**RESULTS**

Over the course of 6 years (Spawn Years 2016-2021), an average of 1856 (± 646) natural-origin female steelhead were sampled and PIT-tagged pre-spawn each year at Lower Granite Dam (LGR), making up the pre-spawn dataset (N = 11,135 total, Table 1). Females made up an average of 65% (± 5%) of the natural-origin steelhead run each year.During downstream post-spawning migration, an average of 385 (± 279) natural-origin female steelhead kelts were encountered by the Kelt Reconditioning Program (KRP) at the LGR juvenile bypass (JBS) each year (N = 2310 total), making up the post-spawn dataset. Most natural-origin steelhead encountered post-spawn were female (71% (± 6%)).A total of 321 of the females encountered post-spawn had been tagged pre-spawn at LGR. Of these, 20 were excluded: 19 due to genetic screening: 14 were of hatchery origin (4.4%), 4 were of undetermined sex and origin (NG, 1.2%), and 1 was male (0.3%). Additionally, one fish that had already repeat spawned (age 2.1S at time of tagging at LGR) was excluded (0.3%). After exclusions, an average of 50 (± 27) had been tagged pre-spawn at LGR adult ladder each year (N = 301 total). Of those encountered, an average of 190 (± 98) were collected each year (N = 1142 total), about half of the total that were encountered. Of the females collected, 160 had been tagged pre-spawn at LGR. After the exclusion of 10 fish described above (9 of hatchery origin, 1 had already repeat spawned), an average of 25 (± 12) of the collected females had been tagged pre-spawn at LGR each year (N = 150 total).

Of the natural-origin females tagged pre-spawn at LGR, a total of 1077 fish were detected migrating downstream post-spawn in Spawn Years 2016-2021. Downstream migration detection efficiency averaged 15% ± 16% per year. Both detection rate and detection efficiency increased dramatically in 2020 and 2021 when the spillway array came online. After the application of the detection efficiency estimate for each year, the estimates for yearly female downstream migration rate averaged 80% ± 20% per year (Figure 1). Each year, an average of 50 (± 27) or 3% (± 1%) tagged females were encountered and an average of 25 (± 12) or 2% (± 1%) tagged females were collected (Figure 1). Over time, encounter and collection rates converged. Both encounter and collectionrates tended to increase to a peak in 2019, followed by a decline.

A total of 144 fish tagged pre-spawn at LGR were detected on a second spawning migration one or two years later, and thus make up the repeat spawners (RS, 1.3% of total natural-origin female steelhead tagged). One third of these were released from the KRP (Reconditioned RS, N = 48), and two thirds returned naturally (Natural RS, N = 96). Two fish were excluded from the Natural RS due to being confirmed as previous RS. An average of 0.57% (± 0.56%) of those tagged pre-spawn at LGR were detected on a repeat spawning migration as Reconditioned RS, and an average of 0.88% (± 0.67%) as Natural RS (Figure 2). Repeat spawner detections peaked in 2018 for both groups and tended to decrease thereafter.

A total of 312 natural-origin female steelhead released from the KRP were detected migrating upstream (making up the full Reconditioned RS dataset, N = 119 consecutive, 193 skip, not restricted to pre-spawn tagged fish, Figure 3), including the 48 that were tagged pre-spawn (described above). Of the 96 Natural RS that were detected migrating upstream (described above), both post-spawn life histories were also represented (N = 76 consecutive, 20 skip). No fish were found to skip more than one year before returning to spawn again. On average, 77% (± 12%) of Reconditioned RS were skip spawners (with the exclusion of 2018, N = 68 consecutive, 1 skip, see below), compared to the average of 29% (± 22%) skip spawners in Natural RS. The probability of returning as a skip spawner was greater in Reconditioned RS, significantly so in years 2016, 2019, and 2020 (P = 1.95 x 10-6, 0.01, and 6.40 x 10-5, respectively). On average, the Reconditioned RS contributed a 2.7x greater proportion of skip spawners to the repeat spawning run.

In 2018, fall sampling identified 102 skip spawners from the first spawn year 2018 collection (non-mature at the time of sampling). One was released accidently in fall of 2018, and the other 101 were held as skip spawners. One out of 101 fish survived, re-matured, and was released in fall 2019 as a skip spawner. The other 100 died due to a mechanical failure during the summer of 2019. Though first spawn year 2018 collections yielded the release of 68 consecutive and only 1 skip (described above), there were 100 more potential skip spawners. Therefore, the pattern of majority skip spawners among Reconditioned RS still holds true for first spawn year 2018 despite exclusion of this year from analysis.

When measured prior to first spawning, fork lengths of Ocean Age 1 fish that later became repeat spawners averaged 589 ± 30 mm. Ocean Age 2 repeat spawners averaged 709 ± 51 mm prior to first spawning. When lengths were standardized within each group the odds of skip spawning decreased with length in all groups, but this relationship was marginally nonsignificant. For every 1SD change in fish length, the odds of skip repeat spawning changed by a factor of 0.66 (p = 0.079; 95% CL: 0.4-1.03).

Ocean Age 1 fish were majority consecutive spawners in both Natural RS (N = 29, 73%) and Reconditioned RS (N = 19, 68%, Supplemental Table 1). Ocean Age 2 fish were majority consecutive spawners in Natural RS (N = 34, 85%) but Reconditioned RS were majority skip spawners (N = 9, 64%). Among Ocean age 1 repeat spawners, Reconditioned RS were 1.31-fold more likely to be skip spawners than Natural RS (p = 0.62, not significant; 95% CL: 0.45-0.3.83, Figure 4). Among Ocean age 2 repeat spawners, Reconditioned RS were 10.4-fold more likely to be skip spawners than Natural RS (p = 0.001; 95% CL: 2.52-42.89, Figure 4).

In Natural RS, the largest proportion of repeat spawners assigned to the Grand Ronde management unit, whereas in Reconditioned RS, the largest proportion assigned to the Salmon River management unit (Supplemental Table 2). All management units and genetic stocks were represented in all years for both groups (Supplemental Table 2, Supplemental Table 3). The Clearwater River management unit contained the highest proportion of skip spawning Reconditioned RS and the lowest proportion of skip spawning Natural RS. The Salmon River management unit contained the highest proportion of consecutive spawning Reconditioned RS, whereas the Clearwater River management unit contained the highest proportion of consecutive spawning Natural RS.

On average, 11,938 (± 3387) natural-origin steelhead were estimated to have returned each year in 2017-2021, of which an average of 7,863 (± 2824) were female (65% ± 5%).An annual average of 94 (± 87, N = 471 total) females were estimated to have returned as Natural RS, and an annual average of 52 (± 30, N = 262 total) females released from the KRP were detected migrating upstream as Reconditioned RS.The KRP increased the annual number of natural-origin repeat spawning female steelhead by 56%.

A total of 401 natural-origin female steelhead were released from the KRP in fall of 2016-2021, with an average 67 (± 30) released per year (Spawn Years 2017-2022, Supplemental Table 4).An average of 76% (± 11%, 53 ± 27) of those released were subsequently detected migrating upstream through the LGR fish ladder PIT arrays (N = 317 total for release years 2016-2021). However, of the known reproductively ready females released (including borderline reproductively ready females), an average of 93% (± 11%, 55 ± 28) were detected moving upstream. An average 8% (± 5%) of the fish released were not reproductively ready and were not expected to migrate upstream. Additionally, some fish (N = 14) were released with unknown reproductive readiness. In 2020, all 6 females released with unknown reproductive status were detected migrating upstream, resulting in an upstream detection rate of 109%. An average of 5% (± 2%, 3 ± 1) of all released fish were detected migrating downstream, and an average of 18% (± 9%, 11 ± 6) were not detected after release.

From first spawn years 2016-2021, a total of 312 Reconditioned RS were detected migrating upstream through LGR after release, either ~6 or ~18 months later (Figure 6). An average of 28% (± 8%, 52 ± 23) of natural-origin female steelhead collected each year by the KRP were detected migrating upstream following release.