removed prior to canning. To account for this loss, we used a wastage rate (Wa) of 0.40, as reported for Chinook Salmon (Myers et al. 1998; Yoshiyama and Moyle 2010). We did not attempt to account for whole fish that were discarded due to spoilage or other factors common in canneries during that era (Yoshiyama and Moyle 2010); therefore, our estimate of Wa is likely to be conservatively low. We then divided the total weight of the harvest by the average historical weight of Queets River winter steelhead (9.8 lb [4.4 kg]; Washington Department of Game 1934) to estimate the total number of winter steelhead harvested. Finally, to expand the number of harvested winter steelhead to a total run size, we used contemporary wild winter steelhead harvest rates (R) to estimate the fraction of the total run harvested by the cannery. Because catch expansion estimates are sensitive to assumed harvest rates (e.g., Cramer and Caldwell 2020), we used a range of plausible values for R (0.28, 0.38, and 0.44) corresponding to the 25%, 50% (median), and 75% quantiles of contemporary annual harvest rates for Queets River wild winter steelhead. These values were used to establish the expected range around the reconstructed abundance estimate. These harvest rates are similar to the range of historical harvest rates ($R = 0.28$–0.57) observed in Columbia River salmon and steelhead fisheries during the same era (Craig and Hacker 1940).

Approach 2: abundance estimates from the 1948–1960 winter steelhead catch.— For our second approach, we expanded the combined annual commercial and recreational fisheries catch from the period 1948–1960 in all four populations to estimate total annual run sizes. To expand annual catch records, we used values for harvest rates and the length of the fishing season relative to the duration of the total winter steelhead migration period to estimate the historical run sizes (N) as

$$N = \frac{C}{RP}, \tag{4}$$

where C is the reported catch, R is the harvest rate, and P is the proportion of the historical run that was available to harvest relative to that for the contemporary period.

The parameter P is necessary to estimate because the proportion of the total wild winter steelhead run that was available to fishers differed between the historical and contemporary periods. Fishing occurred over a relatively greater proportion of the wild winter steelhead run during the contemporary period due to changes in wild winter steelhead migration timing (see Results) and in the timing of the fishery. An additional challenge is that fishing effort was inconsistent for portions of the fishing season in both the historical and contemporary periods. To address these challenges, we truncated the catch series to include only the part of the season for which fishing was relatively consistent across years and then calculated the proportion of the total run fished during that period using the estimated migration timing distributions (see Figure 2).

During the historical period, fishing effort was sporadic in March and April; we therefore truncated the historical catch series to only include catches from December

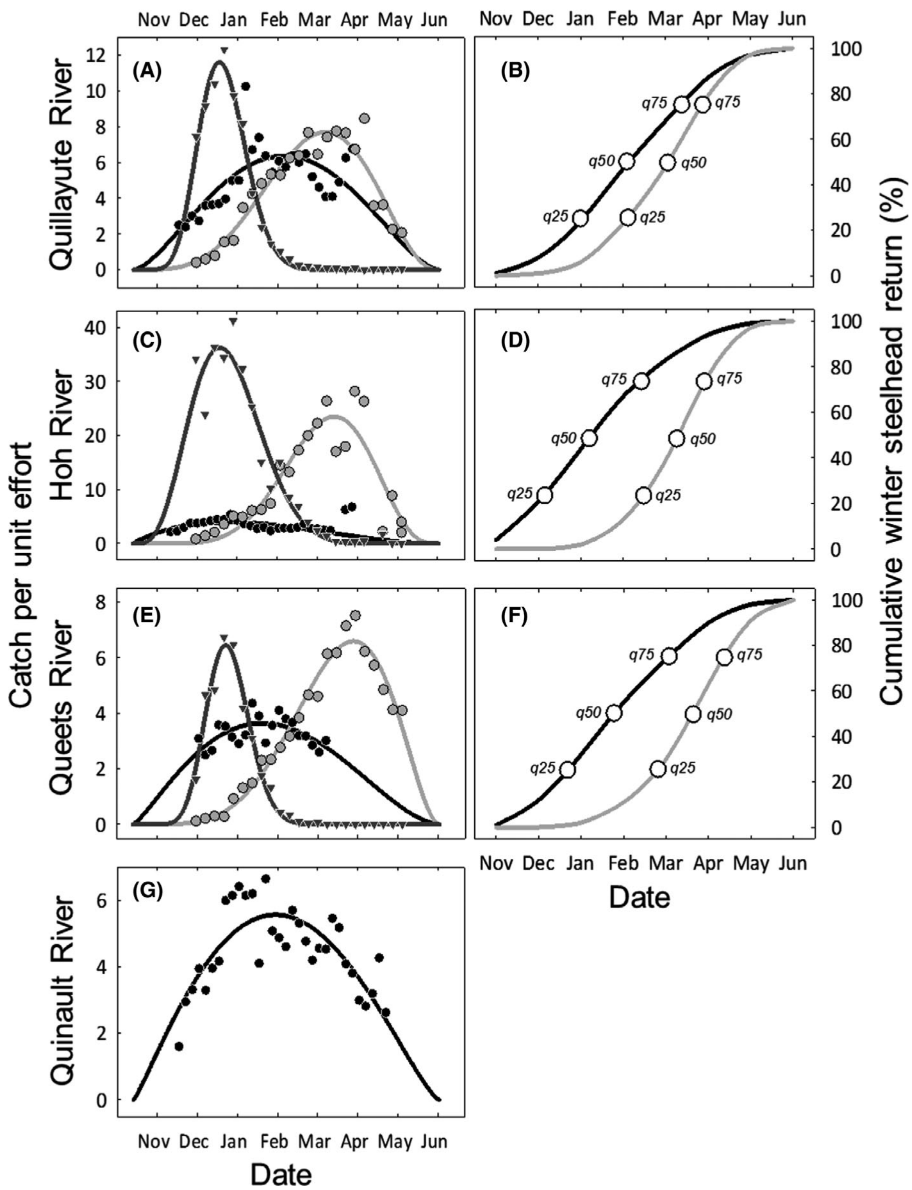

FIGURE 2. Historical (circa 1955–1963) and contemporary (2000–2017) migration timing estimates based on CPUE of wild and hatchery winter steelhead (left panels) in the **(A–B)** Quillayute, **(C–D)** Hoh, and **(E–F)** Queets rivers, and comparison of cumulative run timing with estimates of dates at which 25% (*q*25), 50% (*q*50), and 75% (*q*75) of the run had passed for historical and contemporary wild winter steelhead (right panels). Dark gray lines and triangles represent contemporary hatchery returns; black lines and black circles represent historical wild returns; and light gray lines and light gray circles represent contemporary wild returns. Run timing estimation in the **(G)** Quinault River was limited to the historical period because contemporary CPUE data were not available.

through February. The historical value of P (P_{hist}) ranged from 58% to 63%, meaning that approximately 58–63% of the run was fished historically (Table 3). During the contemporary period, fishing effort in the Hoh and Quillayute rivers was sporadic after March and we truncated the contemporary catch series to only include catches from December through March. In the Queets River, contemporary fishing effort was sporadic after April and we truncated the contemporary catch series to only include catches from December through April. The contemporary value of P (P_{curr}) ranged from 76% to 91% among the study populations (Table 3). Because contemporary CPUE data were not available at weekly intervals for the Quinault River, we estimated P_{curr} using the average for the Hoh and Quillayute River populations (Table 3). The Queets River population was excluded from this average in order to maintain a consistent truncation period. The P was then calculated as P_{hist}/P_{curr}. For example, for the Quillayute River, P_{hist} was 60% and P_{curr} was 78%, resulting in $P = 0.77$ (Table 3).

Values for R were approximated by using the median contemporary harvest rates for each population but differed slightly from the approach used to expand Queets River cannery records in that contemporary values of R were calculated as the catch during the truncated period divided by the total run size over the entire season. Because estimates for R used for this analysis were based on only a portion of the fishing season, values in Table 3 are slightly lower than the total harvest rates that were used to expand Queets River cannery records.

We accounted for uncertainty around the catch expansion estimates in several ways. First, for each annual estimate, we used the 25% quantile for R and $0.2{\cdot}P$ and the 75% quantile for R and $1.2{\cdot}P$ to calculate upper and lower estimate bounds, respectively. We also provided point estimates for each population by using the mean annual catch for the entire historical period. We calculated upper and lower bounds for this point estimate in the same way as was done for each annual estimate. Finally, we found that the interannual variation in estimates produced from the historical catch series was typically greater than the variation around the point estimates for any given year. Consequently, we also present the distributions of annual point estimates for each population in our results.

Approach 3: abundance estimates from historical CPUE, circa 1950s to 1963.— For our third approach, we used historical commercial fishery CPUE data from about the mid-1950s through 1963 (Table 2) to estimate mean annual run size for this period. Since catch is equal to the product of capture efficiency (q), effort (E), and run size, the historical run size (N) can be estimated by dividing CPUE by q:

$$N = \frac{C}{(Eq)} = \frac{\text{CPUE}}{q}. \tag{5}$$

Although historical capture efficiency data were not available, we were able to estimate efficiency for the contemporary (2000–2017) commercial fisheries in the Quillayute and Queets rivers because we had data on catch, effort, and run size (i.e., $q = C/ER$). We presumed that fishers were historically less efficient than contemporary fishers due to changes in fishing gear and methods. For example, contemporary fishers use jet boats to drift the nets downstream and actively fish the river, whereas during the historical period fishers primarily set nets from the bank to passively capture fish (Pettit 1950; Washington Department of Fisheries et al. 1973). During the historical period, commercial fishers used multifilament nets made of organic materials (Potter and Pawson 1991), but fishers now use more efficient monofilament gill nets. Washington (1973) found that monofilament nets were 2.2 times more efficient at catching salmon than multifilament gill nets. We therefore produced point estimates from the CPUE analysis by assuming that contemporary capture efficiency was two times the historical capture efficiency. We believe that this is a conservative assumption because additional changes to fisheries practices are likely to have affected capture efficiency. To account for uncertainty in the difference in capture efficiency between periods, we estimated

TABLE 3. Contemporary (1980–2017) median harvest rates (R) for wild winter steelhead and the proportion of the run that was fished during the historical period (1948–1960; P_{hist}) and the contemporary period (P_{curr}). Median harvest rates and the ratio of the proportions of the run fished (P) in each study period were used to estimate historical mean annual winter steelhead abundance from historical fisheries catch records. Upper and lower bounds for R and P (shown in parentheses) are the 25% and 75% quantiles for each parameter.

		Proportion of run fished		
Population	R	P_{hist}	P_{curr}	P (P_{hist}/P_{curr})
Quillayute River	0.23 (0.20, 0.26)	0.60	0.78	0.77 (0.61, 0.92)
Hoh River	0.24 (0.19, 0.35)	0.63	0.76	0.82 (0.66, 0.99)
Queets River	0.31 (0.23, 0.39)	0.62	0.91	0.68 (0.54, 0.82)
Quinault River	0.39 (0.33, 0.47)	0.58	0.77	0.75 (0.6, 0.9)

lower and upper bounds for the point estimates. The lower bound assumed that contemporary capture efficiencies were equal to historical capture efficiencies, whereas the upper bound assumed that contemporary capture efficiencies were three times the historical capture efficiencies.

We excluded contemporary Hoh River data from this analysis because contemporary CPUE values were abnormally high (Figure 2) and produced nonsensical historical run size estimates that were less than the reported catch. No CPUE data were available for the Quinault River. We therefore averaged capture efficiency estimates for the Quillayute and Queets River fisheries and applied this average to all populations.

Approach 4: winter steelhead abundance estimates from watershed size.— For our final approach, we developed an empirical relationship between adult winter steelhead abundance and the linear extent of accessible stream habitat (measured in stream kilometers [SKM]), a proxy for basin-scale winter steelhead capacity, in several West Coast winter steelhead populations. Similar approaches based on watershed size have been used to estimate Coho Salmon smolt production and adult Chinook Salmon abundance (Bradford et al. 1997; Liermann et al. 2010). For this analysis, we collected information from watersheds with either census counts or estimates of winter steelhead from the first half of the 20th century and prior to hatchery winter steelhead propagation. We identified eight watersheds with suitable winter steelhead information (Appendix Table A.1), including four California or Oregon coastal watersheds with census counts at weirs or fish ladders and four Puget Sound, Washington, watersheds for which Gayeski et al. (2011) estimated historical winter steelhead abundance. The winter steelhead estimates of Gayeski et al. (2011) are based on peak catch records from a single year (1895), whereas our objective was to estimate mean winter steelhead abundances that we could compare with mean estimates derived from our other approaches. We therefore adjusted the 1895 peak catch estimates of Gayeski et al. (2011) by using the mean winter steelhead catch for the period 1893–1909 to estimate mean winter steelhead abundance for Puget Sound rivers (Table A.1).

To relate winter steelhead abundance to watershed size, we assembled winter steelhead SKM for the eight reference watersheds and the four OP study watersheds. Winter steelhead SKM were available either in the primary sources or calculated from digital fish distribution maps within a geographical information system (Table A.1). Based on an inspection of the data, we fitted a power law relationship between mean winter steelhead abundance and SKM ($A = a\text{SKM}^b$), which translates to a linear relationship between log(abundance) and log(SKM) (e.g., Liermann et al. 2010). After verifying that the log–log relationship was approximately linear and that the variance was constant, we fitted the model using simple linear regression and then used this fitted model to predict winter steelhead abundance from SKM for the four OP watersheds. Because we were interested in predicting the historical winter steelhead population sizes, we used 95% prediction intervals rather than CIs to estimate the upper and lower bounds of the regression-based point estimates.

Question 3: How has contemporary wild winter steelhead abundance changed relative to historical abundance, and are there wild winter steelhead abundance trends during the contemporary period (1980–2017)?.— In addition to estimating historical winter steelhead abundance, we assembled the available contemporary winter steelhead harvest and escapement data as reported by the fisheries co-managers (i.e., Washington Coast Treaty Tribes and WDFW). These included data on wild winter steelhead harvest and escapement from 1980 to 2017 in the Hoh, Quillayute, and Queets rivers and from 1980 to 2013 in the Quinault River. From these data, we calculated the contemporary mean wild winter steelhead run size for each river. To estimate the percent change in abundance between the historical and contemporary periods, we compared our ensemble historical estimates to the mean abundances both for the entire contemporary period and for the last available 5 years of the contemporary period. We also used simple linear regression to test for trends in wild winter steelhead abundances during the contemporary period. For this final analysis, wild winter steelhead abundance was log transformed prior to regressing run size on return year.

RESULTS

Question 1: Historical and Contemporary Winter Steelhead Run Timing

Analysis of CPUE data indicated that run timing of wild winter steelhead in the Quillayute, Hoh, and Queets rivers has changed from the historical period, with contemporary runs generally beginning later and occurring over a narrower range of dates (Figure 2). Two metrics of run timing ($q25$ and $pJan1$) provided evidence that wild winter steelhead runs began significantly earlier in all three rivers during the historical period (Table 4). During the contemporary period, the $q25$ ranged from 33 d (95% CI = 24–40 d) later in the Quillayute River to 71 d (95% CI = 62–82 d) later in the Hoh River (Table 4). The percentage of wild winter steelhead migrating before January 1 ($pJan1$) during the contemporary period was between 18% (95% CI = 14–23%) and 43% (95% CI = 35–50%) less than the $pJan1$ during the historical period in the Quillayute and Hoh rivers, respectively (Table 4).

The reduction of earlier-returning wild winter steelhead also corresponded with a significant shift in the $q50$ within the Quillayute and Hoh rivers (Figure 2).

Estimated $q50$ occurred 25 d (95% CI = 16–33 d) and 61 d (95% CI = 47–71 d) later during the contemporary period in the Quillayute and Hoh rivers, respectively (Table 4). The magnitude of the shift in $q50$ in the Queets River was similar to that in the other populations, occurring 54 d (95% CI = −23, 70 d) later during the contemporary period. Confidence intervals for differences in $q50$ did not include zero except for the Queets River (Table 4).

Because wild winter steelhead runs began later during the contemporary period, the breadth of run timing was also more compressed (Figure 2). For example, the IQR was 16 d (95% CI = 6–29 d) shorter in the Quillayute River and 26 d (95% CI = 11–53 d) shorter in the Hoh River, representing a 24% and 37% reduction, respectively, from the historical IQRs (Table 4). Results for the Queets River were similar, with the contemporary IQR reduced by 22 d (95% CI = −4, 83 d), or 31% less than the historical IQR; however, as with $q50$, the CIs for IQR differences spanned zero for the Queets River.

As expected, we found differences in the timing and duration of hatchery and wild winter steelhead runs during the contemporary period, with hatchery winter steelhead returning earlier and over a narrower range of days than contemporary wild winter steelhead (Figure 2). Estimates of $q25$ indicated that contemporary hatchery runs began from 67 d (95% CI = 60–74 d) earlier in the Quillayute River to 72 d (95% CI = 69–74 d) earlier in the Hoh River relative to contemporary wild winter steelhead (Table 4). The $q50$ for hatchery winter steelhead ranged from 77 d (95% CI = 76–79 d) earlier in the Hoh River to 86 d (95% CI = 80–92 d) earlier in the Queets River relative to contemporary wild winter steelhead (Table 4). The IQR for hatchery winter steelhead ranged from 8 d (95% CI = 6–10 d) shorter in the Hoh River to 27 d (95% CI = 18–36 d) shorter in the Queets River relative to contemporary wild winter steelhead (Table 4). In all three rivers, the run timing of hatchery winter steelhead overlapped with that of the earlier-returning wild winter steelhead, which were prominent during the historical period but greatly reduced during the contemporary period (Figure 2). Lastly, while Quinault River migration timing for contemporary wild and hatchery winter steelhead was not available for comparison with historical patterns, historical Quinault River winter steelhead migration timing was similar to that in the other study rivers (Figure 2).

Question 2: Historical Winter Steelhead Abundance

Approach 1: historical estimates from Queets River cannery records in 1923.— In 1923, 1,500 cases of wild winter steelhead were packed at the Queets River cannery, with each case containing 48 cans at 1 lb (0.45 kg) per can, or 48 lb (22 kg) per case. This is equivalent to a total weight of canned winter steelhead of 72,000 lb (32,659 kg). Based on a wastage rate of 0.40 and a mean weight of 9.8 lb (4.4 kg) per Queets River winter steelhead, the number of wild winter steelhead processed in 1923 was equivalent to 12,245 fish. Assuming a cannery exploitation rate equivalent to the median contemporary exploitation rate (0.38), the total 1923 Queets River return of wild winter steelhead was estimated to be 32,223 fish, with upper and lower bounds of 43,732 and 27,829 fish based on 75% and 25% quartiles of contemporary exploitation rates (0.44, 0.28), respectively.

Approach 2: historical estimates from the 1948–1960 commercial and recreational catch expansion.— Expanding commercial and recreational winter steelhead catch based

TABLE 4. Change from the historical study period (circa 1955–1963) to the contemporary study period (2000–2017) in the Julian dates at which 25% ($q25$) and 50% ($q50$) of winter steelhead runs had passed, the number of days that elapsed between when 25% and 75% of the run had passed (interquartile range [IQR]), and the percentage of the run that had passed by January 1 (*pJan1*). The 95% confidence intervals for each migration timing metric change are shown in parentheses.

Migration timing metric	Quillayute River	Hoh River	Queets River
	Wild contemporary–wild historical[a]		
$q25$	33 (24, 40)	71 (62, 82)	63 (37, 87)
$q50$	25 (16, 33)	61 (47, 71)	54 (−23, 70)
IQR	−16 (−29, −6)	−26 (−53, −11)	−22 (−83, 4)
pJan1 (%)	−18 (−23, −14)	−43 (−50, −35)	−31 (−42, −18)
	Wild contemporary–hatchery contemporary[b]		
$q25$	67 (60, 74)	72 (69, 74)	71 (63, 79)
$q50$	79 (74, 84)	77 (76, 79)	86 (80, 92)
IQR	21 (13, 28)	8 (6, 10)	27 (18, 36)
pJan1 (%)	−71 (−76, −67)	−62 (−64, −61)	−68 (−77, −59)

[a]Differences in migration timing metrics were calculated for contemporary wild steelhead relative to historical wild steelhead. For example, relative to the historical migration timing, the $q25$ date for the contemporary Hoh River population now occurs 71 d later, the IQR is 26 d shorter, and the *pJan1* is 43% less.

[b]Differences in migration timing metrics were calculated for contemporary wild steelhead relative to contemporary hatchery steelhead. For example, relative to the contemporary hatchery steelhead migration timing, the $q25$ date for the Hoh River contemporary wild population occurs 72 d later, the IQR is 8 d longer, and the *pJan1* is 62% less.

on estimates of harvest rates and the proportion of the run that was fished, we estimated a mean annual historical run size for the Quillayute River of 22,567 winter steelhead (lower and upper bounds for the historical mean = 16,733, 31,591; Table 5). For the Quillayute River, annual variability within the historical period based on the lowest and highest single-year estimates ranged from 6,702 winter steelhead in 1948 to 34,757 winter steelhead in 1951 (Figure 3). In the Hoh River, catch expansion resulted in an estimated mean annual historical run size of 15,923 winter steelhead (lower and upper bounds = 9,023, 24,901; Table 5). The lowest and highest single-year estimates for the Hoh River were 7,118 and 24,684 winter steelhead in 1948 and 1956, respectively (Figure 3). In the Queets River, we estimated a mean historical run size of 19,875 winter steelhead (lower and upper bounds = 13,025, 32,878). The lowest and highest single-year estimates for the Queets River during that period were 6,191 and 52,200 winter steelhead in 1960 and 1954, respectively (Figure 3). During the peak estimate year in the Queets River, which was the largest estimated run size among all years and all populations, over 14,000 winter steelhead (Table A.2) were harvested, including over 5,200 winter steelhead in the month of December alone. The historical mean estimate for the Quinault River was 13,743 winter steelhead (lower and upper bounds = 9,345, 20,258), with the lowest and highest single-year estimates of 7,475 and 30,332 winter steelhead in 1956 and 1952, respectively. Historical estimates for all populations and years in the historical catch series as well as their upper and lower bounds are given in Table A.2.

Approach 3: CPUE-based historical estimates, circa 1955–1963.— We expanded historical CPUE data using contemporary capture efficiency averaged across populations to estimate the historical abundance of winter steelhead (Table 6). Under a scenario in which contemporary capture

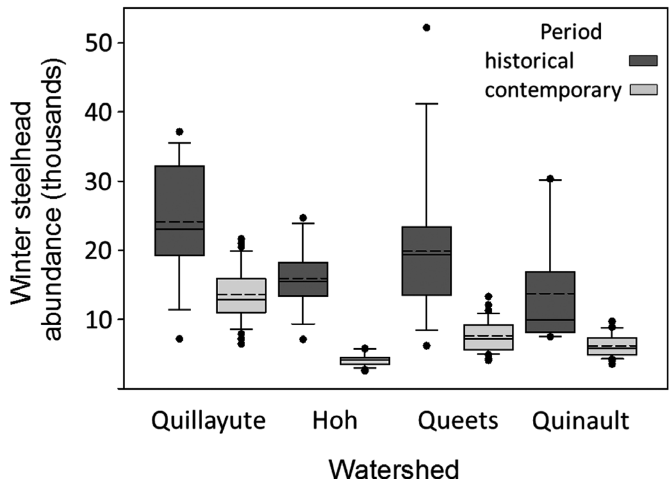

FIGURE 3. Box plots of historical (1948–1960; dark gray) and contemporary (circa 1980–2017; light gray) wild winter steelhead abundance estimates for Olympic Peninsula watersheds. Historical estimates are based on commercial and recreational fisheries catch expansion. Contemporary estimates are from reported harvest and escapement counts. Dashed lines within the boxes represent mean values; solid lines within the boxes represent median values; and whiskers extend to data that are no more than 1.5 times the interquartile range. Top lines of boxes denote the 75th percentile, and bottom lines denote the 25th percentile. Filled circles denote outliers.

efficiency was twice the historical period's capture efficiency (see Data Analysis), we estimated winter steelhead abundances of 23,391 in the Quillayute River, 22,226 in the Quinault River, 14,160 in the Hoh River, and 13,553 in the Queets River (Table 6). Upper and lower bounds to these estimates (based on contemporary capture efficiencies being three times greater than and equal to historical capture efficiencies, respectively) are presented in Table 6.

Approach 4: historical estimates from watershed size.— Accessible SKM, our proxy for basin-scale steelhead capacity, ranged from approximately 10 to 1,473 km, and mean adult winter steelhead population sizes ranged from 432 to 47,222 fish for the eight watersheds used to parameterize the empirical relationship between SKM and winter steelhead abundance (Table A.1). Accessible SKM for the four study rivers ranged from 339 to 675 km (Table A.1).

The linear regression model provided a good fit for the log-transformed data: log(population size) = 1.71 +

TABLE 5. Mean (SD in parentheses) of the annual number of wild winter steelhead caught during 1948–1960 in commercial and recreational fisheries in the Quillayute, Hoh, Queets, and Quinault rivers; and mean annual winter steelhead population size estimated by expanding the catch to account for harvest rates and the proportion of the steelhead run that was fished. Catch numbers include only those fish caught from December 1 to February 28 due to inconsistent fishing effort outside of this period across years. Upper and lower bounds for population size estimates (shown in parentheses) are based on the lower and upper bounds for parameters *R* and *P* given in Table 3.

Population	Mean annual catch (SD)	Mean estimated population size
Quillayute River	3,970 (1,337)	22,567 (16,733, 31,591)
Hoh River	3,138 (885)	15,923 (9,023, 24,901)
Queets River	4,187 (2,347)	19,875 (13,025, 32,878)
Quinault River	3,977 (2,313)	13,743 (9,345, 20,258)

TABLE 6. Estimates of historical (circa 1955–1963) wild winter steelhead run size based on reported commercial fisheries CPUE (fish caught per fisher-day). Lower and upper bounds are shown in parentheses.

Population	CPUE-based mean population estimate
Quillayute River	23,391 (11,695, 35,086)
Hoh River	14,160 (7,080, 21,240)
Queets River	13,553 (6,776, 20,329)
Quinault River	22,226 (11,113, 33,339)

0.91·log(SKM) ($F_{1,6} = 130.07$, $P < 0.001$, $R^2 = 0.96$; Figure 4). Based on this relationship, estimates of winter steelhead population size (with 95% prediction intervals) were 19,571 (7,910–48,423) for the Quillayute River, 10,431 (4,247–25,615) for the Hoh River, 12,144 (4,945–29,821) for the Queets River, and 14,723 (5,986–36,215) for the Quinault River (Table 7).

Ensemble estimates of historical winter steelhead abundance.— We produced ensemble estimates of historical winter steelhead abundance by averaging the point estimates generated from approaches 2–4 described above. We present these estimates in Table 7. The coefficient of variation (CV) for the ensemble estimates, which is a relative measure of variation among analysis approaches, was lowest for the Quillayute River, where estimates from the different approaches were relatively consistent (CV = 9%), and highest for the Queets and Quinault rivers (CV = 27% for both rivers). In the case of the Queets River, the estimate based on historical catch expansion (approach 2) was approximately 47% and 64% higher than those based on CPUE data (approach 3) and SKM data (approach 4), respectively. In the Quinault River, the estimate based on CPUE was approximately 50% and 62% higher than those based on SKM and catch expansion, respectively. In the Hoh River, variability among estimate approaches was moderate (CV = 21%), with the SKM approach producing an estimate that was 26% and 43% lower than those based on the CPUE and catch expansion, respectively. There was a tendency for the SKM approach to produce the lowest estimates among the different approaches, but as is evident from the Quinault River estimates, this was not always the case (Table 7). Thus, no single approach consistently produced the greatest deviation from the ensemble mean estimates across populations.

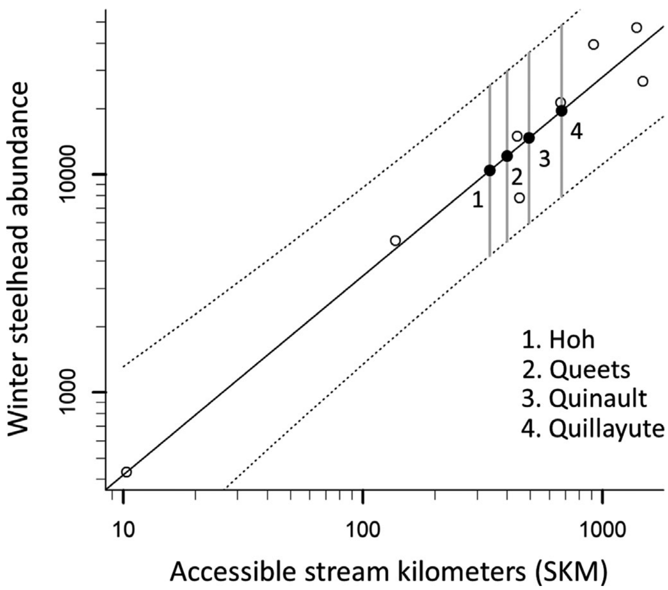

FIGURE 4. Relationship between watershed accessible stream kilometers (SKM) and wild winter steelhead abundance. Open circles are observed patterns from eight U.S. West Coast (California, Oregon, and Washington) steelhead populations. Filled circles (95% prediction intervals = gray vertical lines) are predictions of steelhead abundance for the Quillayute, Hoh, Queets, and Quinault rivers based on their accessible SKM.

Question 3: Contemporary Winter Steelhead Abundance and Trends

During the contemporary period, mean wild winter steelhead abundances ± SD were 13,595 ± 3,963 fish in the Quillayute River, 4,206 ± 856 fish in the Hoh River, 7,648 ± 2,265 fish in the Queets River, and 6,181 ± 1,647 fish in the Quinault River (Table 7). These population sizes are lower by 38% in the Quillayute River, 69% in the Hoh River, 50% in the Queets River, and 63% in the Quinault River compared to the respective ensemble mean historical estimates for each river (average of approaches 2–4; Table 7).

Trends in wild winter steelhead abundance during the contemporary period provided evidence for significant declines in the Hoh, Queets, and Quinault rivers (Figure 5). For example, the decline in Hoh River winter steelhead returns since 1980 was equivalent to a loss of 513 adults (95% CI = 320–710 adults) per decade (linear regression on log-transformed abundance; $F_{1,36} = 29.01$, $P < 0.001$). In

TABLE 7. Comparison of historical mean annual wild winter steelhead abundance estimates based on cannery record data, expansion of historical commercial and recreational catch data, historical commercial fishery CPUE (fish caught per fisher-day), and accessible stream kilometers (SKM) of habitat; an ensemble historical (circa 1948–1960) mean estimate; the contemporary (circa 1980–2017) mean estimate; and the percent decline of each population relative to the ensemble historical estimate.

Population	Cannery records	Historical catch	Historical CPUE	Accessible habitat (SKM)	Ensemble historical abundance estimate[a]	Contemporary mean abundance	Percent decline[b]
Quillayute River		22,567	23,391	19,571	21,843	13,595	38
Hoh River		15,923	14,160	10,431	13,505	4,206	69
Queets River	32,659	19,875	13,553	12,144	15,191	7,648	50
Quinault River		13,743	22,226	14,723	16,897	6,181	63

[a]Ensemble historical estimate does not include cannery records.
[b]Percent decline is the difference between the ensemble historical abundance estimate and the contemporary mean abundance.

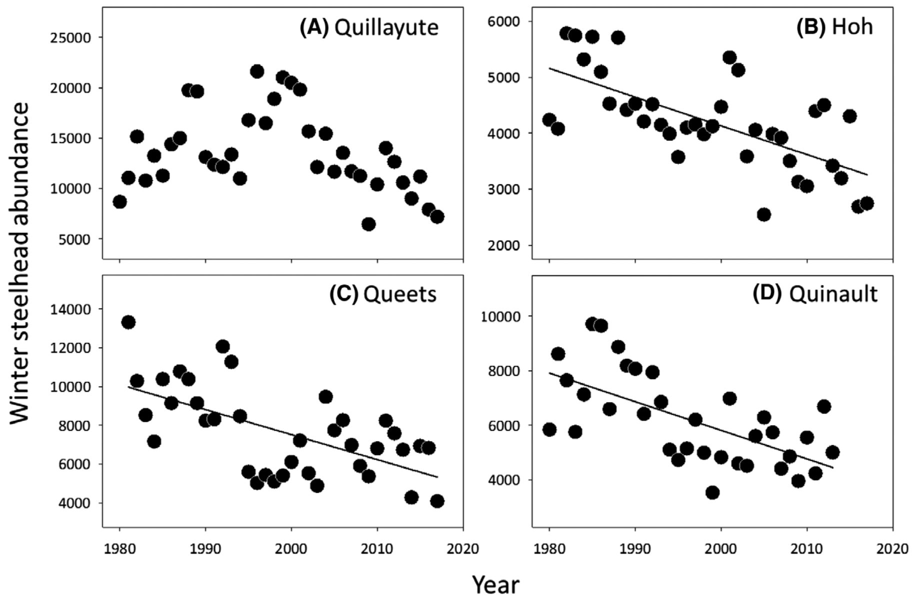

FIGURE 5. Contemporary trends (circa 1980–2017) in wild winter steelhead abundance in the **(A)** Quillayute River, **(B)** Hoh River, **(C)** Queets River, and **(D)** Quinault River. Black lines represent best-fit linear regression models.

the Queets River, the decline was equivalent to a loss of 1,220 adults (95% CI = 640–1,820 adults) per decade ($F_{1,36}$ = 19.56, $P < 0.001$). In the Quinault River, the decline was equivalent to a loss of 1,052 adults (95% CI = 590–1,510 adults) per decade ($F_{1,32} = 21.20$, $P < 0.001$). There was not a simple linear trend for contemporary wild winter steelhead returns in the Quillayute River (Figure 5). Wild winter steelhead returns increased from 8,671 fish in 1980 to a peak of 21,615 fish in 1996 but have since declined at a rate of 5,533 fish/decade (Figure 5).

The 2017 wild winter steelhead returns were among the lowest ever recorded (Figure 5). In 2017, the Queets River had its lowest wild winter steelhead return on record (4,087 fish), the Quillayute River had its second-lowest return on record (7,189 fish), and the Hoh River had its third-lowest return on record (2,742 fish). In 2013, the last year for which data were available on the Quinault River, the return was also among the lowest ever recorded (4,966 fish). Comparing our ensemble mean historical estimates to the most recent 5-year period available for each population, wild winter steelhead returns have declined by 67% in the Quillayute River, 80% in the Hoh River, 73% in the Queets River, and 71% in the Quinault River.

DISCUSSION

A better understanding of the past can better inform contemporary recovery goals and strategies for depleted populations (Swetnam et al. 1999; Bonebrake et al. 2010). Our analysis of multiple historical data sources for OP wild winter steelhead provides important context for understanding the contemporary conservation status of these populations. We provide evidence for striking shifts in wild winter steelhead run timing and declining adult abundance from the early/mid-20th century to the present, both of which have likely compromised the resilience of these populations.

Migration timing represents a significant component of life history diversity in anadromous fish (McElhany et al. 2000). In OP wild winter steelhead, migration timing change primarily reflects the decline of earlier-returning fish, as indicated by the approximately 20–40% reductions in the proportion of fish returning from November through December. Peak run timing of wild winter steelhead is now 1–2 months later than during the historical period, and run timing has also contracted by as many as 26 d (a 37% reduction in IQR) in some populations. Thus, the declines in earlier-migrating fish and the narrowing range of migration timing represent a substantial reduction in the historical population diversity that underpinned OP winter steelhead runs.

Corresponding with changes in migration timing, multiple lines of evidence point to substantial decreases in the abundance of OP wild winter steelhead between the historical and contemporary periods. The magnitude of decline in mean wild winter steelhead abundance between these time periods ranged from approximately 39% to 70%. Furthermore, significant downward trends in wild winter steelhead run sizes since 1980 suggest that comparisons of mean abundance between historical and contemporary periods do not capture the full extent of depletion in these populations. For instance, mean abundances during the most recently available 5-year period for each population indicate that wild winter steelhead have declined 67–80%

from the ensemble mean abundance of the historical period. This magnitude of decline is similar to that reported in several other studies of historical Pacific salmon abundance. For example, Price et al. (2019) found a 56–99% reduction in Sockeye Salmon *O. nerka* stock abundance in the Skeena River, British Columbia, from the onset of industrial fishing (circa 1913) to the present. Meengs and Lackey (2005) estimated an 80–90% reduction in coastal Oregon salmon populations, and similar population declines have been estimated throughout the Pacific Northwest (e.g., Chapman 1986; Brown et al. 1994; Gresh et al. 2000; Yoshiyama and Moyle 2010; Gayeski et al. 2011). To place OP winter steelhead declines in a deeper historical context, we also note that most data sources available for our analyses are from an era following commercial cannery exploitation. Thus, the circa 1948–1960 historical period that was the primary focus of our analyses was likely preceded by an earlier period of population decline. For example, from the very limited cannery records available we estimated that the 1923 Queets River winter steelhead run was more than double our ensemble estimate for the circa 1948–1960 historical period. Consequently, our comparisons of contemporary OP winter steelhead population abundances to those from the circa 1948–1960 historical period almost certainly underestimate the declines in winter steelhead abundance from the pre-cannery era.

A variety of interacting effects has likely contributed to changes in the migration timing and abundance of wild winter steelhead. Although our study was not designed to quantify the underlying causes of these changes, we suggest that there are strong linkages between shifts in migration timing and the declines in wild winter steelhead production. Changes in run timing can shorten breeding seasons, reduce phenotypic diversity, and lower population productivity (Tillotson and Quinn 2018). More protracted anadromous fish migrations, like those that we estimated to occur historically for wild winter steelhead, can allow fish to temporally stagger the use of spawning habitat (Gharrett et al. 2013), thereby reducing density-dependent effects on juvenile survival and increasing local habitat capacity (Chandler and Bjornn 1988).

Migration timing is also often associated with the spatial structure of breeding locations in anadromous fish populations (e.g., Everest 1973; Stewart et al. 2002; Beacham et al. 2012). On the OP, McMillan et al. (2007) observed spatial correlations with spawn timing in the Quillayute River, where spawning higher in the stream network in smaller stream channels occurred about 1 month earlier than that in the lowermost main-stem spawning reaches. Cederholm (1984) also found that earlier-returning Queets River wild winter steelhead were more likely to spawn in smaller tributaries, while main-stem spawning tended to occur several weeks later in the season. Importantly, Cederholm (1984) observed this occurrence in low-elevation tributary streams, so the pattern of earlier spawn timing in tributaries is not necessarily limited to higher-elevation headwaters as might be inferred solely from the results of McMillan et al. (2007); rather, this pattern appears to be associated with stream size.

Given the apparent correlation between run timing and spawning locations, declines in earlier-returning wild winter steelhead could be at least partly attributable to higher impacts to tributary streams from human land use. Although our study watersheds have a substantial proportion of habitat protected within the Olympic National Park, forestry is a dominant land use outside of the park. Timber harvest reached peak intensity from the 1950s through the 1980s, resulting in stream habitat degradation, including reduced amounts of instream wood and increased mass wasting and sediment delivery (Smith 2000; Martens et al. 2019). In addition, the construction of extensive forestry road networks impeded fish migration at many stream crossings, blocking anadromous fish access to tributary habitats (Smith 2000). Thus, stream habitats have been altered in ways that are known to reduce salmonid growth, survival, and reproductive success (Meehan and Bjornn 1991; Bisson et al. 1992), and these impacts may have disproportionately affected the use of tributary streams by winter steelhead. Consequently, the contraction of migration timing—particularly the loss of early returning fish—may be linked to the loss of productive tributary habitat. The resulting spatial contraction in winter steelhead habitat use could reduce juvenile production by strengthening the effects of local density dependence (Einum et al. 2008; Teichert et al. 2011; Finstad et al. 2013; Atlas et al. 2015). Thus, while we do not believe that the full extent of wild winter steelhead declines is explained solely by the losses of earlier-migrating fish, these losses are likely to have played a substantial role since the contraction of migration timing is linked to a number of known demographic mechanisms that decrease anadromous fish production and population resilience (Tillotson and Quinn 2018).

Declines of earlier-migrating wild winter steelhead are also likely associated with the introduction of hatchery winter steelhead into the study rivers (Cederholm and TU 1984; Bahls 2001). Most of the hatchery winter steelhead stocks used in OP rivers are derived from a combination of the Chambers Creek winter steelhead population (a stock originally native to Puget Sound, Washington) and the Cook Creek stock from the Quinault River, both of which were selectively bred to return as adults from November through early January (Crawford 1979; Cram et al. 2018). Our analyses demonstrate that contemporary hatchery winter steelhead migration timing in OP rivers is consistent with this history of artificial selection. They also illustrate a striking overlap in the timing of hatchery winter steelhead migrations with the early portion of historical wild winter steelhead migrations that have been depleted, leading to several plausible hypotheses for hatchery winter steelhead contributions to changes in wild winter steelhead runs.

Hatchery populations may have direct and indirect effects on wild salmonid populations. Direct effects are well known and include competition, genetic introgression, and reduced fitness in the wild (e.g., Weber and Fausch 2003; Kostow and Zou 2006; Araki et al. 2008; Christie et al. 2012). We expect these impacts to be particularly acute for wild fish that have greater temporal overlap with hatchery fish, such as similar adult migration timing. Although the selection of hatchery winter steelhead stocks used in OP rivers was intended to minimize impacts to wild winter steelhead through the temporal segregation of runs (Crawford 1979), our analyses demonstrate that the timing of hatchery winter steelhead migration completely overlaps with the early part of the historical wild winter steelhead returns. The lack of temporal segregation between hatchery and wild stocks suggests a potentially high exposure of earlier-migrating wild winter steelhead to direct hatchery impacts. For example, Seamons et al. (2012) found that a segregated winter steelhead hatchery program using the Chambers Creek stock failed to prevent interbreeding with wild winter steelhead in nearby Forks Creek, Washington. After three generations of hatchery stocking, the proportion of wild-ancestry smolts and adults declined by 10–20% and up to 80% of naturally produced winter steelhead were hatchery × wild hybrids (Seamons et al. 2012). Consequently, the direct effects of hatchery winter steelhead have likely contributed to depletion of earlier-returning wild winter steelhead.

Indirect effects of hatcheries may have also contributed to wild winter steelhead declines. For example, production of hatchery winter steelhead can lead to mixed-stock in-river fisheries in which recreational and commercial fisheries targeting hatchery winter steelhead subject earlier-returning wild winter steelhead to high and potentially unsustainable harvest rates (Cederholm and TU 1984; Naish et al. 2007; Cram et al. 2018). Contemporary fishing effort is highest from December through mid-January, corresponding with the timing of hatchery winter steelhead returns and thereby providing the potential for fisheries-induced directional selection against earlier-migrating wild winter steelhead (Quinn et al. 2007; Tillotson and Quinn 2018). Migration and reproductive timing are strongly heritable in winter steelhead (Carlson and Seamons 2008; Abadía-Cardoso et al. 2013) and are therefore highly responsive to selection in fisheries. Additionally, indirect effects of hatchery populations may interact with other potential stressors. For example, if earlier-returning wild winter steelhead declined in part due to an era of habitat impacts, as described above, their subsequent response to habitat restoration could be suppressed by harvest in recreational and commercial fisheries targeting hatchery winter steelhead (WDFW Commission 1996, cited by Bahls 2001).

Considerable uncertainty is associated with any effort to reconstruct historical Pacific salmon and steelhead runs given the incomplete information available from the past. We approached this challenge by examining multiple data sources to explore a range of plausible historical scenarios (e.g., Swetnam et al. 1999; Bonebrake et al. 2010). Individual approaches may contain bias or may be highly sensitive to their underlying assumptions. For example, our historical abundance estimates based on SKM, a proxy for basin-scale winter steelhead capacity, were lower than those produced by other approaches in three of the four study populations. This pattern could reflect environmental differences between the basins used to parameterize this relationship and the OP basins or it could result from sensitivity to bias in the parameter estimates used in our other analyses, such as when using contemporary harvest rates to approximate historical exploitation (Cramer and Caldwell 2020). Because each analytical approach required its own independent set of assumptions, we chose not to rely on any single approach to produce a "best estimate" and instead generated an ensemble estimate for the historical period based on the average of the central tendencies from each analysis method. Averaging across multiple models typically reduces bias that is associated with individual approaches and results in more reliable prediction (Dormann et al. 2018). Further, no single approach consistently produced the greatest deviation from the historical ensemble estimates, suggesting that there was limited systematic bias associated with our approaches. Our ensemble estimates had a mean CV of approximately 21%, which increased our confidence in the reliability of our historical abundance estimates. Given the relative consistency in our estimates derived from several different approaches and the similarities between our findings and the level of depletion reported in other Pacific salmon populations (e.g., Price et al. 2019), we believe that our results provide important historical reference points for the timing and abundance of wild OP winter steelhead runs that can inform efforts to rebuild these declining populations.

As with previous estimates of historical salmon abundance, our investigation indicates that population declines are much greater than had been previously recognized using only contemporary data (Kendall et al. 2017; Cram et al. 2018). This knowledge has pragmatic value in helping to identify the need for conservation action and for informing population rebuilding goals. We also provide an important reference baseline for the historical breadth of winter steelhead migration timing. The loss of earlier-returning OP winter steelhead has not been previously documented. In the absence of this historical information, it appears that the diminished diversity in contemporary winter steelhead migration timing had generally become accepted as the norm, as previous assessments describe these runs as beginning in January, with the majority of fish migrating from March through May (Busby et al. 1996; Johnson et al. 1997; WDFW and Western Washington Treaty Tribes 2002; Cram et al. 2018). Thus, the historical baseline for winter steelhead migration timing may be an especially important reference for population rebuilding efforts because, in addition to the demographic effects discussed previously, it underpins a population's adaptive capacity to keep pace with shifting climatic conditions, such as changing streamflow and temperature regimes (Reed et al. 2011; Manhard et al. 2017; Austin et al. 2020). For example, winter steelhead tend to migrate and spawn earlier in warmer streams (Busby et al. 1996; Brannon et al. 2004), and if streamflows and water temperature regimes on the OP become more similar to those in more southerly climates (Wade et al. 2013), then early migrating life histories may become increasingly important for population resilience. However, rebuilding earlier-timed wild winter steelhead migrations may be challenging without addressing the direct (e.g., competition and introgression) and indirect (e.g., mixed-stock harvest) effects of current hatchery programs.

Conclusions

Most previous investigations of historical Pacific salmon populations have focused on stocks that were already recognized to be highly depleted and were identified as a conservation priority through ESA listings (e.g., Meengs and Lackey 2005; Yoshiyama and Moyle 2010; Gayeski et al. 2011). Our analysis of non-ESA-listed populations, considered until very recently to be healthy, suggests that the lack of historical baselines can underestimate the loss of population diversity and abundance, thereby masking the need for conservation action. Our results for OP winter steelhead demonstrate how even a relatively modest extension of the period of record (e.g., 30 years) can increase the power to identify patterns of change that may not yet be apparent from contemporary monitoring programs. Analyses of historical anadromous fish data can help to overcome the risks of the shifting baseline syndrome and provide important reference points for rebuilding population diversity and abundance.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.

Appendix: Additional Data

TABLE A.1. Accessible stream kilometers (SKM) and mean annual winter steelhead counts for coastal watersheds along the U.S. West Coast.

Location	SKM	Mean annual winter steelhead count	Winter steelhead count years	SKM source[a]	Winter steelhead count source
Waddell Creek, CA	10.30	432	1933–1941	7	7
South Fork Eel River (Benbow Dam), CA	441.10	14,990	1938–1960	1	8
Mad River (Sweasey Dam), CA	136.80	4,976	1941–1942, 1946–1952	1	7
North Umpqua River (Winchester Dam), OR	450.30	7,812	1945–1959	4	5
Stillaguamish River, WA	667.50	21,358	1893–1895, 1898, 1904, 1909	3	2, 3
Nooksack River, WA	918.00	39,444	1893–1895, 1898, 1904, 1909	3	2, 3
Snohomish River, WA	1,389.00	47,222	1893–1895, 1898, 1904, 1909	3	2, 3
Skagit River, WA	1,473.00	26,759	1893–1895, 1898, 1904, 1909	3	2, 3
Queets River, WA	399.90			6	
Quillayute River, WA	674.70			6	
Quinault River, WA	493.90			6	
Hoh River, WA	338.50			6	

[a]Sources: 1 =CDFW 2020; 2 = Cobb 1921; 3 = Gayeski et al. 2011; 4 = ODFW 2020b; 5 = ODFW 2020a; 6 = ONRC 2020; 7 = Shapovalov and Taft 1954; 8 = Taylor 1978.

TABLE A.2. Number of winter steelhead harvested in commercial and recreational fisheries for the Hoh, Queets, Quillayute, and Quinault rivers from 1948 to 1960. The catch for December–February (the period that was consistently fished each season) and the total annual catch in the fisheries are reported. Estimated annual winter steelhead abundance and lower and upper bounds of the estimates are provided for each year of the catch time series.

Population	Year	Dec–Feb catch	Total catch	Estimated total abundance	Estimate lower bound	Estimate upper bound
Hoh River	1948	1,403	1,448	7,118	4,034	11,132
	1949	4,469	4,469	22,678	12,850	35,464
	1950	2,497	2,506	12,673	7,181	19,819
	1951	3,165	3,203	16,063	9,102	25,119
	1952	2,687	2,754	13,633	7,725	21,320
	1953	3,056	3,059	15,508	8,788	24,252
	1954	2,578	3,363	13,080	7,412	20,456
	1955	3,891	3,986	19,746	11,189	30,880
	1956	4,864	5,130	24,684	13,987	38,601
	1957	3,281	3,659	16,651	9,435	26,040
	1958	2,885	3,287	14,640	8,296	22,894
	1959	2,955	3,341	14,995	8,497	23,449
	1960	3,061	3,061	15,534	8,802	24,292
Queets River	1948	2,993	3,203	14,210	9,312	23,506
	1949	5,200	5,337	24,687	16,178	40,837
	1950	4,435	4,494	21,056	13,798	34,831
	1951	4,347	4,686	20,636	13,523	34,136
	1952	4,791	5,320	22,743	14,904	37,622
	1953	5,043	5,699	23,941	15,689	39,603
	1954	10,996	13,985	52,200	34,208	86,349
	1955	4,082	5,183	19,381	12,701	32,060
	1956	2,495	2,967	11,846	7,763	19,595
	1957	2,907	4,143	13,801	9,044	22,829
	1958	2,781	3,198	13,201	8,651	21,836
	1959	3,052	3,486	14,488	9,494	23,965
	1960	1,304	1,304	6,191	4,057	10,240
Quillayute River	1948	1,179	1,251	6,702	4,970	9,383
	1949	5,381	5,803	30,590	22,683	42,823
	1950	5,442	5,478	30,933	22,937	43,303
	1951	6,114	6,144	34,757	25,772	48,656
	1952	2,921	3,389	16,603	12,311	23,242
	1953	3,790	4,545	21,543	15,975	30,159
	1954	3,286	4,686	18,681	13,852	26,152
	1955	3,432	4,242	19,507	14,464	27,308
	1956	3,259	4,045	18,523	13,735	25,931
	1957	3,094	3,855	17,586	13,040	24,619
	1958	4,156	5,124	23,622	17,516	33,068
	1959	4,326	5,037	24,588	18,232	34,421
	1960	5,230	5,230	29,732	22,046	41,621
Quinault River	1948	2,434	2,566	8,409	5,718	12,396
	1949	5,219	5,470	18,032	12,261	26,580
	1950	2,316	2,348	8,002	5,441	11,796
	1951	8,779	9,126	30,332	20,626	44,713
	1952	8,656	9,137	29,908	20,337	44,088
	1953	3,695	3,759	12,769	8,682	18,822
	1954	3,919	6,054	13,541	9,208	19,961
	1955	2,371	2,857	8,191	5,570	12,074

TABLE A.2. Continued.

Population	Year	Dec–Feb catch	Total catch	Estimated total abundance	Estimate lower bound	Estimate upper bound
	1956	2,184	2,360	7,546	5,131	11,123
	1957	2,163	2,949	7,475	5,083	11,018
	1958	2,601	3,425	8,986	6,110	13,246
	1959	2,860	3,252	9,883	6,720	14,568
	1960	4,510	4,614	15,585	10,597	22,973