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Mixed-maturation fisheries compromise productivity and resilience of Chinook salmon

Nick Gayeski[1]✉, Devin Swanson[1], Misty MacDuffee[2] & Andrew Rosenberger[2,3]

Most ocean-type Chinook salmon (*Oncorhynchus tshawytscha*) in the northeast Pacific Ocean are harvested in mixed-stock marine fisheries. Here, multiple populations with varying abundance and productivities are encountered. In addition to being mixed-stock, many of these fisheries encounter both mature and immature Chinook salmon. Hence, these fisheries are better described as mixed-stock and "mixed-maturation" fisheries. Harvest of immature fish can skew the age composition of Chinook salmon populations towards younger, and hence smaller, individuals. This shift reduces the proportion of older and larger Chinook salmon that contribute disproportionately to the productivity of their populations. We developed a deterministic individual-based demographic-genetic model of fall Chinook salmon to evaluate the effects of fisheries that harvest mature and immature Chinook salmon. We then compared these effects on age, size and weight to terminal fisheries that harvest only mature fish, evaluating the benefits to both landed catch and Chinook salmon rebuilding. In our modeled scenarios of mixed-maturation fisheries, we found that immature Chinook salmon can comprise up to 59% of the total numbers of fish caught, and 47% of the total weight of the catch. If instead, these Chinook salmon were not harvested until they reached terminal fisheries as mature adults, they would contribute greater biomass to landed catches. Unharvested and terminally harvested populations retain a more archetypal age and sex structure than contemporary fall Chinook salmon subject to marine mixed-maturation fisheries. Lastly, when harvested at rates that achieve maximum sustainable yield, terminal fisheries allow a greater proportion of larger, older Chinook salmon reach their spawning grounds, thereby increasing the productivity of their populations. The benefits of terminal fisheries would accrue to river-based fishers and communities, and other near terminal locations (such as inlets or estuaries). They would also support rebuilding of depleted Chinook salmon runs.

Keywords Chinook salmon, Age-and-size overfishing, Fisheries-induced selection, Mixed-maturation fisheries, Population structure, Demographic-genetic model

A number of wild Pacific salmon species and populations have exhibited declines in adult body size over recent decades[1]. Chinook salmon (*O. tshawytscha*) in particular have displayed marked declines in size-at-age and declines in the proportion of older, larger individuals, particularly females, in many populations across their range in the eastern Pacific and watersheds from the Pacific Northwest to Alaska[1–12]. Such observations in Chinook salmon have been documented since the 1920s[3,4].

Several likely factors affecting salmon body size have been identified, including marine environmental conditions, interactions with large numbers of hatchery salmon in marine waters[13–15], adverse genetic and ecological interactions with hatchery salmon in freshwater, and the direct and indirect effects of fisheries that impose selection[1,9,16–22]. While changes in the marine ecosystems of the northeastern Pacific have undoubtedly affected the marine growth of Chinook salmon, the role of fisheries-induced selection and potential for demographic and genetic changes in harvested Chinook salmon populations remains poorly analyzed (e.g., 1, 3, 18).

Chinook salmon have the most complex life history of any Pacific or Atlantic salmon. Like all Pacific salmon, Chinook are semelparous and die after spawning. Despite this, generations overlap due to both sexes having multiple maturation ages with males typically 2 to 6, females 3 to 6 and historically up to 7 and 8[24,28]. This broad age structure has resulted in contemporary marine fisheries harvesting both immature and mature Chinook

[1]Wild Fish Conservancy, P.O. Box 402, Duvall, WA, USA. [2]Biologist, Raincoast Conservation Foundation, P.O. Box 2429, Sidney, Canada. [3]Coastland Research, PO Box 4592, Smithers, Canada. ✉email: nick@wildfishconservancy.org

salmon. This is in contrast to most other fisheries on Pacific salmon species which are largely fished on a mature harvest standard[29].

Coastal mixed-stock fisheries that occur in territorial waters (3 nautical miles) of western Canada and the US Pacific Coast and EEZs are of particular relevance to ocean-type Chinook salmon populations originating in British Columbia (BC) and the southern US (Washington, Oregon, Idaho and California). The majority of ocean-type Chinook salmon from these populations (north of the Elk River on the central Oregon coast) migrate north as sub-yearlings to rear inside of the continental shelf in the coastal marine waters from Oregon to Southeast Alaska before attaining their maturation size and age and migrating back to their natal rivers. Unlike most other salmon species harvested as mature fish on their spawning migration, immature Chinook salmon are subject to harvest in marine sport, troll and net fisheries that are managed under the Aggregate Abundance-Based Management (AABM) regime of the Pacific Salmon Treaty. Hence, these coastal mixed-stock fisheries are also "mixed-maturation" fisheries. Ocean-type Chinook salmon bound for rivers in the southern US and BC that escape the AABM fisheries are then subject to one or more state, tribal or BC federal fisheries managed pursuant to domestic salmon plans[23]. As a result of this life-history and migratory pattern, immature ocean-type Chinook salmon are vulnerable to capture in coastal mixed-stock fisheries, where 'vulnerable' denotes their presence within a fishery area with a non-zero probability of capture.

Hereafter, we refer to ocean-type Chinook salmon as "Fall Chinook"[24,25]. While some summer-run populations may also exhibit an ocean-type life history, they generally rear offshore in marine environments[26] and are therefore less vulnerable to coastal mixed stock fisheries than fall populations that rear on the continental shelf. Fall populations also comprise the majority of ocean-type Chinook.

Direct and indirect age overfishing

Harvest of large numbers of immature salmon (captured one or more years before completing their marine growth and becoming mature adults) results in what we refer to as indirect age overfishing. Indirect age- and/or size-overfishing is a distinct phenomenon from direct age-overfishing. Direct age-overfishing occurs when harvesters target older, typically larger individuals either through gear selectivity or by fishing at times or in areas where these fish are disproportionately present relative to their abundance in the overall population. This practice directly reduces the proportion of older, larger fish remaining in the unharvested population, particularly among spawners. In contrast, indirect age-overfishing, reduces the proportion and total abundance of older, larger adults by removing smaller, immature individuals one or more years before they would have matured. The effect of removing immature fish on the population age structure becomes apparent not in the year of the harvest, but in subsequent years as fewer individuals survive to older ages. Additionally, we distinguish age /size overfishing from the similar growth overfishing (when fish are harvested before they reach the size where yield per recruit is optimized[27] because of the nuanced implications for population structure versus yield.

Age-overfishing (direct or indirect) is a result of fishing mortality and is thus independent of ecological conditions in marine waters that may result in adverse growth conditions. The effect of intensive age-selective harvesting on reducing body size is well documented in the fisheries literature[28–37], as life-history theory predicts that increased mortality in older age and size classes generally favors earlier maturation at smaller size[28,30,34]. Indirect age over-fishing is less likely to occur in terminal (e.g., river) or near-terminal (e.g., estuary) fisheries as the majority of Chinook salmon present are returning as mature spawners[36].

In this study, we hypothesize that (indirect) age-overfishing in mixed-maturation fisheries leads to demographic changes in affected Chinook salmon populations, specifically selecting for younger age-at-maturity. When immature fish are harvested, a survival advantage arises for those that mature at younger ages. Genes and genotypes associated with later maturation are reduced in frequency in the spawning population as immature individuals possessing these genes are removed from the population. Fish with genotypes that promote faster growth and earlier reproduction, even at smaller sizes, are more likely to contribute to the next generation before being caught. This selective pressure leads to the evolution of earlier maturation at smaller sizes, demonstrating how mixed-maturation fisheries can cause fisheries-induced evolution.

If this hypothesis is correct, mixed-maturation fisheries are likely to negatively affect the productivity and resilience of existing Chinook salmon populations compared to terminal or near-terminal fisheries. For instance, reductions in the proportion and size of older females can decrease both the size and number of eggs produced per female, reducing fecundity[7,12,38]. Additionally, a decline in the number and proportion of older, larger Chinook can also simplify the population's age structure, diminishing the 'portfolio effect' - the stabilizing influence that arises from having multiple age classes of mature individuals[39,40]. This loss of age structure diversity can reduce a population's ability to withstand and recover from disturbances such as environmental and climate change, fishing pressure, or habitat degradation, ultimately lowering its resilience[39].

To date, the potential selective effects of harvesting immature Chinook in coastal mixed-maturation salmon fisheries have not been closely analyzed, though the potential for such adverse consequences has been identified[1,3,18,29,37]. To investigate this potential for harvest-induced change in the age and size structure of Chinook salmon, we developed an individual-based demographic-genetic model[21,41,42] based on the life-history of fall Chinook salmon.

The model population consists of 6 (post-smolt) age classes (1–6) with an age structure that exhibits a higher proportion of older individuals aged 4 to 6 than the majority of ocean-type Chinook in the latter half of the 20th and first quarter of the 21st centuries (Table 1). Females mature between the ages of 3 and 6, males between the ages of 2 and 6. Individuals genetically assigned to mature at smaller weights and fork lengths (and thus younger ages) are assigned higher daily post-smolt growth rates than larger, older individuals (see Methods). The population is parameterized so that the deterministic unfished (equilibrium) spawner abundance equals (approximately) 1000 (Table 1).

	L2M	L3M	L4M	L5M	L6M	L3F	L4F	L5F	L6F	TM	TF
N1	23	128	172	163	22	81	167	201	43	508	492
P1	0.045	0.252	0.339	0.321	0.043	0.165	0.339	0.409	0.087	0.51	0.49

Table 1. Initial pre-harvest age structure of the model ocean-type Chinook population. *N1* indicates the number of individuals in each age–sex class, and *P1* indicates their proportion in the population. LxM and LxF indicate the length-at-age classes of males and females, respectively. TM and TF indicate the total numbers of each sex.

Harvest scenario	Mean immature catch	Mean mature catch	Proportion immature
MM Troll (H3)	432	296	0.59
MM Gillnet (H4)	226	338	0.40
	Mean Immature Total Catch Weight (lbs.)	**Mean Mature Total Catch Weight (lbs.)**	**Proportion Immature**
MM Troll (H3)	4111	4612	0.47
MM Gillnet (H4)	1213	6998	0.15

Table 2. Proportion of numbers of immature and mature Chinook in the mean total catch in mixed-maturation (MM) harvest scenarios.

We used the model to compare scenarios in which both immature and maturing individuals are harvested in marine fisheries, versus scenarios where only to mature adults are harvested in terminal fisheries just before they reach the spawning grounds. This comparison allows us to address issues related to fisheries induced evolution and associated demographic changes resulting from mixed-maturation fisheries.

To provide a clear focus on the contrasting effects of mixed-maturation and terminal fisheries, we conduct our harvest simulation on a single population. We consider the implications of these effects relative to the population structure, productivity and resilience of fall Chinook salmon. To focus on the primary mechanism of interest, we conduct deterministic equilibrium simulations of harvest, holding post-smolt density-independent mortality at size- and age-specific mean values (see Methods), and omit other complexities of mixed-stock fishery management to isolate the effects of harvest regime. The rationale for this modelling is further considered in the context of our results.

Results

Harvest scenarios evaluated

We evaluated four model harvest simulations: a terminal troll fishery (H1) and a terminal gillnet fishery (H2), both harvesting only mature individuals. We also modelled a mixed-maturation troll fishery (H3) and a mixed-maturation gillnet fishery (H4) both of which had immature and mature fish that were equally vulnerable to harvest. Each scenario was initiated with 100 years (time-steps) of no harvest, followed by 25 years of harvest, followed by a 25 year no-harvest recovery period. Each fishery scenario imposed a population level total harvest mortality rate that achieved the maximum sustainable yield (MSY) measured in total catch weight (lbs.) (see Methods, Table 3). We calculated MSY in terms of total catch weight to explicitly account for age structure effects of harvest. In contrast, expressing MSY in numbers treats all individuals as equivalent and allows the proportions of mature and immature fish in the catch to vary unless age- or size specific restrictions are imposed. Consequently, MSY (and other harvest rates) measured in numbers do not adequately account for the important distinction between the harvest of immature and mature fish in mixed-maturation fisheries (see Methods).

Mixed-maturation fisheries result in substantial harvest of immature Chinook At the end of the 25-year harvest period of our modelled scenarios, we found that 40–59% of the catch in mixed-maturation fisheries consisted of immature Chinook. In the troll scenario (H3) where immature and mature fish were equally vulnerable to harvest, immature Chinook salmon comprised 59% of the total numbers caught, and 47% of the total catch weight (Fig. 5, Table 2). In the gillnet scenario (H4) where immature and mature fish were equally vulnerable, but the mesh size disproportionately selects for larger fish, immature Chinook salmon comprised 40% of the total numbers caught and 15% of the total catch weight (Fig. 5, Table 2). Supplementary S1, Table A provides a summary of the four harvest scenario simulations for total numbers and weights, and average weights of catch and spawners. Supplementary S2, A10 provides a description of gillnet selectivity employed in the model.

Shifts in age

In terms of selective effects on demographics, mixed-maturation fisheries shifted the population toward younger ages at maturity. We found mixed-maturation harvest decreased the mean age of the spawner population by 0.46 years in the troll fishery (4.23 to 3.77) and 0.48 years in the gillnet fishery (4.23–3.75) after 25 years of harvest (Fig. 3. Panel C and D). Comparatively, the mean age of spawners escaping terminal harvest decreased by 0.07 years in the troll (4.23–4.16), but 0.57 years in the terminal gillnet (4.23–3.66) after 25 years of harvest (Fig. 3

Panel A & B, Table 4, S1 Table E). The proportions of the two oldest spawner ages (5 and 6) are reduced by more than 10% in the mixed-maturation fisheries (S1, Table B).

Mean weights of individual spawners that escaped mixed-maturation fisheries showed a similar trend, declining by 20.8% in the troll and 21.9% in the gillnet fishery from the preharvest weight (about 4 lbs.; 18.3 lbs. to 14.5 and 14.3 lbs. respectively, Fig. 1. Panel E; Fig. 2. Panel C & D). In contrast, the mean weight of spawners escaping the terminal troll declined by only 2.7% (to 17.8 lbs.), whereas those escaping the terminal gillnet fishery experienced a 27.3% decrease (to 13.3 lbs.) (Fig. 1. Panel E; Fig. 2 Panel A & B; S1 Table A). Standard errors were consistently low for all scenarios, ranging from a maximum of 0.068 for terminal harvest scenario H1 and a minimum of 0.002 for pre-terminal harvest weight.

Shifts in individual and overall catch weights

Terminal fisheries (H1, H2) produced higher total and average harvest weights over 25 years than mixed-maturation fisheries. In terms of overall catch weight, smaller catches were observed in the mixed-maturation troll and gillnet fisheries compared to their corresponding terminal fisheries. The MSY catch weight in the mixed-maturation troll fishery was 34% lower than the terminal toll (12295 lbs. and 8725 lbs. respectively; Fig. 4. Panels A & C). Similarly, MSY catch weights in mixed-maturation gillnet fishery were 40% smaller than the terminal gillnet (12,336 lbs. and 8211 lbs. respectively) (Fig. 4, Panels B &D; S1 Table A). In both gear types, terminal fishing scenarios resulted in higher mean total harvest weight and greater mean catch weight, than the corresponding mixed-maturation scenarios (Figs. 1, 4, 5).

Demographic effects within catch and spawners

Overall, mixed-maturation harvest reduced the proportion of older age classes (ages 4–6) in the catch and spawning populations relative to terminal fisheries. The age composition of both sexes shifted toward younger fish with smaller average catch weights (Fig. 1. Panel F; Fig. 3 Panel C & D). While total and mean catch weights were higher in terminal fisheries, mixed-maturation fisheries had a greater numerical catch, due to the harvest of immature fish.

In both terminal fishery scenarios, age-5 Chinook salmon dominate the total mean catch weight over the 25-year harvest period (38% and 47% of troll and gillnet catch, respectively) (Fig. 4, panel A & B, S1 Table D). Additionally, age 6 Chinook salmon comprise four times the total catch weight in the terminal fishery compared to the mixed-maturation scenarios (Fig. 4, Panels A – D; S1, Table D). Gillnet fisheries disproportionately removed older and larger individuals due to gear selectivity. Gillnet selectivity results in age-5 Chinook salmon comprising the greatest proportion of the total catch weight in the mixed-maturation scenario. In contrast, in the mixed-maturation troll scenario, age-4 fish dominate the catch, accounting for 44% (Fig. 4. Panel C; S1 Table D). Mixed-maturation fisheries also reduced the proportion of the two oldest age classes compared to terminal fishery (S1, Table C) and decreased the average weight of the spawning population (Fig. 1. Panel E; Fig. 2. Panel C & D). These changes impair the ability of the harvested population to recover toward the pre-fishery age structure compared to the terminal scenarios (S1, Table E). Importantly, over the 25-year harvest period the two terminal MSY scenarios (H1 and H2) achieve greater total and average catch weights than the mixed-maturation MSY scenarios (Fig. 1. Panels D and F; Fig. 4, Panels AB & CD; S1, Table A).

Spawner weights were largest in the terminal troll (H1). In all other cases, spawner weights during the harvest period were lower than during pre- and post-harvest periods. In addition, average spawner weights did not recover to pre-harvest levels during the post-harvest period, again with the exception of the terminal troll scenario (Fig. 1. Panel E; Fig. 2. Panel B-D, and Table 2).

With the exception of the terminal troll scenario, the mean catch age is greater than the mean spawner age (Fig. 3. Panels B-D). This effect is most pronounced in the terminal gillnet scenario. Again with the exception of the terminal troll scenario, the mean spawner age does not recover to the pre-harvest mean during the 25-year post-harvest period (Fig. 3).

Harvest impacts on egg deposition

We found mean fecundity per female was highest in the terminal troll, followed by the mixed-maturation troll and gillnet fisheries (7% and 9% lower, respectively). Harvest effects on fecundity are also reflected in the age-specific egg deposition and in the proportional contribution of female spawners of each age class (S1 Tables B and F). However, comparing total egg deposition between the mixed-maturation and terminal scenarios shows mixed-maturation fisheries produce 11% more total eggs than the terminal fishery (S1 Table F, Column 6), due the higher number of female spawners at MSY and the smaller number of mature fish that can be harvested at MSY in mixed-maturation fisheries.

When examining the change from pre-harvest to harvest, we found mixed-maturation fisheries increased reliance on younger spawners. In the mixed-maturation harvest scenarios (H3 and H4) the proportion of eggs contributed by the youngest females (ages 3 and 4) increases from 40% contribution in the pre-harvest period to 50% and 52%, respectively after harvest, making populations more reliant on younger, less fecund spawners. The terminal gillnet scenario exacerbates this trend, increasing the proportion of total egg deposition by age 3 and 4 spawners to 54% (S1, Table F). When comparing the shift from pre-harvest to terminal troll harvest, the contribution of the youngest females (ages 3 and 4), shifts by less than 1% (S1 Table F). In the troll scenarios, the lowest average fecundity is observed in the mixed-maturation fishery (H3), where the average fecundity is 200 eggs per female lower than the pre-fishery or the post-fishery averages. For the gillnet scenarios, both the terminal and the mixed-maturation fisheries (H2, H4) result in average fecundities that are 350 to 500 eggs per female lower than the pre-fishery averages (S1, Table G).

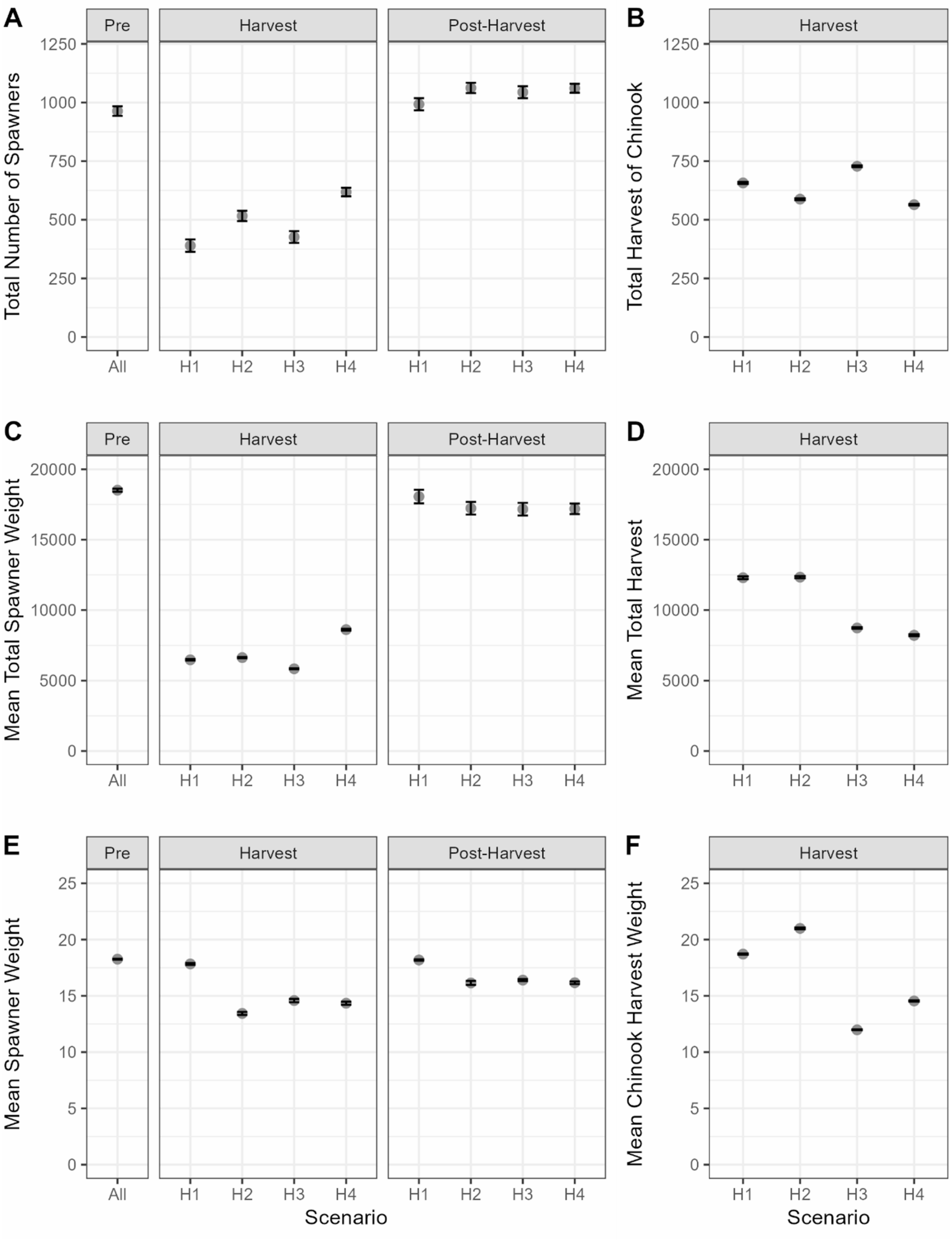

Fig. 1. Mean and standard errors of the number of total spawners (**A**), catch (**B**) and total catch weights (lbs., **D**), and mean catch weights (**F**), for all four scenarios in the harvest and post-harvest periods (simulation years 101 – 125 and 126 – 150, respectively). Labels: H1: Terminal troll; H2: Terminal gillnet; H3: Mixed-maturation troll; H4: Mixed-maturation gillnet.

Reduced egg deposition by older, larger females reduces mean fecundity and has implications for population structure, however, a tradeoff occurs if we consider total fecundity as a measure of productivity (mean number of eggs multiplied by the spawner abundance). Using this metric as a measure of population productivity, both gillnet fisheries outperform the terminal troll scenarios (S1, Table F). This effect is reversed or moderated when

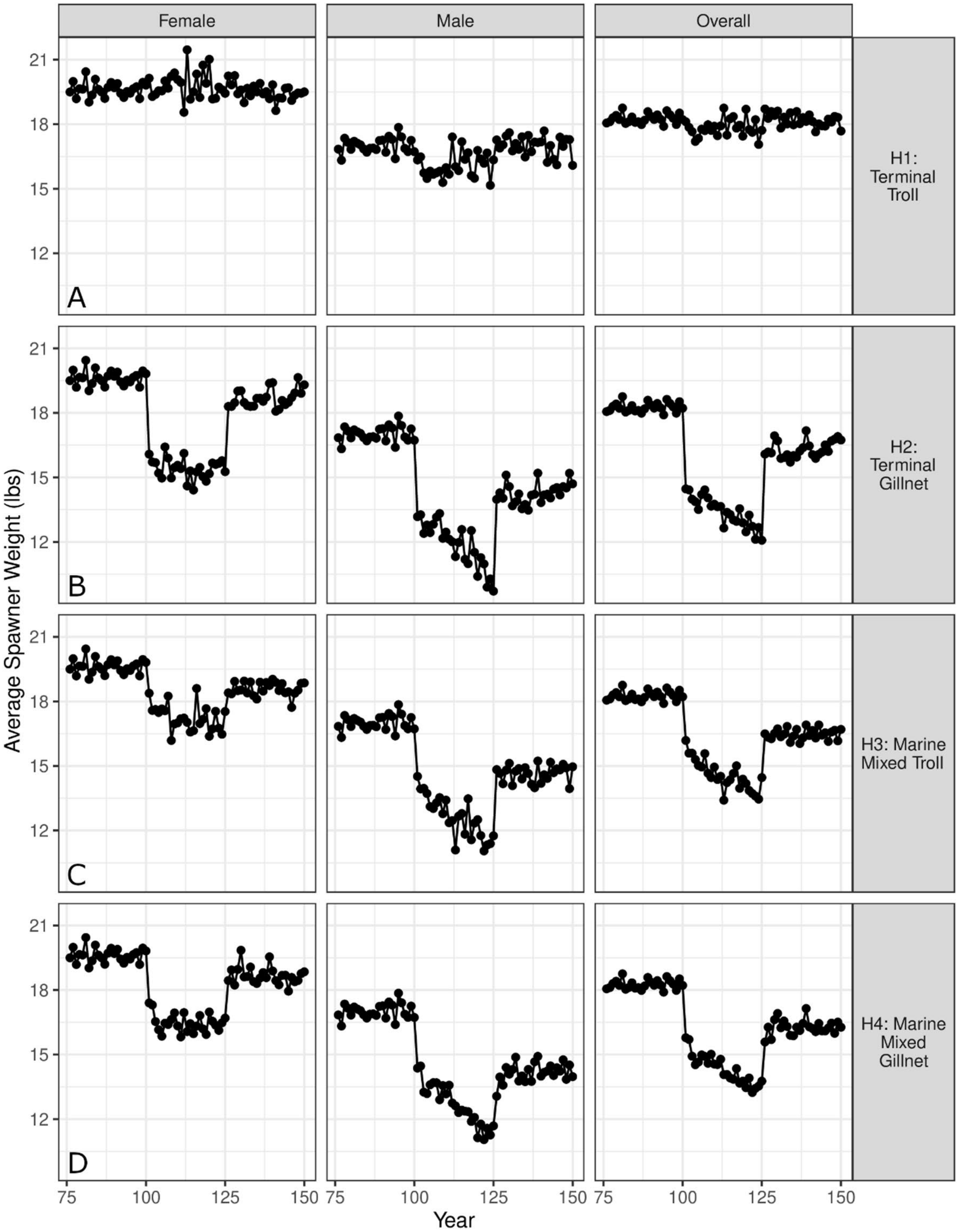

Fig. 2. Average spawner weights (lbs.) for each harvest scenario. Pre harvest stabilization period are years 76-100, harvest simulation years are 101–125, and post-harvest years are 126–150. Labels: H1: Terminal troll; H2: Terminal gillnet; H3: Mixed-maturation troll; H4: Mixed-maturation gillnet.

mean age-specific fecundity is considered due to the troll scenario having equal or higher proportions of total egg deposition contributed by older age classes (S1, Table G).

Effects to the productivity and resilience of the population

Table 3 shows the differences in population productivity over the course of the 25-year harvest period compared to the last 25 years of the pre-harvest period as measured by the alpha parameter of the Ricker stock-recruit model (see Methods). Mean Ricker α declined under mixed-maturation fisheries relative to terminal fisheries.

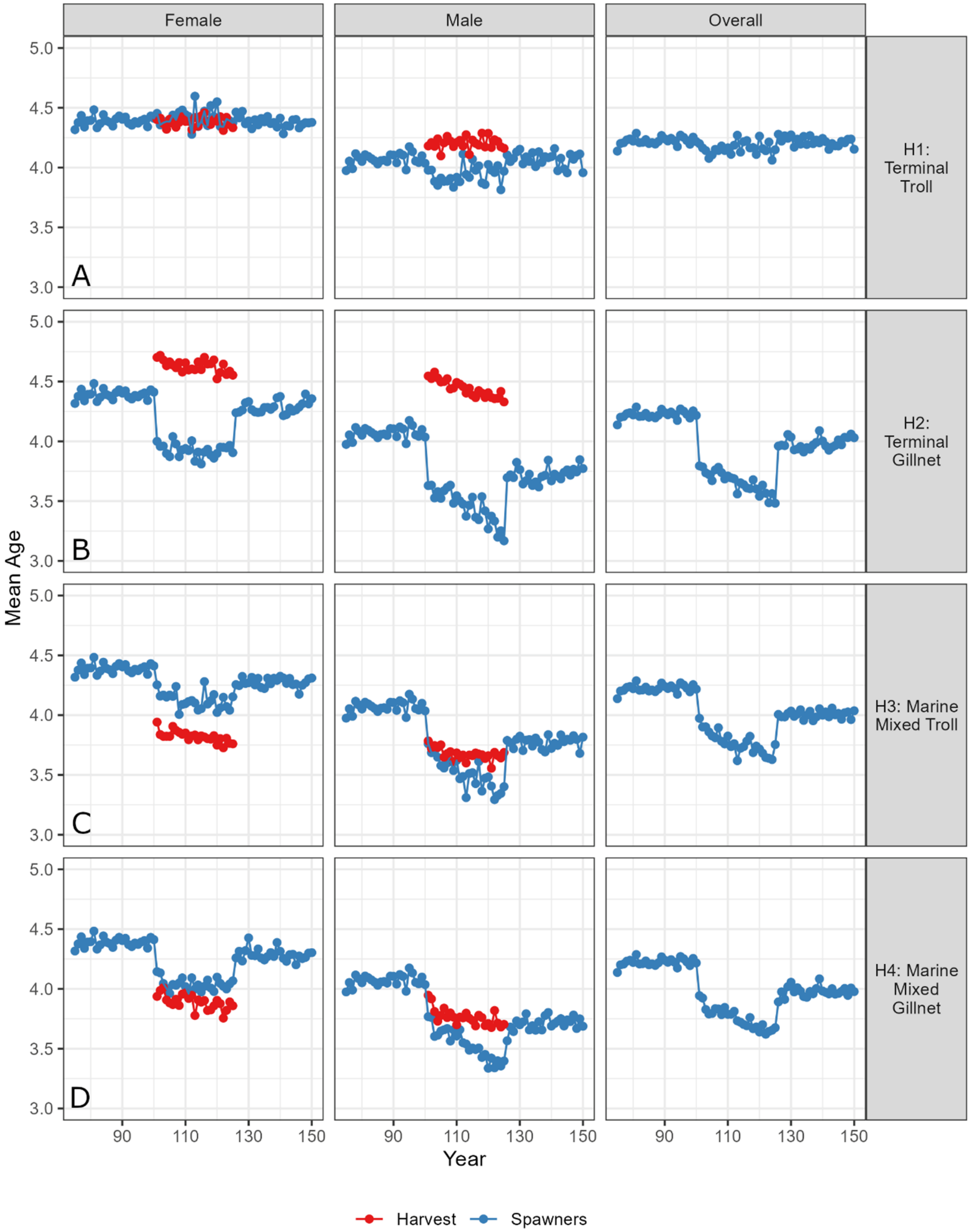

Fig. 3. Average age of spawners and harvested Chinook salmon of each sex for each harvest scenario. Pre harvest stabilization period are years 76-100, harvest simulation years are 101 – 125, and post-harvest years are 126 – 150. Labels: H1: Terminal troll; H2: Terminal gillnet; H3: Mixed-maturation troll; H4: Mixed-maturation gillnet.

The terminal troll fishery had the highest α (4.88), close to the unfished value (5.13) (Table 3). For the pre-harvest years, the estimated mean value of alpha (5.13) was only slightly lower than the analytic calculation of the mean that assumed all spawners in each age class had the same mean weight, length, and fecundity. The decline in the mean alpha in the two mixed-maturation scenarios and the terminal gillnet are one and two units lower (terminal gillnet and mixed-maturation, respectively) than alpha at the end of the pre-harvest equilibrium.

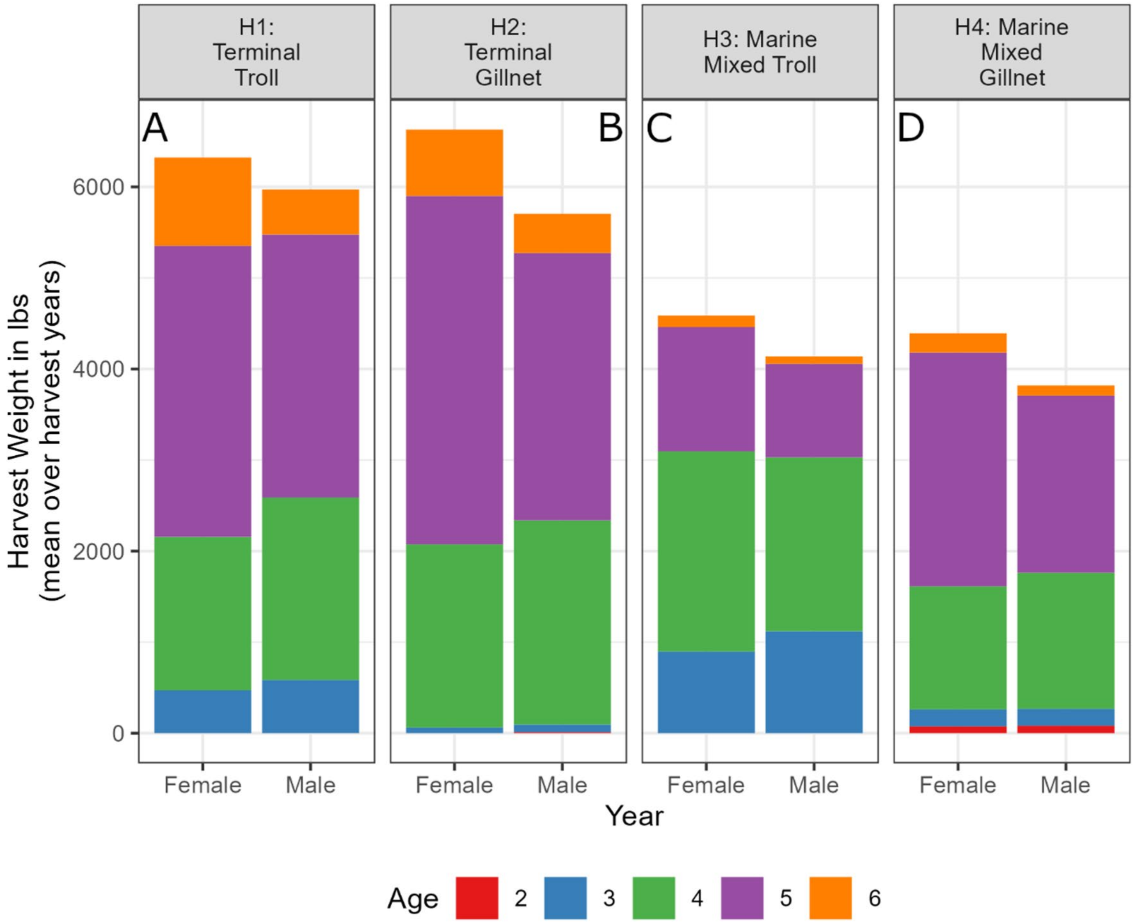

Fig. 4. Total weight of harvest by age class and sex averaged for the 25-year harvest period in all four harvest scenarios.

Following Capdevila et al.[43] we define population (demographic) resilience as a combination of resistance to change following a disturbance (harvest) and the ability to recover afterward. Resistance is measured by the extent to which the population retains its pre-harvest structure, while recovery is assessed by the time required to return to its pre-harvest state or the extent of its movement toward the unfished equilibrium within a given period (25 years in our case).

Our results show that only the terminal troll scenario shows resistance to change in population structure during the harvest period, and a post-harvest return to the unfished population structure by year 25 (simulation year 150). In the terminal troll, both mean spawner weight and age exhibit little change from the last 25 years of the pre-harvest period to the end of the post-harvest period, remaining at 18.2 pounds and 4.23 years for both sexes combined (Fig. 2 Panel A; Fig. 3 Panel A; S1 Tables A and E). The next closest scenario to the terminal troll in terms of resistance to population structure change, is the terminal gillnet. While the terminal gillnet demonstrates a gradual recovery toward the pre-harvest population structure, it remains incomplete after the post-recovery period. The population attains an average spawner weight of 16.3 lbs. with an approximate age of 4.0 years (S1 Tables A and E, respectively).

In terms of the age composition of the spawning population after the 25-year post-harvest period, the two mixed-maturation fisheries display greater recovery than the terminal gillnet fishery. The proportion of spawners of ages 5 and 6 combined averaged over the 25-year post-harvest period of the terminal troll scenario is 0.502 compared to 5.06 for the last 25 years of the pre-harvest period. This compares with 0.347 for proportion of ages 5 and 6 in the terminal gillnet scenario, 0.468 for the mixed-maturation troll scenario, and 0.476 for the mixed-maturation gillnet scenario.

Discussion

We compared the effects of fisheries targeting only mature fish with those capturing both mature and immature Chinook salmon on population age structure. We found that mixed-maturation fisheries, in which mature and immature individuals are equally vulnerable to harvest, impose directional selective pressures that shift populations toward faster growth and earlier maturation. These changes result in a truncation of size and age structure, with fewer older, larger individuals contributing to the spawning population. At the demographic level, these shifts arise from changes in the relative fitness of genotypes associated with maturation age and size.

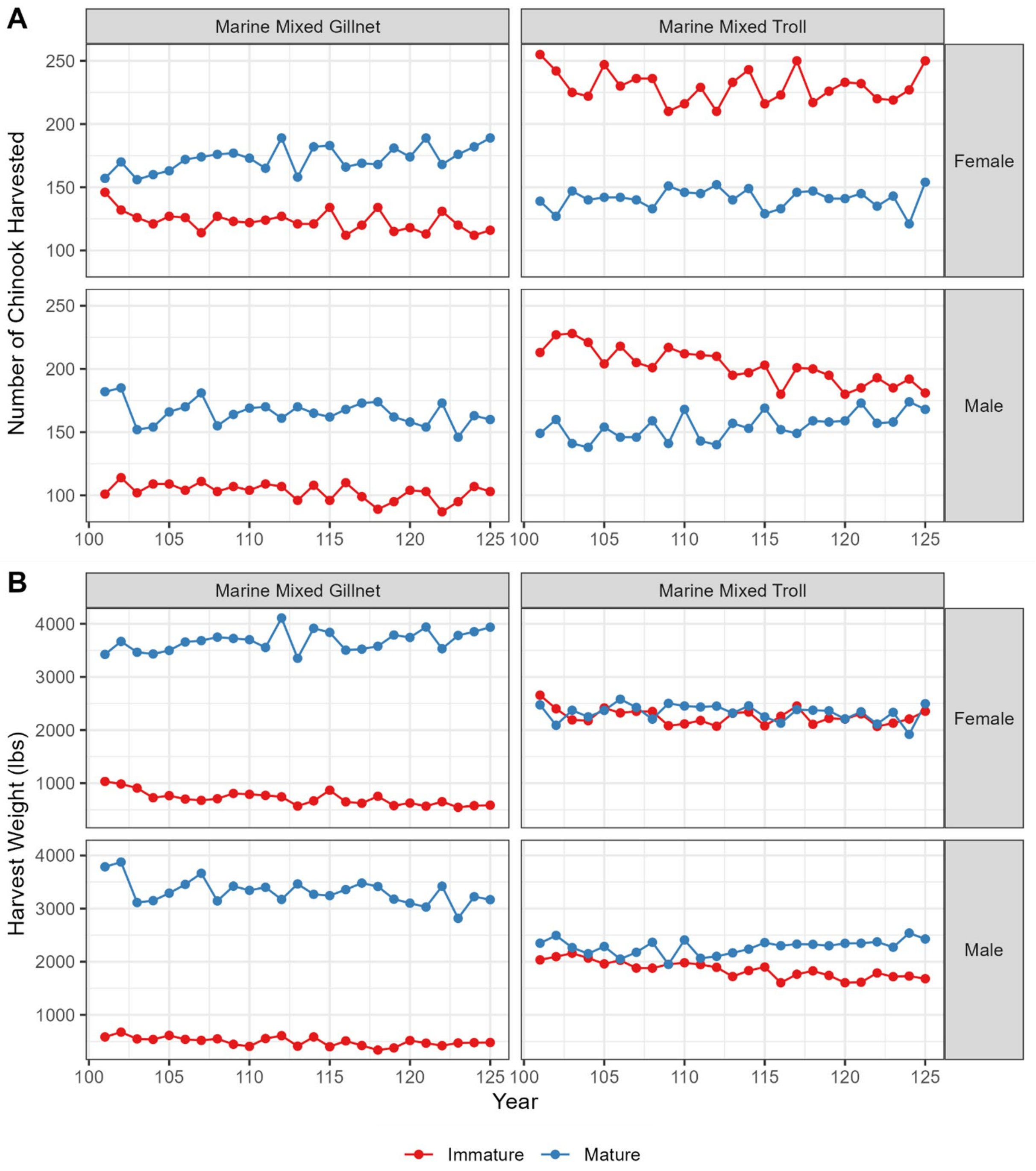

Fig. 5. Catch numbers and weights of immature and mature Chinook salmon of each sex in the two mixed-maturation fishery scenarios.

Importantly, this form of fisheries-induced selection operates through changes in gene and genotype frequencies rather than through alterations to the underlying genetic architecture of maturation. As a result, such changes can occur over relatively short timescales. This pattern is consistent with multi-decadal studies of Atlantic salmon, which show shifts in allele frequencies at loci associated with age at maturity without corresponding changes in genetic architecture[20,35,44,45]. By incorporating bet-hedging in maturation strategies (see Methods), our model retains the full range of growth rates and maturation phenotypes observed in the pre-harvest population, with shifts in allele frequency remaining reversible under realistic exploitation rates.

Relative to terminal fisheries, mixed-maturation fisheries reduce mean catch weight at MSY and shift both catch and spawner age structure toward younger ages through the harvest of immature individuals. This truncation of age structure decreases mean spawner weight and alters age composition in ways that are associated with reduced yield. Consequently, recovery toward pre-harvest age structure is slower, and long-term productivity and harvest performance are diminished compared to terminal harvest strategies.

Harvest scenario	Alpha (central 95% posterior interval)
20 Yr. Pre-Harvest (Spawner Years 76 to 95)	5.13 (3.71 to 6.76)
20 Yr. Term Troll (Spawner Years 101 to 120)	4.88 (3.92 to 5.76)
20 Yr. Term GN (Spawner Years 101 to 120)	4.04 (3.42 to 4.90)
20 Yr. MM Troll (Spawner Years 101 to 120)	3.01 (2.48 to 3.77)
20 Yr. MM GN (Spawner Years 101 to 125)	3.13 (2.71 to 3.66)

Table 3. Ricker alpha values from stock-recruit analyses of years 76 to 95 of the unfished period and years 101 to 120 of each of the four harvest periods, where MM is mixed-maturation, Term is terminal, and GN and gillnet.

Demographic effects to catch and spawners from different gear types

Differences between gear types reflect the underlying selectivity of the fisheries. Gillnet fisheries, particularly those using ~ 8-inch mesh, selectively remove larger, older individuals, whereas troll fisheries tend to harvest Chinook more in proportion to their availability in the population. This size- and age-selective removal contributes to differences in the resulting spawner age structure, with gillnet fisheries disproportionately reducing older age classes and thereby amplifying age-structure truncation relative to troll fisheries.

Productivity and resilience

Differences between harvest regimes have important implications for the maintenance of age structure diversity, particularly the contribution of older, larger female Chinook. The loss or reduced representation of these age classes can influence fecundity and reproductive potential, with consequences for both productivity and population resilience.

From a resilience perspective, harvest strategies that retain a broader age structure are expected to enhance both resistance to disturbance and the rate of recovery, consistent with theory linking demographic diversity to stability in variable environments. In this context, a terminal fishery (particularly not those selecting for larger sizes) is more likely to maintain population structure with a broader age distribution than a mixed-maturation fishery, which reduces the proportion of older age classes.

Although all modelled harvest strategies ultimately allow recovery toward pre-harvest conditions, but the differences in recovery trajectories highlight the importance of harvest strategy and gear selectivity in shaping the timescale over which resilience is observed. These results also support the notion that our modelled population structure is generally resilient under MSY-based harvest scenarios, but maintaining age structure diversity plays a role in determining the timelines of recovery.

In our modelled scenarios (for convenience and lack of data), we assumed that all eggs were of equal size with equal probability of surviving to emergence, and emergent parr were of the same size with the same density dependent survival to the smolt stage (see Methods). In reality, larger female Chinook salmon deposit larger and better provisioned eggs that positively correlate with fitness traits important for survival such as size, growth rate, swimming ability, and behavior[47–50]. In this way, the comparisons between mixed-maturation and the terminal fishery scenarios may exaggerate the benefits of mixed-maturation fisheries on population productivity as measured by total egg deposition. As such, total egg deposition may not be an ideal measure of population productivity of Chinook because it ignores the influence of female age on the quality of total egg deposition.

The alpha parameter of the Stock Recruitment relationship is a key measure of population productivity in fisheries science, with higher and lower alpha values reflecting higher and lower reproductive capacity (recruits per spawner), respectively. Declines in the mean Ricker alpha value during the harvest period indicate reduced intrinsic productivity under mixed-maturation relative to terminal fishery scenarios. In contrast, the terminal troll maintained an alpha value close to the unfished conditions (mean $\alpha = 4.88$ versus 5.13 pre-harvest), suggesting a greater capacity to preserve reproductive potential under MSY based harvest.

The shifts in fecundity and age structure found in our results have important implications for population resilience. We considered resilience as the resistance of populations to change following a disturbance, and their subsequent recovery[43]. Capdevila et al.[43] use measurements of short-term population growth following disturbances, and any of its longer-term consequences, to quantify demographic resilience (for relevant discussion also see[51–53]. While we do not develop metrics to explicitly examine population resilience, it is generally acknowledged that populations with more complex demographics are more resilient to environmental and other perturbations (e.g.[54–56]. For example, harvest strategies that result in the loss of older, more fecund individuals may undermine long-term population stability and reproductive potential. Increased reliance on younger spawners may reduce the buffering capacity of populations against environmental variability, as younger fish generally produce fewer eggs that may have lower fitness and may not be able to reach or successfully spawn in upper reaches of streams with larger substrates[28]. Carvalho et al.[39] found that in fall-run Chinook salmon populations, greater age structure diversity buffered against disturbances by reducing fluctuations in population size and harvest levels. Their study concluded that maintaining age structure diversity promotes the stability of salmon populations under increasingly variable environmental conditions, more so than populations with less age structure diversity.

Intrinsic productivity is another measure of population resilience, as increased productivity under compensatory density-dependent dynamics means that populations can rebound from disturbance more quickly[57]. Other authors suggest that salmon resilience can be improved by allowing salmon to express their maximum life-history variation[58]. Healey[59] lists seven traits of resilient salmon, including phenotypic plasticity (age variation) and life-history (variation in size for example), with variability in these traits being key to increased resilience. Based on approaches to measuring resilience such as those described above, our work suggests that terminal troll fisheries, in comparison with the other types and locations of fisheries examined, may better maintain population structure with a broader age distribution.

Comparisons to other relevant Chinook salmon harvest models

To the best of our knowledge, our model is the first Chinook harvest model to explicitly simulate the inheritance of alleles at multiple loci controlling the annual growth rate and maturation size. In this way, our framework captures genetic processes that influence reproductive output under harvest. Differences in total egg deposition between harvest and non-harvest periods reflect the demographic consequences of harvest-induced changes in population structure.

Other models have explored the potential for harvest to select for changes in Chinook salmon life-history phenotypes, including two relevant simulation models of Chinook salmon harvest. We note key similarities and differences between the simulation models and our model.

Hard[16] measured quantitative genetic parameters from a breeding experiment conducted on hatchery-origin Chinook salmon and employed them in a model to estimate the selective effects of marine mixed-maturation harvest and terminal harvest of mature Chinook using similar gear types to ours. Their two gear types were longline (identical to our troll) that harvested fish greater than 500 mm and a gillnet that harvested fish between 500 and 930 mm. Using estimates of the genetic variance/covariance (G) matrix, selection differentials, breeding values, and heritabilities, the model quantified phenotypic and genetic responses to harvesting under different scenarios.

Unlike our individual-based framework, Hard's model did not simulate individual mating, inheritance of quantitative alleles, or full life cycle processes from egg deposition through to maturation, harvest, and spawning. Nonetheless, it demonstrated that both gear types across harvest scenarios produced changes in the mean and distributions of spawning lengths and age, with a shift toward younger and smaller individuals relative to the unfished conditions.

Consistent with our results, Eldridge et al.[36] reported that harvest can alter both the number and age composition of harvested fish and spawners, with reductions relative to the unfished populations. This pattern is expected under positive genetic correlations between growth and maturation traits (i.e. faster growth resulting in earlier age at maturity).

However, in contrast to our findings, reduction in mean age and size were associated only with "high-seas" fisheries (comparable to our marine mixed-maturation scenario). Their terminal longline fishery did not affect mean length (size) and their terminal gill net scenario -which was parameterized to harvest with a slot limit between 500 and 930 mm, resulted in an increased mean length of mature fish. This was likely due to the escape of fish exceeding the upper size limit and contributing to the spawning population.

These differences may also reflect assumptions regarding harvest rates. Eldridge et al.[36] applied a fixed harvest rate of 50%, whereas we modeled specific harvest rates (up to 70%, Table 6) to achieve MSY measured in total catch weight.

A final distinction between the Eldridge et al.[36] model and our approach lies in the representation of age-at-maturity. In our model, age-at-maturity emerges from the interaction between genetically controlled growth rate, maturation size and annual survival rates, rather than through fixed age-length relationships This allows age-at-maturity to respond dynamically to harvest induced effects on growth and size, providing a more mechanistic representation of life history variation.

Bromaghin et al.[46] developed an individual-based simulation model to explore the effects of historical gillnet fisheries in Alaska's Yukon River. These salmon have experienced a long-term decline in size and age since at least the 1960s. Consistent with the genetic approaches of Hard[16] and Eldridge et al.[36] their model incorporated heritable variation in growth and age at maturity. However genetic structure was represented implicitly i.e. it tracked effects at the population, not individual, level. Simulations of gillnet harvest showed consistent declines in length-at-age and average age at maturity in both the catch and the spawning population, reflecting strong size selective pressure imposed by large mesh gillnets. Model simulations of recovery indicated that reversing these changes required substantial reduction in harvest rates, and in many cases, elevated escapements simulated over multiple years.

Bromaghin et al. focused on terminal, in river gillnet fisheries that targeted matured fish. Their results are consistent with our terminal gillnet scenario, demonstrating that size selective harvest on its own can drive shifts toward younger smaller spawners. Across these studies and our model, the changes occur without alteration to the underlying genetic architecture of maturation, and instead, reflect shifts in gene and genotype frequencies. As also shown by Miettinen et al. (2024[45], these effects are reversible when the harvest pressures were sufficiently reduced, though recovery times varied based on management interventions.

Implications of defining MSY in terms of catch weight versus numbers in mixed-maturation fisheries

Contrary to conventional approaches, we modeled maximum sustainable yield (MSY) in terms of catch weight rather than numbers of fish. Our rational for doing so is because numerical MSY implicitly treats all caught fish as equivalents (in terms of their contribution to the spawning population) and assumes that they are distributed across age and size classes in the same proportion. This assumption holds up much better in fisheries where catch aligns with the population structure on the spawning grounds, like a terminal troll on mature fish (Table 6), but it breaks down in fisheries that harvest unevenly across maturity states or size classes (i.e. marine mixed-maturation).

In mixed-maturation fisheries, the fish available to be caught include those that don't contribute to the spawning population. As a result, applying a numerical MSY derived from the unfished equilibrium can lead to overestimation of sustainable harvest rates. This is because the denominator (total numbers vulnerable to the fishery) includes immature fish, and impacts to population structure are later realized in the spawning population that drives recruitment (fewer future spawners, younger age structure, lower productivity). This mismatch between the exploited population and the population that determines recruitment complicates the interpretation of numerical harvest rates (Table 6).

In conclusion, these differences highlight that MSY defined in terms of numbers does not adequately capture the demographic consequences of harvest in age structured populations with varying maturities. In contrast, defining MSY in terms of catch weight better reflects changes in age and size structure, and thus provides a more appropriate basis for evaluating sustainable harvest in fisheries that alter maturation patterns and spawner composition.

Conclusion

Our individual-based Chinook salmon model evaluates how different harvest regimes and gear types are likely to influence the demographic structure and productivity of Pacific coast fall Chinook salmon populations. Specifically, we compared terminal and mixed-maturation fisheries and their effects on life-history traits, productivity, and returns to harvesters (measured by catch number and catch weight). By elucidating the trade-offs in these harvest regimes, our model provides insights into their relative benefits to fishers and population resilience.

Overall, terminal fisheries provide greater harvest benefits than mixed-maturation fisheries, recognizing these benefits disproportionately favour river-based rather than marine-based, fishers. Additionally, harvest strategies that truncate age structure and reduce productivity can slow recovery of at-risk Chinook populations and/or limit future harvest opportunities. In this regard, we found that terminal fisheries are more likely to maintain population structure with a broader age distribution and a higher mean spawner weight, associated with productivity and resilience. These results are relevant to Canada's Wild Salmon Policy and should be of value to those concerned with the long-term sustainability of wild Chinook salmon populations, harvest opportunities, and the rebuilding of depleted and at-risk populations.

Methods

Our individual-based model simulates demographic and selected genetic processes of each individual in the population and is thus capable of considering individual variation in demographic and relevant genetic characteristics within size- and/or age-classes. As such, the model is stochastic at the individual level, but deterministic at the population level (i.e., no environmental variation in age-specific post-smolt survival). Our model was derived in large part from the Individual Based Salmon Ecological Genetic Model of Castellani et al.[42] and parameterized to reflect the life-history of fall Chinook salmon. Juvenile fall Chinook salmon become smolts as sub-yearlings, migrating seaward within several weeks or months of emerging from the spawning gravel[27,28,60]. We also incorporated model approaches developed by Bromaghin et al.[46] to evaluate fisheries selectivity of an in-river gillnet fishery for Yukon River Chinook salmon. The model was written in C++, and figures were generated using R (R Core Team 2024).

We model a single Chinook population with a fall life-history and a size- and age structure likely to be representative of a late 19th and early 20th century population prior to the development of intensive coastal mixed-stock and mixed-maturation fisheries. As such, the model population contains a higher proportion of older individuals (ages 5 and 6) than the majority of fall Chinook salmon populations in the latter half of the 20th century and the first two decades of the 21st century. The model population is based on a combination of data for fall Chinook salmon from the Fraser River, BC in the mid-1960s[60] and the Hanford Reach Upriver Bright population in the middle Columbia River between 1920 and 1990[61]. Similar to Bromaghin et al.[46], our model population is best viewed as representing a generic historical fall Chinook salmon population with concomitant higher than average survival rates compared to recent survival rates experienced by most extant Chinook populations.

Model limitations and simplifying assumptions

We applied two simplifying assumptions to focus attention on the potential effects of mixed-maturation fisheries on the age and size structure of the population. First, our model simulations are deterministic in that they do not incorporate environmental variation in the density-independent survival of post-smolt stages. We focus on the effects of harvest under an assumed mean marine environment. Variation in marine survival that alters the mean stage-to-stage survival of post-smolt age classes affects the numbers that recruit to fisheries, not their relative size at a given age. Consequently, immature Chinook will always be smaller than if allowed to grow to maturity prior to harvest in terminal fisheries. Stochastic simulations incorporating post-smolt environmental variation will not be more informative about the primary effects of mixed-maturation versus terminal fisheries on population structure. Our deterministic model, which effectively applies an equilibrium analysis, is sufficient to delineate the difference between the two fishery regimes.

Although our model of population dynamics is deterministic, stochasticity is incorporated for several life history traits (mating, fecundity, egg to fry survival, daily growth rate, length at maturity, harvest vulnerability of length classes). Random variations occur at each annual time step of a model simulation and produce small variations in year-to-year population numbers. These variations account for the fact that our pre-harvest population attains a stochastic equilibrium rather than a constant population size. Supplement File S2, A6 lists the life-history parameters that include year-to-year random variation. Supplement File S3 provides a detailed description of the equilibrium abundance.

Second, we model harvest in both mixed-maturation and terminal fishery scenarios as occurring immediately prior to spawning. While this does not represent the timing of most mixed-maturation fisheries, it enables us to focus on the maximum size that immature Chinook attain at the end of each model year (which starts and ends with spawning). Modeling mixed-maturation harvest that occurs several months before spawning results in higher catches of individuals smaller in size-at-age than at spawning. This occurs because, although the fish avoid the natural mortality that would happen between the harvest period and entry to terminal areas, they also forgo the additional growth that would occur during that period. While this natural mortality could affect the numeric performance of terminal fisheries (particularly if freshwater migration is included[62,63], both immature and mature fish harvested earlier will be smaller than if harvested close to the time of spawning.

Conversely, slightly more immature fish in older age classes would be harvested in earlier fisheries than just prior to spawning, because immature fish in the younger age classes would be less vulnerable than immediately prior to spawning time. This would likely reduce the numbers and proportions of older mature fish over time compared to mixed-maturation harvest conducted closer to spawning. While the details of more realistic harvest timing will be of interest in a particular real case, it will not affect our basic contrast between mixed-maturation and terminal fisheries.

Model population structure

The model population consists of the following stages: eggs, parr (post-emergent fry), smolts, and post-smolts of ages 1 to 6 (Supplementary File S2, Figure A; A1, Table A). Males and females are modeled separately. Males mature between the ages of 2 (ocean age 1) and 6 (ocean age 5); females between the ages of 3 (ocean age 2) and 6 (ocean age 5). Spawning is modeled as occurring on November 1 of each model year, and fry (called "parr") are modeled as emerging from the gravel and completing yolk absorption on May 1 of the following calendar year. All parr are assumed to have a common size (weight and fork length) at the time of emergence, S2, Figure A; A1, Table A. Figure 6 shows the distribution of fork lengths at each maturation age.

Genetics control the probability of maturing at an adult size within length intervals reflective of the growth trajectories of the majority of males and females at each possible age of maturity. Figure 6 shows the distribution of fork lengths at each maturation age. S2, Table A, column 7 lists the mean fork lengths (mm) of all ages and life-stages. Size at maturity is greater than 350 mm fork length (FL) for males and greater than 520 mm for females. Genetic control is parameterized following the approach of Castellani et al.[42] and Piou[64]. The general features are described in the **Genetics** section below. Additional details are given in S2. Sections A2 to A4.

Both growth and survival are modeled from the parr stage forward. Ricker-type density dependence applies to survival of newly emerged parr from May 1 to smolt at July 1 (60 days) at which time smolts migrate to marine waters (See **Parr-to-smolt growth and survival** below).

Growth and density-independent survival of smolts is calculated to November 1 of the migration year (123 days) at which time smolts are referred to as "age 1", the age they will attain if they survive to their next birthday on May 1 of the following year. Growth and survival from the smolt stage forward is modeled using the joint growth-and-mortality model of McGurk[65]. Parr are assumed to grow to the smolt stage in accordance with the growth rate component of the McGurk model, but survival to the smolt stage is subject to the (size-independent) Ricker density-dependent equation. From age-1 forward growth, survival, potential harvest and maturation occur at annual time steps. Harvest in both marine and terminal fisheries occurs immediately prior to adult spawning. We parameterized the parr-to-smolt Ricker equation so that in conjunction with the egg-to-parr survival rate and the age- and stage-specific density independent survival rates of the McGurk model, the unfished adult population has a Ricker spawner recruit relationship with an alpha value of 5.24, a beta value of 604 (number of spawners that produce the maximum average recruitment, Rmax) (S2, A5 Table A), and a deterministic equilibrium adult population size of 1000. (A5, Table A; S3, Table A). The model life-stages and related equations, parameters and values are shown in S2, A1 Tables A, B, and C.

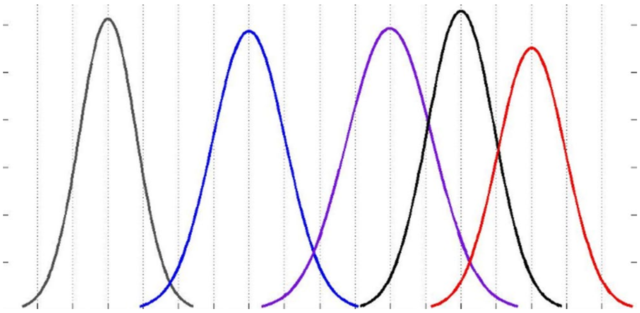

Fig. 6. Maturation lengths in mm at ages 2 to 6 from 10000 simulated random values drawn from each of the five possible bivariate-normal distributions of daily growth rates and maturation lengths, colored age groups L2 to L6 from left to right.

Genetics

We follow Castellani et al. in employing an additive quantitative genetics model for the inheritance of size at maturity. The daily growth rate in weight and the weight at maturity of each offspring are controlled by a single set of 20 biallelic loci. Each fertilized egg inherits a maternal and a paternal allele having a value of 0 or 1 at each locus.

The genotypic value of each locus is the average value of the two alleles contributed by each parent. The "allelic value" of each locus is then determined by multiplying the genotypic value (0, 0.5, or 1) by a locus-specific weight. The weights decline exponentially from a maximum value at locus 1 to a minimum at locus 20 such that there are a small number of genes (loci) which have a relatively large effect on daily growth and size-at-maturity, and the remaining loci have exponentially smaller influence. See S2, A2, Table A and Figure B for an illustration.

The sum of the 20 weighted loci constitutes the total genetic effect or breeding value of an individual, which then determines the daily growth rate and maturation size of each offspring as described below. Following[42], we name this total genetic effect sPhi (Sφ), where the value of Sφ ranges from a minimum of 0 (when all 20 loci are homozygous for the "0" allele) to a maximum of 1 (when all 20 loci are homozygous for the "1" allele).

Depending on the age of each female spawner, each Sφ value within a specified range (e.g., >0.2 and $<=0.4$) then determines the probability of an individual maturing at one of three of the five possible weight and length intervals (L2 to L6) by virtue of inheriting a daily growth rate (GR) in weight (g/g body weight) and a target weight at maturity (Wmat). Random variation in the actual daily growth rate and maturation weight of each individual is incorporated by drawing from a bivariate normal distribution with mean growth rate (GRx) and standard deviation (GRxsd), a mean maturation weight (Wxmat) and standard deviation (Wxmatsd), and a fixed correlation coefficient (rho) between GRx and Wxmat. As the target mean maturation weights of the model population were determined from target fork lengths (Lmat) according to the allometric equation $W = aL^g$ (S2, A1, Eq. 1.1), maturation weight is then converted to maturation length (Lxmat) via the inverse of the allometric weight-length equation (S2, A1, Eq. 1.2).

The maturation length (Lxmat) for each maturation age x is equal to the maturation length that an individual with mean growth rate (GRx) would attain at age x, where $x = 2$ to 6 for males and 3 to 6 for females. Thus, we model the genetic determination of the mean growth rate and maturation weight values assigned to offspring as canalized. This constitutes a form of "diversification bet-hedging" against unpredictable environmental variability (including harvest mortality) that can fundamentally affect the fitness of different maturation ages[66–71].

After mating and spawning occur, parr emerge and undergo density-dependent survival to the smolt stage. Sex is then assigned randomly to each smolt based on each individual's total allelic value with an equal probability of being male or female as described above and in S2, A3.

We also calculated several other quantities relevant to quantitative genetic models, including heritabilities, correlations between daily growth rates (GR) and maturation weight and length (Lmat) within and between age classes, and female age-specific reproductive values. These may be found in Supplement File S2, sections A7, A8, and A9, respectively.

Spawning and mating

The mean fecundity of a female is determined by its fork length[38] based on the Pearson equation used by Bromaghin et al.[46]. The number of eggs is randomly drawn from a normal distribution with mean fecundity and a standard deviation chosen to achieve an appropriate random variation in fecundity at each female age.

Mating is modeled as size-selective following the approach of[46]. Each female spawner is chosen at random, then a male is chosen at random. Whether or not the male "proposes" to the female is determined based on the relative (fork) lengths of each individual. If the female "accepts" the male's proposal mating occurs and each of the females' eggs receives one allele from each parent at each of the 20 loci that determine the offspring's probability of maturing within a specific length-interval. Once mating occurs, the female is removed from the class of potential mates and placed in the spawner population. Males remain in the candidate pool and may mate with one or more other females. The equations and parameter values for fecundity and mate choice are described in S2, Section A4 with parameter values listed in S2, A4 Tables A and B.

Egg development and parr emergence

All fertilized eggs are assumed to be the same size and survive to become parr on May 1 according to a random binomial survival probability (S2, A4, Table C and Eq. [4.3]). Surviving parr are assigned a common fork length of 37 mm and weight of 0.3545 g (details in S2, A1, Table B). A 37 mm fork length was chosen based on literature values for fall Chinook salmon[24], page 336]); the weight is derived by applying the allometric length-weight equation (aL^g), where $a = 0.00000373$ and $g = 3.18$ (S2, A1).

Parr-to-smolt growth and survival

Parr survive to become smolts on July 1 according to a Ricker density-dependent function and grow according to the growth component of the McGurk equation, as described in S2, A5. Parameter values are given in S2, A5, Table B. The Ricker model equation for the parr-to-smolt transition is.

$$\mathrm{ps}\ \ (\mathrm{parr\ survival})\ \ =\ \alpha_{\mathrm{parr}} *\ \ (-\mathrm{n}_{\mathrm{parr}}/\beta_{\mathrm{parr}}) \tag{1}$$

where α_{parr} is the parr-to-smolt productivity parameter, β_{parr} is the parr carrying capacity parameter, and n_{parr} is the total number of parr on May 1. The total number of parr surviving to the smolt stage (nsm) is thus

$$\mathrm{nsm}\ (\mathrm{number\ of\ smolts})\ \ =\ \alpha_{\mathrm{parr}} *\ \mathrm{n}_{\mathrm{parr}} *\ \ (-\mathrm{n}_{\mathrm{parr}}/\beta_{\mathrm{parr}}) \tag{2}$$

Length age	Sm-A1	A1-A2	A2-A3	A3-A4	A4-A5	A5-A6
L2	0.34	0.31	NA	NA	NA	NA
L3	0.34	0.31	0.59	NA	NA	NA
L4	0.35	0.31	0.59	0.74	NA	NA
L5	0.35	0.31	0.59	0.71	0.78	NA
L6	0.38	0.32	0.59	0.71	0.78	0.83

Table 4. Stage-to-stage survival rates for each length/age class of Chinook salmon as estimated using McGurk[66]. The mean smolt to adult survival rate is 0.048. Smolt (Sm) and A1- A6 represent age classes 1 through 6. L2 - L6 are the age length categories.

Size	Age 2 (L2)	Age 3 (L3)	Age 4 (L4)	Age 5 (L5)	Age 6 (L6)
Fork Length, mm (inches)	450 (18)	650 (26)	850 (33.5)	950 (37.4)	1050 (41.3)
Weight, grams (lbs)	1020 (2.25)	3283 (7.24)	7712 (17.0)	10,984 (24.2)	15,094 (33.3)

Table 5. Mean age-specific lengths and weights of the fall Chinook salmon model population pre 20th century.

Smolts and sub-adults grow and experience density-independent survival based on the allometric relationships of smolt to adult survival in McGurk[65](S2, A5 with parameter values in S5 Table B). The growth coefficient is the value of the growth rate assigned on the basis of the individual's maturation genotype (S^{φ}) that determines which bivariate normal distribution of growth rate (GR) and target maturation weight (Wmat) and length (Lmat) the individual inherits (see S2, A3 Genetic assignment of instantaneous growth rate in weight (g/g/day) and maturation weight to individual offspring).

A key outcome of our modeling approach is that individuals genetically predisposed to mature at smaller sizes and younger ages have higher growth rates than individuals programmed to mature at longer lengths, greater weights and generally, older ages (see S2, A12.1, Table A for details).

The McGurk integrated growth and survival model was originally programmed to estimate the smolt-to-adult survival rates by incorporating the effects of both size and rate of growth between the smolt and mature adult stages. However, since the model is parameterized with instantaneous mortality rates it can be used for a variety of times steps. Table 4 lists the stage-specific annual survival rates for each length/age class derived from the McGurk model. The mean cohort smolt-to-adult survival rate from values shown in Table 4 is 0.048. While 4.8% is in the higher range of recent survival rates for Chinook populations coast wide (see[72–74], this rate would be representative of survival in our turn of the century population. Importantly, it allows us to identify the role of harvest in initially facilitating the younger age-at-maturity and smaller size-at-age that has been documented over many decades. For parameter values of the McGurk model see S2, A5, Tables B.

Harvest, maturation and spawning

Harvest is modeled to occur immediately prior to spawning on November 1. Harvest is modeled randomly based on a MSY exploitation rate (h_msy) that applies equally to all vulnerable individuals (that is, each vulnerable individual undergoes a Bernouilli trial). The MSY exploitation rate may be modified for each of five contiguous length intervals of mature individuals (L2-L6) and each of four contiguous length intervals of immature individuals (L2-L5). Harvest rates can then be stratified by length and maturation stage. Terminal fishery scenarios are modeled only on mature adults, with harvest vulnerabilities of immatures of all length intervals set equal to 0. Mixed-maturation fishery scenarios can explore a range of vulnerabilities of both mature and immature individuals, including minimum length thresholds and drop-off and non-retention mortalities of sublegal size matures and immatures (see S2, A10). Mature individuals that survive harvest move to the mating/spawning population at the end of each annual time-step. Unharvested immatures undergo growth and survival to the next time step (S2, Figure A).

Model initialization

The model is initialized as a colonization process by a spawning population of 508 males ages 2 to 6, and 492 females ages 3 to 6. The proportions of ages in each sex are chosen to achieve a target adult equilibrium population of approximately 1000 individuals, a sex ratio of approximately 1:1 and target age/sex proportions. At equilibrium males slightly outnumber females as a result of their having five possible ages at maturity compared to four for females. Since the model is length-/weight- and not age-based, we refer to the initial spawning population by length-intervals associated with the dominant maturation age within each interval, as shown below in Fig. 6. At initialization, these can be thought of as equal to the mean fork length in millimeters of the maturation age of each sex. Table 5 shows the age-specific mean fork length and weight of each age-at-maturity. Stage-specific weight of each maturation age from parr to mature adult are in S2, A1 Table B, and corresponding fork lengths are in S2, A1 Table C. We evaluated the time it takes to attain a stochastic equilibrium by running the model without harvest for 1000 time-steps (years) and examining the distributions of spawner sexes and ages at several 25-year intervals (approximately six generations) and at the final year of each 25-year period. We determined

Harvest scenario	Fishery	Gear type	(h MSY)	Maturity	(v)	Size category (mm)	(s)	Actual harvest rate (ha)
H1	Terminal MSY	Troll	0.65	Immature	0.0	NA	NA	0
				Mature	1.0	> 610	1.0	0.65
H2	Terminal MSY	Gillnet	0.70	Immature	0.0	NA	NA	0
				Mature	1.0	< 783 783 – 158 > 1158	0.1 1.0 0.4	0.07 0.70 0.28
H3	Mixed Maturation MSY	Troll	0.45	Immature/ Mature	1.0	< 610	0.0	0.0
						≥ 610	1.0	0.45
H4	Mixed Maturation MSY	Gillnet	0.50	Immature / Mature	1.0	< 783 783–1158 > 1158	0.1 1.0 0.4	0.05 0.50 0.20

Table 6. Four harvest scenarios, H1 through H4, with their MSY harvest rates, vulnerabilities of immature Chinook to harvest, size vulnerabilities to different gear types, and actual harvest rates. Harvest rate (h msy) is a weight based MSY specific to each fishery; v is the vulnerability of immature fish to harvest, s is the size selective vulnerability of mature and immature fish, and the harvest rate (ha) for each scenario-maturity-size-gear combination is calculated by h_msy $*v*s$.

that the model achieves its stochastic equilibrium by year 100. Supplement S3 provides the characteristics of the equilibrium abundance. Summary data for a 1000-year non-harvest simulation is provided in S4.

Modeling harvest

We ran the model for 100 years without harvest, allowing the population to achieve a stochastic equilibrium following the initial colonization. We then ran each harvest scenario for 25 years, followed by 25 years of no harvest. We chose 25 years of harvest as a reasonable length of time for harvest to impact the demographics and genotype frequencies of the population in a time frame relevant to short-term management, but short enough that fisheries-induced evolution via mutations that change the genetic architecture of maturation is unlikely (see also [36]). Similarly, we chose 25 years for the post-harvest recovery as a relevant time frame to evaluate the response of the harvested population and its ability to recover demographically and genetically. This provides a measure of resilience in the population to the impacts of harvest scenarios on the age and size structure of the population.

The model can simulate harvest with either a minimum length limit, as appropriate to a troll fishery, or with a lower and upper size limit, as may occur in a gillnet fishery due to the mesh size selectivity. To evaluate the impact of troll and gillnet harvest in terminal and mixed-maturation fisheries on Chinook salmon demographics, we examined four harvest scenarios that explore the main features of these approaches. All scenarios were run with the same seed for the random number generator and initiated with 100 years of no harvest (pre-fishery scenario) to attain the same equilibrium spawner abundance and age/sex composition prior to the start of the harvest period.

The four scenarios consist of two troll fisheries (one terminal (H1)) and one mixed-maturation (H3), and two gillnet fisheries (one terminal (H2) and one mixed-maturation (H4)). All scenarios use harvest rates that achieve MSY in the total weight of the catch.

For each scenario, the approximate MSY harvest rate (h_msy) was estimated by trial-and-error by running each 150-year simulation set to several different harvest rate values over intervals of 0.05 (e.g., 0.60, 0.65, 0.70) and choosing the value that generated the largest total weight of the catch. We measured MSY in terms of catch weight rather than catch numbers because doing so accurately represents the difference between mixed-maturation and terminal fisheries. Measuring harvest using individual fish overlooks the age and size distribution of the catch, potentially obscuring population level impacts that we are concerned with, especially when comparing mixed-maturation and terminal fisheries. Still, we acknowledge this approach may not be directly comparable to MSY yields based on numeric catch.

We evaluate harvest impacts at MSY for all four scenarios. We chose MSY because it best reflects the variability in the productivity of long-term yields when comparing different management strategies. Using MSY provides a theoretical maximum perpetual "sustainable" catch weight that reveals the impact of harvesting immature Chinook salmon in mixed-maturation compared with terminal fisheries. It also reveals the performance of terminal fisheries for achieving greater catch weight with fewer numbers of salmon than is possible in mixed-maturation fisheries.

While strict adherence to MSY harvest varies with the management framework, MSY is a foundational concept in Pacific salmon management. For example, MSY based reference points guide population status and escapement goals under Canada's Wild Salmon Policy. Under the Magnuson-Stevens Act, US fisheries are generally managed to achieve optimum yields derived from MSY or meet escapement goals that produce MSY [75].

The features of each of the four scenarios are listed in Table 6. For terminal fishery scenarios, vulnerabilities (v) of all immatures were set equal to 0, and all matures were set to 1.0. For mixed-maturation fishery scenarios, vulnerability of all matures and immatures were set equal to 1.0. Thus, our mixed-maturation harvest simulations assume that all immatures of sizes vulnerable to the fishing gear are equally likely to be captured by the fisheries as mature individuals. The actual harvest rate for each maturity and size strata is simply calculated as.

H_msy $*v*s$. Harvest of each vulnerable individual, *i*, age-2 to age-6 is calculated as.

$$\mathrm{H}i = \mathrm{Bernouilli}\,(\mathrm{h\_msy} * \mathrm{v}i * \mathrm{s}i) \tag{3}$$

Here, h_msy is the fishery-specific base harvest rate that achieves the maximum mean catch weight given the life-stage and length-specific vulnerability to the gear; v*i* is the degree of vulnerability of individual *i* to the gear; and *si* is the selectivity of the gear for individuals of age/size *i*. Further details are in S2, A10 and Table 6 below.

Measuring the effects of harvest on resilience and productivity
We characterize resilience of the population to harvest impacts as the extent to which the population recovers towards its unfished equilibrium size and age structure at the end of the 25-year post-harvest period (simulation year 150). We measure the impact of each harvest scenario on the productivity of the population by the alpha parameter of the Ricker stock-recruit equation.

$$\mathrm{R}\ \ (\text{number of adult recruits}) \ = \alpha_{\mathrm{spawners}} * \ \mathrm{n}_{\mathrm{spawners}} * \ \ (-\mathrm{n}_{\mathrm{spawners}}/\beta_{\mathrm{spawners}}) \tag{4}$$

Estimated over each of the 25-year harvest period compared to the value estimated from the final 25 years of the pre-harvest period (time steps 76 to 100). The parameters of the Ricker model were estimated for 20 cohorts from the end of the 100-year pre-harvest period (simulation years 76 to 95) and for 20 cohorts from the first 25 years of each of the four 25-year harvest periods (simulation years 101 to 120). Because age-6 recruits from the final year of each of the 20-year spawner and recruit time series would not return until the 26th year (101 or 126), we estimated the number of age-6 recruits from spawning years 95 and 120 as the average number of age-6 recruits from the three preceding years (92–94 and 117–119, respectively). This created stock-recruit time series of 20 years for the pre-harvest and harvest periods.

Additional model assumptions
We assumed that all immature Chinook salmon were as vulnerable to harvest as mature individuals of the same size, implying they rear in the same areas where matures are present and fishing occurs. While likely true for many Pacific Salmon Treaty marine Chinook salmon fisheries, there may be exceptions. Vulnerabilities of immature Chinook to the fishing gears less than 1 (see Methods), in the neighborhood of, e.g., 0.5 would moderate the effects of mixed-maturation troll and gillnet fisheries documented in our simulations. But the general effect of shifting the age-distribution of the population (both the total return and the spawning population) would still occur and likely be significant for population fitness.

Data availability

All data generated or analyzed in the current study are included in the published article and its supplementary files.

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Author contributions

Nick Gayeski conceived the modeling study.Misty MacDuffee and Andrew Rosenenberger checked and contributed life history information embodied in the modelMisty MacDuffee provided editorial review of the manuscript.Devin Swanson coded the model in C++.

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Declarations

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to N.G.