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Quality over Quantity: Conservation hatchery intervention diversifies outmigration size and timing of juvenile Coho Salmon (*Oncorhynchus kisutch*)

By

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THESIS

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Abstract

Climate change is altering environmental conditions and negatively affecting a wide range of species and taxa. In California, endangered Coho Salmon (*Oncorhynchus kisutch*) have been reduced to critically low abundances, and the total production of hatchery individuals has increased dramatically in response. Evidence shows that production hatcheries are severely diminishing the biocomplexity of wild salmon populations in streams where stocking occurs, but there has been no assessment into whether conservation hatcheries are also homogenizing the life history events of the populations they aim to protect. Maintaining diversity will be critical for populations to persist and adapt to global change. The Tomales Bay metapopulation of coho includes the putatively-wild Lagunitas Creek and the hatchery-supported Walker Creek. We compare Fork Length (FL), mass (g), and outmigration timing of Lagunitas Wild (LW), Walker Hatchery (WH), and Walker Natural Origin (WNO) smolts in 2022 and 2023. By comparing smolt data for the three subpopulations in both years, we attempted to determine if conservation hatcheries that prioritize genetic diversification in breeding pairs can produce offspring with variability at the time of outmigration. Lagunitas Wild (LW) coho were the smallest on average in both years but exhibited the highest abundance of coho smolts and variability in size and outmigration timing. Conversely, Walker Hatchery (WH) coho exhibited the lowest smolt abundance and lowest variation in important life history characteristics. In both years, WH and Walker Natural Origin (WNO) coho outmigrated at significantly different rates when compared to LW, but were not significantly different from each other in 2023. These differences indicate that ongoing conservation interventions to the Tomales Bay metapopulation are improving biocomplexity during outmigration, an important factor to consider under a rapidly changing climate.

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Introduction

Climate change is causing species across environments to adjust life histories and acclimate to novel environments, forcing natural resource managers to reconsider long-term conservation strategies (Cobben et al., 2012; Mawdsley et al., 2009). Anadromous salmonids (*Oncorhynchus spp.*), in particular, face a host of threats associated with climate change (Moyle et al. 2017), with populations located near the southern ends of their ranges exhibiting the highest extinction risk (Hare and Mantua, 2000; National Research Council, 1996). Over the last few decades, concerns over the decreases in wild population abundances and their long-term persistence have led to systematic increases in the total production of hatchery individuals for commercial exploitation (Hillborn and Winton, 1993; Olla et al., 1998). While salmon hatcheries have been shown to sustain populations of special concern (Osborne et al., 2020), there are inherent and distinct compromises that could limit the overall effectiveness of such actions. Possible tradeoffs include competition with wild conspecifics (Tatara and Berejikian, 2012), lower survival of hatchery individuals post release (McIntyre, 1985; Riley et al., 2004), disease (Peeler and Murray, 2004), and increased straying that may result in outbreeding depression and the domestication of wild stocks (Jones et al., 2018; Keefer and Caudill, 2014; Naish et al., 2007; Quinn, 1993). Despite these concerns, hatchery fish can promote adult returns (James et al., 2023), increase abundances across life stages (Venditti et al., 2018), and preserve genetic diversity in declining stocks (Van Doornik et al., 2011). In functionally extirpated populations, the release of both adults and juveniles has been used to supplement abundances (Arahamian et al., 2003), as well as maintain niche space and ecosystem function (Kostow, 2009; Pearsons and Temple, 2007).

The portfolio effect is often cited as a critical strategy for the conservation of threatened and endangered salmonid species (DuFour et al., 2015). At its simplest, the portfolio effect states

that in a changing environment, total population collapse is less likely when there is increased diversity in the timing of outmigration and other life history traits among subpopulations (Schindler et al., 2010; Oliver et al., 2015). Wild salmonid species naturally exhibit significant diversity in life history strategies (Quinn, 2005), but there is growing apprehension that production hatcheries, whose sole goal is to increase abundances for commercial and recreational fishing, is causing reductions in biocomplexity (Huber et al. 2024). In salmon populations, biocomplexity refers to the variety of characteristics that divide populations, and includes the variation in timing of life history events triggered by environmental cues among individuals and subpopulations, and is important for maintaining portfolio effects (Hilborn et al., 2003). Salmon from production hatcheries tend to have lower life history diversity compared to wild populations, and cause domestication in the wild populations that inhabit the same tributaries, (Sharma et al., 2005; Kostow, 2009; Huber et al., 2024). However, in highly imperiled stocks where harvest is barred, the focus shifts from boosting abundances to maintaining localized diversity (Naish et al., 2007). The goal of conservation hatcheries is to preserve and protect declining stocks by producing hatchery individuals that are genetically similar to the original populations, often through using individuals from local tributaries for broodstock where native populations still exist (Fisch et al., 2015, Utter and Epifano, 2002). However, to date there has been no attempt to discern if conservation hatcheries have the same deleterious effects on life history diversity as production hatcheries.

Many salmonid populations have become hatchery dependent and would not exist without conservation intervention (Moyle et al., 2017). In California, salmonid populations are faced with increasingly frequent droughts, coupled with atmospheric rivers in wet years, that together reduce juvenile survival in the freshwater environment (Munsch, 2022). Ocean warming and acidification

also reduce adult growth rates and survival (Haigh et al., 2015; Moltumyr et al., 2020). As the climate changes, maintaining phenotypic and phenological diversity in salmonid populations is critical in buffering against environmental variation and stochastic events (Schindler et al., 2010; Price et al., 2021). Recent studies have attempted to shift the importance of prioritizing genetic diversity to centering the maintenance of biocomplexity as the primary marker of hatchery intervention success (Williams et al., 2003; Osborne et al., 2020), but those studies heavily favor production hatcheries, not conservation hatcheries (Meek et al., 2020). Understanding the effects of conservation hatcheries on wild salmon diversity will be critical in safeguarding these populations in the future.

Coho Salmon (*Oncorhynchus kisutch*) in the Central California Coast Evolutionary Significant Unit (CCC-ESU) have shown dramatic reductions in abundance over the last century and were listed as federally threatened in 1996 and endangered in 2005 (Brown and Moyle, 1991; Katz et al., 2013). While climate change plays a major role in these declines (Crozier et al., 2019), other anthropogenic shifts have exacerbated these issues, including reductions in spawning and rearing habitat (Brown et al., 1994), alterations to hydrologic regimes (Grantham et al., 2012, NMFS 2012), the legacy effects of logging, mining, and agriculture (Moyle et al., 2008, Lamothe-Ammerlaan et al., 2017), and the introduction of invasive species (Moyle et al., 2017). Numerous populations south of the San Francisco Bay have been declared functionally extirpated (Spence and Williams, 2011) and Tomales Bay, in Marin County, California, was named a priority watershed for coho recovery by the National Marine Fishery Service (NMFS) in 2008 because it supports the largest presumed wild run of coho south of the Noyo River (Spence et al., 2008, NOAA, 2013). Tomales Bay also offers an ideal system to study the effects of hatchery intervention on biocomplexity in the context of the portfolio effect. The two largest tributaries,

Lagunitas Creek and Walker Creek (Figure 1), historically supported large runs of CCC Coho Salmon, but abundances have plummeted over the last few decades (Moyle et al., 2017). Lagunitas Creek maintains the southernmost population of fully wild, self-sustaining coho in North America (NOAA, 2013), but Walker Creek has relied heavily on hatchery releases of both adults and juveniles since the 1970s to prevent local extirpation (Spence and Williams, 2011).



Figure 1. Site Map of the Tomales Bay Watershed. This map shows the Tomales Bay Watershed and the location of the two main tributaries used for this study. The Walker Creek Watershed Boundary is designated by the dark blue outline and Walker Creek mainstem and its tributaries are indicated by the light blue lines. The location of the four PIT antennas that were in operation during this study are indicated with blue triangles. Soulajule Dam marks the end of anadromy for salmonids in Walker Creek and is represented by the light blue square. The location of the Walker Creek smolt trap is indicated by the light blue hexagon. The juvenile hatchery coho were released on the Walker Creek Ranch property at the light blue pin in both years of the study. The Lagunitas Creek Watershed Boundary is indicated by the dark red outline and mainstem Lagunitas and its tributaries are indicated by the lighter red lines. Peter's Dam (dark red square) and Seeger Dam (light red square) mark the end of anadromy in Lagunitas Creek. The location of the Lagunitas smolt trap is indicated by the red hexagon.

Coho Salmon have a three-year life cycle, with some variation in key life history events that mark their progression from egg to spawner (Sandercock, 1991). In the CCC-ESU, spawning typically occurs between November-February, and juveniles rear in stream for two winters before outmigrating in the following spring as smolts (Lestelle, 2007). Most individuals spend two summers in the ocean before returning to their natal streams in their third year to spawn (Pearcy and Fisher, 1988). Reduced biocomplexity in salmon stocks is often cited as an accelerant for population loss (Carlson and Satterthwaite, 2011). A lack of size and outmigration timing diversity are important factors that indicate reduced biocomplexity, and are correlated with smolt survival and adult returns (Simmons et al., 2022). Smolt size corresponds to growth rates and competitive abilities (Einum and Kvingedal, 2011), and a larger smolt indicates increased fitness (Tatara and Berejikian, 2012), because density-dependent mortality from competition and predation is a significant stressor in the freshwater environment (Moore and Berejikian, 2017, (Osterback et al., 2014). The timing of when coho enter the estuary is also an important phenological event, because early juvenile outmigration reduces overcrowding in streams (Jones et al., 2015; Simenstad et al., 1982), and seasonal predator and prey abundances in the estuary determine smolt growth and survival prior to ocean entry (Moore and Berejikian, 2017).

The purpose of this study is to determine if conservation hatchery practices that prioritize genetic diversity in breeding pairs can also produce juveniles of variable sizes and phenologies similar to wild populations. Specifically, we examined three populations of CCC coho within the Tomales Bay complex to determine the effect of hatchery intervention on outmigration diversity during 2022 and 2023. These three populations include Walker Creek Hatchery (WH), Walker Creek Natural Origin (WNO), and Lagunitas Creek Wild (LW). All Lagunitas smolts were presumed wild, and all hatchery juveniles stocked in Walker were tagged, meaning that any Walker

smolt without a Coded Wire Tag (CWT) or Passive Integrated Transponder (PIT) tag are presumed WNO. We hypothesize that (i) WH will exhibit the lowest variation in FL, mass, and outmigration timing compared with WNO and LW, and that (ii) LW will exhibit the highest variation in FL and mass.

Materials and Methods

Study Area

The CCC-ESU spans coastal drainages from Redwood Creek in Humboldt County to Aptos Creek in Santa Cruz County, USA (Spence and Williams, 2011). Coho in the CCC-ESU have been listed as federally endangered since 2005 (Brown and Moyle, 1991; Katz et al., 2013). The Walker Creek watershed is approximately 122 km² and drains into the northern end of Tomales Bay, five km before its confluence with Bodega Bay (Niemi and Hall, 1996; Rooney and Smith, 1999). Soujlajule Dam blocks migration of anadromous fish to roughly 32 km of historical spawning and rearing habitat. Walker Creek has historically been used for cattle ranching and gravel mining with roughly 95% of the watershed still actively operated as private cattle ranchland, (Marin Resource Conservation District, 2011; Tomales Bay Watershed Council, 2004). Hatchery intervention in Walker Creek commenced in 1976 after summer electrofishing surveys found only eight coho juveniles rearing in the entire watershed (Kelley, 1976), but the first two adult stockings in 1979 and 1980 failed to produce viable offspring (Brown and Moyle, 1991). Interventions have routinely included hatchery adults and juveniles since 2008 (NOAA, 2023).

Lagunitas Creek is approximately 270 km² and is the largest river system in Marin County, CA, USA (NMFS, 2012). Lagunitas drains into Tomales Bay at its southern end, roughly 18 km south of the Walker Creek terminus (Niemi and Hall, 1996). Approximately 37 km of historical

coho spawning and rearing habitat in mainstem Lagunitas Creek is currently blocked by Peter's Dam, located just upstream of the confluence with San Geronimo Creek, and 59 km of stream habitat is blocked by Seeger Dam on Nicasio Creek, the second largest tributary to Lagunitas (Ettlenger and Andrew, 2001). Similarly to Walker Creek, the Lagunitas Creek Watershed has historically been used for cattle ranching as well as timber harvest, but nearly 50% of the watershed has been converted to state park or open space land (Niemi and Hall, 1996; Tomales Bay Watershed Council, 2004).

Hatchery Procedures

The Don Clausen Fish Hatchery at Lake Sonoma, also known as the Warm Springs Conservation Hatchery, rears coho for the Russian River Captive Broodstock Program (USACE, 2021). Since 2001, this hatchery has been breeding coho from the Russian River and surrounding watersheds, and as of 2008, surplus individuals slated for the Russian River have been released into Walker Creek to boost coho abundance. Prior to spawning, adult coho are given a PIT Tag and genetic samples are removed to be studied at the National Oceanic and Atmospheric Association Southwest Science Center (NOAA SFSC). These genetic samples are used to create a matrix to determine which females should be spawned with corresponding males to minimize inbreeding and maximize genetic diversity for eventual release of juveniles into the wild. Program coho are then carefully spawned based on the genetic matrix created by the NOAA SFSC and reared at the hatchery until release. Broodstock are predominantly collected as young-of-the-year (YOY) from various Russian River tributaries and natural-origin YOY from surrounding watersheds (USACE, 2021). Any individual that is descended from a hatchery coho or population where hatchery coho are stocked is considered Natural Origin (USACE, 2021). Individuals meant for captive rearing

are typically taken from Lagunitas Creek or Olema Creek (the largest tributary to mainstem Lagunitas), and some broodstock are also taken from adult coho that return to the hatchery.

To identify WH fish from WNO and LW, all WH coho were implanted with a Coded Wire Tag (CWT) by hatchery staff, and a subset of individuals received PIT Tags to monitor their freshwater rearing patterns and overwinter survival as part of a separate project. PIT Tagging was conducted by the University of California, Davis, California Department of Fish and Wildlife (CDFW), and California Trout in October of 2021 and 2022, and PIT tagging procedures largely followed those of Lusardi et al. (2020). Coho were collected into tanks and moved to the tagging station in aerated buckets, where they were anesthetized using one to three teaspoons of buffered tricaine methanesulfonate (MS-222), wet weighed (g), and measured for fork length (FL). A small incision was then made into the anterior body cavity using scalpels, and a Biomark APT12 High Performance PIT Tag (12mm) was inserted into the cavity, before the individual was placed in a recovery bucket. Once the tagged individual regained swimming ability, it was moved to a new holding tank and kept for 30 days to ensure minimal tag shedding. The hatchery individuals were then transported via aerated truck to the Walker Creek Ranch Outdoor Education Center in November of 2021 and 2022, where the tagged juveniles were released within roughly 10m of the WCR PIT antenna. During 2021, we PIT tagged a total of 1100 hatchery individuals and 2100 individuals during 2022.

Smolt Trapping

The Walker Creek smolt trap was a channel-spanning fyke net trap (Figure 2) and was operated between 29 March 2022 to 26 May 2022, and 12 April 2023 to 07 June 2023. The Lagunitas Creek smolt trap was a floating rotary screw trap (Figure 3) and was operated between 22 March 2022 to 02 June 2022, and 04 April 2023 to 01 June 2023. Trap installation for both

tributaries was delayed in 2023 due to high flows from heavy rains in March 2023. The Walker smolt trap was monitored daily in both years following CDFW protocols (Tonty et al., 2023), but the Lagunitas smolt trap was operated on a schedule based off of flow and the new moon (Ettliger, 2023). In Walker Creek, salmonids were removed from the trap and placed into holding buckets to be processed. All coho smolts over 65 mm FL were scanned for PIT tags or CWTs, and the presence/absence of a tag determined if an individual was WH or WNO, respectively. All PIT tagged coho were placed into a bucket treated with Alka Seltzer and measured for FL and mass. All PIT tagged coho were measured and weighed as part of a separate project. The first 30 CWT WH coho were dosed and processed, and the first 30 WNO coho were processed. Scale samples were collected from the 30 WNO coho for parental genetic analysis at the Southwest Fishery Science Center in Santa Cruz, CA, USA. Once all measurements had been taken from the first 30 WH and WNO coho, the remaining coho smolts were scanned for tags and tallied. In Lagunitas, salmonids were removed from the trap before being placed in a bucket dosed with MS-222, the first 20 coho smolts were processed, and the rest were tallied before being released downstream.



Figure 2. Walker Creek Smolt Trap. This picture shows the Walker Creek channel, spanned by a downstream migrant fyke net trap. A gap is maintained at the river left edge for migratory steelhead. The trap is operated by California Department of Fish and Wildlife staff and maintained daily for the duration of the season.



Figure 3. Lagunitas Creek Rotary Screw Trap. The drum of the trap faces upstream and the floating box at the back is where individuals are held prior to release. The trap is adjusted so that flows allow for the drum to spin between 3-8 revolutions per minute (RPM). In the event of high flows, the trap is disengaged to reduce smolt mortality. In the event of reduced flows, plywood baffles are installed upstream of the trap to direct flow into the drum to maintain RPMs. The rear of the trap is netted to maximize smolt capture.

Statistical Analyses

In order to determine if fish size varied between the three populations, we first tested for data normality using a Shapiro-Wilk test. As FL and mass data were not normally distributed, we log-transformed these variables and retested for normality. If any of the three populations were still not normally distributed for a given metric, we conducted a Kruskal-Wallis test to assess differences in FL and mass variance among the populations. Where significant variance was found, a post-hoc Dunn Test was done to determine which populations differed statistically.

To analyze variance in the distribution of individuals caught in the trap per day across the three populations, we again assessed normality. We used a Shapiro-Wilk test for the WH and WNO

populations, but employed an Anderson-Darling test for LW because abundance in both years was higher than the limits required for a Shapiro-Wilk test. As the distributions were not normally distributed for all populations, a Kruskal-Wallis and post-hoc Dunn test was used to compare the distribution of individuals caught in the trap per day.

Fish outmigration is heavily influenced by streamflow, and both Lagunitas and Walker Creek have different hydrologic regimes as a result of dam impairment, and surface and groundwater inputs. To account for this, we used stream gauge data measuring discharge every 15 minutes from both tributaries and calculated the average daily flow for each creek. To determine the role of flow in outmigration behavior between populations, we used a Negative Binomial Generalized Linear Model. We selected this model because the response variable (daily trap catch) is a count variable showing overdispersion (Cheng and Gallinat, 2004), and flow is a covariate that impacts the number of individuals caught in each trap per day (Kastl et al., 2022). Two Negative Binomial GLM models were used to compare daily trap catches for the two Walker populations against Lagunitas, keeping discharge for each tributary constant as a predictive covariate for downstream migration. The model compares the variation in daily trap catch rates as a function of each population, their respective daily average flows, and calculated unexplained factors. Date and year are also included to determine the role interannual variance on outmigration behavior between cohorts. By including population as a factor, and streamflow, date, and year as covariates, the model intrinsically accounts for the variation in Lagunitas and allows us to compare daily trap catch for WH vs. LW in the first equation (Table 5) and WNO vs. LW in the second (Table 6), incorporating the influence of the variables in both systems. The equations for the models are:

$\log(\text{Daily Catch Abundance}) = \beta_0 + \beta_{\text{WH}} * \text{Origin WH} + \beta_{\text{CFS}} * \text{CFS} + \beta_{\text{Date}} * \text{Date} + \beta_{\text{Year}} * \text{Year} + \epsilon$	(1)
$\log(\text{Daily Catch Abundance}) = \beta_0 + \beta_{\text{WNO}} * \text{Origin WNO} + \beta_{\text{CFS}} * \text{CFS} + \beta_{\text{Date}} * \text{Date} + \beta_{\text{Year}} * \text{Year} + \epsilon$	(2)

where $\log(\text{Daily Catch Abundance})$ represents the natural logarithm of the daily trap counts, β_0 represents the intercept term, or the expected log count of individuals caught per day when all predictors are zero, β_{WH} and β_{WNO} indicates the difference in the expected log count of Daily Catch Abundance between WH (Walker Hatchery) or WNO (Walker Natural Origin) and the reference category, which is LW (Lagunitas Wild), and β_{CFS} , β_{Date} , and β_{Year} all represent the change in the expected log count of Daily Catch Abundance associated with a one-unit increase in their respective variables, holding all other variables constant.

Results

Fork Length and Body Mass

During 2022, a total of 2,023 were measured for FL and mass between the two tributaries (Figure 4, Table 1). The WH population exhibited the lowest abundance (298 of 385 individuals measured for FL and mass), the WNO population was the largest on average (713 of 1,647 individuals measure), and LW exhibited the highest abundance (1,012 of 7,188 individuals measured) but was smallest on average. None of the populations were normally distributed for FL or mass, except for WH. Significant differences in FL were apparent for the three populations after log-transforming the data (Kruskal-Wallis test, Chi-squared = 502.22, df = 2, p-value < 2.2e-16), and the post-hoc Dunn Test revealed that WNO was significantly larger than WH (adjusted p-value = 1.23e-03), and LW was significantly smaller than WH (adjusted p-value = 1.43e-35) and WNO (adjusted p-value = 9.09e-103). Significant variation in mass also existed between populations

(Kruskal-Wallis test, Chi-squared = 438.93, df = 2, p-value < 2.2E-16), and the post-hoc Dunn test revealed WNO was significantly larger than WH (adjusted p-value = 1.58e-31) and LW was significantly smaller than WH (6.79e-90) and WNO (adjusted p-value = 3.21e-03).

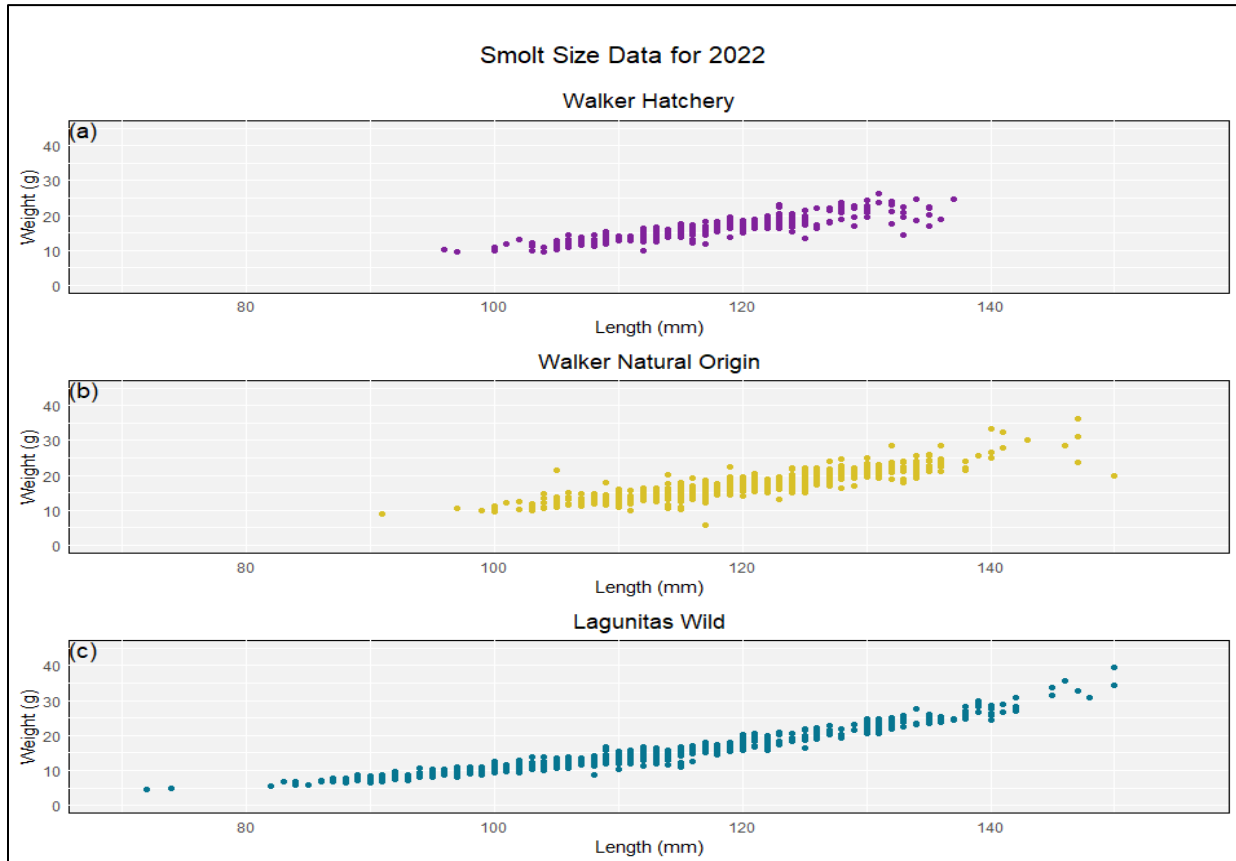


Figure 4. Smolt size, fork length (mm) and wet weight (g) for the three coho populations measured in 2022. Each dot represents an individual coho for (a) Walker Hatchery (WH) individuals (purple, n = 298), (b) Walker Natural Origin (WNO) individuals (yellow, n = 713), and (c) Lagunitas Wild (LW) individuals (blue, n = 1012). All individuals were captured between 22 Mar 2022 and 02 June 2022.

Table 1. Coho smolt size data in 2022. This table shows the summary statistics for all individuals measured in 2022. Fork Length (FL) was measured to the nearest millimeter (mm) and weight measured to the nearest tenth of a gram. Only a subset of coho for each day are measured due to time constraints, and a sample of the population is used to determine overall trends for a given day.

Walker Hatchery			Walker Natural Origin			Lagunitas Wild		
Measure	Fork Length (mm)	Weight (g)	Measure	Fork Length (mm)	Weight (g)	Measure	Fork Length (mm)	Weight (g)
Max	137	26.2	Max	165	47.2	Max	150	39.6
Min	96	9.5	Min	91	5.8	Min	72	4.4
Average	118	16.3	Average	120	17.3	Average	109	13.5
SE	0.5	0.2	SE	0.3	0.1	SE	0.4	0.2
95% CI Lower	117	15.9	95% CI Lower	120	17.0	95% CI Lower	108	13.2
95% CI Upper	118	16.7	95% CI Upper	121	17.5	95% CI Upper	109	13.8
Number Measured	298		Number Measured	713		Number Measured	1012	
Number Captured	385		Number Captured	1647		Number Captured	7188	
% Measured	77%		% Measured	43%		% Measured	14%	

In 2023, a total of 1,814 smolts were measured for FL and mass between the two tributaries (Figure 5, Table 2). Again, the WH coho exhibited the lowest abundance (283 captured, 277 measured for FL and mass), but were the largest on average, and WNO had 784 individuals measured of the total 3,163. The LW population again exhibited the highest abundance (753 of 7,683 individuals measured for FL and mass), and were the smallest on average. None of the populations were normally distributed after log transformation, and significant differences were apparent for the three populations in FL (Kruskal-Wallis test, Chi-squared = 811.28, df = 2, p-value < 2.2e-16) and mass (Kruskal-Wallis test, Chi-squared = 735.19, df = 2, p-value < 2.2e-16). The post-hoc Dunn test revealed that WH was significantly larger than WNO (adjusted p-value = 4.29Ee-03) and that LW was significantly smaller than WH (adjusted p-value = 7.42e-94) and WNO (adjusted p-value = 7.42e-94; LW vs. WNO adjusted p-value = 2.20e-127). In both years,

the WH coho had the lowest intrapopulation variation for FL and mass, while LW exhibited the highest.

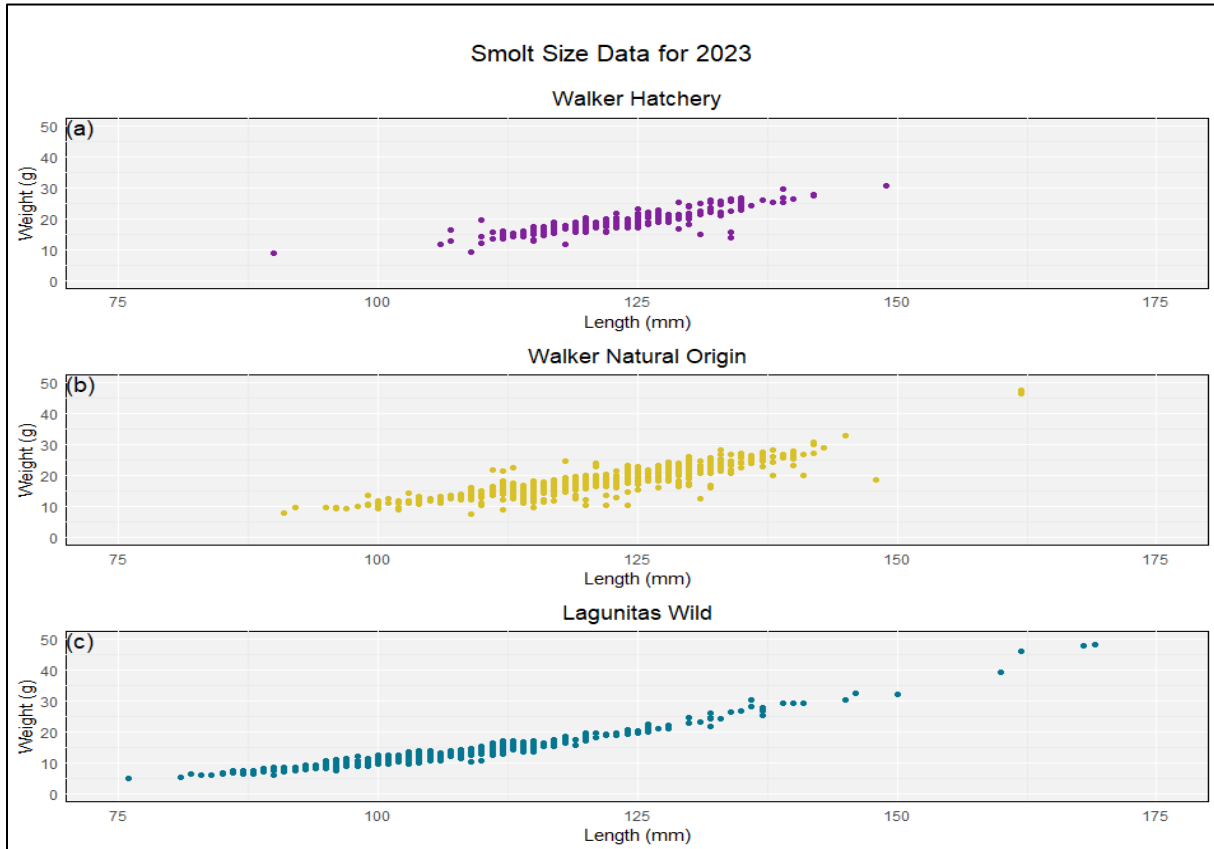


Figure 5. Smolt size, fork length (mm) and wet weight (g) for the three coho populations measured in 2023. Each dot represents an individual coho for (a) Walker Hatchery (WH) individuals (purple, $n = 277$), (b) Walker Natural Origin (WNO) individuals (yellow, $n = 784$), and (c) Lagunitas Wild (LW) individuals (blue, $n = 753$). All individuals were captured between 04 Apr 2023 and 07 June 2023.

Table 2. Coho smolt size data in 2023. This table shows the summary statistics for all individuals measured in 2023. Only a subset of coho for each day are measured due to time constraints, and a sample of the population is used to determine overall trends for a given day.

Walker Hatchery			Walker Natural Origin			Lagunitas Wild		
Measure	Fork Length (mm)	Weight (g)	Measure	Fork Length (mm)	Weight (g)	Measure	Fork Length (mm)	Weight (g)
Max	149	30.6	Max	162	47.5	Max	177	53.7
Min	90	9.0	Min	91	7.6	Min	76	5.0
Average	122	18.7	Average	120	17.9	Average	105	12.6
SE	0.4	0.2	SE	0.3	0.2	SE	0.4	0.2
95% CI Lower	121	18.3	95% CI Lower	120	17.6	95% CI Lower	104	12.3
95% CI Upper	123	19.1	95% CI Upper	121	18.2	95% CI Upper	106	13
Number Measured	277		Number Measured	784		Number Measured	753	
Number Captured	283		Number Captured	3163		Number Captured	7683	
% Measured	98%		% Measured	25%		% Measured	10%	

Outmigration Behavior

During 2022, a total of 9,220 coho smolts migrated from both tributaries between 22 Mar 2022 to 02 June 2022 in Lagunitas (72 days) and 29 Mar 2022 to 26 May 2022 in Walker (58 days) (Figure 6, Table 3). The WH outmigration window lasted 53 days and peaked on 01 May 2022. The WNO outmigration window lasted the entire Walker smolt trapping season at 58 days and peaked on 06 May 2022. The LW outmigration window lasted the whole Lagunitas smolt trapping season at 72 days and peaked on 02 May 2022. The same statistical analyses used to identify variance in size were used to analyze the total number of individuals caught in each trap per day between the three populations (Kruskal-Wallis test, Chi-squared = 728.93, df = 2, p-value <2.2E-16). The post-hoc Dunn test showed significant differences in daily trap catches between all three

populations (WH vs. WNO adjusted p-value $3.67e-10$; LW vs. WH adjusted p-value = $2.31e-12$; LW vs. WNO adjusted p-value = $5.39e-156$).

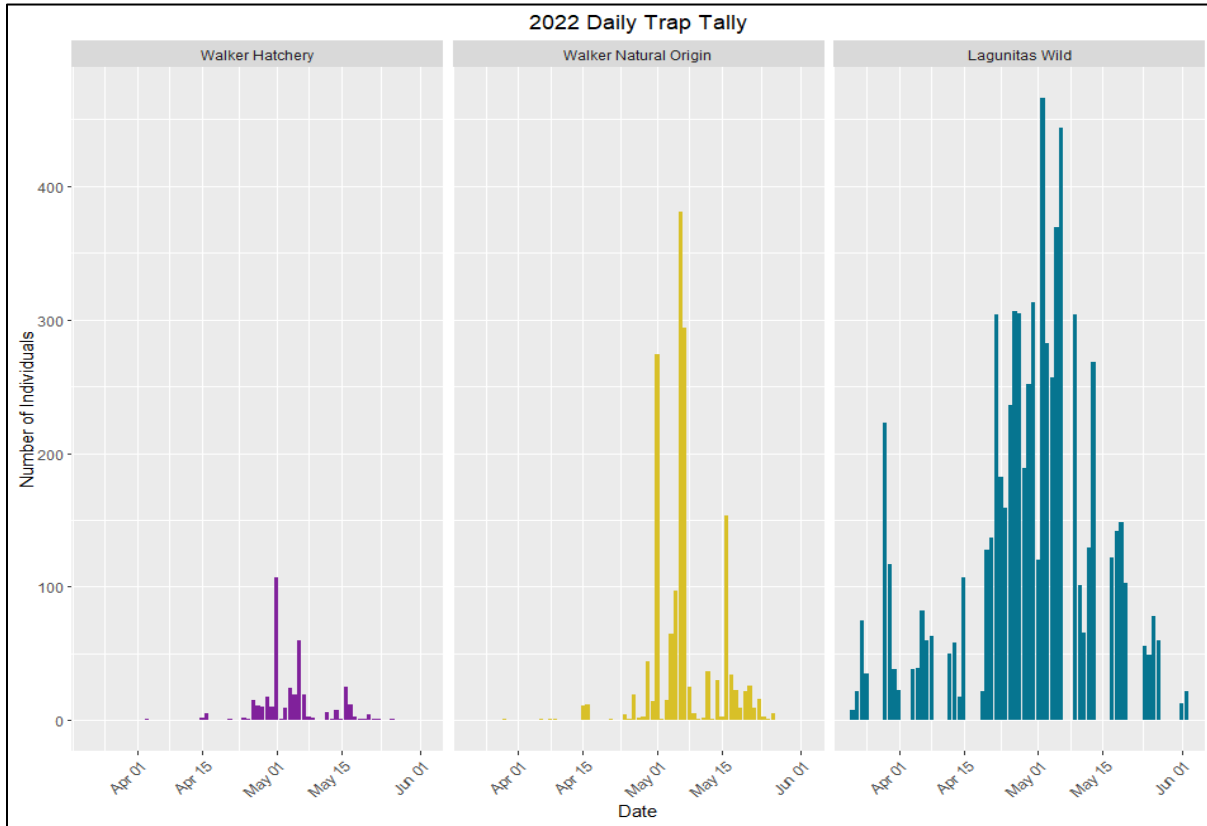


Figure 6. Daily trap counts for coho smolts in 2022. This graph shows the total number of smolts caught per day during the 2022 smolt trapping season. Walker Hatchery (WH) smolts (purple bars, $n = 385$), Natural Origin (WNO) smolts (yellow bars, $n = 1,647$), Lagunitas Wild (LW) smolts (purple bars, $n = 7,188$).

Table 3. Summary of Outmigration for 2022. This table provides detailed information on the outmigration patterns for each tributary during 2022, including key metrics and observations for each population.

2022 Outmigration Summary						
Origin	Number of Individuals	First Capture	Last Capture	Outmigration Duration	Peak Number	Peak Date
Walker Hatchery	385	4/3/2022	5/26/2022	53 days	107	5/1/2022
Walker Natural Origin	1,647	3/29/2022	5/26/2022	58 days	381	5/6/2022
Lagunitas Wild	7,188	3/22/2022	6/2/2022	72 days	466	5/2/2022

In 2023, a total of 11,129 coho smolts migrated from both tributaries between 04 Apr 2023 and 01 June 2023 in Lagunitas (58 days) and 12 Apr 2023 and 07 June 2023 in Walker (56 days) (Figure 7, Table 4). Trap installation in both tributaries was delayed due to heavy rains and high March flows. The WH outmigration window lasted 58 days and peaked on 28 Apr 2023. WH overwinter survival was 26.5% lower in 2023 (102 fewer individuals). The WNO outmigration window lasted 50 days and peaked on 29 Apr 2023. Overwinter survival was 47.9% higher for the WNO coho in 2023 (1,516 more individuals). The LW outmigration window lasted 58 days and peaked on 27 Apr 2023. Overwinter survival was 6.4% higher for LW coho in 2023 (495 more individuals). Normality tests showed none of the populations were normally distributed, and the statistical analysis showed significant variation between the three populations (Kruskal-Wallis test, Chi-squared = 2818.5, df = 2, p-value <2.2E-16). The post-hoc Dunn test revealed there was no significant variation in outmigration between the WH and WNO populations in 2023 (adjusted p-value = 3.10e-01), but that both populations were significantly different from LW (LW vs. WH adjusted p-value = 6.70e-63; LW vs. WNO adjusted p-value = 0.00e+00). In both years, the WH coho again exhibited the lowest intrapopulation variation in outmigration timing and the LW coho exhibited the highest.

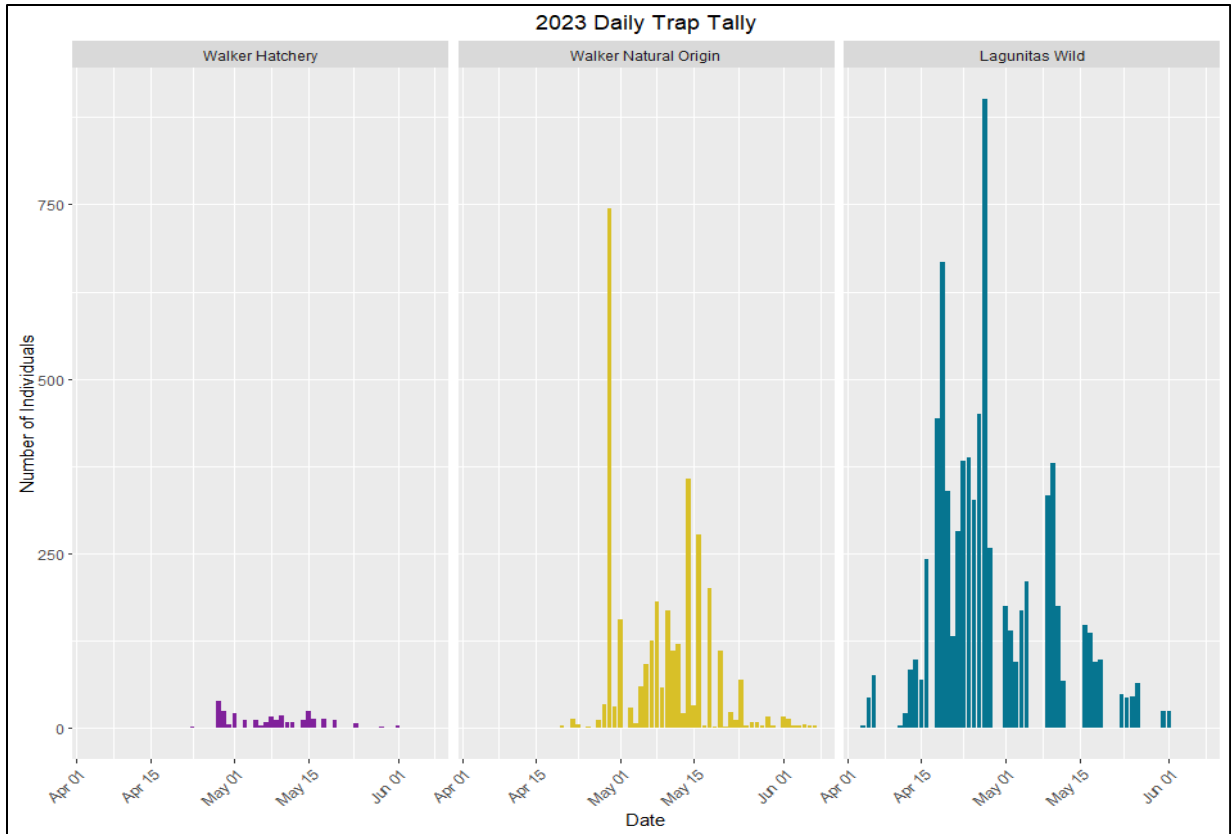


Figure 7. Daily trap counts for coho smolts in 2023. This graph shows the total number of smolts caught per day during the 2023 smolt trapping season. Walker Hatchery (WH) smolts (purple bars, n = 283), Natural Origin (WNO) smolts (yellow bars, n = 3,163), Lagunitas Wild (LW) smolts (purple bar, n = 7,683).

Table 4. Summary of Outmigration for 2022. This table provides detailed information on the outmigration patterns for each tributary during 2023, including key metrics and observations for each population.

2023 Outmigration Summary						
Origin	Number of Individuals	First Capture	Last Capture	Outmigration Duration	Peak Number	Peak Date
Walker Hatchery	283	4/12/2023	6/2/2023	58 days	39	4/28/2023
Walker Natural Origin	3,163	4/18/2023	6/7/2023	50 days	745	4/29/2023
Lagunitas Wild	7,683	4/4/2023	6/1/2023	58 days	901	4/27/2023

Downstream Migration Flow Modeling

The models compared the total number of individuals caught in the trap per day as a function of Origin (WH vs. LW), CFS (Daily Average CFS in Walker vs. Daily Average CFS in Lagunitas), Date, and Year. The first model compared WH to LW (Table 5), and found that Origin ($Pr(>|z|) = < 2.2e-16$), CFS ($Pr(>|z|) = 1.2e-06$), Date ($Pr(>|z|) = 6.7e-04$) and Year ($Pr(>|z|) = 5.4e-04$) were all significant predictors of the number of individuals caught in the trap per day. The second model compared WNO and LW (Table 6), with the same equation and variables, and found that Origin ($Pr(>|z|) = 3.1e-11$), CFS ($Pr(>|z|) = 4.0e-06$), Date ($Pr(>|z|) = 8.0e-04$) and Year ($Pr(>|z|) = 4.5e-04$) were also all significant predictors of the number of individuals caught in the trap per day. While all variables held significance, both Origin and CFS had the highest impact on the number of individuals caught in the trap per day when comparing the Walker populations to Lagunitas.

Table 5. Negative Binomial Generalized Linear Model (GLM) Results for Walker Hatchery vs. Lagunitas Wild. This table displays the estimates, standard errors, z-values, and p-values ($Pr(>|z|)$) obtained from the Negative Binomial GLM analysis conducted to compare outmigration behavior between Walker Hatchery and Lagunitas Wild in both years. The estimates represent the model's coefficients, while the standard errors, z-values, and p-values assess the statistical significance of the coefficients, indicating the impact of predictor variables on the outcome variable within the model.

Equation (1): Negative Binomial GLM of WH vs. LW				
Predictor	Estimate	Std. Error	z value	$Pr(> z)$
(Intercept)	-1.4e+04	4.2e+03	-3.5e+00	5.4e-04
Origin WH	-3.0e+00	1.8e-01	-1.6e+01	<2.2e-16
CFS	-2.0e-02	4.0e-03	-4.9e+00	1.2e-06
Date	-1.9e-02	5.6e-03	-3.4e+00	6.7e-04
Year	7.3e+00	2.1e+00	3.5e+00	5.4e-04

Table 6. Negative Binomial Generalized Linear Model (GLM) Results for Walker Natural Origin vs. Lagunitas Wild. This table displays the estimates, standard errors, z-values, and p-values ($\Pr(>|z|)$) obtained from the Negative Binomial GLM analysis conducted to compare outmigration behavior between Walker Natural Origin and Lagunitas Wild in both years. The estimates represent the model's coefficients, while the standard errors, z-values, and p-values assess the statistical significance of the coefficients, indicating the impact of predictor variables on the outcome variable within the model.

Equation (2): Negative Binomial GLM of WNO vs. LW				
Predictor	Estimate	Std. Error	z value	$\Pr(> z)$
(Intercept)	-1.6e+04	4.7e+03	-3.5e+00	4.5e-04
Origin WNO	-1.4e+00	2.1e-01	-6.6e+00	3.1e-11
CFS	-2.3e-02	4.9e-03	-4.6e+00	4.0e-06
Date	-2.1e-02	6.3e-03	-3.4e+00	8.0e-04
Year	8.3e+00	2.4e+00	3.5e+00	4.5e-04

Discussion

In this study, we attempted to answer the question of whether or not conservation hatcheries that prioritize genetic diversity can also create individuals with variation in biocomplexity, by comparing three salmon stocks that create a metapopulation in Tomales Bay. Coho show substantial life history variation as juveniles (Quinn, 2005), particularly during freshwater rearing and downstream migration, and such differences across cohorts can increase the number of adult returns by providing a diversity of individuals that can survive variable environmental conditions (Jones et al., 2021). Both the size of an individual and the timing of their outmigration are important factors in smolt fitness and survival (Einum and Kvingedal, 2011; Tatara and Berejikian, 2012; Moore and Berejikian, 2017; Osterback et al., 2014). In 2022, the WH coho had the lowest abundance and lowest variation in size, and the WNO coho were the largest on average. In 2023, the WH coho remained the least abundant and least variable, but were the largest on average, and the total number of WNO coho nearly doubled. In both years, the LW coho were the most abundant, smallest on average, and had the highest variation for FL and mass. The lower abundance and variability of WH coho align with expectations, given the size-based selection that occurs from

hatchery rearing and tagging practices (Kostow, 2004; Metcalfe et al., 2003), and the documented lower fitness and survival of hatchery individuals post-release (LeVay, 2007; Connor et al., 2004). Notably, the high variation observed in LW coho may explain their persistence as the southernmost wild coho population in North America (Spence and Williams, 2011). This aligns with the principle that diversity increases community stability (Schindler et al., 2010).

Streamflow plays an important role in salmonid dynamics, affecting growth rates, phenology, and survival across life stages (Addo et al., 2023; Watz et al., 2023). High winter flows may benefit rearing juveniles by activating floodplains and increasing food availability (Warren et al., 2015; Katz et al., 2017), but can also increase mortality if juveniles are unable to find velocity refuge (Warren et al., 2015; Bellmore, 2022). Streamflow is also a significant trigger for smolt outmigration (Silva et al., 2020). In 2022, all three populations outmigrated at different rates, even with discharge factored in as a covariate (Table 5). In 2023, while there was no significant difference in outmigration timing between WH and WNO, both differed from LW (Table 6). Both tributaries experienced substantial variation in peak flow between years, with Walker Creek seeing a more than 50-fold increase in peak discharge in 2023 compared to 2022, and Lagunitas Creek experiencing an increase exceeding 120-fold in 2023 (Figure 8).

The models indicate that both origin of the individual (e.g., WH, WNO, and LW) and discharge were significant predictors of the number of individuals captured in the trap per day, with higher discharge corresponding to reduced catches. Changes in streamflow across years as a result of climate change will affect the longevity of salmonid populations across their range (Munsch, 2022), but increased streamflow during outmigration has been linked to increased smolt survival in both wild and hatchery salmonids (Notch et al., 2020). The results of the model also indicate that both Date and Year significantly affected the outmigration behavior of the three

populations. The variation in daily trap catches in response to date could be attributed to daily photoperiod or lunar phase, as longer days and darker nights have been shown to increase outmigration numbers in salmonid smolts (Spence and Dick, 2014). Additionally, as the season progresses, a higher percentage of individuals will have already left the system, so the number of individuals caught in the trap decreases over time. Year also significantly affected daily trap catch, and this could be caused by a variety of factors, including variation in returning spawner abundance (Bradford et al., 1997), annual streamflow (Munsch, 2022), predator abundance (Hostetter et al., 2013), or a plethora of biotic and abiotic factors that change between years. While the higher flows in 2023 could be the primary driver of increased WNO and LW smolt abundances (47.9% and 6.4%, respectively), it is unclear what caused the 26.5% reduction in overwinter survival of the WH smolts. Increased mortality could be a result of inferior competitive ability in the freshwater environment (Tatara and Berejikian, 2012), or higher mortality from predation (Kostow, 2009). Future monitoring efforts should focus on freshwater dynamics in Walker to better understand the interannual survival of the hatchery juveniles post-release.

Commercial hatcheries have faced increasing criticism for exacerbating declines in wild salmon populations through overharvest, exceeding environmental carrying capacities, and diminishing genetic integrity (Naise et al., 2007; Brannon et al., 2004; Beamish et al., 1997; Bingham et al., 2014). They also contribute to disease transmission, reduced survival rates, and decreased adaptability to climate change in wild populations (Nekouei et al., 2019; Weber and Fausch, 2003; Sharma et al., 2005; Kostow, 2009). While studies have extensively documented these negative effects in production hatcheries, few have explored whether conservation hatchery practices, aimed at maximizing genetic diversity and preserving local adaptations, can maintain or enhance biocomplexity at the metapopulation level (Neff et al., 2011). Research suggests that

maintaining variability is vital for the long-term survival of salmonids in the face of climate change (Muñoz et al., 2017), and conservation hatcheries focus on minimizing extinction risk by prioritizing genetic diversity, selecting for adaptive traits, and mimicking natural rearing conditions (Osborne et al., 2020; Näslund and Johnsson, 2016; Ward, 2006; Fisch et al., 2015). The Don Clausen Fish Hatchery follows similar protocols for coho breeding in Walker Creek (USACE, 2021). In both years of this study, the WH coho had the lowest abundance and lowest variation in terms of size and outmigration timing. These results suggest that while the WH coho population may lack diversity when considered in isolation, it contributes significant variation to its natural origin and wild counterparts within the broader metapopulation context.

Climate change has been directly linked to the loss of biodiversity across species and a variety of taxa (Habibullah et al., 2022). Organisms that have evolved to local environments may no longer be suited to novel conditions (Gallagher et al., 2013), and phenological shifts have already caused mismatches in biological interactions across trophic levels (Bellard et al., 2012). Genetic variation has been linked to physiological, phenotypic, and phenological diversity within populations (Doi et al., 2010), and the loss of any diversity poses a significant threat to population longevity because it is the basis through which evolutionary processes act (Väinölä and Johannesson, 2017). Maintaining biocomplexity in declining populations is an advantageous strategy for reducing extinction risks within the context of global change (Schindler et al., 2010; Meek et al., 2020). The two-year timeframe of this study may be too short to capture the full scale of interannual variability in coho from Tomales Bay, but it provides a concrete estimation of Walker coho abundances and insights into coho metapopulation dynamics in the CCC-ESU. While WH coho may lack intrapopulation biocomplexity, they showed variation in size and behavior during outmigration compared with WNO and LW. These differences suggest that conservation

hatchery intervention diversified life history timing and size during outmigration in the Tomales Bay metapopulation. Future studies should examine the effects of such interventions on adult returns at decadal time scales to better understand long-term metapopulation dynamics in the context of CCC-ESU conservation and, specifically, portfolio effect theory. As climate change continues to affect salmonids across the Pacific, understanding whether to produce hatchery fish for abundance, genetic diversity, or life history variation will be paramount to salmonid conservation.

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