Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 13:41–68, 2021

ISSN: 1942-5120 online
DOI: 10.1002/mcf2.10134

FEATURED PAPER

Hatchery-Origin Stray Rates and Total Run Characteristics for Pink Salmon and Chum Salmon Returning to Prince William Sound, Alaska, in 2013–2015

E. Eric Knudsen,*[1] Peter S. Rand, and Kristen B. Gorman
Prince William Sound Science Center, 300 Breakwater Avenue, Cordova, Alaska 99574, USA

David R. Bernard
D. R. Bernard Consulting, LLC, 2481 Northwest 87th Avenue, Ankeny, Iowa 50023, USA

William D. Templin
Department of Fish and Game, Division of Commercial Fisheries, 333 Raspberry Road, Anchorage, Alaska 99518, USA

Abstract
Pacific salmon hatcheries support important commercial fisheries for Pink Salmon *Oncorhynchus gorbuscha* and Chum Salmon *O. keta* in Prince William Sound (PWS), Alaska. State policy mandates that hatchery-produced fish must not negatively impact natural populations, which can occur during mixed fisheries and via ecological and genetic interactions. Therefore, we quantified the spatial and temporal overlap of natural- and hatchery-origin salmon (1) as they migrated into PWS and (2) in PWS spawning streams. Intensive sampling during 2013–2015, combined with ancillary agency harvest and hatchery composition data, also allowed us to estimate the hatchery, natural, and total run sizes. Estimated annual proportions (SE in parentheses) of hatchery fish in the preharvest run ranged from 0.55 (0.01) to 0.86 (0.03) for Pink Salmon and from 0.51 (0.03) to 0.73 (0.02) for Chum Salmon. Proportions of hatchery fish across all sampled PWS spawning streams were much lower, ranging from 0.05 (0.03) to 0.15 (0.07) for Pink Salmon and from 0.03 (0.03) to 0.09 (0.03) for Chum Salmon. In both species, relatively high instream proportions of hatchery fish tended to be geographically localized, while many streams exhibited low proportions. The estimated total PWS runs were 50–142 million Pink Salmon and 2.3–5.4 million Chum Salmon. Commercial fisheries harvested 94–99% of hatchery-origin fish of both species, 27–50% of natural-origin Pink Salmon, and 17–20% of natural-origin Chum Salmon. Despite very high harvest rates on hatchery-produced fish, an estimated 0.8–4.5 million hatchery Pink Salmon and 30,000–90,000 hatchery Chum Salmon strayed into PWS spawning streams. Our findings provide context for further research on the relative productivity of hatchery- and natural-origin salmon spawning in streams, density-dependent survival, improvements in fidelity to hatchery release sites, the influence of hatchery production on escapement management and policy, and refinements in harvest management precision in PWS.

*Corresponding author: eericknudsen@gmail.com
[1]Retired.
Received December 10, 2019; accepted August 20, 2020

Pacific salmon *Oncorhynchus* spp. (hereafter, "salmon") are well known for their natal philopatry, or homing behavior, wherein adult salmon return to the same stream from which they emerged as fry (Quinn 2018). Philopatry reduces the likelihood that individuals disperse. This leads to local adaptation and fine-scale patterns of spatial genetic structure across populations (Avise 2000; Quinn 2018). Although salmon populations are known to be locally adapted, some amount of straying (returning to spawn in nonnatal streams) is also thought to be advantageous to maintain population resilience and robustness, facilitate recolonization, and expand territories (Keefer and Caudill 2014; Quinn 2018; Yeakel et al. 2018). Straying rates can be highly variable among species, years, locations, and ages of salmon (Westley et al. 2013; Keefer and Caudill 2014; Quinn 2018). Previous research has primarily focused on straying by Chinook Salmon *O. tshawytscha*, Coho Salmon *O. kisutch*, and steelhead *O. mykiss* (Labelle 1992; Quinn 1993; Schroeder et al. 2001; Ford et al. 2015). In contrast, fewer studies have examined straying by Pink Salmon *O. gorbuscha* (Thedinga et al. 2000; Mortensen et al. 2002; but see Brenner et al. 2012) or Chum Salmon *O. keta* (but see Lin et al. 2011; Brenner et al. 2012; Zhivotovsky et al. 2012). Despite a growing interest in the ecology of straying by salmon, we still lack a thorough understanding of the ecological, evolutionary, and fishery management implications of this phenomenon, especially with regard to hatchery-supported populations.

Keefer and Caudill (2014) identified four knowledge gaps and current challenges that must be addressed to improve our understanding of straying by salmonids, including (1) the lack of study designs that explicitly address spatial scale, (2) overcoming the bias introduced by not identifying all strays *from* or *into* a population, (3) quantifying both donor and recipient rates of straying, and (4) resolving the ambiguity around temporary and permanent straying (see Table 1 for definitions of terms relevant to this study). Meeting these challenges will not only advance the understanding of straying as a biological phenomenon but also provide important insight into managing risks associated with hatchery straying in regions supporting wild salmon.

Although many hatchery programs are primarily designed to enhance commercial fishing opportunities, some returning hatchery-origin salmon that escape fisheries stray away from their natal hatchery and into natural spawning streams (e.g., Brenner et al. 2012; Zhivotovsky et al. 2012). Importantly, concerns have been raised about genetic introgression between natural- and hatchery-origin salmon (Naish et al. 2007; Jasper et al. 2013) and ecological interactions, including displacement of wild spawners by hatchery-origin spawners (e.g., Kostow 2009; Rand et al. 2012). Further concerns arise when fisheries targeting hatchery-origin salmon sometimes overharvest comingled, nontarget, natural-origin salmon, which might also reduce the locally adapted diversity of less-productive or smaller populations (Gayeski et al. 2018 and references therein).

TABLE 1. Salmon straying terminology as used in the present paper (see Keefer and Caudill 2014).

Term	Definition
Hatchery-origin proportion	The fraction of a sampled population composed of first-generation hatchery-origin fish
Stray	An individual salmon that returns from the ocean to a nonnatal location
Permanent stray	A stray salmon that spawns, senesces, and dies in a spawning location. All stream strays in this study were permanent because we only sampled dead or moribund salmon
Stray rate	The estimated proportion, or fraction, of individuals in one population that migrated to or from another population
Recipient stray rate	The fraction of nonnatal-origin salmon in a local spawning population
Donor stray rate	The fraction of a salmon population that strays from the natal location to one or more nonnatal locations
Wild salmon	Salmon that spawn in the wild and have little or no ancestral hatchery influence. In Alaska policy, a wild salmon stock may include rehabilitation with hatchery fish, but that is not the purpose of Prince William Sound hatcheries
Natural-origin salmon	Any salmon that was spawned naturally but might have one or more hatchery-origin ancestors. In Alaska policy, natural-origin salmon are considered wild

Prince William Sound (PWS), Alaska, is a key region for consideration of the ecological, evolutionary, and fisheries management issues raised by the straying of hatchery-origin salmonids into natural salmon spawning systems. Prince William Sound naturally produces exceptionally large numbers and biomass of Pink Salmon and Chum Salmon each year. Pink Salmon have a 2-year life cycle, with the odd-year natural run sizes usually larger than the even-year runs (e.g., see data in Vega et al. 2019). Chum Salmon return to spawn in PWS streams mostly after 2–5 years at sea (Clark et al. 2018). Pink Salmon are known to utilize at least 892 PWS streams of varying sizes and Chum Salmon use at

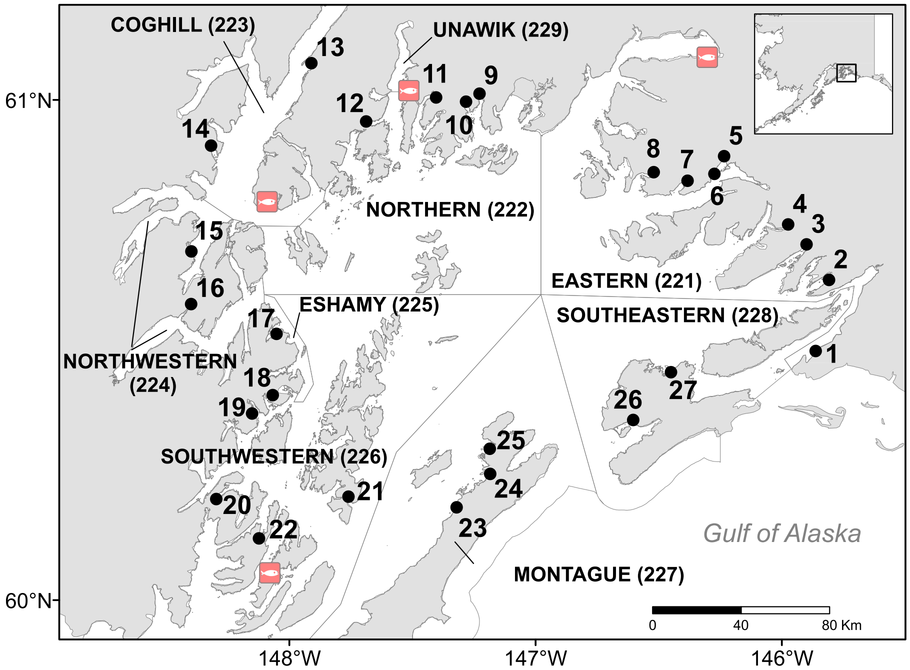

FIGURE 1. Pink Salmon study streams in PWS, Alaska (numbers correspond to the stream numbers and descriptions in Table 4). Commercial fishing management districts are denoted by solid black lines. Locations of Pink Salmon hatcheries are identified by the fish symbols within red squares (clockwise from lower left): Armin F. Koernig Hatchery, Wally Noerenberg Hatchery, Cannery Creek Hatchery, and Solomon's Gulch Hatchery.

least 326 PWS streams, as determined from the Alaska Anadromous Waters Catalog (Johnson and Blossom 2019). Additionally, there are four Pink Salmon hatcheries (Figure 1) and two Chum Salmon hatcheries plus a Chum Salmon remote release facility in PWS (Figure 2); these are operated by private, nonprofit corporations under permits from the state of Alaska. Hatchery Pink Salmon and Chum Salmon are released as fry, with the intention of increasing harvest in common property fisheries (Hilborn and Eggers 2000; Wertheimer et al. 2004). Commercial salmon fisheries in PWS include substantial catches of hatchery-origin as well as naturally produced salmon. For example, during 2013–2015 in PWS, hatchery-origin Pink Salmon comprised 72–93% of the 39–90 million annual commercial common property harvests, while hatchery-origin Chum Salmon comprised 68–95% of the 1.1–3.3 million annual commercial harvests (Vercessi 2014, 2015; Stopha 2016). However, hatchery-induced costs to PWS natural production that could be accounted for when calculating the actual hatchery contributions to total catches are open for debate (Hilborn and Eggers 2000; Wertheimer et al. 2001, 2004; Amoroso et al. 2017).

From its inception, the hatchery program in Alaska was developed to support fisheries under a precautionary approach, including a definition of guiding principles, development of a permitting system, and establishment of policies to control and mitigate potential risks (McGee 2005; Heard 2012; Evenson et al. 2018). According to the Alaska State Policy for the Management of Sustainable Salmon Fisheries

> . . .effects and interactions of introduced or enhanced salmon stocks on wild salmon stocks should be assessed; wild salmon stocks and fisheries on those stocks should be protected from adverse impacts from artificial propagation and enhancement efforts. [From Title 5 Alaska Administrative Code (AAC) Chapter 39.222:page 2.]

This and other policies, such as the Alaska Fish Health and Disease Control Policy (5 AAC 41.080), the Management of Mixed-Stock Salmon Fisheries (5 AAC 39.220), the Salmon Escapement Goal Policy (5 AAC 39.223), Application of (regional) Fishery Management Plans (5 AAC 39.200), and Alaska Department of Fish and Game (ADFG) Genetic Policy (Davis et al. 1985), require the conservation of wild stocks and consideration of interactions among natural- and hatchery-origin salmon (Stopha 2017).

The state mandate to protect wild salmon from adverse effects of artificial propagation and enhancement efforts prompted the establishment of the Alaska Hatchery Research Project (AHRP) in 2012. The AHRP mandate was to investigate the effects of hatcheries on the productivity of naturally spawning Pink Salmon and Chum Salmon in PWS and Chum Salmon in Southeast Alaska (SEAK). A science panel composed of experienced fisheries scientists from ADFG, the University of Alaska, Alaskan aquaculture associations, and the National Marine Fisheries Service

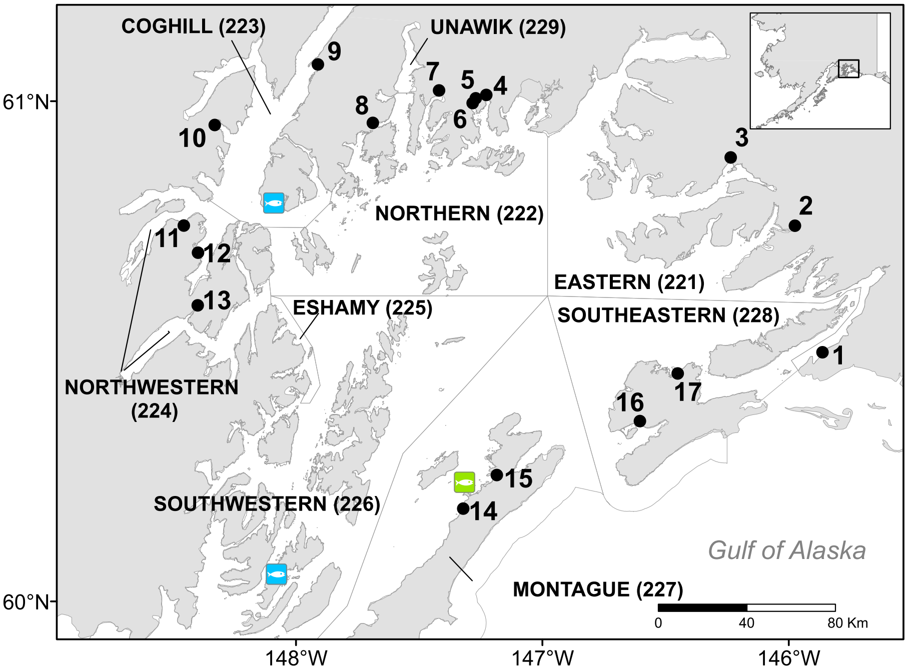

FIGURE 2. Chum Salmon study streams in PWS, Alaska (numbers correspond to the stream numbers and descriptions in Table 5). Commercial fishing management districts are denoted by solid black lines. Locations of Chum Salmon hatcheries are shown (clockwise from lower left): Armin F. Koernig Hatchery (fish symbol in blue square), Wally Noerenberg Hatchery (fish symbol in blue square), and the Port Chalmers remote release site (fish symbol in green square).

oversees the AHRP. When developing the AHRP, the science panel raised a focal question: "What are the extent and annual variability of straying by hatchery-produced Pink Salmon in PWS and Chum Salmon across PWS and SEAK?" Here we report on the AHRP-guided investigation of the relative spatial and temporal distribution of natural- and hatchery-origin adult Pink Salmon and Chum Salmon in nearshore marine waters and on spawning grounds of PWS during 2013–2015. This study was feasible because all PWS hatchery-produced Pink Salmon (beginning in 1995) and Chum Salmon (1996) are identifiable by hatchery- and year-specific, thermally marked otoliths (Volk et al. 2005; Stopha 2019). The SEAK results are reported by Josephson et al. (in press).

The rigor and novelty of this study lie in the sampling design implemented across time and space, including sampling of migrating adult natural- and hatchery-origin fish during their late ocean phase prior to commercial harvest and stream sampling to characterize the natural- and hatchery-origin composition of the run and estimate abundance-weighted hatchery-origin proportions (i.e., recipient hatchery stray rates) in streams. To date, managers have also lacked reliable estimates of spawner escapement for PWS Pink Salmon and Chum Salmon and instead have relied on aerial survey-based indices due to the region's remoteness and the large number of spawning streams. Without such statistically rigorous escapement estimates, total natural run sizes were also unknown, as were harvest rates and donor hatchery stray rates. Data produced by our study allowed for these previously unattainable estimates.

The three main objectives of our study were to estimate the following for Pink Salmon and Chum Salmon separately during 2013–2015: (1) the probability of occurrence, relative abundance and timing, and abundance-weighted proportions of preharvest natural- and hatchery-origin fish as they entered PWS; (2) the probability of occurrence, relative run timing, and abundance-weighted proportions of natural- and hatchery-origin fish sampled in spawning streams, in management districts, and throughout the entire PWS region; and (3) the PWS-wide total run size, harvest, and escapement for natural- and hatchery-origin fish, the harvest rates specific to each group, and hatchery-origin donor stray rates.

METHODS

To address our study objectives, we collected field data using (1) an ocean test fishery that sampled nine ocean entrance stations and (2) stream surveys that sampled from 27 Pink Salmon and 17 Chum Salmon spawning streams (see Figures 1–3). General methods are described here, while specific field protocols are detailed by Knudsen et al. (2016). Hatchery-origin salmon occurrence was estimated in two ways for both ocean stations and spawning streams: probability of occurrence and estimated

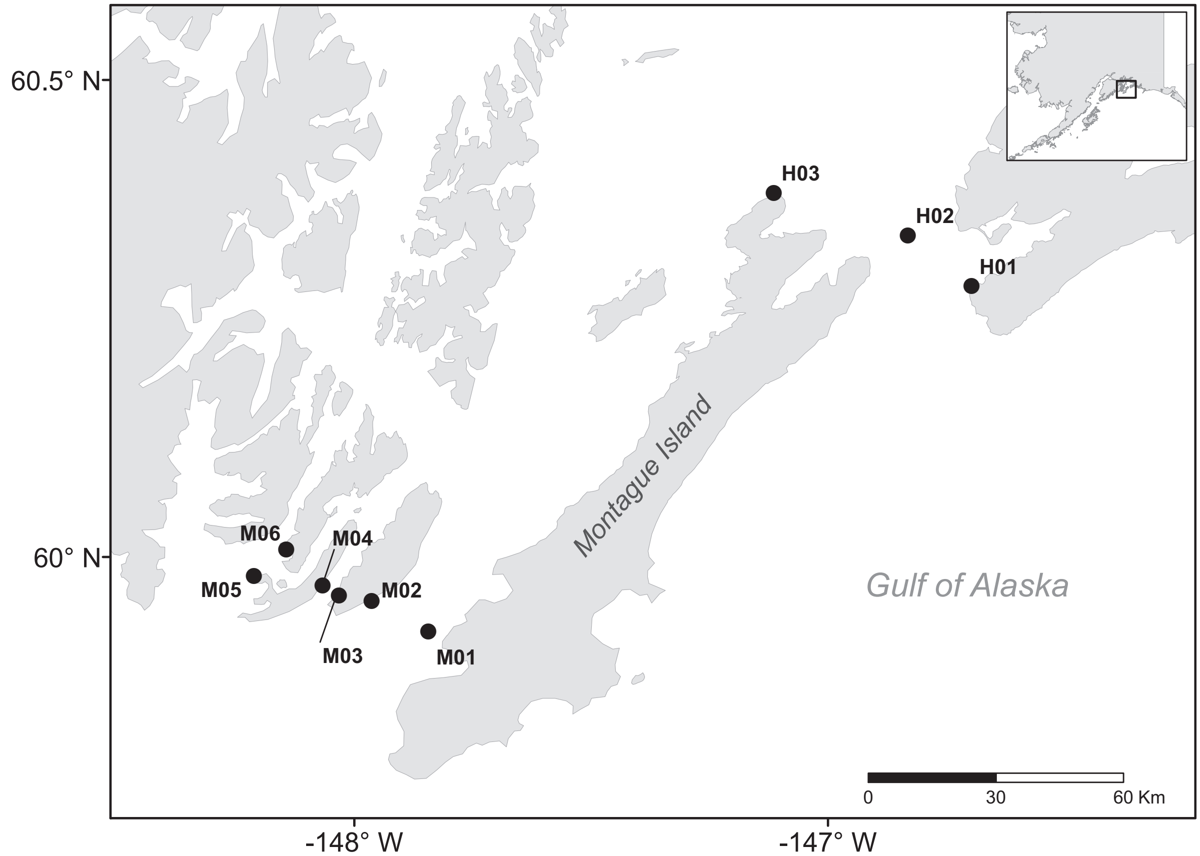

FIGURE 3. Ocean sampling stations where test fishing occurred near the entrances of PWS, Alaska (H = Hinchinbrook Entrance stations; M = Montague stations).

proportions, weighted by relative abundance, as further described below (both presented as fractions). Examining the probability of occurrence allowed us to test for differences in the relative presence of natural- and hatchery-origin salmon across space (i.e., ocean stations and districts) and over time (i.e., annual and within season). In the final stage of the analysis, we combined the ocean and stream hatchery proportion estimates with ancillary data on commercial fishery catches and hatchery returns to generate estimates of total run size, total harvests, total stream escapements, and harvest rates for natural- and hatchery-origin Pink Salmon and Chum Salmon in each year of the study (the latter presented as a percentage).

Ocean data collection.— Ocean sampling during 2013–2015 was designed to provide spatially and temporally explicit estimates of the occurrence and relative abundances of natural- and hatchery-origin Pink Salmon and Chum Salmon migrating into PWS prior to harvest by commercial fisheries. Sampling was first stratified by nine test fishing stations (Figure 3). Three stations were spaced approximately equidistant across the largest, easternmost Hinchinbrook Entrance (H01, H02, and H03), and two each of the remaining six stations were spaced across three entrances to PWS just west of Montague Island: two at the entrance to Montague Strait (M01 and M02), two in Latouche Passage (M03 and M04), and two in the entrance to Prince of Wales Passage (M05 and M06; Figure 3). Station locations were selected systematically to document abundance and hatchery–natural proportions without bias relative to normal fishing operations or hatchery location. Most hatchery production occurs in the west side of PWS (Figures 1 and 2).

For all 3 years of our study, ocean test fishing was conducted aboard a 9.8-m commercial fishing vessel using a drift gill net from the middle of May to the end of August. The vessel made sets at each test fishing station using a 366-m (200-fathom) gill net consisting of four 91.5-m (50-fathom) panels with different stretch mesh sizes of 111, 121, 130, and 140 mm (4.375, 4.750, 5.125, and 5.500 in). Each panel was 60 meshes deep, or about 6–8 m (3.3–4.4 fathoms) deep. The net was usually fished for 1 h, with shorter times and/or more drifts in cases of large catches, small catches, vessel traffic, weather, or the presence of marine mammals. All nine stations were fished over a 2-d cruise (trip), and two trips were scheduled per week. Each fishing event is referred to as a "visit." This sampling scheme was repeated for the entire study season contingent on weather. Date, time, latitude, and longitude were recorded at (1) the start and end of any periods of net setting; (2) the beginning and end of any drift; and (3) the start and end of any net retrieval. Once the net was retrieved, fish were removed and enumerated by species. The predetermined number of fish to retain for otolith removal and biological measurements was 20 per species from each Hinchinbrook Entrance station and 10 per species from each Montague station (because of the greater number of stations at the Montague entrances). Catches that exceeded those targets were systematically subsampled to acquire the predetermined sample size, and the rest of the catch was released if alive. Retained fish were tagged with a color-coded Floy tag to later distinguish sampling station, stored on ice, and returned to the ADFG laboratory in Cordova. Otoliths from all specimens were subsequently removed and read by trained personnel at the ADFG Cordova laboratory to determine natural or hatchery origin following the methods described by Volk et al. (2005).

Probability of hatchery-origin salmon among migrants from the ocean.— We applied a generalized linear model (GLM; Agresti 1996) to determine whether there were statistically significant differences in the probability of sampling hatchery-origin fish across time and space in our ocean test fishery. We used the following GLM to determine how the main effects of year, station, and trip explained variation in the probability of sampling hatchery-origin individuals for each species:

$$\log\left(\frac{H}{1-H}\right)_s = \alpha_s + \beta_{1,s}\text{Year} + \beta_{2,s}\text{Trip} + \beta_{3,s}\text{Station} + \varepsilon_s, \tag{1}$$

where H is the probability of sampling hatchery-origin salmon during test fishing; Trip (twice-weekly sampling visits) is a temporal, ordinal variable; Station is a categorical variable that indicates the ocean station where fish were captured; s is the species collected (Pink Salmon or Chum Salmon); α_s and $\beta_{n,s}$ are fitted coefficients; and ε is an error term. Sampled fish were designated as either natural origin (0) or hatchery origin (1) based on laboratory examination of otoliths. We implemented the GLM in the R statistical environment (version 3.4.1; R Core Team 2017), specifying a binomial distribution and logit link function. We applied type II chi-square analysis of deviance tests ($\alpha = 0.05$) to determine significance for main effects. We modified equation (1) to account for Year × Station and Trip × Station interactions. We determined whether the inclusion of interaction terms significantly improved the model fit through a likelihood ratio test. For cases in which interaction terms were significant, we explored the relationships by plotting these predicted probabilities (on the response scale, converted from the logit scale) across a range of values of the covariate using the "effects" package in R (Fox 1987, 2017). We conducted multiple comparisons based on estimated z-values (Wald statistic, testing the hypothesis that the effect of a particular covariate is 0 using a two-tailed test, $P < 0.05$), and we compared across main effects using Tukey's method implemented in R (R Core Team 2017) using the "multcomp" package (Hothorn 2017). To facilitate description of our results (in text and in plots), the response variable in the model (an odds ratio) was converted to a probability of sampling hatchery-origin individuals ($P[H]_{\text{ocean}}$). We also evaluated power (i.e., the probability of avoiding a type II error) by applying the GLM to bootstrapped data sets in a two-tailed test ($\pi = 0.80$) to determine whether sample sizes in our study were sufficient to draw reliable inferences on the effects of each covariate and their interactions in the model (see Supplement 1 available separately online).

Estimating relative abundance and hatchery proportions of returning salmon.— The ocean station sampling design described above was used to examine abundance patterns of migrating adult Pink Salmon and Chum Salmon. Fishing effort (E) during each visit to a station was calculated as

$$E = \sum_{d=1}^{D}(\text{Net fathoms})_d \left(\frac{\text{Minutes to set}}{2} + \text{Drift minutes} + \frac{\text{Minutes to retrieve}}{2}\right)_d, \tag{2}$$

where D is the number of drifts during a visit to a test fishing station. Note that the net was assumed to be less effective by half while being deployed or retrieved. The CPUE was calculated as the sum of the target species' catches over all drifts during one visit to each test fishing station divided by E above. Observations of CPUE were then used as standardized units that described relative abundance at each station over the immigration season for each species.

Data from otolith marks identifying the natural or hatchery origin of fish captured at test fishing stations were also used to derive and compare unbiased estimates of the proportions of hatchery-origin salmon for (1) each station on each visit ($\hat{p}_{\text{st}}$), (2) the entire season at each station ($\hat{p}_{\text{s}}$), and (3) all stations combined for the entire season ($\hat{p}$; i.e., one annual estimate for all PWS entrances). Samples from the nine ocean stations were assumed to provide a good representation of natural- and hatchery-origin contributions to the mixed populations as they returned to PWS. Methods for handling missed sampling events and derivations of the estimates are described in Appendix 1, and calculation of approximate variances for these weights and proportions are described in Supplement 2.

Stream data collection.— The objective of stream sampling was to estimate the probability of occurrence and proportions of hatchery-origin Pink Salmon and Chum Salmon spawning in selected recipient PWS streams, in commercial management fishing districts, and for PWS streams as a whole. The sampling design consisted of stratifying by the eight PWS fishery management districts for Pink Salmon (Figure 1) and six of the districts for Chum Salmon (two of the districts have negligible Chum Salmon populations; Figure 2). Within districts, streams were chosen randomly with replacement and with a probability proportional to their population size based on the 25-year average of spawner abundance indices generated from aerial surveys by ADFG over the years 1986–2010 (Botz et al. 2014). The number of streams to sample for this study was allocated across PWS districts proportional to district run size (summed abundance indices) according to procedures outlined by Cochran (1977). Streams were selected without regard to hatchery proximity. Study streams remained consistent throughout the study (Figures 1 and 2).

Each sampled stream was visited three to five times from mid-July through late September during each year of the study. Pink Salmon in Paddy, Erb, Hogan Bay, Spring (in the Eastern District [221]), and Stockdale creeks were sampled more frequently for a related study of the relative reproductive success of natural- and hatchery-origin Pink Salmon, resulting in a higher temporal sampling resolution for those streams. During each stream visit, otolith samples were taken from dead or moribund Pink Salmon and Chum Salmon and the number of dead individuals of these species was enumerated for later weighting of the relative proportions of natural- and hatchery-origin spawners by visit. As in the ocean test fishing, otoliths were delivered to ADFG's Cordova laboratory, where they were examined to determine whether the fish were of natural or hatchery origin.

Probability of hatchery-origin fish in spawning streams.— Similar to the ocean entrance analyses, we applied a GLM to explain the probability of sampling hatchery-origin individuals in the stream spawning populations:

$$\log\left(\frac{H}{1-H}\right)_s = \alpha_s + \beta_{1,s}\mathrm{Year} + \beta_{2,s}\mathrm{Day} + \beta_{3,s}\mathrm{District} + \varepsilon_s, \quad (3)$$

where H is the probability of sampling hatchery-origin salmon during stream surveys; Day is a temporal, continuous variable; District is a categorical variable representing the location of the stream in PWS; s is the species collected (Pink Salmon or Chum Salmon); α_s and $\beta_{n,s}$ are fitted coefficients; and ε is an error term. Fish were designated as either natural origin (0) or hatchery origin (1) based on laboratory examination of otoliths collected from each sampled carcass. We modified equation (3) to account for Year $\times$ District and Day $\times$ District interactions. We determined whether inclusion of interaction terms significantly improved the model fit through a likelihood ratio test. For cases in which the interaction terms were significant, we explored the relationships by examining the predicted probabilities (on the response scale, converted from the logit scale) across a range of values of the covariate using the "effects" package in R (Fox 1987, 2017). Following methods like those used for our ocean sampling analysis, we carried out multiple comparisons of group means for factors that were identified as having a significant effect, and we produced summaries after transforming the response variable from an odds ratio to a probability ($P[H]_{\mathrm{stream}}$). We also evaluated power in these models using the same approach as described above for the ocean sampling (see Supplement 1).

Estimating hatchery proportions in spawning populations.— Data on the natural and hatchery origin of fish sampled in streams were weighted by counts of dead individuals from each stream visit to derive unbiased estimates of the proportions of hatchery-origin salmon ($\overline{q}_i$) in individually sampled spawning streams following the procedures developed by Thompson (1992; Appendix 2). Estimation of the hatchery-origin fish proportion per district $\overline{q}$ accounted for the variety of streams in a district by the initial selection of small, medium, and large populations for sampling within each district based on their recent stream-specific aerial abundance indices. An unbiased estimate of the hatchery proportion $\hat{q}$ for a species across all PWS districts was obtained by weighting the stream estimates by the ADFG district-wide aerial abundance indices. These estimated q-values are analogous to the pHOS (proportion of hatchery-origin spawners) values described by Paquet et al. (2011). Complete derivations for spawning stream hatchery-origin proportions are given in Appendix 2, and methods for their approximate variances are described in Supplement 3.

Estimating sound-wide harvest management parameters.— Hatchery-origin proportions estimated for Pink Salmon and Chum Salmon at ocean entrances and later in PWS streams (as described above), combined with PWS harvest statistics, enabled estimation of total PWS run sizes, harvests, escapements, and harvest rates for both natural- and hatchery-origin fish. The change-in-ratio method (Udevitz 2013) was used to estimate the aggregate annual run sizes and annual spawner abundances for PWS populations. Methods used to derive the estimates and their variances are detailed in Appendix 3. Resulting estimates for harvest were divided by estimated run sizes to

TABLE 2. Annual test fishing total catches of Pink Salmon and Chum Salmon at PWS ocean entrance stations, the number of fish that were sampled for hatchery-marked otoliths and used to calculate hatchery probability and proportion, the probability of hatchery fish occurrence in the catch ($P[H]_{ocean}$), and the estimate of the weighted overall proportion that were of hatchery origin ($\hat{p}$) in 2013–2015.

Year	Test fishing catch	Number sampled	$P(H)_{ocean}$	$SE(P[H]_{ocean})$	$\hat{p}$	$SE(\hat{p})$
			Pink Salmon			
2013	3,458	515	0.553	0.0152	0.679	0.016
2014	9,400	1,615	0.835	0.0100	0.864	0.030
2015	12,060	2,278	0.412	0.0119	0.549	0.004
			Chum Salmon			
2013	1,305	947	0.669	0.0199	0.725	0.019
2014	1,198	908	0.549	0.0225	0.511	0.029
2015	2,022	1,296	0.667	0.0172	0.688	0.015

estimate harvest rates for natural- and hatchery-origin salmon in each year of our study.

RESULTS

Population Characteristics at Ocean Entrances

Test fishing yielded catches of 24,918 Pink Salmon and 4,525 Chum Salmon during 2013–2015. In total, 4,408 Pink Salmon and 3,151 Chum Salmon captured at the ocean entrance stations were analyzed to determine their origin (Table 2). For each species, we first report the results of the GLM-estimated probability of occurrence of hatchery-origin individuals across all stations ($P[H]_{ocean}$), followed by the results of CPUE estimates that were applied to the hatchery-origin occurrence data to derive abundance-weighted hatchery proportions.

Pink Salmon.— The probability of an ocean-sampled Pink Salmon being of hatchery origin ($P[H]_{ocean}$) was highest in 2014 (0.84), while the lowest $P(H)_{ocean}$ was estimated to occur in 2015 (0.41; Table 2). The model identified odd years (2013 and 2015) as having significantly lower $P(H)_{ocean}$ (about 30% lower) relative to 2014 (Figure 4A). The greater value of $P(H)_{ocean}$ in 2014 was likely an effect of the well-documented pattern of smaller PWS natural Pink Salmon run sizes in even years.

Values of $P(H)_{ocean}$ showed consistency across many of the Montague stations (M02–M06), with $P(H)_{ocean}$ values between 0.72 and 0.81 (Figure 4B). Station M01 in Montague Strait and the three stations in Hinchinbrook Entrance (H01–H03) showed significantly lower $P(H)_{ocean}$, and the lowest $P(H)_{ocean}$ (0.15) was observed at the extreme eastern station in Hinchinbrook Entrance (H01; Figure 4B). Pink Salmon $P(H)_{ocean}$ was greater in the later part of the run, rising significantly from a low of 0.30 to a high of over 0.70 by the end of the run (Figure 4C). The temporal dynamics observed at station H01 also led to a significant interaction effect in the GLM (Year × Station and Trip × Station): at H01, the $P(H)_{ocean}$ in 2013 was lower than that in 2015, which did not occur at any of the other stations, and $P(H)_{ocean}$ at stations H01 and H02 declined over time through the season, whereas the reverse pattern was observed at all of the other stations (Supplements 4 and 5).

Pink Salmon CPUE data indicated that their abundance increased after mid-June and peaked in early August, and they were still entering PWS when sampling ended at the end of August (Figure 5; Supplement 5). The CPUE of Pink Salmon was generally much greater than that of Chum Salmon (note the relative scales in Figures 5 and 6 and Supplement 5). Pink Salmon CPUE was relatively uniform across stations over the 3 years, although station H02—the only station far from land—consistently ranked lowest in CPUE (Figure 6; Supplement 5). Mean Pink Salmon CPUEs were generally greater in the Montague (western) stations compared to the Hinchinbrook Entrance (eastern) stations (Figure 6).

The overall PWS Pink Salmon CPUE-weighted hatchery-origin proportions at ocean stations ranged from 0.55 (SE = 0.02) to 0.86 (SE = 0.03) over the 3 years (Table 2). The weighted proportions of hatchery-origin fish in the Pink Salmon run during the two odd years were lower (0.68 in 2013; 0.55 in 2015) than the proportion in 2014, reflecting larger runs of natural-origin fish in those years. The weighted hatchery-origin proportions by ocean station illustrated the tendency of hatchery-origin Pink Salmon to predominate in the runs through the Montague entrances, while natural-origin fish predominated in the Hinchinbrook Entrance (Figure 7).

Chum Salmon.— Annual values of $P(H)_{ocean}$ for Chum Salmon ranged from 0.55 to 0.67 (Table 2), with the 2014 value being lower than those of the other 2 years (Figure 4D); the effect was significant but small and not likely to be biologically meaningful. Chum Salmon $P(H)_{ocean}$ was consistent across many of the Montague stations (M02–M06), with $P(H)_{ocean}$ values between 0.65 and 0.79 (Figure 4E). Station M01 at the entrance to Montague Strait and two of the three stations in Hinchinbrook

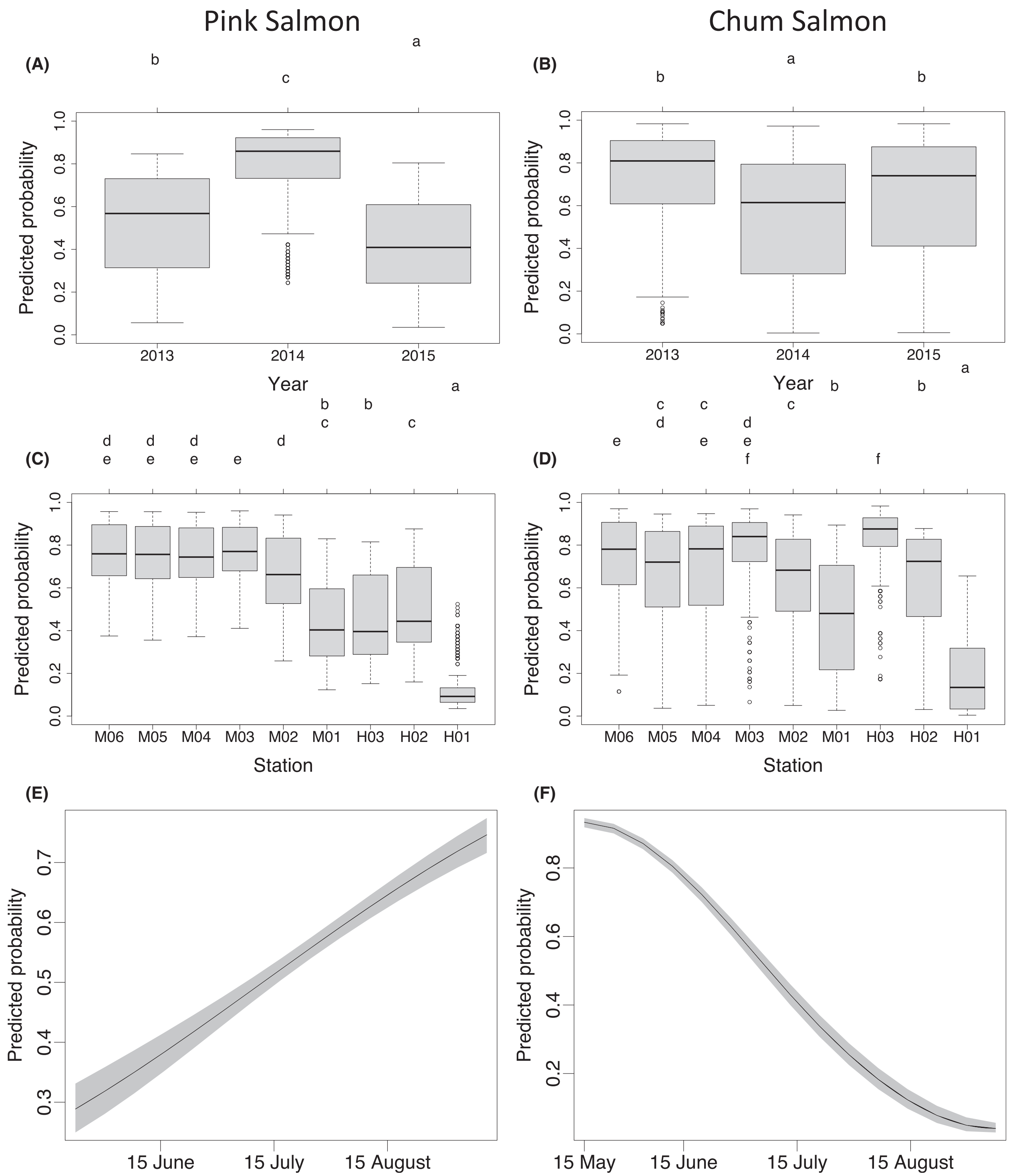

FIGURE 4. Predicted probabilities of observing hatchery-origin **(A–C)** Pink Salmon and **(D–F)** Chum Salmon: (A, D) at PWS ocean stations by year; (B, E) across ocean stations (ordered west to east); and (C, F) in samples at ocean stations through the season (shaded area = 95% CI). Samples were obtained on twice-weekly cruises (Trips) from mid-May to the end of August during 2013–2015. Bars sharing the same letter along the top margin of the box plots are not statistically different (Tukey's test: $P < 0.05$). In the box plots, means are included as filled circles, horizontal bars are the medians, boxes bound the lower and upper quartiles (25% and 75%), whiskers bound the minimum and maximum values, and open circles represent outliers. See text for a description of the general linear model.

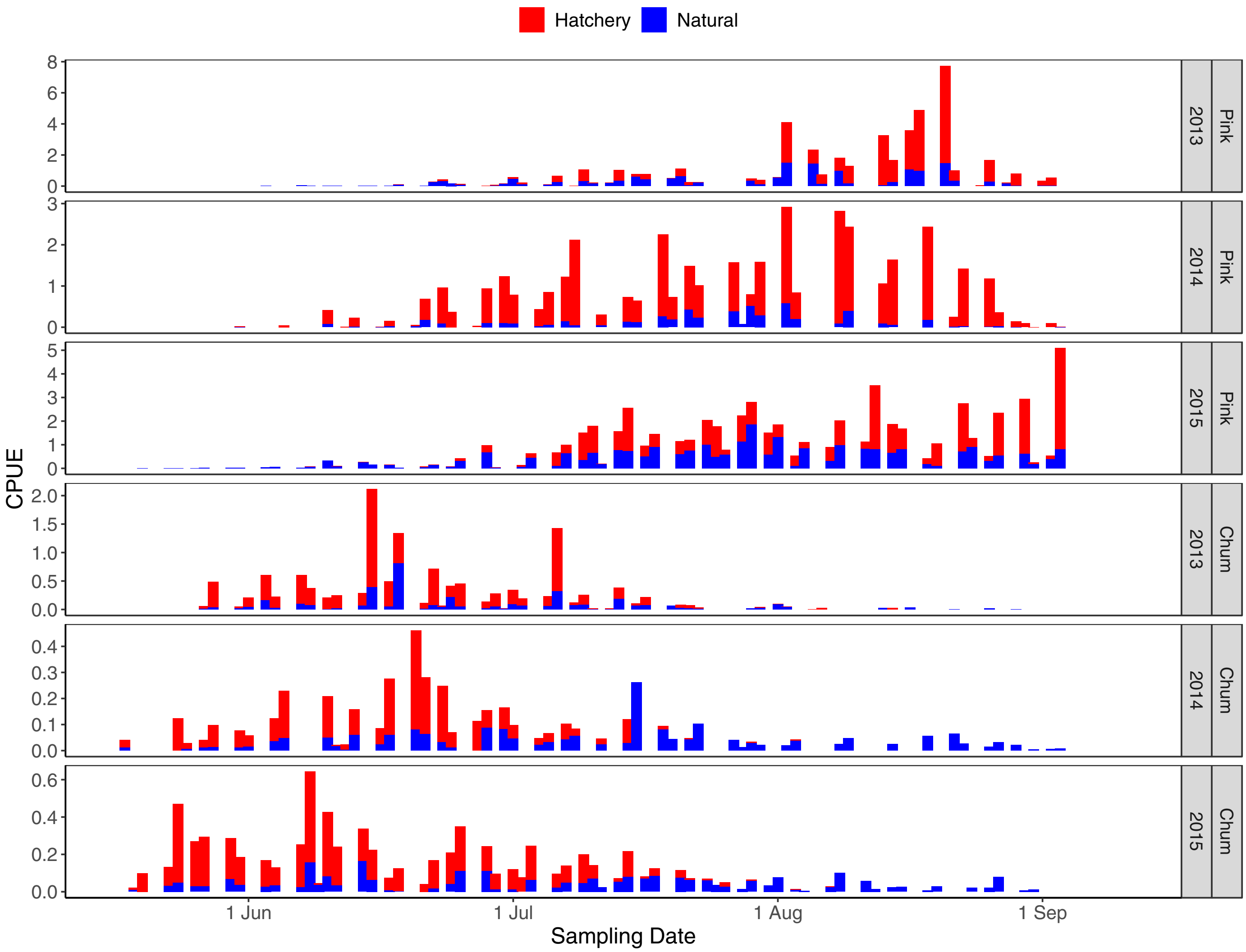

FIGURE 5. Pink Salmon (top three rows) and Chum Salmon (bottom three rows) CPUE for hatchery- and natural-origin fish across all sampling dates in PWS. Data are additive per sampling date for all nine ocean stations combined. Note that CPUE scales vary and that Pink Salmon are more abundant than Chum Salmon.

Entrance (H01 and H02) showed significantly lower $P(H)_{\text{ocean}}$ (Figure 4E). The lowest Chum Salmon $P(H)_{\text{ocean}}$ (0.18) was observed at the extreme eastern station in Hinchinbrook Entrance (H01), similar to the results for Pink Salmon (Figure 4B, E). Probability of hatchery Chum Salmon occurrence over time showed a pattern opposite that of Pink Salmon, with high $P(H)_{\text{ocean}}$ at the beginning of the run (0.90) but declining significantly to nearly zero by the end of the run (Figure 4F). There was a Year × Station interaction for $P(H)_{\text{ocean}}$, resulting from a different annual ranking of $P(H)_{\text{ocean}}$ at station H01 (the 2014 value was greater than the 2013 value) and station M04 (the 2015 value was greater than those of the other years) relative to the other stations (Supplement 6).

Results for CPUE indicated that Chum Salmon appeared first in mid-May, peaked by mid-June, and became rare after mid-July (Figure 5; Supplement 5). Station H02 consistently ranked lowest in Chum Salmon CPUE, similar to Pink Salmon (Figure 6). Unlike Pink Salmon, there was no notable difference in average Chum Salmon CPUE between the Montague stations and the Hinchinbrook Entrance stations (Figure 6).

The overall preharvest, CPUE-weighted hatchery-origin proportions of Chum Salmon ranged from 0.51 (SE = 0.03) to 0.73 (SE = 0.02; Table 2). Chum Salmon hatchery proportions were greater in 2013 and 2015 than in 2014, a pattern in contrast to that observed for Pink Salmon (Table 2). The weighted hatchery proportions by ocean station exhibited a tendency of hatchery-origin Chum Salmon to predominate at most of the stations except for the easternmost stations in the Montague and Hinchinbrook entrances (i.e., M01, H02, and especially H01; Figure 7).

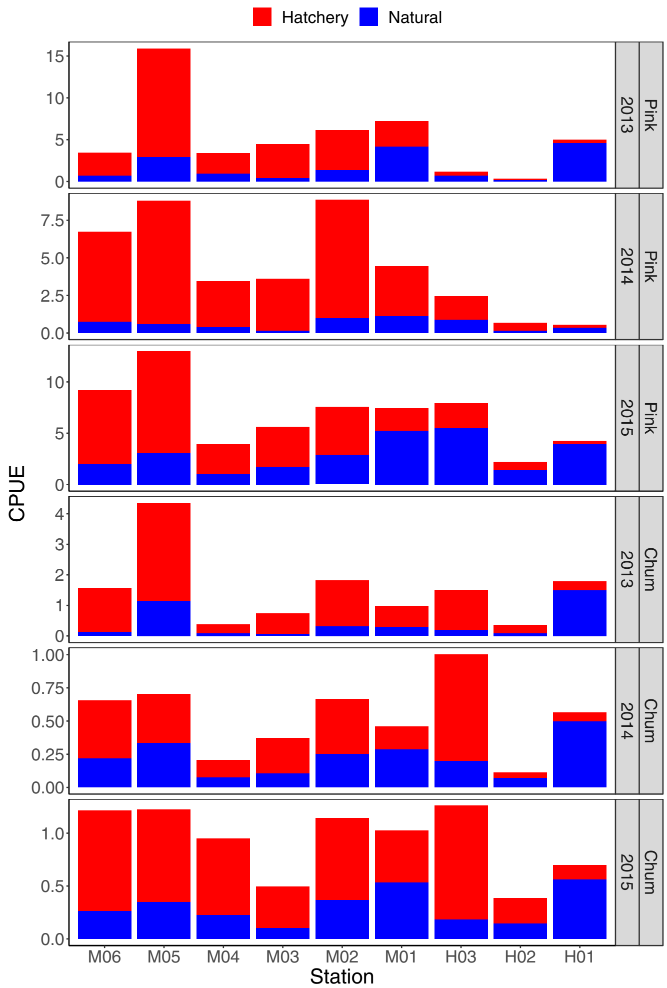

FIGURE 6. Pink Salmon (top) and Chum Salmon (bottom) CPUE for hatchery- and natural-origin fish across PWS ocean stations. Data are additive per station for all sampling visits combined. Note that CPUE scales vary and that Pink Salmon are more abundant than Chum Salmon.

Population Characteristics in Spawning Streams

We collected and processed 54,806 Pink Salmon otoliths from 385 visits to 27 study streams and 16,543 Chum Salmon otoliths from 178 visits to 17 study streams during 2013–2015 (Figures 1 and 2; Table 3). For each species, we first report the results of the GLM-estimated probability of occurrence of hatchery-origin individuals across all streams ($P[H]_{\text{stream}}$), followed by the abundance-weighted hatchery-origin proportions for PWS streams, management districts, and all of PWS.

Pink Salmon.— The probability of hatchery-origin Pink Salmon occurrence in PWS streams (Figure 1) was 0.04–0.20 and varied by year in a pattern similar to that observed in the ocean test fishery—higher $P(H)_{\text{stream}}$ was observed during the even year (0.20 in 2014) than during the two odd years (0.04 in 2013; 0.07 in 2015), with 2013 and 2014 being significantly different (Table 3; Figure 8A). The Eshamy (225) and Southwestern (226) districts exhibited the highest probabilities of hatchery-origin Pink Salmon (0.74 and 0.32, respectively), while the lowest $P(H)_{\text{stream}}$ values were estimated for districts in the eastern region of PWS (Eastern District [221]: 0.02; Southeastern District [228]: 0.01; Figure 8B). Different temporal dynamics across districts led to significant interaction terms in the GLM. Streams in the Southwestern (226) and Montague (227) districts exhibited higher $P(H)_{\text{stream}}$ in 2014 relative to the other years, whereas 2014 had the lowest $P(H)_{\text{stream}}$ for Pink Salmon in the Northwestern District (224), contributing to a significant Year × District interaction (Supplements 7 and 8). The temporal pattern of $P(H)_{\text{stream}}$ also mirrored that of the ocean sampling, with $P(H)_{\text{stream}}$ being nil at the start of the season (in early July) and increasing over the season to 0.55 by late September (Figure 8C). Some western districts exhibited a marked increase in $P(H)_{\text{stream}}$ over the season (e.g., Northern [222], Eshamy [225], Southwestern [226], and Montague [227] districts), whereas no such trend was observed among eastern districts (i.e., Eastern [221] and Southeastern [228]), thereby contributing to a significant Day × District interaction in the model (Supplements 7 and 8).

The overall Pink Salmon hatchery-origin proportions (SE in parentheses) across all streams, weighted by the aerial survey indices in each district, were 0.04 (0.03) in 2013, 0.15 (0.07) in 2014, and 0.11 (0.05) in 2015 (Table 3). At the spatial scale of individual streams, hatchery-origin Pink Salmon were observed in most streams and years sampled across PWS (Table 4; Supplement 9). Comstock Creek in the Eshamy District (225) consistently had the highest estimated hatchery-origin proportions over the 3 years, ranging from 0.81 to 0.90 (Table 4). Among the 27 streams, 15 streams consistently exhibited Pink Salmon hatchery-origin proportions less than 0.20 (Table 4). Hummer Creek in the Coghill District (223) and Paulson Creek in the Northwestern District (224) had hatchery proportions slightly greater than 0.20 in 2015 but not in the other 2 years. Besides Comstock Creek, streams that had notably greater hatchery proportions within at least one of the sampling years were Long Creek, Delta Creek, and the Siwash River in the Northern District (222); Paddy, Erb, Johnson, and Hogan Bay creeks in the Southwestern District (226); and Cabin and Stockdale creeks in the Montague District (227; Table 4). Six of the 27 sampled Pink Salmon streams exceeded hatchery-origin proportions of 0.40 in one or more years (Table 4).

Hatchery-origin proportions of PWS Pink Salmon at the spatial scale of the fishery management district varied from less than 0.05 in the Eastern (221), Coghill (223), and Southeastern (228) districts up to 0.89 in the Eshamy District (225), with a wider range of proportions across the western districts (Figure 9; Supplement 10).

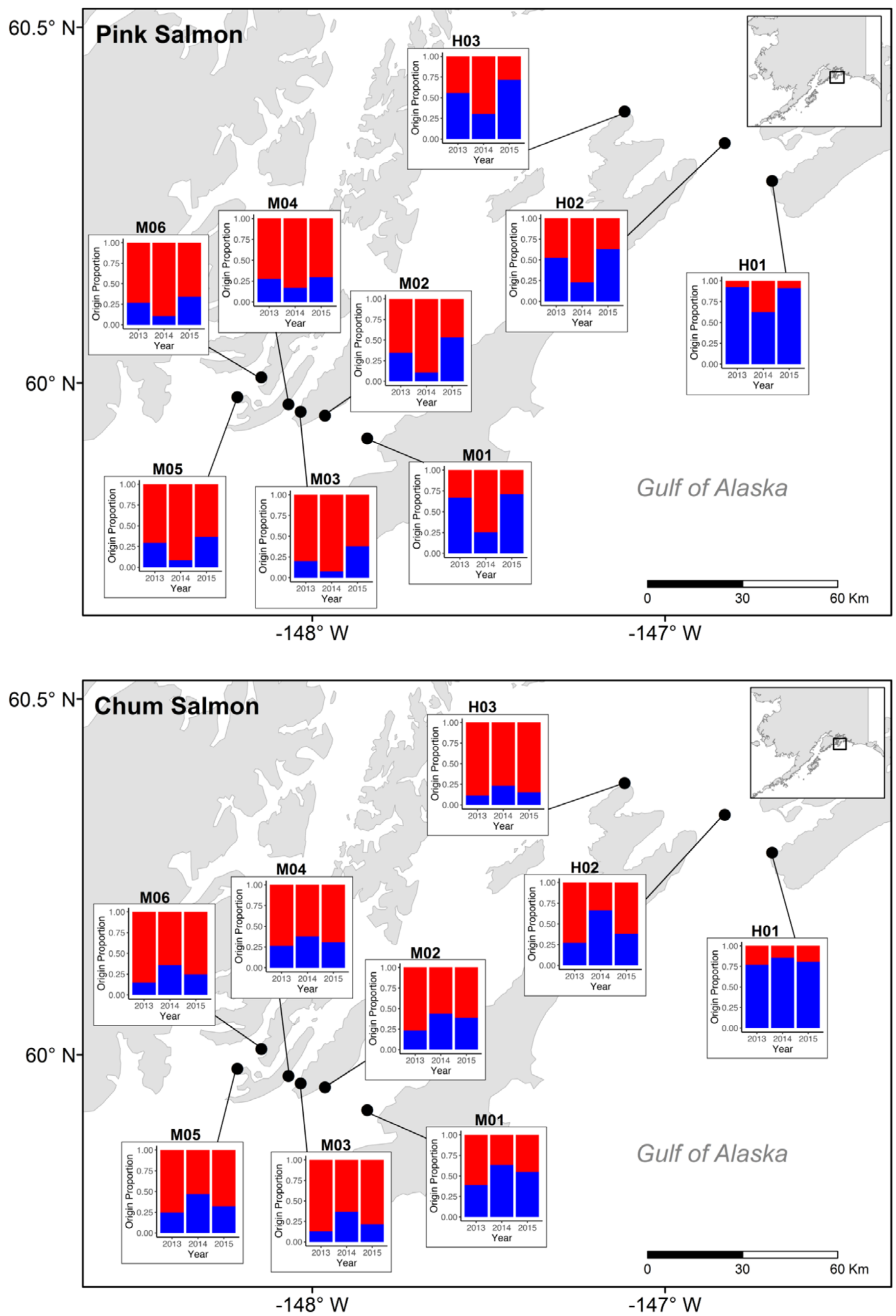

FIGURE 7. Estimated hatchery-origin proportions (red) compared to natural-origin proportions (blue) for Pink Salmon (top) and Chum Salmon (bottom) at each PWS ocean station in each year.

Particularly high proportions occurred in the Eshamy District because there was only one study stream in that district (Comstock Creek), and it had the highest proportion of hatchery-origin Pink Salmon among all of the study streams. However, the Eshamy District is a relatively minor contributor to overall PWS Pink Salmon escapement, representing less than 1% of total PWS aerial-based escapement in 2013–2015, so it did not strongly influence the overall hatchery proportion of strays for PWS. The Southwestern District (226) had the second-highest district-wide hatchery-origin proportion of Pink Salmon over the 3 years (Figure 9). The Northern (222), Northwestern (224), and Montague (227) districts had hatchery proportions ranging from less than 0.01 to

TABLE 3. Annual combined sampling of Pink Salmon and Chum Salmon in PWS spawning streams, the number of fish that were sampled for hatchery-marked otoliths for calculating hatchery probability and proportion, the probability of hatchery fish occurrence across all streams ($P[H]_{\text{stream}}$), and the estimate of the weighted overall proportion that were of hatchery origin ($\hat{q}$) in 2013–2015.

Year	Number sampled	$P(H)_{\text{stream}}$	SE($P[H]_{\text{stream}}$)	$\hat{q}$	SE($\hat{q}$)
		Pink Salmon			
2013	15,966	0.044	0.002	0.045	0.029
2014	16,909	0.199	0.006	0.147	0.071
2015	21,931	0.071	0.002	0.105	0.052
		Chum Salmon			
2013	5,864	0.067	0.005	0.028	0.025
2014	4,452	0.063	0.006	0.033	0.009
2015	6,227	0.087	0.006	0.092	0.029

nearly 0.40. Most districts exhibited greater hatchery proportions in 2014 than in 2013 and 2015 (Figure 9; Supplement 10).

Chum Salmon.— The probabilities of hatchery-origin Chum Salmon occurrence in PWS streams ($P[H]_{\text{stream}}$; Figure 2) were markedly lower than those of Pink Salmon, ranging from 0.06 in 2014 to 0.09 in 2015 (Table 3; Figure 8D). Values of $P(H)_{\text{stream}}$ were significantly lower in 2013 and 2014 than in 2015, but the size of the effect was very small and unlikely to be biologically significant (Figure 8D). We observed the highest $P(H)_{\text{stream}}$ of 0.92 in the Montague District (227), a value that was significantly higher than those in all other districts (range of 0.02–0.05 across the other districts; Figure 8E). Hatchery-origin Chum Salmon were more commonly observed in the early part of the run ($P[H]_{\text{stream}} = 0.09$), with probabilities declining significantly over time to approximately 0.02 by the end of the season in September (Figure 8F; Supplement 8). Because of the unique dynamics observed in the Montague District (227), significant interactions of Day × District and Year × District were detected. Values of $P(H)_{\text{stream}}$ in the Montague District ranged from 0.70 in 2014 to greater than 0.90 in 2013—a range much greater than that observed for any other district in PWS. In addition, the rate of decline in $P(H)_{\text{stream}}$ over the season in the Montague District was much more pronounced than that observed in any other PWS district (Supplement 11).

The PWS-wide Chum Salmon hatchery-origin proportions in sampled streams were very similar for 2013 (0.03; SE = 0.03) and 2014 (0.03; SE = 0.01), but the proportion was higher in 2015 (0.09, SE = 0.03; Table 3). Hatchery-origin Chum Salmon were detected in all study streams in PWS, although not in every year (Table 5). Cabin Creek (Montague District [227]) consistently had the highest Chum Salmon hatchery proportion among all study streams, ranging from 0.80 to 0.97 (Table 5; Supplement 12). Neighboring Swamp Creek in the same district had the next-highest proportions of hatchery fish in 2013 (0.60) and 2015 (0.79), although no Chum Salmon were found in Swamp Creek during 2014. Two Northern District (222) streams had hatchery Chum Salmon proportions greater than 0.20 during single years: Siwash River (0.33 in 2015) and Long Creek (0.26 in 2013). All other Chum Salmon study streams and years exhibited hatchery proportions less than 0.12 (Table 5). Hatchery-origin Chum Salmon generally entered spawning streams earlier than their natural-origin conspecifics (Supplement 8).

The Montague District (227) consistently stood out as having the highest stray proportion of Chum Salmon for any district across PWS over the 3 years (Figure 9; Supplement 13). All other districts had lower hatchery-origin proportions, with the Eastern (221), Coghill (223), and Southeastern (228) districts all having the lowest average hatchery-origin proportion (0.02) in PWS during 2013–2015 (Supplement 13).

Overall Run Sizes and Run Components

Pink Salmon.— The estimated run size $\hat{R}$ (SE in parentheses) of PWS Pink Salmon in 2013, 2014, and 2015 was 109 (3.0), 50 (2.3), and 142 (5.5) million, respectively (Table 6; Figure 10). Estimated hatchery run size ($\hat{R}_H$) was larger than the estimated natural run ($\hat{R}_W$) in each year, with $\hat{R}_H$ (SE in parentheses) estimated at 74 (0.7), 43 (0.7), and 78 (3.0) million in 2013, 2014, and 2015, respectively, representing 68, 86, and 56% of the total run (Figure 10). Odd-year cohorts were more abundant on the spawning grounds, with estimated numbers of naturally produced Pink Salmon spawners ($\hat{S}_W$; SE in parentheses) of 18 (2.7) and 38 (2.7) million in 2013 and 2015 but only 5 (1.8) million in 2014 (Table 6). Estimated recipient proportions ($\hat{q}$) of hatchery-origin strays on the spawning grounds reflected this trend (0.05, 0.15, and 0.11 for 2013, 2014, and 2015, respectively; Table 3), perhaps indicating a dilution of the recipient stray rate in years of greater natural-origin spawner escapement. The number of hatchery-origin Pink Salmon spawning in the wild ($\hat{S}_H$),

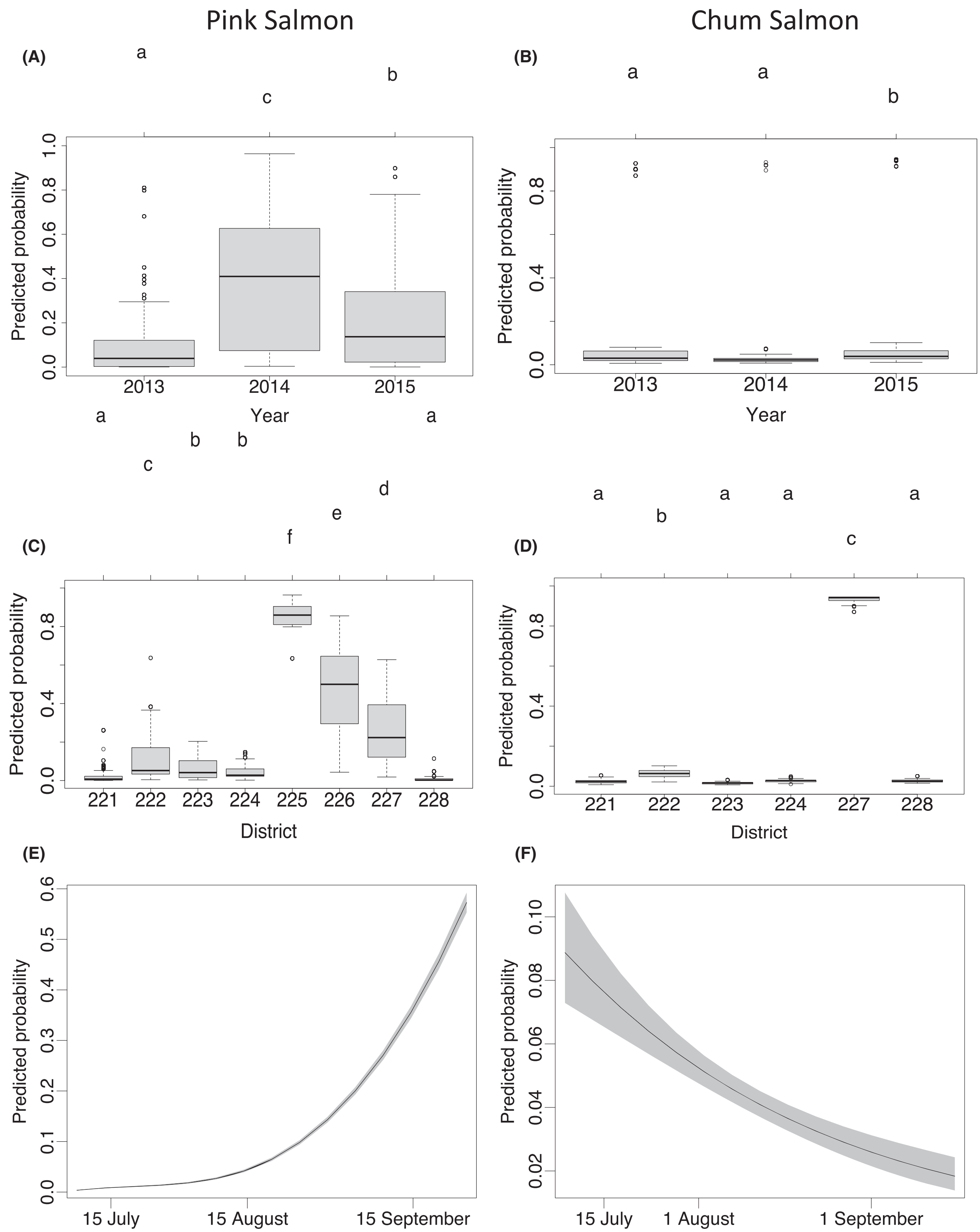

FIGURE 8. Predicted probabilities of observing hatchery-origin **(A–C)** Pink Salmon and **(D–F)** Chum Salmon: (A, D) in PWS streams by year; (B, E) across fishery management districts; and (C, F) in samples from PWS streams through the season (shaded area = 95% CI). Bars sharing the same letter along the top margin of the box plots are not statistically different (Tukey's test: $P < 0.05$). In the box plots, means are included as filled circles, horizontal bars are the medians, boxes bound the lower and upper quartiles (25% and 75%), whiskers bound the minimum and maximum values, and open circles represent outliers. See text for a description of the general linear model.

TABLE 4. Summary of hatchery proportions by stream for PWS Pink Salmon in 2013–2015. Counts of dead salmon were taken during each visit to weight the hatchery proportions of salmon sampled at each visit, thus producing weighted average seasonal hatchery proportions for each stream. Stream numbers correspond to stream locations depicted in Figure 1. Additional details about Pink Salmon stream sampling results are presented in Supplement 9.

			Average hatchery proportion weighted by counts per visit[a]		
Stream number	Stream name	District	2013	2014	2015
1	Hartney Creek	Eastern (221)	0.024	0.072	0.011
2	Spring Creek	Eastern	0.031	0.040	0.009
3	Sheep River	Eastern	0.000	0.013	0.002
4	Beartrap River	Eastern	0.025	0.001	0.013
5	Sunny River	Eastern	<0.001	0.022	0.016
6	Short Creek	Eastern	0.006	0.081	0.039
7	Fish Creek	Eastern	<0.001	0.054	0.026
8	Lagoon Creek	Eastern	0.016	0.077	0.055
9	Long Creek	Northern (222)	0.070	0.415	0.161
10	Spring Creek	Northern	0.002	0.017	0.037
11	Delta Creek	Northern	0.010	0.294	0.172
12	Siwash River	Northern	0.098	0.367	0.324
13	Coghill River	Coghill (223)	0.018	0.099	0.000
14	Hummer Creek	Coghill	0.020	0.197	0.206
15	Paulson Creek	Northwestern (224)	0.058	0.005	0.212
16	West Finger Creek	Northwestern	0.025	0.000	0.053
17	Comstock Creek	Eshamy (225)	0.868	0.899	0.807
18	Paddy Creek	Southwestern (226)	0.154	0.595	0.328
19	Erb Creek	Southwestern	0.113	0.228	0.214
20	Bainbridge Creek	Southwestern	0.174	0.000	0.169
21	Hogan Bay Creek	Southwestern	0.640	0.915	0.583
22	Johnson Creek	Southwestern	0.370	0.712	0.387
23	Swamp Creek	Montague (227)	0.063	0.125	0.130
24	Cabin Creek	Montague	0.103	0.321	0.107
25	Stockdale Creek	Montague	0.163	0.735	0.240
26	Constantine Creek	Southeastern (228)	0.000	0.023	0.006
27	Double Creek	Southeastern	0.002	0.048	0.013

[a]The number of dead salmon was used as a weighting factor in analyses.

expressed as a percentage of the entire hatchery run $\hat{R}_H$, provides the donor stray rate from the hatchery population: 1.0, 2.0, and 5.8% in 2013, 2014, and 2015, respectively. Although these donor stray rates are low, because of the large hatchery production, they correspond to $\hat{S}_H$ (SE in parentheses) absolute numbers ranging from 0.8 (0.6) to 4.5 (2.9) million hatchery fish in natural spawning streams (Table 6).

The PWS Pink Salmon common property fishery harvested between 70% and 88% of the total run in 2013–2015 (Figure 10). However, most of the harvest was directed at hatchery-origin Pink Salmon. The PWS-wide harvest rates on hatchery-origin fish were consistently high (94–99%), while harvest rates on the natural-origin run varied from 27% to 50% over the 3 years, with the lowest natural-origin harvest rate occurring in the year of the lowest natural-origin run size (2014; Table 6).

Chum Salmon.— The estimated run size $\hat{R}$ (SE in parentheses) of Chum Salmon during 2013, 2014, and 2015 was 5.4 (0.2), 2.3 (0.2), and 3.7 (0.1) million, respectively (Table 6; Figure 10). Estimated hatchery run size ($\hat{R}_H$) was greater than wild production (R_W) in 2013 and 2014, but the run sizes were similar in 2015. The R_H (SE in parentheses) was estimated at 3.9 (0.04), 1.2 (0.01), and 2.6 (0.03) million for 2013, 2014, and 2015, respectively; thus, the hatchery run was 72, 51, and 69% of the total run in each year. Estimated spawner abundance of natural-origin Chum Salmon ($\hat{S}_W$; SE in parentheses) was similar in all 3 years at 0.9–1.3 (0.1–0.2) million (Table 6; Figure 10). Estimated PWS-wide recipient proportions ($\hat{q}$)

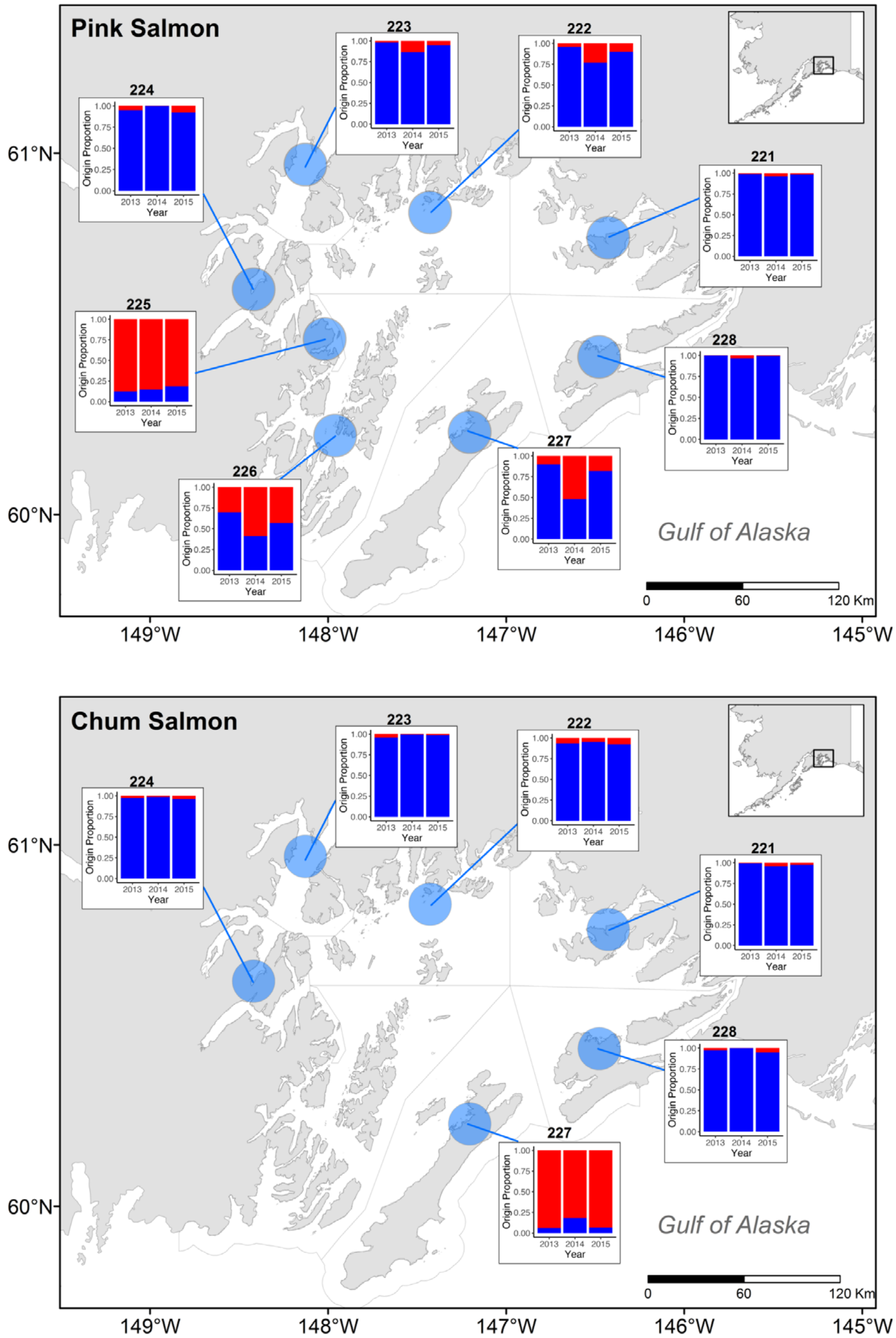

FIGURE 9. Estimated instream (recipient) spawner hatchery proportions (red) compared to natural proportions (blue) for Pink Salmon (top) and Chum Salmon (bottom) in each PWS management district during each year.

of hatchery-origin strays on the spawning grounds were 0.03, 0.03, and 0.09 in 2013, 2014, and 2015, respectively (Table 3), although the otolith-based hatchery-origin proportion estimates revealed extremely high hatchery-origin proportions in the Montague District (227). The number of hatchery-origin Chum Salmon spawning in the wild ($\hat{S}_H$), expressed as a percentage of the entire hatchery run $\hat{R}_H$, provides the donor stray rate from the hatchery population: 1.0, 2.5, and 3.5% in 2013, 2014, and 2015, respectively. Although these donor stray rates are low, they correspond to $\hat{S}_H$ (SE in parentheses) absolute numbers of 30,000–90,000 (10,000–30,000) hatchery Chum Salmon in

TABLE 5. Summary of hatchery proportions by stream for PWS Chum Salmon in 2013–2015. Counts of dead salmon were taken during each visit and used to weight the hatchery proportion of salmon sampled at each visit, thus producing weighted average hatchery proportions for each stream. Stream numbers correspond to stream locations depicted in Figure 2. Additional details about Chum Salmon stream sampling results are presented in Supplement 12.

			Average hatchery proportions weighted by counts per visit[a]		
Stream number	Stream name	District	2013	2014	2015
1	Hartney Creek	Eastern (221)	0.005	0.034	0.022
2	Beartrap River	Eastern	0.005	0.051	0.014
3	Sunny River	Eastern	0.001	0.038	0.003
4	Long Creek	Northern (222)	0.261	0.058	0.075
5	Vanishing Creek	Northern	0.045	0.025	0.027
6	Spring Creek	Northern	0.023	0.000	0.009
7	Wells River	Northern	0.021	0.065	0.045
8	Siwash River	Northern	0.049	0.120	0.326
9	Coghill River	Coghill (223)	0.049	0.000	0.008
10	Mill Creek	Coghill	0.042	0.003	0.011
11	Blackstone Creek	Northwestern (224)	0.093	0.000	0.065
12	Paulson Creek	Northwestern	0.056	0.043	0.040
13	West Finger Creek	Northwestern	0.017	0.015	0.038
14	Swamp Creek[b]	Montague (227)	0.601	NA	0.794
15	Cabin Creek	Montague	0.965	0.803	0.897
16	Constantine Creek	Southeastern (228)	0.005	0.000	0.036
17	Double Creek	Southeastern	0.039	0.001	0.026

[a]The number of dead salmon was used as a weighting factor in hatchery proportion estimates.

[b]Data were collected and hatchery proportions were calculated at the stream level, but Swamp Creek was not included in the district or sound-wide hatchery proportion estimations for 2014 because no Chum Salmon returned to that stream in 2014.

PWS natural spawning streams during the 3 years because of the large hatchery production (Table 6).

Harvest rates in the Chum Salmon fishery were between 59% and 76% of the total run in 2013–2015 (Figure 10). As with Pink Salmon, the common property harvests in PWS are directed at hatchery-origin Chum Salmon: most hatchery-origin Chum Salmon were harvested (96–99%), while the fishery harvested 17–20% of the natural-origin run during the 3 years of our study (Table 6).

DISCUSSION

This is the largest and most comprehensive investigation to date on hatchery-origin Pink Salmon and Chum Salmon from their entry into PWS to their eventual fate in harvests or as stray spawners in the streams of PWS. Our study included a test fishery that was designed to provide unbiased estimates of hatchery- and natural-origin proportions for both species during their return migration into PWS prior to exposure to the fishery. By sampling dead and moribund fish from selected streams within each district, we could also estimate recipient hatchery-origin stray rates for each stream, each district, and PWS as a whole. The ADFG routinely samples the commercial harvest to estimate the relative harvests of natural- and hatchery-origin salmon (see Stopha 2019; Vega et al. 2019). Combining our estimates of hatchery- and natural-origin fractions of both prefishery and spawning fish with fractions in total catches allowed us to quantify the relative contributions of both the hatchery- and natural-origin components of the total run over a 3-year period (2013–2015). From this, we estimated the overall hatchery fish donor stray rate to PWS escapement. This study advances understanding of the dynamics of hatchery fish straying across PWS and provides new estimates of spawner escapement and total run size by hatchery and natural origin.

Adult Return Migration Patterns

Examination of the probabilities of sampling natural- and hatchery-origin fish and the hatchery–natural proportions over space and time revealed patterns that build on previous understanding of the adult return migrations of both species. First, relative abundance (based on CPUE) of combined hatchery and natural Pink Salmon appeared

TABLE 6. Estimates (millions of fish; with approximate SEs in parentheses) for natural-origin (W) and hatchery-origin (H) Pink Salmon and Chum Salmon in the run (R) and all spawners (S) in PWS during 2013–2015. Harvest rates are shown as a proportion of the total run (HR) and separately for natural-origin (HR_W) and hatchery-origin (HR_H) Pink Salmon and Chum Salmon.

Parameter	2013 estimate (SE)	2014 estimate (SE)	2015 estimate (SE)
	Pink Salmon		
$\hat{R}$	108.87 (3.0)	49.61 (2.25)	141.78 (5.53)
$\hat{R}_W$	34.95 (2.71)	6.75 (1.80)	63.94 (2.68)
$\hat{R}_H$	73.92 (0.69)	42.86 (0.67)	77.84 (2.96)
$\hat{S}$	18.36 (3.01)	5.78 (2.25)	42.98 (5.53)
$\hat{S}_W$	17.53 (2.74)	4.93 (1.80)	38.47 (2.73)
$\hat{S}_H$	0.83 (0.60)	0.85 (0.66)	4.51 (2.94)
HR	0.83 (0.02)	0.88 (0.04)	0.70 (0.03)
HR_W	0.50 (0.04)	0.27 (0.09)	0.40 (0.02)
HR_H	0.99 (0.01)	0.98 (0.02)	0.94 (0.03)
	Chum Salmon		
$\hat{R}$	5.44 (0.16)	2.34 (0.15)	3.71 (0.11)
$\hat{R}_W$	1.50 (0.15)	1.14 (0.14)	1.16 (0.09)
$\hat{R}_H$	3.94 (0.04)	1.19 (0.01)	2.55 (0.03)
$\hat{S}$	1.28 (0.16)	0.95 (0.15)	1.03 (0.11)
$\hat{S}_W$	1.25 (0.15)	0.92 (0.14)	0.93 (0.09)
$\hat{S}_H$	0.04 (0.03)	0.03 (0.01)	0.09 (0.03)
HR	0.76 (0.02)	0.59 (0.04)	0.73 (0.02)
HR_W	0.17 (0.02)	0.20 (0.03)	0.19 (0.02)
HR_H	0.99 (0.01)	0.97 (0.01)	0.96 (0.01)

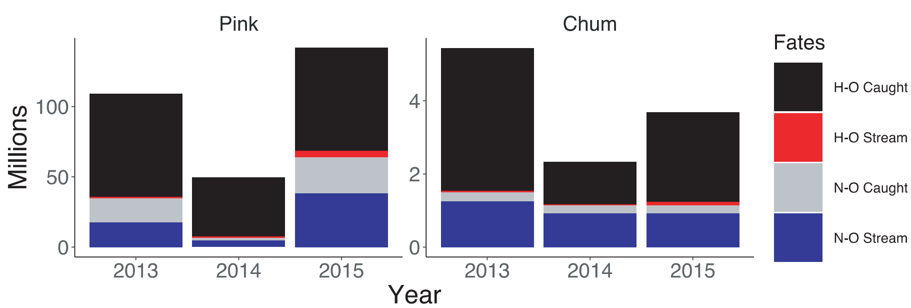

FIGURE 10. Estimated spawner abundance ($\hat{S}$) and catch ($\hat{C}$; millions of fish) of Pink Salmon (left) and Chum Salmon (right) by origin (H–O = hatchery origin; N–O = natural origin) in PWS during 2013–2015. The tops of the histogram bars represent total estimated run sizes by species and year. Note that the scale for Pink Salmon is much greater than the scale for Chum Salmon.

to be greater in the Montague (western) entrances than in the Hinchinbrook Entrance (eastern), although there was no similar pattern for Chum Salmon (Figure 6). Second, natural-origin Pink Salmon—and to a lesser extent Chum Salmon—tended to occur in higher proportions at the eastern PWS entrance (Hinchinbrook Entrance) and hatchery-origin proportions were generally greater at the western (Montague) entrances (Figure 6). This suggests preferred migration routes and differences in orientation by hatchery or natural origin in the ocean prior to entering PWS. Pink Salmon instream spawner hatchery fractions were similarly lowest in the Eastern (221) and Southeastern (228) districts (Figure 9; Supplement 10), perhaps at least partly explaining the tendency for greater proportions of hatchery-origin fish entering PWS from the west. The locations of Pink Salmon hatcheries (Figure 1) in northern and western PWS may influence adult immigration through the western PWS entrances, as they constitute the most direct pathway from the ocean to the hatcheries. Although there are no comprehensive analyses of returning adult oceanic migration routes in the literature, related information indicates a tendency to enter

TABLE 7. Comparisons of recipient hatchery fish stray proportions between earlier studies and the present study. Single values are from 1 year of observations, whereas ranges represent observations from multiple years. Methods for within-stream hatchery fish proportion estimates were comparable among the studies.

Stream number[a]	Stream (district)	1997[b]	2008–2010[c]	2013–2015
	Pink Salmon			
1	Hartney Creek (221)		0.00–0.039	0.011–0.072
9	Long Creek (222)		0.026–0.086	0.07–0.415
12	Siwash River (222)		0.011–0.370	0.098–0.367
15	Paulson Creek (224)		0.038	0.005–0.212
16	West Finger Creek (224)		0.000–0.013	0.000–0.053
18	Paddy Creek (226)	0.65		0.154–0.595
19	Erb Creek (226)	0.61		0.113–0.228
20	Bainbridge Creek (226)		0.086–0.141	0.000–0.174
21	Hogan Bay Creek (226)	0.78		0.583–0.915
22	Johnson Creek (226)		0.179–0.412	0.370–0.712
23	Swamp Creek (227)		0.018–0.071	0.063–0.130
	Chum Salmon			
1	Hartney Creek (221)		0.000–0.037	0.005–0.034
2	Beartrap Creek (221)		0.000–0.005	0.005–0.051
3	Sunny River (221)		0.00–0.003	0.001–0.038
4	Long Creek (222)		0.028–0.314	0.058–0.261
6	Spring Creek (222)		0.059	0.000–0.023
7	Wells River (222)		0.021–0.074	0.021–0.065
8	Siwash River (222)		0.051–0.626	0.049–0.326
10	Mill Creek (223)		0.000–0.142	0.003–0.042
13	West Finger Creek (224)		0.015–0.061	0.015–0.038
16	Constantine Creek (228)		0.0–0.012	0.000–0.036

[a]Refer to Figure 1 for Pink Salmon stream locations or Figure 2 for Chum Salmon stream locations.
[b]From Joyce and Evans (2000).
[c]From Brenner et al. (2012). Average annual hatchery proportions were weighted by the relative stream-specific escapement for Pink Salmon but not for Chum Salmon.

through the Montague entrances over the Hinchinbrook Entrance. These observations are consistent with the theory that salmon likely respond to geomagnetic cues for navigation and that salmon orient themselves in the ocean prior to arrival at the entrances to inshore waterbodies (see Putman et al. 2014a, 2014b; Quinn 2018 and references therein). Brodeur et al. (2003) documented juvenile salmon emigrating westward from the Montague entrances to the Shelikof Straits near the Alaska Peninsula. It is conceivable that returning adult salmon follow this same path in reverse by relying on magnetic cues (Putman et al. 2014a, 2014b).

We chose the ocean stations with the intention of covering all major entrances systematically and thoroughly. Local fishermen know that catches of both species are greater along the shoreline; therefore, to maximize our chances for good estimates of hatchery proportions, most stations were established just offshore of the entrance capes (Figure 3). Because the Hinchinbrook Entrance is so large, we added one station (H02) in open water away from shore. Although the CPUE was lowest at the only open-water station (H02), as expected, the hatchery proportions there were usually similar to those at the two adjacent nearshore stations (H01 and H03) in each year (Figure 6). We acknowledge the presence of several smaller entrances, each on the far east and west ends of PWS, that were unsampled; neither of these entrances is thought to be a significant migratory pathway (C. W. Russell, ADFG, personal communication).

Stray Rates in Spawning Streams

Our estimates of Pink Salmon hatchery stray rates are in line with estimates derived from previous Alaska studies. Donor stray rates into naturally spawning aggregates of Pink Salmon in SEAK were estimated to be 4.4–6.7% (Thedinga et al. 2000; Mortensen et al. 2002), which is comparable to donor rates reported here (1.0–5.2%), although those studies may have been biased by sampling only a few streams rather than sampling a set of streams that are more representative of all streams in the area.

Our estimated Pink Salmon donor stray rates are also similar to findings from the Fraser River (2.5%; Pess et al. 2012). These donor stray rates are consistent with the idea that Pink Salmon stray no more than other salmon species (Quinn 1993).

Other studies have sampled streams to estimate hatchery proportions in PWS as we did, although the manner in which streams were selected differed across these studies. Joyce and Evans (2000) selected streams on the western side of PWS in the general location of hatcheries. Brenner et al. (2012) selected streams based on their distance from where hatcheries released fish. We selected streams based on their expected number of spawners regardless of stream distance from hatcheries. Protocols for selecting streams to sample in these three studies differed because the studies' objectives differed. Due to this difference, only results from streams that were common among studies are comparable (Table 7). Pink Salmon hatchery stray rates in 1997 (Joyce and Evans 2000) and 2008–2010 (Brenner et al. 2012) were mostly similar to our findings, with a few exceptions (Table 7). Variations observed among years are likely attributable to a combination of varying interannual survival rates, run sizes, and harvest patterns.

Only a few previous studies have focused on hatchery Chum Salmon straying. Piston and Heinl (2012) concluded that recipient hatchery-origin proportions in SEAK fishery management subregions ranged from 0.02 (Northern Southeast Outside) to 0.14 (Northern Southeast Inside), a range that brackets the range observed in this study (0.03–0.09; Table 3). Josephson et al. (in press), using the same methods as ours and in the same years, reported summer Chum Salmon recipient stray rates of 0.03–0.06 across SEAK, with rates in individual streams ranging from 0.00 to 0.85. McConnell et al. (2018) documented a recipient hatchery stray rate of 0.51 for Chum Salmon in a single SEAK stream. In the only other study of straying by PWS hatchery Chum Salmon (comparable to our study except that the authors did not weight their average stray proportions by escapement as we did), Brenner et al. (2012) reported stray rates mostly similar to ours in streams that were common to both studies (Table 7).

Although the proportions of hatchery-origin Chum Salmon spawners in most streams sampled in our study were less than 0.10, they were anomalously high in the Montague District (227; Table 5; Figure 9), similar to the findings of Brenner et al. (2012), who reported a hatchery proportion of over 0.90 for Chum Salmon in the Chalmers River. Chum Salmon released at Port Chalmers in the Montague District are raised at Wally Noerenberg Hatchery and transferred to holding pens at the remote release site (Figure 2), where they are reared for approximately 12 weeks prior to release. Our two study streams in the Montague District (Swamp and Cabin creeks on Montague Island) were close to this remote release site and had high proportions of hatchery-origin Chum Salmon (0.60–0.89). Otolith marks on the hatchery-origin fish sampled in these creeks indicated that most originated from the on-site Wally Noerenberg Hatchery remote release (AHRP, unpublished data), and although these fish were incubated in a distant hatchery, they most likely imprinted to water in Port Chalmers prior to release. This remote release site was originally chosen partly because of low wild-origin Chum Salmon spawning abundance in neighboring streams, which was thought to have resulted from uplift following the 1964 earthquake (Roys 1965). It was also chosen because the location focused fishing effort on hatchery-origin Chum Salmon in an area that was somewhat separated from the main migratory pathway of natural-origin salmon. The straying distance for these fish is relatively short and demonstrates the tendency to home to the remote release location after imprinting at a later life history stage (postembryonic). Use of off-site, remote rearing locations has been found to increase straying for Coho Salmon (Labelle 1992) and Chinook Salmon (Candy and Beacham 2000) relative to the use of natal rearing facilities. In addition, the lack of consistent natural spawning in these streams (e.g., no Chum Salmon were found in Swamp Creek during 2014) indicates that the effects on natural-origin Chum Salmon may be limited. On the other hand, the abundance of hatchery-origin Chum Salmon in these local streams could be compromising the postearthquake recovery of natural Chum Salmon.

Both donor and recipient stray rates estimated for PWS as well as other locations are influenced to an unmeasured degree by harvest management decisions, which can vary annually. We estimated donor stray rates for the entire PWS region only rather than generating a more localized estimate. We also found PWS-wide harvest rates of hatchery fish exceeding 94%. At the present rate of hatchery salmon production, lower hatchery-origin harvest rates could result in higher donor stray rates.

Although we did not include distance from hatcheries as a covariate in our GLM, we did observe patterns at the district level that were consistent with the hypothesis that streams closest to hatcheries often have higher proportions of hatchery-origin individuals, as noted from previous studies in this region (Joyce and Evans 2000; Brenner et al. 2012; Otis et al. 2018) and other salmon studies (Unwin and Quinn 1993; Pascual and Quinn 1994; Keefer and Caudill 2014 and references therein). The Eastern (221), Northern (222), and Southeastern (228) districts consistently exhibited lower $P(H)_{\mathrm{stream}}$ and hatchery-origin proportions than other districts (Figure 9; Supplements 10 and 13). Very few Pink Salmon strays from Solomon Gulch Hatchery in the Eastern District (221) were found in this study, but Brenner et al. (2012) observed a high Pink Salmon recipient hatchery-origin stray rate in a stream close to that hatchery. Our results are generally consistent with a hatchery proximity hypothesis given the association of higher recipient stray rates in certain local streams (Tables 4 and 5) and in districts containing hatchery release sites (Figures 1, 2, and 9). Josephson et al. (in press) noted the same hatchery proximity pattern for summer Chum Salmon straying in SEAK. Higher proportions in streams near hatcheries might also be a result of Alaska's policy of avoiding hatchery siting on or near productive spawning streams. Higher recipient stray proportions might be expected in small spawning aggregates within streams near hatcheries. Beyond the hatchery proximity hypothesis, we observed a geographical tendency toward greater hatchery Pink Salmon recipient stray rates in certain other streams and districts over the 3 years (Table 4; Figure 7). These greater hatchery stray rates could in some cases be strongly influenced by harvest management decisions, such as closures in outer fishing zones to protect natural stocks bound for inner zones, resulting in increased straying of hatchery fish into local streams (Russell, personal communication).

The broad spatial extent of straying by hatchery-origin fish is also a topic of great interest. Prince William Sound hatchery-origin Pink Salmon have been observed in lower Cook Inlet streams situated 240–480 ocean kilometers away from PWS (Otis et al. 2018). Otis et al. (2018) sampled 13 streams during 2014–2017 and found that in most stream × year combinations, PWS hatchery-origin Pink Salmon were present, ranging as high as 87% in one sample. Although not yet fully understood, these observations demonstrate that the geographic scope of hatchery straying may be broader than previously documented in Alaska. Future alignment of field and analytical methods across PWS and Cook Inlet will allow for a direct comparison of results and a broader assessment of hatchery fish straying patterns.

Stream weights for estimating hatchery-origin proportions at the district and PWS levels were based on aerial and ground surveys of spawning population indices, adding uncertainty that was not reflected in our estimated SEs. The goal of stream selection for our study was to represent small, medium, and large populations in each district, with the number of streams per district weighted by the relative importance of each district to the overall PWS production. However, ADFG aerial and ground survey streams were not initially chosen randomly—instead, larger populations were more likely to be surveyed. In addition, aerial surveys tend to observe and count a lower fraction of larger spawning populations (Jones et al. 1998). On the other hand, unweighted results in our study showed that distributions of strays across streams and across districts were not uniform: many streams with larger populations or far from hatcheries had virtually no strays at all. Under those circumstances, uncertainty in weights based on aerial surveys would be relatively small.

Measurement error in the reading of otoliths for our study was demonstrably negligible. Volk et al. (1999) estimated that the probability of misreading a marked fish as a nonmarked fish was 2%, while the probability of misreading a nonmarked fish as a marked fish was 6%. Since then, quality control systems have been implemented for validation readings, whereby a large portion of the otoliths are read twice to discover those that might have been misread and a third reader then helps to resolve differences (Haught et al. 2019). We believe that our misread rates were much lower than those reported by Volk et al. (1999) because we had many instream hatchery salmon fractions that were less than 0.01, which would not have been possible with misread rates as high as 6%.

This research demonstrates that hatchery salmon are overlapping in some PWS streams, which raises concerns about possible effects on the fitness of wild populations, as observed in other salmon species in other locations (e.g., Leider et al. 1990; Araki et al. 2007; McConnell et al. 2018). Potential effects of hatchery strays could be expected to increase as their percentages in local populations increase (Chilcote et al. 1986, 2011; Reisenbichler and Rubin 1999), although large effects are not always found in the presence of high hatchery stray proportions (Jasper et al. 2013). The potential for hatchery-origin immigrants to affect the fitness of a wild recipient population might also be expected to be higher when hatchery stocks are domesticated (Berejikian and Ford 2004; Araki et al. 2008). There is evidence that introgression can occur in Chum Salmon in PWS (Jasper et al. 2013). The AHRP includes a fitness study that is related to our study; in the fitness study, the productivity of hatchery-origin Pink Salmon in PWS is being compared to that of natural-origin salmon in natural stream environments (C. Habicht and K. Shedd, ADFG, unpublished data). Combining this information into an assessment of the potential effect of hatchery-origin strays on natural Pink Salmon and Chum Salmon populations in PWS has not yet been completed.

Harvest Management Implications

Our findings provide information that should prove useful to ADFG in managing harvest and hatcheries in PWS. The intensive sampling of natural- and hatchery-origin fish at the ocean entrances and in spawning streams provided the opportunity for first-ever estimates of the PWS total run sizes and escapements by origin (Table 6). Previously, estimates were only available for total harvest, harvest of natural- and hatchery-origin fish, and an index of mixed-origin escapement based on aerial surveys. As an index, the aerial surveys were never meant to estimate total escapement, but it is interesting to note that total escapement (hatchery plus natural) reported for this study was 3.5, 7.3, and 5.8 times greater than aerial escapement indices for Pink Salmon and 2.6, 3.2, and 1.8 times greater than aerial indices for Chum Salmon in 2013, 2014, and 2015, respectively (see Table 6; Vega et al. 2019). Furthermore, aerial survey-based escapement index counts include non-trivial numbers of hatchery-origin fish that obscure natural-origin components of escapement in some streams (e.g., Tables 4 and 5). Current escapement goals have been developed to ensure natural production from streams at levels that provide consistent harvestable surpluses. Hatchery strays have been included in escapement assessments since hatchery releases began more than 40 years ago, and escapement goals are based on consistent, long-term assessments that contain this usually unmeasured contribution. Escapement goals for PWS Pink Salmon and Chum Salmon are re-evaluated by ADFG regularly on a 3-year cycle during which the proportions of hatchery-origin fish in some escapement estimates can be considered. On a broader scale, our results encourage further investigation of the potential influence of hatchery fish on index stream fish counts, natural production, and escapement goal policy in PWS.

Estimated size of the Pink Salmon hatchery return in odd years (70 and 77 million) was substantially higher than the even-year return (43 million; $\hat{R}_H$ in Table 6) even though hatchery fry releases were relatively consistent through the years (see Vega et al. 2019). This may indicate that Pink Salmon hatchery releases have higher survival in odd brood years than in even brood years. One possible explanation for this is predator swamping, wherein the predators of migrating fry may become saturated in years of high overall (hatchery-plus natural-origin) Pink Salmon emigration from PWS, because natural escapement and resultant brood fry are also much greater during odd years ($\hat{R}_W$; Table 6). Timing of release has long been under study by aquaculture corporations in the region, and we suspect that higher odd-year survival of hatchery Pink Salmon may result from the degree of interactions between hatchery- and natural-origin juveniles and the impact that predators may exert at this early life stage (Willette et al. 2001; Chenoweth et al. 2017). High densities of juvenile co-emigrants have been identified as a strategy that increases protection from predators in freshwater salmonid systems (Furey et al. 2016). On the other hand, higher densities of conspecifics in the ocean may in some cases have negative effects on overall survival (Ruggerone and Irvine 2018). Research on the density-dependent survival of PWS hatchery-origin salmon and how it might affect the magnitude of straying in this ecosystem deserves greater attention.

Pink Salmon and Chum Salmon produced by PWS hatcheries are intended to be fully harvested by fisheries or captured for use as hatchery broodstock, limiting the potential genetic interaction with natural spawners. Our results indicate that the existing flexible management system, informed by in-season sampling for hatchery or natural origins in commercial harvests (see Vega et al. 2019), is likely meeting its objective to harvest most of the hatchery-origin fish while achieving natural spawner escapement goals, at least on a broad scale. During the 3 years of our study, estimated harvest rates on the PWS-wide hatchery-origin portions of the runs for both species were in the range of 95–99%. This was achieved while limiting the PWS-wide natural-origin exploitation in both species to more modest harvest rates (21–53%; Table 6), although some individual populations are likely subject to higher (or lower) harvest rates. Even though most hatchery-origin fish that enter PWS are harvested (95–99%), this also represents potential hatchery donor straying rates in the range of 1–5% into spawning streams. We found that even this low donor stray rate can represent large numbers of recipient hatchery-origin strays in the escapement of certain districts and in certain streams (Tables 4 and 5). This is driven by the overall large abundance of the hatchery returns (Pink Salmon: 42.8–77.3 million; Chum Salmon: 1.2–3.0 million). High harvest rates on hatchery-origin salmon concurrent with the moderate harvest rates on natural-origin salmon observed during our study demonstrate that current management practices are effective and flexible when balancing exploitation of hatchery and natural stocks. Managers have many tools available (e.g., moving harvest into or away from terminal areas) to achieve both harvest and escapement, but use of these tools is most effective when near-real-time information on run timing, abundances, and hatchery presence in the harvest is available. Improvements in the flow of information have the largest influence on the efficacy of management decisions. Management is not the only way to reduce donor straying: additional research into methods that increase the fidelity of hatchery-origin salmon to their release locations would also potentially reduce the occurrence of hatchery salmon in natural escapements.

Another potential issue is the relative effect of focusing intensive fishing effort on hatchery-origin fish. Although this study documented very different harvest rates on hatchery- versus natural-origin stocks during 2013–2015, the harvest rates likely are unevenly experienced by the various natural-origin stocks. Some natural-origin fish may be protected, while other natural populations in the path of intensive hatchery-targeted fishing may be overfished. Furthermore, because most of the harvest effort targets hatchery-origin fish, some natural populations away from hatchery areas may be able to withstand additional harvest. While none of these issues is directly addressed by the present findings, they all deserve further attention. We therefore underscore the importance of continuing to evaluate the interactions among hatchery and natural production, prosecution of the fisheries, and achievement of harvest and escapement objectives in this highly complex and variable system. For example, salmon run reconstruction models like those reported by Templin et al. (1996) and Cunningham et al. (2018) could be further refined—together with detailed information on natural- and hatchery-origin stock identification, migratory pathways, and run timing—to better understand the system and maintain sustainable harvests into the future, as was also recommended by Gayeski et al. (2018).

This study provides important insight into when and where biological and ecological interactions may occur between hatchery- and natural-origin Pink Salmon and Chum Salmon in PWS and the potential effects that may occur as a result. This should prove useful in evaluating future actions to limit the degree of interaction among hatchery and natural populations. For certain local streams receiving a high percentage of hatchery-origin salmon, care should be taken to not dilute the genetic characteristics or reduce natural production.

ACKNOWLEDGMENTS

This article is dedicated to the late Michele Buckhorn of Prince William Sound Science Center (PWSSC), who provided oversight and leadership of the ocean test fishing component of the project during 2013–2014. Many energetic and skilled seasonal field technicians assisted with fieldwork for both the ocean and stream components of our study. This project would not have been possible without their tremendous work, which was regularly conducted under difficult conditions. We particularly thank the crew leaders A. Asada, R. Blackadar, D. Crowther, G. Dunne, K. Froning, J. Jablonski, J. McMahon, R. McGuire, M. Roberts, D. Roberts, and K. Ruck. We especially recognize the field leadership of Neil Durco (now deceased), who worked multiple seasons on this project and significantly contributed to the success of several field crews. We thank B. Reynolds, captain of the F/V *Rebound*, for collecting and processing the ocean specimens for this study. Captains M. Cline of the M/V *Cathy G* and D. Janka of the M/V *Auklet* provided logistical support for the field crews. We thank Randall Davis and his Texas A&M University summer field camp technicians for their support in data collection. R. Busch and colleagues with Resource Data, Inc., provided Android apps and an SQL database for the project as well as technical data management. D. Crowther provided invaluable assistance on the graphics used in the paper. Staff of PWSSC provided administrative and logistical support. Research was conducted in accordance with state of Alaska fish resource permits (F2013-266, SF2014-163, and SF2015-230) in addition to an Institutional Animal Care and Use Permit approved by PWSSC. We thank the ADFG Cordova otolith laboratory staff for analyzing the large numbers of otoliths for this study. The paper was substantively improved by constructive reviews from P. Westley, A. Wertheimer, M. Adkison, C. Habicht, J. Hard, W. Smoker Jr., S. Haught, C. Russell, J. Botz, and two anonymous reviewers. The AHRP Science Panel provided guidance on our study and valuable input on the manuscript. The data used in this paper are available at https://knb.ecoinformatics.org/view/doi%3A10.5063%2FF1QV3JXF. There is no conflict of interest declared in this article.

REFERENCES

Agresti, A. 1996. An introduction to categorical data analysis. Wiley, New York.

Amoroso, R. O., M. D. Tillotson, and R. Hilborn. 2017. Measuring the net biological impact of fisheries enhancement: Pink Salmon hatcheries can increase yield, but with apparent costs to wild populations. Canadian Journal of Fisheries and Aquatic Sciences 74:1233–1242.

Araki, H., B. A. Berejikian, M. J. Ford, and M. S. Blouin. 2008. Fitness of hatchery-reared salmonids in the wild. Evolutionary Applications 1:342–355.

Araki, H., B. Cooper, and M. S. Blouin. 2007. Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. Science 318:100–103.

Avise, J. C. 2000. Phylogeography: the history and formation of species. Harvard University Press, Cambridge, Massachusetts.

Berejikian, B. A., and M. J. Ford. 2004. Review of relative fitness of hatchery and natural salmon. NOAA Technical Memorandum NMFS-NWFSC-61.

Botz, J., T. Sheridan, A. Weise, S. Moffitt, and R. Brenner. 2014. 2013 Prince William Sound area finfish management report. Alaska Department of Fish and Game, Fishery Management Report 14-43, Anchorage.

Brenner, R. E., S. D. Moffitt, and W. S. Grant. 2012. Straying of hatchery salmon in Prince William Sound, Alaska. Environmental Biology of Fishes 94:179–195.

Brodeur, R. D., K. W. Myers, and J. H. Helle. 2003. Research conducted by the United States on the early ocean life history of Pacific salmon. North Pacific Anadromous Fish Commission Bulletin 3:89–131.

Candy, J. R., and T. D. Beacham. 2000. Patterns of homing and straying in southern British Columbia coded-wire tagged Chinook Salmon (*Oncorhynchus tshawytscha*) populations. Fisheries Research 47:41–56.

Chenoweth, E. M., J. M. Straley, M. V. McPhee, A. Atkinson, and S. Reifenstuhl. 2017. Humpback whales feed on hatchery-released juvenile salmon. Royal Society Open Science 4:170180.

Chilcote, M. W., K. W. Goodson, and M. R. Falcy. 2011. Reduced recruitment performance in natural populations of anadromous salmonids associated with hatchery-reared fish. Canadian Journal of Fisheries and Aquatic Sciences 68:511–522.

Chilcote, M. W., S. A. Leider, and J. J. Loch. 1986. Differential reproductive success of hatchery and wild summer-run steelhead under natural conditions. Transactions of the American Fisheries Society 115:726–735.

Clark, J., S. Haught, S. Vega, and R. Brenner. 2018. Salmon age, sex, and length samples from Prince William Sound and Copper River, 1960–2018. Alaska Department of Fish and Game, Division of Commercial Fisheries, Cordova.

Cochran, W. G. 1977. Sampling techniques. Wiley, New York.

Cunningham, C. J., T. A. Branch, T. H. Dann, M. Smith, J. E. Seeb, L. W. Seeb, and R. Hilborn. 2018. A general model for salmon run reconstruction that accounts for interception and differences in availability to harvest. Canadian Journal of Fisheries and Aquatic Sciences 75:439–451.

Davis, B., B. Allee, D. Amend, B. Bachen, B. Davidson, T. Gharrett, S. Marshall, and A. Wertheimer. 1985. Genetic policy. Alaska Department of Fish and Game, Juneau.

Evenson, D. F., C. Habicht, M. Stopha, A. R. Munro, T. R. Meyers, and W. D. Templin. 2018. Salmon hatcheries in Alaska—a review of the implementation of plans, permits, and policies designed to provide protection for wild stocks. Alaska Department of Fish and Game, Special Publication 18-12, Anchorage.

Ford, M. J., A. Murdoch, and M. Hughes. 2015. Using parentage analysis to estimate rates of straying and homing in Chinook Salmon (*Oncorhynchus tshawytscha*). Molecular Ecology 24:1109–1121.

Fox, J. 1987. Effect displays for generalized linear models. Sociological Methodology 17:347–361.

Fox, J. 2017. Effects: effect displays for linear, generalized linear, and other models. R package version 4.0-0. Available: https://cran.r-project.org/web/packages/effects/index.html. (November 2020).

Furey, N. B., S. G. Hinch, A. L. Bass, C. T. Middleton, V. Minke-Martin, and A. G. Lotto. 2016. Predator swamping reduces predation risk during nocturnal migration of juvenile salmon in a high-mortality landscape. Journal of Animal Ecology 85:948–959.

Gayeski, N. J., J. A. Stanford, D. R. Montgomery, J. Lichatowich, R. M. Peterman, and R. N. Williams. 2018. The failure of wild salmon management: need for a place-based conceptual foundation. Fisheries 43:303–309.

Haught, S., J. Morella, and S. Vega. 2019. Estimating wild and hatchery contributions of Pacific salmon stocks in Prince William Sound management area fisheries. Alaska Department of Fish and Game, Regional Operational Plan ROP.CF.2A.2019.03, Cordova.

Heard, W. R. 2012. Overview of salmon stock enhancement in Southeast Alaska and compatibility with maintenance of hatchery and wild stocks. Environmental Biology of Fishes 94:273–283.

Hilborn, R., and D. Eggers. 2000. A review of the hatchery programs for Pink Salmon in Prince William Sound and Kodiak Island, Alaska. Transactions of the American Fisheries Society 129:333–350.

Hothorn, T. 2017. Multcomp: simultaneous inference in general parametric models. R package version 1.4-8. Available: https://cran.r-project.org/web/packages/multcomp/index.html. (November 2020).

Jasper, J. R., C. Habicht, S. Moffitt, R. Brenner, J. Marsh, B. Lewis, E. C. Fox, Z. Grauvogel, S. D. R. Olive, and W. S. Grant. 2013. Source–sink estimates of genetic introgression show influence of hatchery strays on wild Chum Salmon populations in Prince William Sound, Alaska. PLoS (Public Library of Science) ONE [online serial] 8(12):e81916..

Johnson, J., and B. Blossom. 2019. Catalog of waters important for spawning, rearing, or migration of anadromous fishes—Southcentral Region, effective June 1, 2019. Alaska Department of Fish and Game, Special Publication 19-03, Anchorage.

Jones, E. L., T. J. Quinn, and B. W. Van Alen. 1998. Observer accuracy and precision in aerial and foot survey counts of Pink Salmon in a Southeast Alaska stream. Transactions of the American Fisheries Society 18:832–846.

Josephson, R., A. Wertheimer, D. Gaudet, E. E. Knudsen, B. Adams, D. R. Bernard, S. C. Heinl, A. W. Piston, and W. D. Templin. In press. Proportions of hatchery fish in escapements of summer-run Chum Salmon in Southeast Alaska, 2013–2015. North American Journal of Fisheries Management.

Joyce, T. L., and D. G. Evans. 2000. Otolith marking of Pink Salmon in Prince William Sound salmon hatcheries. Alaska Department of Fish and Game, *Exxon Valdez* Oil Spill Restoration Project Final Report, Cordova.

Keefer, M. L., and C. C. Caudill. 2014. Homing and straying by anadromous salmonids: a review of mechanisms and rates. Reviews in Fish Biology and Fisheries 24:333–368.

Knudsen, E., P. Rand, K. Gorman, J. McMahon, B. Adams, V. O'Connell, and D. Bernard. 2016. Interactions of wild and hatchery Pink Salmon and Chum Salmon in Prince William Sound and Southeast Alaska: progress report for 2015. Prince William Sound Science Center, Cordova, Alaska.

Kostow, K. 2009. Factors that contribute to the ecological risks of salmon and steelhead hatchery programs and some mitigating strategies. Reviews in Fish Biology and Fisheries 19:9–31.

Labelle, M. 1992. Straying patterns of Coho Salmon (*Onchorhynchus kisutch*) stocks from southeast Vancouver Island, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 49:1843–1855.

Leider, S. A., P. L. Hulett, J. J. Loch, and M. W. Chilcote. 1990. Electrophoretic comparison of the reproductive success of naturally spawning transplanted and wild steelhead trout through the returning adult stage. Aquaculture 88:239–252.

Lin, J. E., R. Hilborn, T. P. Quinn, and L. Hauser. 2011. Self-sustaining populations, population sinks or aggregates of strays: Chum (*Oncorhynchus keta*) and Chinook salmon (*Oncorhynchus tshawytscha*) in the Wood River system, Alaska. Molecular Ecology 20:4925–4937.

McConnell, C. J., P. A. H. Westley, and M. V. McPhee. 2018. Differences in fitness-associated traits between hatchery and wild Chum Salmon despite long-term immigration by strays. Aquaculture Environment Interactions 10:99–113.

McGee, S. G. 2005. Salmon hatcheries in Alaska—plans, permits, and policies designed to provide protection for wild stocks. Pages 317–331 *in* M. Nickum, P. Mazik, J. Nickum, and, D. MacKinlay, editors. Propagated fish in resource management. American Fisheries Society, Symposium 44, Bethesda, Maryland.

Mortensen, D. G., A. C. Wertheimer, J. M. Maselko, and S. G. Taylor. 2002. Survival and straying of Auke Creek, Alaska, Pink Salmon marked with coded wire tags and thermally induced otolith marks. Transactions of the American Fisheries Society 131:14–26.

Naish, K. A., J. E. Taylor III, P. S. Levin, T. P. Quinn, J. R. Winton, D. Huppert, and R. Hilborn. 2007. An evaluation of the effects of conservation and fishery enhancement hatcheries on wild populations of salmon. Advances in Marine Biology 53:61–194.

Otis, E. O., G. J. Hollowell, and E. G. Ford. 2018. Observations of Pink Salmon hatchery proportions in selected lower Cook Inlet escapements, 2014–2017. Alaska Department of Fish and Game, Special Publication SP18-11, Anchorage.

Paquet, P. J., T. Flagg, A. Appleby, J. Barr, L. Blankenship, D. Campton, M. Delarm, T. Evelyn, D. Fast, J. Gislason, P. Kline, D. Maynard, L. Mobrand, G. Nandor, P. Seidel, and S. Smith. 2011. Hatcheries, conservation, and sustainable fisheries—achieving multiple goals: results of the Hatchery Scientific Review Group's Columbia River basin review. Fisheries 36:547–561.

Pascual, M. A., and T. P. Quinn. 1994. Geographical patterns of straying of fall Chinook Salmon, *Oncorhynchus tshawytscha* (Walbaum), from Columbia River (USA) hatcheries. Aquaculture Research 25(S2):17–30.

Pess, G. R., R. Hilborn, K. Kloehn, T. P. Quinn, and M. Bradford. 2012. The influence of population dynamics and environmental conditions on Pink Salmon (*Oncorhynchus gorbuscha*) recolonization after barrier removal in the Fraser River, British Columbia, Canada. Canadian Journal of Fisheries and Aquatic Sciences 69:970–982.

Piston, A. W., and S. C. Heinl. 2012. Hatchery Chum Salmon straying studies in Southeast Alaska, 2008–2010. Alaska Department of Fish and Game, Fishery Manuscript Series 12-01, Anchorage.

Putman, N. F., E. S. Jenkins, C. G. Michielsens, and D. L. Noakes. 2014a. Geomagnetic imprinting predicts spatio-temporal variation in homing migration of Pink and Sockeye salmon. Journal of the Royal Society Interface 11:20140542.

Putman, N. F., M. M. Scanlan, E. J. Billman, J. P. O'Neil, R. B. Couture, T. P. Quinn, K. J. Lohmann, and D. L. G. Noakes. 2014b. An inherited magnetic map guides ocean navigation in juvenile Pacific salmon. Current Biology 24:446–450.

Quinn, T. P. 1993. A review of homing and straying of wild and hatchery-produced salmon. Fisheries Research 18:29–44.

Quinn, T. P. 2018. The behavior and ecology of Pacific salmon and trout, 2nd edition. University of Washington Press, Seattle.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Rand, P. S., B. A. Berejikian, A. Bidlack, D. Bottom, J. Gardner, M. Kaeriyama, R. Lincoln, M. Nagata, T. N. Pearsons, M. Schmidt, W. W. Smoker, L. A. Weitkamp, and L. A. Zhivotovsky. 2012. Ecological interactions between wild and hatchery salmonids and key recommendations for research and management actions in selected regions of the North Pacific. Environmental Biology of Fishes 94:343–358.

Reisenbichler, R. R., and S. P. Rubin. 1999. Genetic changes from artificial propagation of Pacific salmon affect the productivity and viability of supplemented populations. ICES (International Council for the Exploration of the Sea) Journal of Marine Science 56:459–466.

Roys, R. S. 1965. Effect of March 27, 1964 earthquake on Pink and Chum Salmon streams of Prince William Sound. Pages 42–71 *in* Post-earthquake fisheries evaluation report. Alaska Department of Fish and Game, Juneau.

Ruggerone, G. T., and J. R. Irvine. 2018. Numbers and biomass of natural- and hatchery-origin Pink Salmon, Chum Salmon, and Sockeye Salmon in the North Pacific Ocean, 1925–2015. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 10:152–168.

Schroeder, R. K., R. B. Lindsay, and K. R. Kenaston. 2001. Origin and straying of hatchery winter steelhead in Oregon coastal rivers. Transactions of the American Fisheries Society 130:431–441.

Stopha, M. 2016. Alaska fisheries enhancement annual report 2015. Alaska Department of Fish and Game, Regional Information Report 5J16-03, Anchorage.

Stopha, M. 2017. Alaska fisheries enhancement annual report 2016. Alaska Department of Fish and Game, Regional Information Report 5J17-04, Anchorage.

Stopha, M. 2019. Alaska fisheries enhancement annual report 2018. Alaska Department of Fish and Game, Regional Information Report 5J19-01, Juneau.

Templin, W. D., J. S. Collie, and T. R. Quinn. 1996. Run reconstruction of the wild Pink Salmon fishery in Prince William Sound, 1990–1991. Pages 499–508 *in* S. D. Rice, R. B. Spies, D. A. Wolfe, and B. A. Wright, editors. Proceedings of the *Exxon Valdez* oil spill symposium. American Fisheries Society, Symposium 18, Bethesda, Maryland.

Thedinga, J. F., A. C. Wertheimer, R. A. Heintz, J. M. Maselko, and S. D. Rice. 2000. Effects of stock, coded-wire tagging, and transplant on straying of Pink Salmon (*Oncorhynchus gorbuscha*) in southeastern Alaska. Canadian Journal of Fisheries and Aquatic Sciences 57:2076–2085.

Thompson, S. K. 1992. Sampling. Wiley, New York.

Udevitz, M. S., editor. 2013. Change-in-ratio, volume 2. Wiley, New York.

Unwin, M. J., and T. P. Quinn. 1993. Homing and straying patterns of Chinook Salmon (*Oncorhynchus tshawytscha*) from a New Zealand hatchery: spatial distribution of strays and effects of release date. Canadian Journal of Fisheries and Aquatic Sciences 50:1168–1175.

Vega, S. L., C. W. Russell, J. Botz, and S. Haught. 2019. 2017 Prince William Sound area finfish management report. Alaska Department of Fish and Game, Fishery Management Report 19-07, Cordova.

Vercessi, L. 2014. Alaska Salmon Fisheries Enhancement Program 2013 annual report. Alaska Department of Fish and Game, Fishery Management Report 14-12, Anchorage.

Vercessi, L. 2015. Alaska Salmon Fisheries Enhancement Program 2014 annual report. Alaska Department of Fish and Game, Fishery Management Report 15-15, Anchorage.

Volk, E. C., S. L. Schroder, and J. J. Grimm. 1999. Otolith thermal marking. Fisheries Research 43:205–219.

Volk, E. C., S. L. Schroder, and J. J. Grimm. 2005. Otolith thermal marking. Pages 447–463 *in* S. X. Cadrin, K. D. Friedman, and J. R. Waldman, editors. Stock identification methods. Elsevier, London.

Wertheimer, A. C., W. R. Heard, and W. W. Smoker. 2004. Effects of hatchery releases and environmental variation on wild-stock productivity: consequences for sea ranching of Pink Salmon in Prince William Sound, Alaska. Pages 307–326 *in* K. M. Leber, S. Kitada, H. L. Blankenship, and T. Svåsand, editors. Stock enhancement and sea ranching. Blackwell Publishing, Hoboken, New Jersey.

Wertheimer, A. C., W. W. Smoker, T. L. Joyce, and W. R. Heard. 2001. Comment: a review of the hatchery programs for Pink Salmon in Prince William Sound and Kodiak Island, Alaska. Transactions of the American Fisheries Society 130:712–720.

Westley, P. A. H., T. P. Quinn, and A. H. Dittman. 2013. Rates of straying by hatchery-produced Pacific salmon (*Oncorhynchus* spp.) and steelhead (*Oncorhynchus mykiss*) differ among species, life history types, and populations. Canadian Journal of Fisheries and Aquatic Sciences 70:735–746.

Willette, T. M., R. T. Cooney, V. Patrick, D. M. Mason, G. L. Thomas, and D. Scheel. 2001. Ecological processes influencing mortality of juvenile Pink Salmon (*Oncorhynchus gorbuscha*) in Prince William Sound, Alaska. Fisheries Oceanography 10:14–41.

Yeakel, J. D., J. P. Gibert, T. Gross, P. A. H. Westley, and J. W. Moore. 2018. Eco-evolutionary dynamics, density-dependent dispersal and collective behaviour: implications for salmon metapopulation robustness. Philosophical Transactions of the Royal Society B: Biological Sciences 373:20170018.

Zhivotovsky, L. A., L. K. Fedorova, G. A. Rubtsova, M. V. Shitova, T. A. Rakitskaya, V. D. Prokhorovskaya, B. P. Smirnov, A. M. Kaev, V. M. Chupakhin, V. G. Samarsky, V. P. Pogodin, S. I. Borzov, and K. I. Afanasiev. 2012. Rapid expansion of an enhanced stock of Chum Salmon and its impacts on wild population components. Environmental Biology of Fishes 94:249–258.

SUPPORTING INFORMATION

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

Appendix 1: Derivation of Hatchery Proportions by Ocean Station, Season, and Year

The proportion of hatchery-origin fish in the catch (or sample) from a specific visit (date) at a specific station was estimated as

$$\hat{p}_{\mathrm{st}} = \frac{z_{\mathrm{st}}}{m_{\mathrm{st}}}, \tag{A.1.1}$$

where s is a test fishing station, t is a visit (date), m_{st} is the number of individuals of the target species sampled in the catch at test fishing station s during visit t for which origin was determined, and z_{st} is the number of individuals within m_{st} that were identified as being of hatchery origin. When hatchery proportions were estimated for each ocean station over the entire season, they

TABLE A.1.1. The four possible outcomes of ocean sampling visits at each test fishing station and their consequences for visit t to station s when estimating hatchery proportions in the yet-to-be-fished runs of Pink Salmon and Chum Salmon in PWS during 2013–2015. Dummy variables λ_{st} and ω_{st} are used in equations (A.1.2), (A.1.3), and (A.1.7) to express the outcomes.

Outcome	Comments	Dummy variables	Adjustments
1. Target species caught; origin determined for all or some of the catch	Determination for only "some" due to subsampling of large catches	$\lambda_{st} = 1$; $\omega_{st} = 1$	None
2. Target species caught; origin not determined for any of the catch	One target species caught; unable to determine origins from otoliths	$\lambda_{st} = 0$; $\omega_{st} = 1$	Visit excluded when estimating proportions but not when estimating CPUE
3. No target species caught	CPUE = 0	$\lambda_{st} = 0$; $\omega_{st} = 1$	Visit excluded when estimating proportions but not when estimating CPUE
4. No fishing	Weather	$\lambda_{st} = 0$; $\omega_{st} = 0$	Visit excluded from all calculations

were weighted by CPUE to produce unbiased estimates. Ideally, weights would be based on numbers of the target species (N) passing near each test fishing station during a visit in relation to all individuals of the target species passing during the season:

$$W_{st} = \frac{\lambda_{st} N_{st}}{\sum_{t'=1}^{T_s} \lambda_{st'} N_{st'}}, \quad \text{(A.1.2)}$$

where t' represents visits to test fishing station s during the season, including visit t; and $\lambda_{st} = 1$ if the visit t to test fishing station s resulted in outcome 1 or $\lambda_{st} = 0$ otherwise (Table A.1.1). Because the N-values are unknown, CPUE was used as a surrogate. Catch (C) is a function of fishing effort (E), catchability (c), and abundance such that $C = cEN$, which makes $N = \text{CPUE}(1/c)$. Substitution into equation (A.1.2) above provides estimated weights in terms of CPUE:

$$\hat{W}_{st} = \frac{\lambda_{st}\text{CPUE}_{st}(1/c_s)}{\sum_{t'=1}^{T_s} \lambda_{st'}\text{CPUE}_{st'}(1/c_s)} = \frac{\lambda_{st}\text{CPUE}_{st}}{\sum_{t'=1}^{T_s} \lambda_{st'}\text{CPUE}_{st'}}, \quad \text{(A.1.3)}$$

as long as the catchability is the same during all visits at test fishing station s. Fishing protocols at each test fishing station were standardized over the duration of ocean fishing, so the estimate for the proportion of hatchery fish at a specific test fishing station for the season was then calculated as

$$\hat{p}_s = \sum_{t=1}^{T_s} \hat{W}_{st}\hat{p}_{st}. \quad \text{(A.1.4)}$$

Equation (A.1.4) is an unbiased estimator for the hatchery proportion, with random sampling without replacement through a two-stage design for each test fishing station; visits are the first sampling stage, and fish comprise the second (subsampling) stage.

The estimated mean proportion of hatchery-origin salmon of the target species in the overall PWS run was then calculated as the weighted average of the estimated proportions for test fishing stations:

$$\hat{p} = \sum_{s=\text{H01}}^{\text{H01...M06}} \hat{W}_s \hat{p}_s. \quad \text{(A.1.5)}$$

Here, the weights were based on the estimated mean CPUE for each test fishing station:

$$\hat{W}_s = \frac{\overline{\text{CPUE}}_s}{\sum_{s'=\text{H01}}^{\text{H01...M06}} \overline{\text{CPUE}}_{s'}}, \quad \text{(A.1.6)}$$

$$\overline{\text{CPUE}}_s = \frac{\sum_{t=1}^{T_s} \omega_{st}\text{CPUE}_{st}}{\sum_{t=1}^{T_s} \omega_{st}}, \quad \text{(A.1.7)}$$

where $\omega_{st} = 1$ if visit t to test fishing station s resulted in outcome 1, 2, or 3; and $\omega_{st} = 0$ if the visit resulted in outcome 4 (Table A.1.1). Two different multipliers, λ and ω, were required because a CPUE of 0 (outcome 3) provides no information on the proportion of hatchery-origin fish in the catch but does provide information on the appropriate weight to be used to estimate the proportion for the entire PWS. Calculation of approximate variances for these weights and proportions is described in Supplement 2.

Appendix 2: Derivation of Hatchery-Origin Proportions in PWS Streams

Data on the hatchery and natural origin of fish sampled in streams were weighted by dead counts from each stream visit to derive unbiased estimates of the proportions of hatchery-origin salmon in sampled spawning streams. Statistics were calculated from samples following procedures developed by Thompson (1992). An unbiased estimate of the district total τ from any multi-stage sampling design in which the streams were chosen for sampling proportional to their average run size with replacement is

$$\tau = \frac{1}{n}\sum_{i=1}^{n}\frac{\tau_i}{\pi_i}, \quad \text{(A.2.1)}$$

where

$$\pi_i = \frac{M_i}{M} \quad \text{and} \quad \tau_i = M_i\overline{q}_i.$$

In this study, τ is an unbiased estimate of the number of hatchery-origin fish on the spawning grounds in an unspecified district, n is the number of streams visited in that district, π_i is the relative size of the ith stream among all streams in the district, M_i is the number of second-stage units (spawning fish) in the ith stream in that district, M is the recent average number of spawning fish in the district, τ_i is the estimated number of hatchery-origin salmon on the spawning grounds in the ith stream, and $\overline{q}_i$ is the estimated proportion of hatchery-origin fish on the spawning grounds of the ith stream. The $\overline{q}_i$ for each stream was calculated by

$$\overline{q}_i = \sum_{v=1}^{V_i} w_{iv}q_{iv}, \quad \text{(A.2.2)}$$

where

$$w_{iv} = \frac{C_{iv}}{\sum_{v'=1}^{V_{iv}} C_{iv'}} \quad \text{and} \quad q_{iv} = \frac{\sum_{j=1}^{m_{iv}} y_{ijv}}{m_{iv}},$$

andwhere v denotes a visit, V_i is the number of visits to the ith stream, C_{iv} is the number of dead salmon of the target species counted during visit v to the ith stream, m_{iv} is the number of the target species sampled during visit v to the ith stream, y_{ijv} is the result of sampling the jth fish ($y_{ijv} = 1$ if the fish is of hatchery origin and 0 otherwise), and q_{iv} denotes the estimated hatchery-origin proportion of postspawners during visit v to the ith stream. The estimated mean proportion over all streams in a district ($\overline{q}$) was calculated by combining equations (A.2.1) and (A.2.2) and dividing the result by the aerial survey-based spawner abundance M of the target species in an entire district:

$$\overline{q} = \tau/M = \frac{1}{M}\frac{1}{n}\sum_{i=1}^{n}\frac{M_i\overline{q}_i}{M_i/M} = \frac{1}{n}\sum_{i=1}^{n}\overline{q}_i. \quad \text{(A.2.3)}$$

An unbiased estimate of the hatchery proportion $\hat{q}$ for a species across all districts is

$$\hat{q} = \sum_{h=221}^{221,\ldots,229} W_h\overline{q}_h, \quad \text{(A.2.4)}$$

where

$$W_h = \frac{A_h}{\sum_{h'=221}^{221,\ldots,229} A_{h'}},$$

and where h denotes the stratum (district) and A_h is the aerial abundance index by ADFG for stratum (district) h in a calendar year. Methods for calculating approximate variances for stream proportions are described in Supplement 3.

Appendix 3: Derivation of Sound-wide Harvest Management Parameter Estimates

Fisheries for Pink Salmon and Chum Salmon in PWS have been managed to concentrate fishing effort toward hatchery salmon and away from natural-origin salmon (e.g., Vega et al. 2019), with the goal of maximizing harvest from each group. Under this policy, the odds of sampling a natural-origin fish in a yet-to-be-fished run should be lower than the odds of sampling a natural-origin fish in the spawning population. Such odds for the yet-to-be fished run (θ_{run}) are

$$\theta_{\text{run}} = \frac{1-p}{p} = \frac{R_W}{R_H}, \quad \text{(A.3.1)}$$

where

$$p = \frac{R_H}{R_W + R_H},$$

and where R_H is the size of the run of hatchery-origin fish and R_W is the size of the run of natural-origin fish. The odds for the run after it has been fished (i.e., in the spawning escapement) are

$$\theta_{\text{esc}} = \frac{1-q}{q} = \frac{S_W}{S_H} = \frac{R_W - C_W}{R_H - C_H}, \tag{A.3.2}$$

where

$$q = \frac{S_H}{S_W + S_H},$$

and where S_H is the number of hatchery strays that survive the fishery (and end up in the spawning stream), S_W is the number of natural-origin fish that end up in the spawning stream, C_W is the "catch" of natural-origin fish (in the common property fishery, in cost recovery, and rack return), and C_H is the "catch" of hatchery-origin fish (in the common property fishery, in cost recovery, and rack return). Equation (A.3.1) can be rearranged such that $R_W = \theta_{\text{run}} R_H$. When this relationship is plugged into equation (A.3.2) and solved for R_H, the result is

$$R_H = \frac{C_W - \theta_{\text{esc}} C_H}{\theta_{\text{run}} - \theta_{\text{esc}}}. \tag{A.3.3}$$

Using the relationship $R_W = \theta_{\text{run}} R_H$ in the context of equation (A.3.3),

$$R_W = \theta_{\text{run}} R_H = \frac{\theta_{\text{run}}(C_W - \theta_{\text{esc}} C_H)}{\theta_{\text{run}} - \theta_{\text{esc}}}. \tag{A.3.4}$$

Further relationships involving catch and spawner abundance are

$$S_W = R_W - C_W = \frac{\theta_{\text{run}}(C_W - \theta_{\text{esc}} C_H)}{\theta_{\text{run}} - \theta_{\text{esc}}} - C_W, \tag{A.3.5}$$

$$S_H = R_H - C_H = \frac{C_W - \theta_{\text{esc}} C_H}{\theta_{\text{run}} - \theta_{\text{esc}}} - C_H, \tag{A.3.6}$$

$$R = R_W + R_H = \frac{(1+\theta_{\text{run}})(C_W - \theta_{\text{esc}} C_H)}{\theta_{\text{run}} - \theta_{\text{esc}}}, \tag{A.3.7}$$

$$S = R - C = \frac{(1+\theta_{\text{run}})(C_W - \theta_{\text{esc}} C_H)}{\theta_{\text{run}} - \theta_{\text{esc}}} - C. \tag{A.3.8}$$

Substituting statistics from ocean sampling ($\hat{p} \rightarrow p$), stream sampling ($\hat{q} \rightarrow q$), and catch sampling ($\hat{C}_W \rightarrow C_W$ and $\hat{C}_H \rightarrow C_H$) into equations (A.3.1)–(A.3.8) produced estimates of run size and spawner abundance (results in Table 6). Harvest rates for salmon of each species were obtained by dividing the estimated catch by the estimated run sizes for both natural- and hatchery-origin Pink Salmon and Chum Salmon in each year (see Table 6).

Standard errors for estimates of run size, spawning abundance, and harvest rates were caculated through parametric Monte Carlo simulations of fractions of hatchery fish in runs from ocean sampling (p), fractions of hatchery fish on the spawning grounds (q), and catches of salmon in fisheries. Simulated values for p, q, and C_H were randomly drawn from normal distributions with means $\hat{p}$, $\hat{q}$, and $\hat{C}_{H_{\text{est}}}$ and their estimated SEs to create a set of values for p, q, and C_H. Each such set of simulated values was used to calculate nine more values: three for run sizes, three for spawning abundance, and three for harvest rates, as per equations above. At the completion of simulating 1,000 such sets for each species × year combination of data, SEs for each simulated variable were calculated as SDs over the 1,000 sets representing each species × year combination. Because of high harvest rates of hatchery salmon, simulations occasionally produced harvest rates $\text{HR}_{H_{\text{sim}}}$ greater than 1.0, a result observed in 71, 18, 13, 138, 0, and 1 out of 1,000 simulations for Pink Salmon and Chum Salmon, respectively, for 2013–2015. The cases in which a simulation produced $\text{HR}_{H_{\text{sim}}}$ exceeding 1.0 were ignored, and SEs were calculated using the remaining simulations. The differences in simulated SEs with and without the impossible harvest rates were less than 0.01.