

ARTICLE

Higher Early Marine Mortality of Steelhead Associated with Releases of Hatchery Coho Salmon but Not Chinook Salmon

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Abstract

Understanding the drivers of mortality during critical life history periods is an important part of increasing our capacity to rebuild depressed salmonid populations. For threatened steelhead *Oncorhynchus mykiss* in Puget Sound, Washington, early marine predation has been implicated as a key source of mortality. Yet, the agents that mediate predation pressure are poorly understood. In this study, we characterize abundances of juvenile Coho Salmon *O. kisutch* and Chinook Salmon *O. tshawytscha* in Puget Sound and relate these abundance patterns to weekly steelhead survival to better understand whether pulses of hatchery-released salmonids mediate steelhead survival. We found that weekly abundances of hatchery Coho Salmon and Chinook Salmon smolts vary by several orders of magnitude across weeks, indicating that large resource pulses are available to salmonid predators. We further found that weekly steelhead survival was significantly negatively related to abundances of hatchery-released Coho Salmon but not Chinook Salmon, which had considerably smaller body sizes than both Coho Salmon and steelhead smolts. Together, our results suggest that releases of Coho Salmon into Puget Sound mediate mortality of steelhead smolts, possibly via increased predation pressure by shared predators.

Top-down forcing processes are critical to understanding variability in abundances of marine and anadromous fish species (Baum and Worm 2009). In the Pacific Northwest, predation pressure on salmonid smolts has increased substantially over the past several decades (Chasco et al. 2017), coinciding with increases in the abundance of some marine mammal populations (Jeffries et al. 2003; Jefferson et al. 2016, 2021). Indeed, in Puget Sound, Washington, predation on salmonid smolts by pinnipeds in general, and harbor seal *Phoca vitulina* in particular, has increased several fold since 1970 and can result in millions of smolts being consumed each month during the peak of smolt migration (Chasco et al. 2017; Thomas et al. 2017; Nelson et al. 2021).

Steelhead *Oncorhynchus mykiss* in Puget Sound are listed as threatened under the U.S. Endangered Species Act due to population declines over the past several decades (NOAA 2007; Scott and Gill 2008). Although mortality of steelhead occurs throughout their life cycle, the early marine migration through Puget Sound represents a critical period of high mortality (Moore et al. 2015). For example, mortality rates of Nisqually River steelhead from the river mouth to the Strait of Juan de Fuca exceed 80% in most years, despite Nisqually steelhead migrating through Puget Sound in just 1–2 weeks (Moore et al. 2015; Moore and Berejikian 2017). The brief migration through Puget Sound combined with high mortality rates suggests that predation, rather than

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longer-acting bottom-up mechanisms like disease or food availability, is a primary cause of mortality (Moore and Berejikian 2017).

Marine survival of other larger-bodied Puget Sound salmonid smolts (i.e., Coho Salmon *O. kisutch* and Chinook Salmon *O. tshawytscha*) has also declined, or remained quite low, over the past few decades (Scott and Gill 2008; Zimmerman et al. 2015; Ruff et al. 2017). Each spring, tens of millions of Chinook Salmon and Coho Salmon are released into Puget Sound, and release timing and size variation have become more compressed in recent years (Nelson et al. 2019a). Marine entry of hatchery-released smolts, along with a smaller number of naturally produced salmonid smolts, results in large pulses of prey that can induce a numerical response and increase localized feeding by predators (Holling 1959; Collis and Beaty 1995; Allegue et al. 2020). For instance, Allegue et al. (2020) showed that harbor seals responded to hatchery releases of Coho Salmon by increasing feeding rates on smolts in estuaries near the river mouth but showed little or no response to smaller Chinook Salmon smolts.

Pulses of one species (e.g., Coho Salmon or Chinook Salmon) can have indirect positive or negative impacts on another species (e.g., steelhead) if both species share a predator (Murdoch and Oaten 1975). Positive impacts could occur if hatchery Coho Salmon and Chinook Salmon reduce predation pressure on steelhead smolts by increasing predator encounters with hatchery salmon and decreasing opportunities to feed on steelhead smolts, or predators may focus attention on more abundant prey (Malick et al. 2009; Moore et al. 2021). In contrast, negative impacts could occur if predators switch to feeding on salmonid smolts, generally, from other prey resources such as Pacific Herring *Clupea pallasii* or Northern Anchovy *Engraulis mordax*, which could be amplified if the predator response to hatchery pulses also results in greater spatial overlap with juvenile steelhead (Moore et al. 2015; Allegue et al. 2020). Determining whether hatchery releases of Coho Salmon or Chinook Salmon increase, decrease, or have no effect on predation mortality of steelhead is an important step in understanding how top-down dynamics impact survival of steelhead in Puget Sound.

Several previous studies have investigated relationships between salmonid survival and the magnitude of hatchery salmonid releases in Puget Sound (e.g., Nelson et al. 2019b; Kendall et al. 2020; Sobocinski et al. 2020); however, these studies focus on the annual time scale, which does not capture the pulsed nature of hatchery salmonid abundances in marine environments. Similarly, these studies tend to focus on total hatchery releases in the Puget Sound region rather than explicitly considering spatial heterogeneity in hatchery releases. In this study, we used a unique long-term data set of spatially and temporally explicit steelhead survival in Puget Sound along with

two complementary data sets of abundance of Coho Salmon and Chinook Salmon smolts to first characterize abundances of Coho Salmon and Chinook Salmon smolts within and across years in several regions of Puget Sound. We then estimated relationships between weekly Coho Salmon and Chinook Salmon abundance patterns and steelhead survival. Combined, this allowed us to evaluate how weekly changes in the abundances of Coho Salmon and Chinook Salmon smolts are related to intra-annual survival of steelhead smolts in Puget Sound.

METHODS

In this study, we indexed nearshore abundances of juvenile Coho Salmon and Chinook Salmon and estimated relationships between weekly Nisqually River steelhead survival and juvenile salmonid abundances. In particular, we indexed abundances of Coho Salmon and Chinook Salmon smolts in Puget Sound using data from hatchery releases and nearshore sampling using a lampara net. We used hatchery release data to estimate weekly nearshore abundances of hatchery Coho Salmon and Chinook Salmon in Puget Sound. Estimates of juvenile salmonid abundance based only on hatchery-origin salmonids, however, ignore abundances of natural-origin salmonid smolts migrating to Puget Sound. Therefore, to index abundances of both hatchery and naturally produced smolts, we used systematic weekly lampara net sampling of the Puget Sound nearshore environment near the mouths of four major river systems: Nisqually, Puyallup, Lake Washington system, and Green–Duwamish (Figure 1A).

The lampara netting locations were chosen to estimate weekly abundance for the four major systems that produce Chinook Salmon that could have an ecological impact along the migratory path of Nisqually River steelhead. These four systems contribute the majority of natural-origin Chinook Salmon in south and central Puget Sound and account for a large proportion of the hatchery Chinook Salmon and Coho Salmon releases. The major river systems further to the north (Skagit, Stillaguamish, and Snohomish) also contribute significant numbers of hatchery- and natural-origin Chinook Salmon and Coho Salmon but are far less likely to affect ecological conditions for migrating Nisqually steelhead because multiple years of data indicate that all steelhead migrate up the west side of Whidbey Island (Moore et al. 2015).

Hatchery releases.—We used hatchery release data for Chinook Salmon and Coho Salmon from the Regional Mark Information System database (RMIS; <http://www.rmpc.org>) to estimate hatchery salmonid abundances in nearshore environments. The RMIS contains detailed records of coded wire tag (CWT) releases of salmonids from hatcheries throughout the North American west coast. Each record in the RMIS describes the total

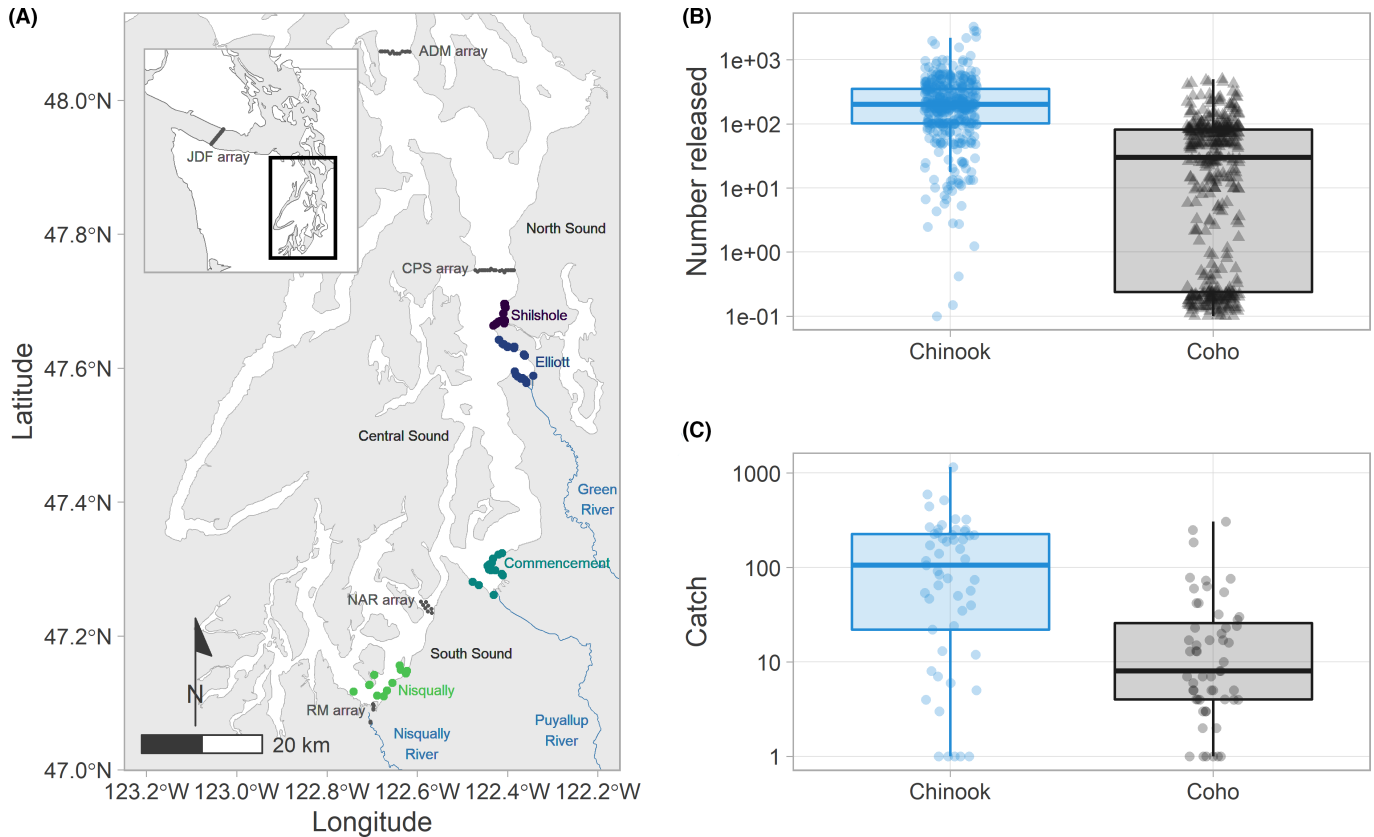


FIGURE 1. Summary of the study area and Coho Salmon and Chinook Salmon hatchery release and lampara catch data. (A) The map of the study area shows the lampara net sampling locations (Nisqually, light green; Commencement Bay, teal; Elliott Bay, blue; Shilshole, purple) and receiver array locations (small dark gray closed circles). The box plots show a summary of (B) hatchery releases of juvenile Chinook Salmon (blue) and Coho Salmon (gray) for the years 2014–2020 and (C) lampara net catches of juvenile Chinook Salmon (blue) and Coho Salmon (gray) for the years 2018–2019. For the box plots, the horizontal line in each box indicates the median, the box dimension represent the 25th to 75th percentile ranges, and the whiskers extend to the minimum and maximum values that occur within 1.5 times the interquartile range; the y -axes are on a log scale, and light dots show all individual releases or catches.

number of salmonids released, number of tagged fish, date of first and last release, CWT number, location of release, and geographic region of release. We downloaded release data from the RMIS database for years 2014–2020 and two geographic regions: South Puget Sound (SPS) and Mid Puget Sound (MPS). These two regions include all releases in Puget Sound south of the Snohomish River, excluding Hood Canal (Figure 1A). For Chinook Salmon, both subyearling and yearling releases were included. We then assigned each tag group a release week number and only included releases for week numbers 16–24 (mid-April through mid-June), which corresponded to the period of available steelhead survival estimates (week number was defined using the ISO 8601 definition).

Three primary factors can influence the timing and abundance at ocean entry of a particular hatchery release group: (1) river distance between release location and Puget Sound, (2) migration speed, and (3) downriver survival. Hatchery releases in SPS and MPS occurred at

distances from <1 to 112 km from Puget Sound. Migration rates of subyearling Chinook Salmon in the Columbia River basin have been shown to range from 12 to 50 km/d (Giorgi et al. 1997; Tiffan et al. 2009). Similarly, an analysis of Skagit River subyearling hatchery Chinook Salmon (see the Supplement available separately online) indicated a median downriver travel rate of 24.2 km/d (Figure S1 available in the Supplement). Based on these migration rates and the geographic distribution of hatchery releases, we included hatchery release groups that were released at sites within 62 km of Puget Sound (Figure S2). We also assumed a conservative 100% survival rate during the downriver migration for both Coho Salmon and Chinook Salmon because survival estimates were not available for systems in our study region.

The included releases accounted for 89% of all Coho Salmon releases and 96% of all Chinook Salmon releases for the years (2014–2020), regions (SPS, MPS), and weeks (16–24) considered (Figure S3). More specifically, for the

period 2014–2020, annual total releases of Chinook Salmon averaged 18.4 million fish, with 17.5 million fish being released from sites within 62 km of Puget Sound. For Coho Salmon, average annual releases were 3.9 million fish, with 3.4 million fish released from sites within 62 km of Puget Sound (Figure S4). There were a total of 853 CWT release groups released at 63 unique release locations (Figure S2). In 155 of the releases (18%), releases potentially occurred over multiple weeks (“last release date” in RMIS data was at least 1 week later than the “first release date”). Because each entry only has a “first release date” and “last release date,” we were unable to calculate exact weekly releases. In these cases, we assumed that all fish were released the first week (62% are listed as forced releases, 20% as volitional, with the remaining 18% not listing a release strategy).

Uncertainties associated with both downriver survival and seawater entry timing of hatchery releases likely increase with distance from Puget Sound. For example, all fish within a single release may not migrate at the same speed and downriver mortality rates may reduce the number of juvenile salmonids entering Puget Sound. Therefore, we conducted a separate analysis that included only releases that occurred within 1 km of Puget Sound. This analysis included a smaller percentage of all hatchery releases (65% of Coho Salmon and 19% of Chinook Salmon), but the close proximity to Puget Sound meant that the numbers of fish entering Puget Sound and the timing of marine entry were more precise (Figure S2).

Lampara net sampling.—Nearshore sampling followed methods described in Rubin et al. (2018). Each of four locations were sampled weekly from April 18 through June 14, 2018, and April 22 through June 13, 2019. Sets were made at 18 sites in Commencement Bay (mouth of the Puyallup River), 17 sites in Elliott Bay (mouth of the Green–Duwamish River), 15 sites near Shilshole Bay (Lake Washington system), and 14 sites near the Nisqually River estuary. A lampara net was used to systematically capture salmonids in the nearshore environment. The net measured 46 m long and 4.5 m deep with 13-mm (stretched) netting in the “bag end” of the net. The lampara net was attached to two boats positioned close to shore in approximately 3–6 m of water depth. The boats moved in opposite directions along the shoreline, fully extending the net. The two boats then moved away from shore, circling back together. The net was then pulled on board one of the boats. All fish captured were loaded into water-filled buckets, netted, and individually identified to species. Chinook Salmon and Coho Salmon were checked for the presence or absence of a CWT and adipose fin clip (both indicating that they were produced from a hatchery) and measured (fork length) to the nearest 1 mm (Figure S5). The abundance of each species from all sampling sites was combined within each of the four locations to

produce an abundance index for each sampling week and location (river system).

Abundance indices.—We calculated separate weekly abundance indices for Coho Salmon and Chinook Salmon and the hatchery and lampara data sets (total of four indices per week). For each index, we first calculated the total species-specific abundance at each sampling location (lampara data) or Puget Sound region (hatchery data). We assumed that Coho Salmon and Chinook Salmon at sites or segments north of the Nisqually River mouth (i.e., Shilshole, Elliott Bay, and Commencement for lampara data and MPS for hatchery data), could influence Nisqually steelhead survival 1 week after steelhead ocean entry (based on steelhead migration timing; Moore et al. 2015). Therefore, abundances at these northern sites were lagged 1 week to match steelhead survival timing (e.g., Coho Salmon sampled at Shilshole in week 17 were assumed to interact with Nisqually River steelhead entering Puget Sound in week 16). We then summed across locations or regions to get a total weekly abundance index that could be compared to weekly steelhead survival from the Nisqually River mouth to the Strait of Juan de Fuca.

Steelhead survival.—Wild steelhead smolts were captured at a rotary screw trap at river kilometer (rkm) 19 (measuring from the river mouth) in the Nisqually River (Figure 1) during the smolt outmigration periods (April–June) of 2014 through 2020. Nisqually steelhead smolt abundances were an order of magnitude smaller than hatchery releases of Coho Salmon and two orders of magnitude smaller than Chinook Salmon releases, with a peak abundance of 133,597 in 2018 (Losee et al. 2021). Captured smolts were anesthetized, weighed, measured (fork length), and implanted with a Vemco V7 2L acoustic transmitter (7 × 15.5 mm, 69 kHz, 30–90 s random ping interval; Vemco, Nova Scotia, Canada) following surgical implantation procedures outlined in Moore and Berejikian (2017). All smolts were held for 18–24 h and released at rkm 19.

Transmitter detections from fixed hydrophones deployed in the Nisqually River estuary and near the Pacific Ocean point of entry were used to estimate the early marine survival of tagged steelhead smolts. Six Vemco V2W hydrophones were deployed at the same locations at the Nisqually River mouth (RM) each year from 2014 to 2019; three VR2Ws were deployed in 2020 within the same geographic range. Thirty Vemco VR3 and VR4 hydrophones maintained by the Ocean Tracking Network spanned the Strait of Juan de Fuca (JDF) at Pillar Point (Figure 1). Cormack–Jolly–Seber mark–recapture models (Cormack 1964; Jolly 1965; Seber 1965) implemented in the RMark package (Laake 2013) for R version 3.6.2 (R Core Team 2019) were used to estimate the probability of detection (p) at the river mouth array and the probability of smolt survival (π) from RM to JDF. To account for

separate (but overlapping) week ranges in steelhead survival across years and allow for segment-specific survival, we fit separate mark–recapture models for each year (2014–2020) (Moore et al. 2021). Each model included parameters for segment-specific π (point of release–RM and RM–JDF) and p (RM and JDF) as well as a week effect on RM–JDF survival to obtain π for each week. Only weeks when greater than four tagged smolts migrated through the estuary were included in the analysis. A value of 0.685 was fixed for p at JDF according to linear regression estimation methods detailed in Melnychuk (2009). Model goodness-of-fit parameters were satisfactory for all models (Fletcher’s c -hat > 1.2; Fletcher 2012).

Statistical models.—We used Bayesian beta regression models to estimate the relationship between weekly steelhead survival estimates from the mark–recapture models and abundance of juvenile salmonids (Ferrari and Cribari-Neto 2004; Simas et al. 2010; Geissinger et al. 2022). We fit separate models for each of the four abundance indices (Chinook Salmon lampara, Chinook Salmon hatchery, Coho Salmon lampara, Coho Salmon hatchery). Each model had point estimates of weekly steelhead survival as the response variable (Table S1 available in the Supplement) and one of the abundance indices as the independent variable. Steelhead survival was assumed beta distributed with a mean μ and precision ϕ . We used a logit link function for μ and a log link function for ϕ but did not include any predictors for ϕ (Simas et al. 2010). We used weakly informative normal prior distributions for the intercept, slope, and ϕ parameters. The abundance indices were standardized to mean zero and unit variance prior to model estimation.

To account for annual changes in mean steelhead survival in the hatchery index models, we also included year-specific effects, which were modeled as annual deviations from the overall intercept. We did not include autocorrelation in the hatchery index models because exploratory analyses showed no evidence for autocorrelation in the weekly survival time series (average weekly AR-1 coefficient across all years was -0.03).

Each regression model was fit using Stan 2.21.0, R 4.1.2, and the brms package (Carpenter et al. 2017; Bürkner 2018; R Core Team 2019; Goodrich et al. 2020). All estimated parameters had a potential scale reduction factor (\hat{R}) less than 1.05 and an effective sample size of at least 1,000, and no divergent transitions were observed. We also assessed chain convergence and model fits using graphical methods (e.g., trace plots) and posterior predictive checks (Gabry et al. 2019).

To test the sensitivity of our results to which releases were included in the hatchery abundance indices, we also fit a set of models where the hatchery abundance indices were calculated only using releases that occurred within 1 km of Puget Sound.

RESULTS

Hatchery Releases

A total of 429 Chinook Salmon and 424 Coho Salmon releases occurred within 62 km of Puget Sound for weeks 16–24 over the period 2014–2020. Average individual hatchery release abundance was five times higher for Chinook Salmon (285,240 fish) compared to Coho Salmon (56,892) (Figures 1B and S3), but the average length of fish released was considerably larger for Coho Salmon (139 mm) compared with Chinook Salmon (82 mm) (Figure 2A). For both Chinook Salmon and Coho Salmon, the majority of releases occurred in the MPS region (487 releases), with fewer releases in SPS (366 releases). Releases of Chinook Salmon tended to be concentrated in

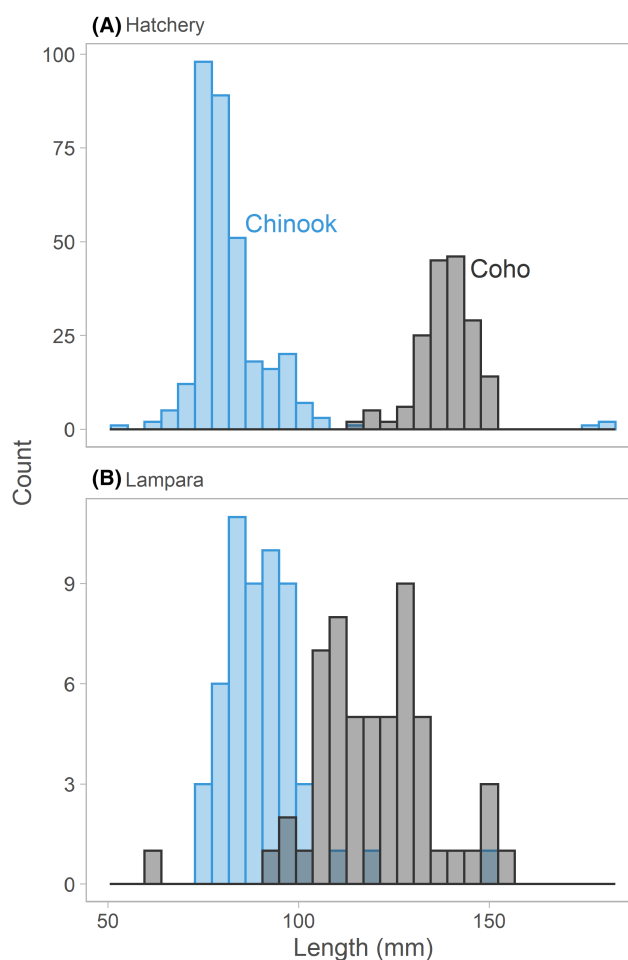


FIGURE 2. Body size distributions (histograms) of Coho Salmon (gray) and Chinook Salmon (blue) for (A) hatchery releases and (B) lampara catches. The y -axis gives the number of observations (mean lengths) in a size bin. For hatchery releases, length is the mean length of all fish in a release group. For lampara catches, length is the daily site- and species-specific average body length of all fish captured, which includes a combination of hatchery- and natural-origin fish.

one or a few weeks, whereas Coho Salmon releases tended to be more spread out over multiple weeks (Figure 3A). For example, in 2015 almost all Chinook Salmon were released during week 19, but Coho Salmon releases were more evenly distributed over several weeks (second row in Figure 3A).

Across all years, the correspondence between the Chinook Salmon and Coho Salmon abundance indices ranged from strongly positive to weakly negative, with a mean correlation across years of 0.19. For example, in 2014 Chinook Salmon and Coho Salmon indices were strongly positively correlated ($r = 0.69$), whereas in 2016 the indices were weakly negatively correlated ($r = -0.22$).

Lampara Catches

Similar to the hatchery releases, Chinook Salmon catches were consistently higher compared with Coho Salmon catches (Figure 1C), with the largest catches occurring at the southernmost sampling site, Nisqually. The mean catch across all sampling events was 117 Chinook Salmon and 23 Coho Salmon. The weekly mean catch of Coho Salmon was highest in Shilshole (40) and lowest in Elliot Bay (7), whereas for Chinook Salmon, mean catch was highest in Nisqually (272) and lowest in Shilshole (23). In 2018 and 2019, catches of Chinook Salmon increased markedly in weeks 20 and 21, respectively, and remained relatively high through week 24 (Figure 4A). In contrast, catches of Coho Salmon in 2018 were highest in weeks 20 and 24 and showed low variation across weeks in 2019. These patterns were also observed in the abundance indices where the Chinook Salmon index peaked in weeks 19 and 21 in 2018 and 2019, respectively, whereas the Coho Salmon index had two peaks in 2018 (weeks 19 and 23) and low variability across weeks (Figure 4B). Similar to the hatchery releases, Coho Salmon were considerably larger on average (123 mm) compared with Chinook Salmon (90 mm) (Figure 2B).

The weekly lampara abundance indices had moderately negative to weakly negative correlations with the abundance indices derived from the hatchery releases. Specifically, the lampara and hatchery indices for Coho Salmon had correlations of -0.10 in 2018 and -0.01 in 2019. The Chinook Salmon indices had correlations of -0.58 and -0.12 in 2018 and 2019, respectively.

Steelhead Survival

At the time of tagging, steelhead smolts were generally larger than both the Chinook Salmon and Coho Salmon sampled in the lampara nets and released from the hatcheries. Tagged steelhead from 2014 to 2020 averaged 205 mm and ranged in size from 180 to 226 mm (Tables 1 and S1). Weekly steelhead survival from the Nisqually River mouth to JDF ranged from a high of 0.73 in week 22 (2016) to a low near 0 in week 18 (2014). Intra-annual

patterns of weekly steelhead survival were quite variable across years (Figure 5). For example, 2019 showed little variability in survival across weeks (standard deviation = 0.04), whereas variability was considerably higher in 2016 (standard deviation = 0.22). Across all years, survival tended to be highest in week 19 (2014, 2017, 2019) and week 22 (2015, 2016, 2020). Lowest survival most often occurred in week 18 (2014–2016, 2018) and week 20 (2018, 2020).

The beta regression models revealed a significant negative relationship between steelhead survival and the abundance of hatchery Coho Salmon (Figure 6A, B; Table 2). In contrast, no relationship was observed between survival and the abundance of hatchery Chinook Salmon (Figure 6A, B; Table 2). The regression models that included the lampara abundance indices showed no significant relationships between survival and abundance of Coho Salmon or Chinook Salmon (Figure 6C, D; Table 2).

The hatchery models fit using the alternative abundance index that only included releases within 1 km of Puget Sound had similar estimates as the models fit using the full abundance indices for both Coho Salmon and Chinook Salmon (Table S2; Figure S6), suggesting our results are not sensitive to potential uncertainties in downriver migration rates or survivals.

DISCUSSION

In this study, we characterized abundance patterns of juvenile Coho Salmon and Chinook Salmon in Puget Sound and estimated relationships between abundance and early marine steelhead survival. We found that (1) nearshore abundances of Coho Salmon and Chinook Salmon (based on hatchery releases and lampara catches) can vary several orders of magnitude across weeks and regions within a year, (2) weekly survival of Nisqually steelhead smolts was low with a median survival of 0.20 through Puget Sound, (3) weekly steelhead survival was significantly negatively related to the abundance of hatchery Coho Salmon smolts but not the abundance of Chinook Salmon smolts, and (4) steelhead survival was not related to Coho Salmon abundance based on lampara catches in the 2 years evaluated, suggesting that the more important impact comes from hatchery releases. Together, these results suggest that hatchery releases of Coho Salmon into Puget Sound contribute to variation in mortality of steelhead smolts as they migrate through Puget Sound.

The significant negative relationship between weekly abundance of hatchery-released Coho Salmon and steelhead survival in Puget Sound could arise (1) from direct competition between Coho Salmon and steelhead smolts for prey resources or (2) indirectly via a predator response to pulses of Coho Salmon entering Puget Sound. Although juvenile Coho Salmon and steelhead likely have

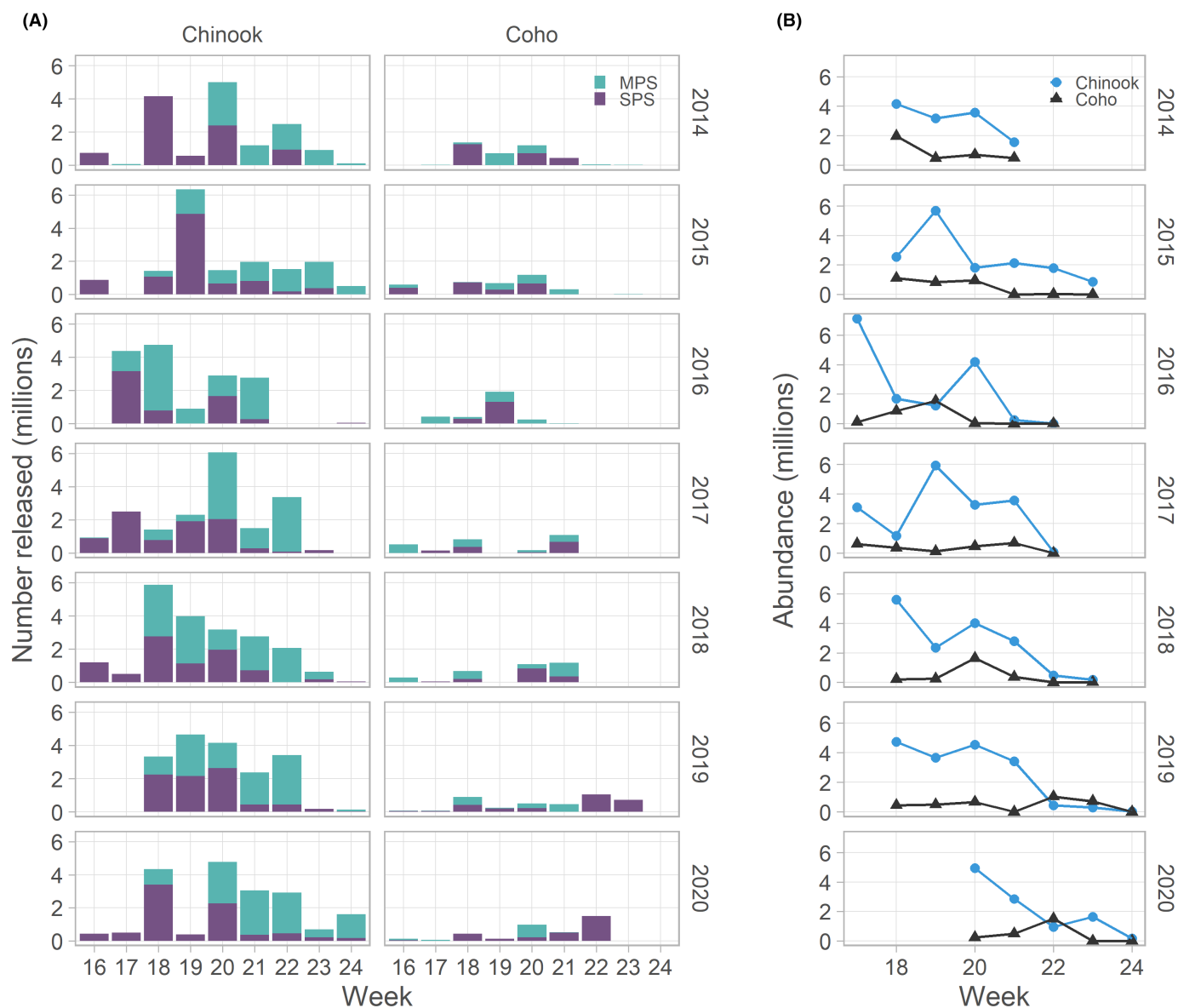


FIGURE 3. Time series of hatchery releases and abundance indices, showing (A) weekly time series of hatchery releases of Chinook Salmon (left column) and Coho Salmon (right column) for each of the Puget Sound regions and (B) abundance indices based on the hatchery releases for Chinook Salmon (blue circles) and Coho Salmon (dark gray triangles) for each year. The x-axis of both figures gives the week of hatchery release.

similar diets while residing in Puget Sound (Daly et al. 2009, 2014), the rapid migration of steelhead through Puget Sound, typically in 1–2 weeks, provides only a short time frame for resource competition to affect survival (Moore et al. 2015, 2021). This rapid movement of Nisqually steelhead, which is similar to other populations in Puget Sound (Moore et al. 2015), suggests that steelhead smolts use Puget Sound more as a migration corridor rather than a rearing environment.

A more likely explanation for the negative relationship is apparent competition, where shared predators of juvenile Coho Salmon and steelhead could cause negative

indirect effects on steelhead by increasing feeding rates on both species when Coho Salmon are abundant and co-occur in space and time (Holt and Bonsall 2017). Because of their greater energetic demands, marine mammals and seabirds likely have a greater impact on steelhead smolt survival than piscine predators. In particular, we suggest harbor seals, harbor porpoises *Phocoena phocoena*, cormorants *Phalacrocorax* spp., western gulls *Larus occidentalis*, and Caspian terns *Hydroprogne caspia* as plausible shared predators in Puget Sound. Harbor seal abundances have increased substantially in Puget Sound since 1970 (Jefferson et al. 2021), and although harbor seals are

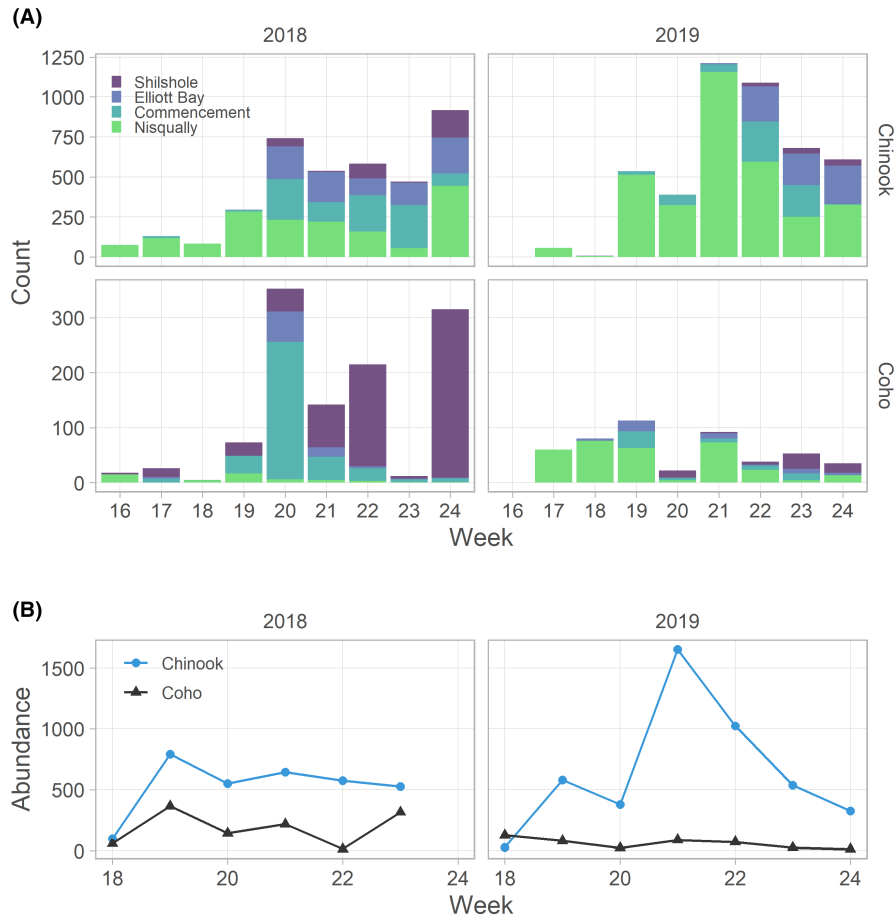


FIGURE 4. Time series of lampara catches and abundance indices, showing (A) weekly time series of lampara catches of Chinook Salmon (top row) and Coho Salmon (bottom row) for each of the four sampling locations and (B) abundance indices based on the lampara catches for Chinook Salmon (blue circles) and Coho Salmon (dark gray triangles) for 2018 (left panel) and 2019 (right panel). The *x*-axis of both figures gives the week of capture in the lampara sampling.

TABLE 1. Annual summary of number (*N*), length, weight, and standard errors (SEs) of tagged steelhead smolts used to estimate survival probabilities from the river mouth to the Strait of Juan de Fuca.

Year	<i>N</i>	Length (mm)	Length SE	Weight (g)	Weight SE
2014	100	194.9	2.7	71.6	3.6
2015	99	200.5	2.4	75.7	2.8
2016	149	200.7	1.9	75.5	2.2
2017	98	205.9	1.6	80.1	1.9
2018	204	210.3	1.7	90.8	2.3
2019	204	213.6	1.7	98.0	2.5
2020	176	201.2	1.8	76.0	2.2

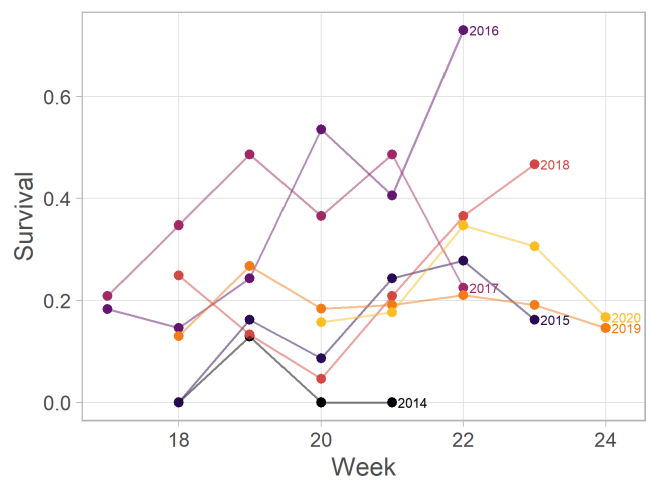


FIGURE 5. Weekly time series of steelhead early marine survival from the Nisqually River mouth to the receiver array in the Strait of Juan de Fuca for years 2014–2020.

generalist predators that feed primarily on clupeids and gadids, they also feed opportunistically on a range of species, including juvenile salmonids (Olesiuk 1993; Thomas

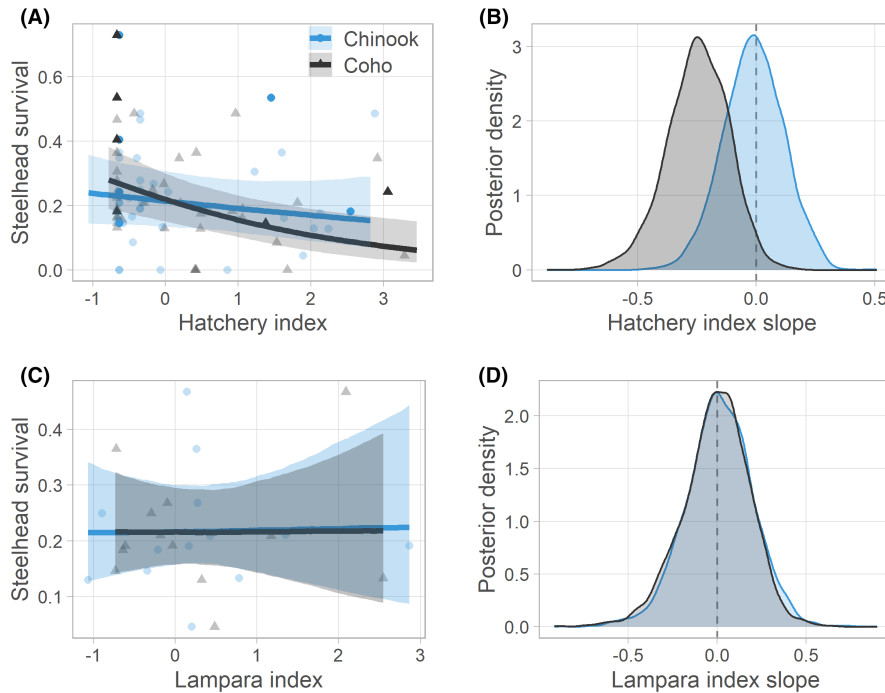


FIGURE 6. Beta regression analysis of steelhead survival and the abundance indices, showing (A) fitted regression lines for the hatchery release abundance index for Chinook Salmon (blue circles) and Coho Salmon (dark gray triangles) with 95% credibility intervals. Bold triangles highlight data for 2016, which was a high Northern Anchovy abundance year. The other graphs show (B) posterior distributions for the hatchery release index effect on steelhead survival, (C) fitted regression lines for the lampara abundance index for Chinook Salmon (blue) and Coho Salmon (dark gray) with 95% credibility intervals, and (D) posterior distributions for the lampara index effect on steelhead survival.

TABLE 2. Summary of posterior distributions for the slope of the abundance index variable in the beta regression models.

Species	Index	Lower 95% CI	Slope	Upper 95% CI
Chinook Salmon	Lampara	-0.37	0.01	0.38
Coho Salmon	Lampara	-0.42	-0.01	0.34
Chinook Salmon	Hatchery (62 km)	-0.41	-0.14	0.12
Coho Salmon	Hatchery (62 km)	-0.69	-0.41	-0.16

et al. 2011, 2017; Lance et al. 2012; Berejikian et al. 2016; Allegue et al. 2020), which can result in considerable smolt mortality (Chasco et al. 2017; Thomas et al. 2017). Harbor porpoise abundances have also increased substantially in Puget Sound in recent years (Jefferson et al. 2016), and there is some evidence that they consume juvenile salmonids, although diet information is limited (D’Alessandro and Duffield 2019). Cormorants, western gulls, and Caspian terns are among the most likely shared avian predators, which have been documented concurrently feeding on Coho Salmon and steelhead in small and large coastal river estuaries (Collis et al. 2002; Ryan et al. 2003; Clements et al. 2012).

A negative indirect effect of predation could arise if predators switch to feeding on salmonid smolts from other prey resources and (indirectly) increase predation of steelhead smolts. Predator responses to resource pulses are commonly observed in terrestrial and aquatic predators (Ostfeld and Keesing 2000; Holt 2008; Nowlin et al. 2008), and marine mammals and piscivorous seabirds are highly mobile predators, making them likely candidates to respond to pulses of released hatchery salmonids (Thomas et al. 2011; Evans et al. 2012; Allegue et al. 2020). Previous studies have indicated that Coho Salmon and steelhead smolts use similar habitats in Puget Sound (Simenstad et al. 1982; Duffy et al. 2005); thus, a predator response to pulses of Coho Salmon may increase the spatial and temporal overlap of predators and steelhead smolts. The hypothesis that predators switch to pulses of Coho Salmon and feed on similar comingling species (steelhead) is most likely when hatchery releases of Coho Salmon occur while steelhead are migrating through nearshore environments, which was the case during the time series we analyzed.

Contrasting the apparent competition hypothesis, Moore et al. (2021) showed that years with high abundances of alternative prey for steelhead predators (Northern Anchovy) in Puget Sound were associated with higher

annual Nisqually steelhead survival rates. Our analysis, however, did not indicate a substantial difference in the Coho Salmon abundance–steelhead survival relationship during high age-1 Northern Anchovy abundance years (e.g., 2016; Figure 6A). This apparent contradiction may be explained by the finer temporal scale investigated in our study (weekly rather than annual). For instance, within a year of high Northern Anchovy abundance, predators may switch from feeding on Northern Anchovy to salmonid smolts only when salmonid smolts are abundant, leading to reduced steelhead survival during these weeks but higher annual survival compared with low Northern Anchovy years. Then when salmonid smolt abundance is lower, predators may return to feeding on Northern Anchovy, causing reduced predation of steelhead smolts and increased weekly survival. This hypothesis is supported by 2016 also having the highest average steelhead survival across weeks among all years (37%). Differences in the temporal availability and behaviors of Coho Salmon and anchovies could also partly explain why changes in abundance may indirectly affect steelhead vulnerability to shared predators. Coho Salmon and steelhead behave similarly after marine entry, which includes a net migration to the Pacific Ocean, whereas anchovies form larger and denser aggregations and exhibit a more patchy distribution in Puget Sound (Duguid et al. 2019). Therefore, Coho Salmon may overlap both spatially and temporally with steelhead to a greater extent than Northern Anchovy, which could attract predators rather than drawing them away.

In contrast to hatchery Coho Salmon, we did not find a relationship between hatchery releases of Chinook Salmon and steelhead survival. This result is consistent with Allegue et al. (2020), which showed that harbor seals did not respond strongly to hatchery releases of Chinook Salmon in the Strait of Georgia. One possible explanation is that Coho Salmon may simply be a more attractive target for predators that results in a feeding response, which could be related to some combination of their larger size, greater energy content, or behavioral patterns. Coho Salmon are typically reared in freshwater for a year prior to release, whereas Chinook Salmon are typically released the same year as hatching (i.e., as subyearlings). As a result of the additional rearing period, Coho Salmon achieve a substantially greater size than Chinook Salmon released in the same year (Duffy et al. 2005). Greater similarity in size between Coho Salmon and steelhead may mean that steelhead are coincidentally consumed by predators feeding on Coho Salmon more so than Chinook Salmon smolts. Coho Salmon smolts also have a higher energy density compared with Chinook Salmon smolts (5.04 kJ/g for Coho Salmon and 3.98 kJ/g for Chinook Salmon; Roby et al. 2003), indicating that Coho Salmon smolts may be a more energetically profitable diet item

than Chinook Salmon smolts. Differences in behavioral patterns (e.g., depth, distance from shore, or differences in schooling behavior) could also result in differences in spatial overlap with steelhead.

We found no evidence of a relationship between the abundance index for Coho Salmon derived from the lampara sampling data and steelhead survival. The lampara abundance index for Coho Salmon was remarkably stable across weeks in both sampling years (i.e., 2018 and 2019), which contrasts with the observed several-fold changes observed in the abundance index derived from hatchery release data. It is possible that nearshore sampling using a lampara net may not properly capture weekly changes in abundance of Coho Salmon or that variation in downstream migration rates smooths the distribution of marine entry timing. Further, Coho Salmon tend to use nearshore habitats less than Chinook Salmon in Puget Sound, moving offshore into deeper habitats shortly after ocean entry, and thus may not be as susceptible to sampling via a lampara net (Simenstad et al. 1982; Duffy et al. 2005).

Results from the models that included hatchery abundance indices derived only using releases within 1 km of Puget Sound showed similar relationships as the indices that included more inland releases. Releases on small tributaries very close to Puget Sound would enter Puget Sound almost immediately upon release and experience less downriver migration mortality compared with releases further upstream. This could result in these tidewater releases contributing a relatively higher proportion to weekly nearshore abundances of hatchery smolts compared with more inland releases that can experience considerable downriver mortality. Similarly, tidewater releases may result in stronger pulses of smolts entering Puget Sound since migration distance to Puget Sound is low; marine entry pulses of releases more inland may be muted due to variability in migration rates within a release resulting in marine entry over several days (Figure S1).

In this study, we used a novel approach that combined long-term data sets of weekly spatially explicit estimates of hatchery smolt abundance and empirically derived wild steelhead smolt survivals to evaluate evidence for relationships between hatchery releases and steelhead survival during the early marine life phase. Combined, our results are consistent with the hypothesis that steelhead smolt mortality is mediated by similarly sized Coho Salmon abundances but not smaller Chinook Salmon, possibly via increased predation pressure by shared predators. Hatcheries are a central part of management of salmonid populations in Puget Sound (WDFW and Puget Sound Tribes 2017), and ecological effects of released hatchery salmonids on natural salmon and steelhead populations have been difficult to identify and quantify (Rand et al. 2012). Mechanistic studies that involve cotagging of released hatchery and wild salmonids to identify predation events hold promise to further

quantify predation risk and develop hatchery release strategies to mitigate potential risk.

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SUPPORTING INFORMATION

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