



# Resurgence of an apex marine predator and the decline in prey body size

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**In light of recent recoveries of marine mammal populations worldwide and heightened concern about their impacts on marine food webs and global fisheries, it has become increasingly important to understand the potential impacts of large marine mammal predators on prey populations and their life-history traits. In coastal waters of the northeast Pacific Ocean, marine mammals have increased in abundance over the past 40 to 50 y, including fish-eating killer whales that feed primarily on Chinook salmon. Chinook salmon, a species of high cultural and economic value, have exhibited marked declines in average size and age throughout most of their North American range. This raises the question of whether size-selective predation by marine mammals is generating these trends in life-history characteristics. Here we show that increased predation since the 1970s, but not fishery selection alone, can explain the changes in age and size structure observed for Chinook salmon populations along the west coast of North America. Simulations suggest that the decline in mean size results from the selective removal of large fish and an evolutionary shift toward faster growth and earlier maturation caused by selection. Our conclusion that intensifying predation by fish-eating killer whales contributes to the continuing decline in Chinook salmon body size points to conflicting management and conservation objectives for these two iconic species.**

age and size structure | fisheries | life-history traits | predation | evolutionary change

Large marine mammal predators can have pronounced effects on marine ecosystems, primarily because of their mobility, size, and high energy demand (1), especially at higher latitudes (2). It is well established that large predators can critically affect food web structure and function, including direct effects on prey populations and indirect trophic cascades (1, 3, 4). However, the implications of changing predation pressure for prey life-history characteristics and phenotypic traits remain poorly understood. This is surprising given mounting evidence for fishing-induced trait changes in harvested populations (5–7) and is particularly important in light of recent conservation efforts leading to recoveries of many large marine mammal populations worldwide. The recoveries have heightened concerns for the potential impacts of apex predators on global fisheries, thus creating new trade-offs for natural resource management and conservation (8, 9).

Chinook salmon (*Oncorhynchus tshawytscha*) are anadromous fish that hatch and rear in freshwater, subsequently migrate to sea to spend 1 to 5 y in the ocean, and finally return to their natal rivers to spawn once and then die (10). In the ocean, these fish often migrate thousands of kilometers and are widely distributed along the west coast of North America, the Gulf of Alaska, and farther west along the Aleutian Islands and into the Bering Sea (11, 12). Chinook salmon have exhibited marked shifts in demographic structure throughout most of the North American range over the past 4 to 5 decades (13–16). In most populations, fish now mature at younger ages, and while the size of younger fish has been stable or increasing, older fish that return to spawn after several years in the ocean are increasingly smaller. In other

words, size at age is declining for older fish but not for younger fish. As a result, the contributions of the largest and oldest fish to populations have declined since the 1970s, a trend that is remarkably consistent among populations (14) along the west coast of North America. The trend toward smaller and younger fish is a pressing concern because Chinook salmon are valuable to commercial, recreational, and subsistence fisheries, and because large fish contribute disproportionately to reproduction. Causes of the observed changes in demographic characteristics have remained elusive, although effects of harvesting, including evolutionary changes, have been hypothesized for decades (17). The widespread loss of the oldest and largest fish indicates a common driver operating at basin-wide spatial scales that has been changing through time. One potential basin-wide driver is the coast-wide recovery of marine mammal predators following successful implementation of the 1972 US Marine Mammal Protection Act.

Killer whales (*Orcinus orca*) are the ocean's ultimate apex predator and are widely distributed throughout the world's oceans. In the northeast Pacific Ocean, three ecotypes are distinguished based on their diet: fish-eating “residents,” mammal-eating “transients,” and “offshore” killer whales that eat fish and other organisms. Resident killer whales, which primarily occupy coastal waters, have nearly tripled in abundance in the northeast Pacific Ocean (18) since the early 1970s (19, 20). Their diets are dominated by salmon, especially Chinook salmon, which have the highest energy content of any salmon, and the whales selectively prey on the largest Chinook salmon (21–24). Killer whales are

## Significance

Recent recoveries of marine mammal populations worldwide have heightened concerns for their potential impacts on global fisheries. While predator-induced reductions in prey abundance have been documented, trait-mediated changes in life-history characteristics are rarely considered. Here we provide a striking example of the impact of a resurging apex marine predator on a commercially important fish species through changes in prey life-history traits. We find that widespread declines in the body size of Chinook salmon over the past 50 y can be explained by intensified predation by growing populations of resident killer whales that selectively feed on large Chinook salmon, thus revealing a potential conflict between salmon fisheries and marine mammal conservation objectives.

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estimated to currently consume over 2.5 million adult Chinook salmon each year (23). Because of declines in fisheries' harvests since the 1980s, these consumption levels by killer whales now exceed the combined annual removals of Chinook salmon by commercial, recreational, and subsistence fisheries (23).

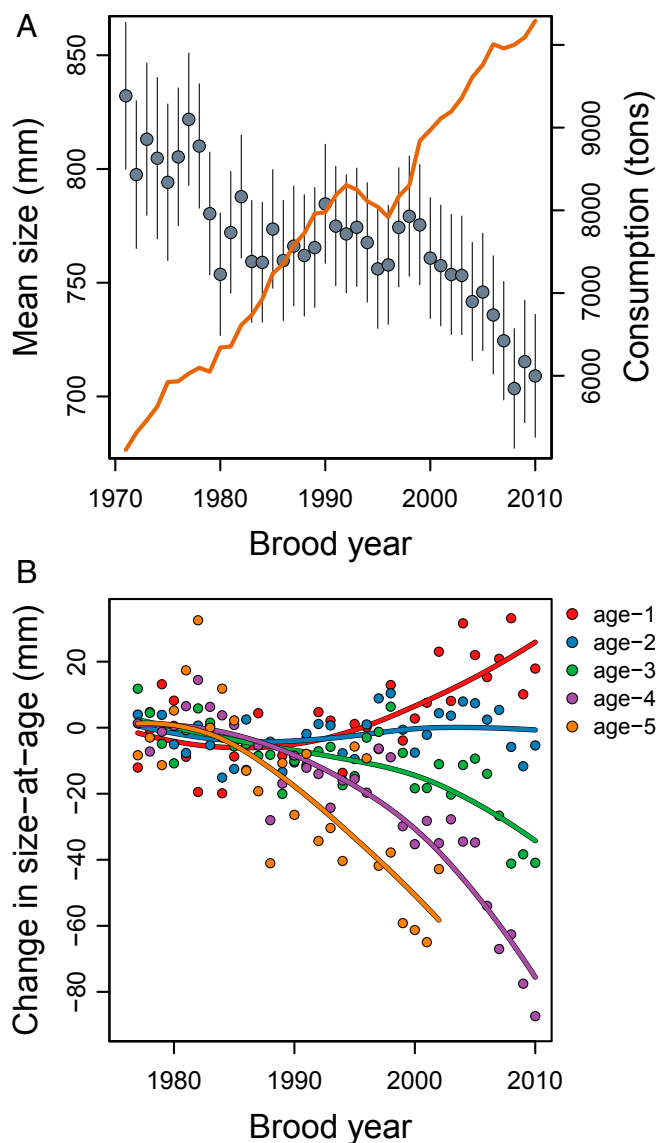
We investigated the potential role of fisheries harvest and predation by growing populations of fish-eating killer whales in causing the shift in demographic structure that has led to precipitous declines in the mean size of Chinook salmon (14). Size-selective predation and fishing both act to alter the age and size composition of prey populations via direct removals and selection for evolutionary changes in life-history traits related to growth and maturation. Over the past 50 y, changes in fishery exploitation of Chinook salmon have occurred independently of the temporal patterns of change in killer whale populations, thus allowing us to distinguish potential effects of each source of mortality on Chinook salmon demographic structure. We developed an age- and size-based population model for Chinook salmon that allowed for the evolution of individual growth trajectories and maturation (*Materials and Methods*). *SI Appendix* contains details on the timing of life-history events, model functions, and parameters (*SI Appendix*, Figs. S1 and S2 and Table S1). We evaluated patterns of predation pressure (intensity and size selectivity) that would be expected to cause changes in the body size of returning Chinook salmon similar to observed size declines given multidecadal changes in fishery harvest rates and contrast these against scenarios without predation or fishing mortality. Our model mimics historical changes in harvest rates and recent increases in predation rates due to a growing number of fish-eating killer whales (*SI Appendix*, Fig. S3). For the past 50 y, the time period during which reliable empirical data were collected, harvest declined and predation pressure increased (23, 25); we evaluate changes in size at age, age composition, and overall mean body size and compare these to observed changes for Chinook salmon along the west coast of North America (Fig. 1) (14).

## Results and Discussion

Model simulations revealed that an increasing rate of size-selective predation is necessary to generate the strong demographic shifts in size at age, age composition, and mean body size observed in North American Chinook salmon since the 1970s. Our results suggest that fish-eating killer whales are currently having a larger effect than fisheries on phenotypic traits and life-history characteristics of Chinook salmon. Further, the direct removal of large maturing fish, primarily via predation, has a larger effect on prey body size than evolutionary changes resulting from selection for faster growth and earlier maturation. Below we detail the results supporting these claims.

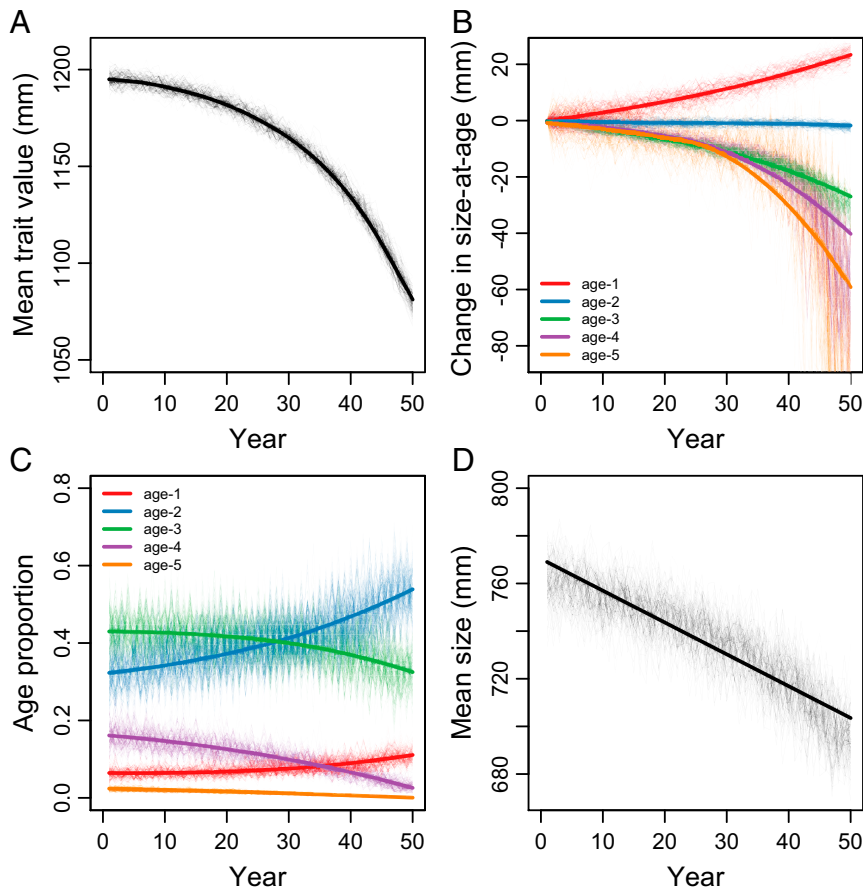
The simulated trends toward smaller and younger individuals in the escapement (Fig. 2), that is, fish that have matured and survived predation and fishing mortality, matches the broad-scale patterns observed in many North American Chinook salmon populations (14). The change in mean size is not linear over time but suggests that mean body size declined particularly rapidly during the late 1970s and again since the late 1990s brood years. The model reproduces observed changes in age composition and size at age of spawners over the past few decades, with increasing proportions and size at age of younger ages and declining proportions and size at age of older ages (Fig. 1 and *SI Appendix*, Fig. S4) (14). These shifts in age composition and size at age result in marked declines in overall mean body size, as seen in both our model simulations (Fig. 2) and the empirical data which suggest declines in mean body length of at least 70 mm (~9%) between brood years 1971 and 2009 (Fig. 1).

Both removals of large, old individuals and evolutionary changes in growth and maturation contribute to changes in mean size in the escapement. We simulated declines in mean size using



**Fig. 1.** Estimated changes in mean size, size at age, and consumption of Chinook salmon along the west coast of North America. (A) Estimated annual mean lengths of Chinook salmon (blue circles) with 90% confidence intervals (bars) and estimated biomass of Chinook salmon consumed in each year by “resident” fish-eating killer whales (orange line), as reported in ref. 23. Consumption estimates were lagged by 5 y to match the brood year of Chinook salmon (years when eggs of a certain cohort of fish were deposited in the gravel). (B) Estimated changes in mean size at age of Chinook salmon (circles; LOESS [locally estimated scatterplot smoothing] smoothers indicate temporal trends) for ocean ages 1 (red), 2 (blue), 3 (green), 4 (purple), and 5 (orange) from linear mixed effects models using the approach presented in ref. 14. Sample sizes by age group prior to 1975 were not sufficient for inclusion in these models. Estimates of changes in Chinook salmon body size were made for fish that have returned to freshwater habitats to spawn and were considered part of the escapement.

a model with and without evolution in growth and maturation traits (Fig. 3) and found declines in mean size to be largest in the evolutionary model (8 to 9% decline, default parameters) with a roughly 1.5 times stronger decline in mean size compared to a model without evolution (5 to 6% decline). This result suggests that evolutionary changes toward smaller maximum size, faster early growth, and maturation at younger ages contribute to declining average sizes, although they might be less important than



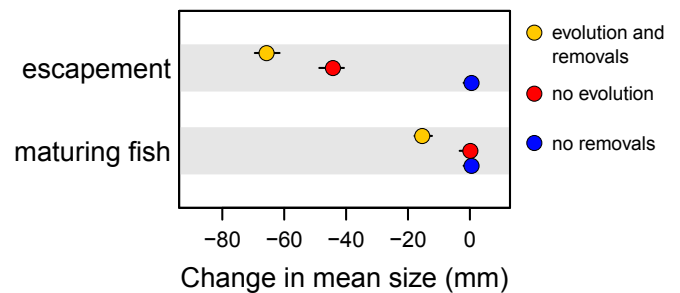
**Fig. 2.** Simulated changes in age-size structure of Chinook salmon. Shown are changes in the age and size composition of the escapement (fish that have matured and survived predation and fishing mortality) based on 100 stochastic runs using default parameter values. The panels show (A) mean trait value (average asymptotic length), (B) change in size at age (relative to initial size), (C) age proportions, and (D) overall mean size. Smooth lines indicate temporal trends using LOESS smoothers fit to median values across stochastic runs. Colors refer to ages 1 (red), 2 (blue), 3 (green), 4 (purple), and 5 (orange).

the direct effects of selective removal by fisheries and apex predators. Evolution in the model simultaneously affected the growth and maturation processes due to an assumed correlation between asymptotic size and the maturation reaction norm, whereby a negative trait correlation implies that smaller maximum sizes result in earlier maturation. This is in line with empirical evidence suggesting that age and size at maturity are heritable traits in Chinook salmon (26, 27) and that the age threshold for maturation in North American Chinook salmon has declined in recent decades (28) coincident with declines in maximum size (14).

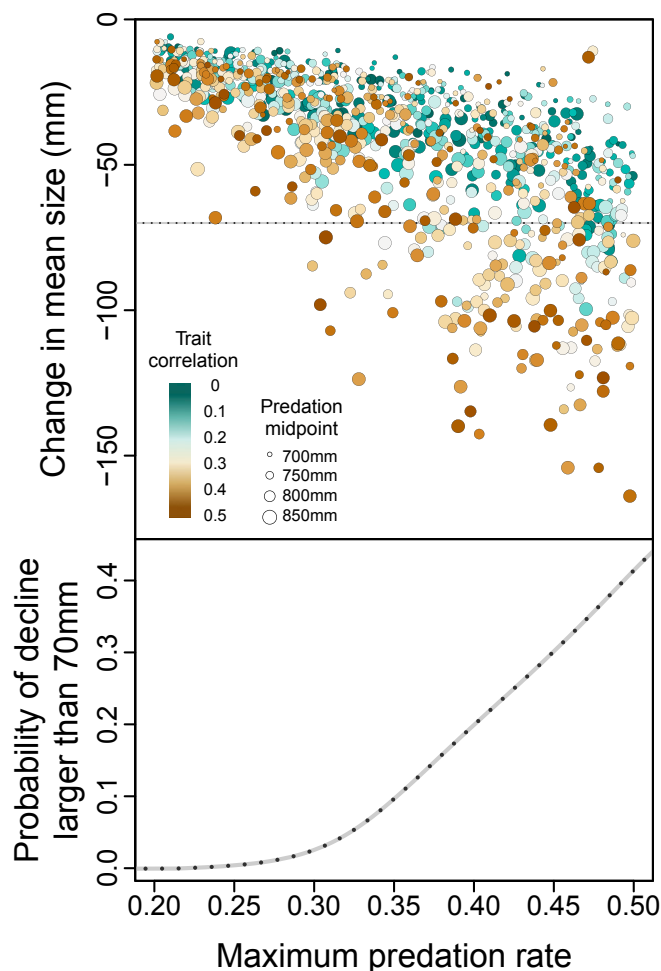
Our results suggest that adaptive evolution toward earlier maturation has contributed to life-history changes in Chinook salmon over the past few decades, as has been seen with the rapid evolution in age at maturity in other salmonids, for example Atlantic salmon (29). The pace of evolutionary change depends on the strength of selection and on heritability in size- and age-related traits. Heritability is the proportion of phenotypic variation attributable to genetic variation among individuals. In our model, it is determined by the trait variance and the variance in growth rate (*SI Appendix, Fig. S5*), which were set such that heritability was similar to values reported for size- and age-related traits in Chinook salmon (27, 30, 31). Nonevolutionary dynamics were simulated by setting the trait variance to zero, such that no trait evolution could occur, and changes in mean size of the escapement would be caused exclusively by selective removals of mature individuals.

Size-selective predation on large individuals has immediate effects on the age and size composition of returning fish and may

select for evolutionary shifts in growth-related traits. Predation mortality disproportionately affected older fish that had grown to larger body sizes and thus caused the strongest decline in size at age among the oldest fish. Size-selective predation predominantly removes larger individuals of a certain age as long as selectivity increases with body size over the range of prey sizes present in that age group. Our simulations revealed that the



**Fig. 3.** Changes in mean size of Chinook salmon when omitting evolution or removals. Shown are changes in mean size for the escapement (upper band) and maturing fish (lower band) over the last 50 y for the model including removals and allowing for trait evolution (yellow) and simulations either omitting evolution (red) or omitting any size-selective removals (blue). Circles represent median values and bars represent 5th and 95th percentiles of 100 stochastic runs.



**Fig. 4.** Change in mean size of Chinook salmon as a function of maximum predation rate based on random permutations of model parameters. (Top) The decline in mean size as a function of maximum predation rate for 1,000 simulations based on randomly drawn parameter values. The empirically estimated size decline of at least 70 mm is indicated by the horizontal line. The size and color of circles reflect the relative values of the two other most important parameters affecting changes in mean size: the predation midpoint (size of circles) and the trait correlation between growth and maturation (color of circles). (Bottom) Results from a quantile regression of simulated size changes that was used to estimate the probability of a size decline of at least 70 mm (threshold) as a function of maximum predation rate.

trend in mean size of the escapement was highly sensitive to predation parameters, specifically the predation rate and midpoint of the size selectivity function (*SI Appendix, Fig. S6*). Declines in mean length on the order of those observed for Chinook salmon populations coast-wide over the past 40 to 50 y (at least 70 mm, or ~9%) were only reproduced with a predation rate of 0.3 or higher toward the end of the simulation (Fig. 4). Based on simulations where all model parameters were drawn randomly from a specified range of reasonable values, the probability of a decline in mean size larger than the 70-mm threshold was 2.5% at a maximum predation rate of 0.3 (Fig. 4) but rapidly increased and reached a probability of over 40% at a maximum predation rate of 0.5 (the full set of responses for the most important parameters is shown in *SI Appendix, Fig. S7*). Therefore, if more than 30% of maturing Chinook salmon are currently being consumed by fish-eating killer whales, a size decline on the order of that observed in the empirical data is plausible, and the decline is likely to continue in the future.

Other marine mammals that have increased in abundance (18), including pinnipeds, also feed on Chinook salmon. Harbor seals (*Phoca vitulina*) can significantly reduce Chinook salmon marine survival (23, 32); however, these predators primarily target Chinook salmon during their residency in estuaries or first year at sea and are not thought to feed selectively on large fish. Yet, lower abundances due to increased early ocean mortality may exacerbate the impact of size-selective predation later in life and may result in a release from competition for resources, thus contributing to changes in growth rates. California sea lions (*Zalophus californianus*) and Steller sea lions (*Eumetopias jubatus*) may target adult Chinook salmon, although consumption from these predators is thought to be a fraction of that consumed by fish-eating killer whales, in part because Chinook salmon represent a small fraction of sea lions' diets. Increasing abundances of other marine predators such as salmon sharks (*Lamna ditropis*) could also be compounding the effects of predation by killer whales if their selectivity patterns are similar and their abundance is large enough to significantly reduce the survival of large Chinook salmon (33–35). Importantly, killer whales are highly selective for the largest fish and are estimated to consume several times more Chinook salmon biomass than other predators (23). We therefore focused our assessment on size-selective predation by fish-eating killer whales.

Fisheries often exert selection on life-history traits by selectively removing larger individuals, and evidence for fishing-induced evolution in exploited species is mounting (5–7, 36, 37). Harvesting had a weaker effect on changes in mean body size of Chinook salmon compared to predation, because harvest rates have declined in recent decades while predation pressure has increased (*SI Appendix, Fig. S3*). Additional model simulations without predation mortality revealed that harvesting alone cannot explain the observed declines in body size of Chinook salmon over the past 50 y, and that the impacts of harvesting were likely stronger during the decades preceding the most recent period for which reliable empirical estimates of changes in mean body size of Chinook salmon exist (*SI Appendix, Fig. S8*). Sufficiently strong harvest rates and selectivity may have caused significant declines in mean size during earlier periods (*SI Appendix, Fig. S9*).

Commercial fisheries for Chinook salmon in coastal waters of the northeast Pacific developed during the late 19th and early 20th century. From the 1920s to the 1970s, harvest removals by commercial fisheries were relatively stable, when each year between 2.2 and 3.8 million fish were captured in commercial fisheries (38). After the late 1970s, harvests of Chinook salmon started to decline, while the production of hatchery-origin fish increased rapidly (38), such that harvest rates were highest prior to the 1970s and have declined since (25, 39, 40). These patterns of changes in fishery exploitation are not concordant with the observed changes in Chinook salmon life history characteristics observed in the last 50 y (14).

Harvest-induced size declines would be expected to continue for multiple generations only in populations that continue to experience sustained or increasing harvest levels. Yet, despite reductions in harvest rates in many populations (25, 41, 42), Chinook salmon continue to return at smaller sizes and younger ages throughout most of their North American range, and size declines have been most pronounced during the last 15 y. Furthermore, size trends are similar in geographically close populations that experience differential fishing pressure and/or selection regimes, as reported for Chinook salmon in Alaska (43). It is also noteworthy that mean body weights of other Pacific salmon have generally declined less than those of Chinook salmon since the mid-20th century, and these species have also been heavily exploited by fisheries (38, 44). Trends toward smaller mean weight in fishery catches of North American Chinook salmon during the 1950s to 1970s were reported almost 40 y ago (45), although it remained speculative to what extent declines in mean catch weight were

caused by harvesting. Our results suggest that the main impact of fishing on the size and age composition of Chinook salmon indeed occurred prior to the 1970s (*SI Appendix, Fig. S8*). Size declines likely continued because the combined removals by fisheries and marine mammal predators have increased continuously over the past century (23, 40). Without increasing predation pressure, average sizes of Chinook salmon should have partly recovered due to reductions in fisheries harvest during the past 40 to 50 y (*SI Appendix, Fig. S9*). To our knowledge, data that would allow reconstruction of average body sizes have not been collected systematically prior to the onset of commercial fishing (but see ref. 46), such that we cannot make inferences about longer-term trends in Chinook salmon body size. However, current population sizes of Chinook salmon are very likely much lower compared to pre-modern times, which could facilitate pronounced effects of size-selective predation compared to previous times when marine mammals may have been abundant, because the magnitude of the predation effect also depends on the abundance of prey (47).

In addition to size-selective predation and harvest mortality, changes in growth conditions at sea can affect the size at age and maturation of Chinook salmon. The growth environment experienced by Chinook salmon in the ocean has clearly changed over the past decades (14), and variation in the slope of change in mean size (Fig. 1) indicates that other factors have contributed to changing demographic structure. While slower growth due to lower ocean productivity or increased competition with other salmonids could contribute to declining size at age of older fish, this is expected to result in later maturation in semelparous Pacific salmon, because slow-growing individuals mature later than fast-growing individuals (48, 49). The observation for Chinook salmon that age at maturation declined along with the size at age of older fish (14) contrasts with other semelparous species such as chum salmon (*Oncorhynchus keta*) (45, 48) and sockeye salmon (*Oncorhynchus nerka*) (13, 50, 51), which have experienced stable or increasing age at maturation while size at age has declined. Fish-eating killer whales feed on other species of Pacific salmon, such as chum and coho salmon, though to a lesser extent (21–24).

The observation that the size at age of young Chinook salmon in the ocean has increased indicates that growth conditions during the salmon's first 1 or 2 y at sea have improved, or that the fish enter the ocean at larger sizes (14). More favorable growth conditions in the ocean could lead to accelerated growth early in life and thus earlier maturation. A potential mechanism causing faster growth is a release from competition, for instance caused by higher early ocean mortality of Chinook salmon due to increased harbor seal abundances (23). However, faster early growth due to higher food abundance is expected to also lead to larger size at age later in life (52, 53), unless feeding conditions continuously deteriorate as the fish grow, or size-selective mortality later in life selects for smaller maximum size. Finally, while increased temperature due to climate warming can cause life-history changes similar to those observed in Chinook salmon, temperatures in the northeast Pacific have not shown spatially consistent and continuously increasing trends over the past few decades (14). Nonetheless, temperature effects could be contributing to observed demographic shifts in Chinook salmon and were not explicitly modeled in this study.

Hatchery practices may have contributed to larger sizes early in life by producing faster-growing smolts that enter the ocean at larger average size (54). Previous work suggests that trends in size at age are similar for wild and hatchery-origin fish, and that wild populations that are not exposed to hatchery introgression or potential competition with hatchery stocks, such as Chinook salmon in western Alaska, have experienced similar declines in the size at age of older fish (14). Furthermore, coast-wide hatchery releases of Chinook salmon increased rapidly in the 1970s and 1980s but have declined steadily since the late 1980s. Changes in hatchery practices may contribute to trends in demographic

characteristics but cannot explain changes in populations that experience little or no competition and introgression from hatchery fish.

Our model was developed to represent the typical life history of North American Chinook salmon. It ignores differences in life-history strategies among populations and regional trends in demographic change, harvest rates, predation pressure, and environmental conditions. For instance, Chinook salmon populations differ in many aspects of their life history, including growth rate, maturation schedule, and marine distribution (11, 14, 55). Hatchery-origin Chinook salmon are only produced in large quantities in the central and southern regions, from California to British Columbia. Furthermore, exposure to killer whale predation depends on the abundances, ocean distributions, and migration routes of both predators and prey. Abundances of fish-eating killer whales have increased continuously over the past decades, with the exception of the southern resident population that inhabits the Salish Sea and coastal waters from California to Vancouver Island. Interestingly, Chinook salmon populations from California and southern Oregon that do not migrate far northward along the coast and likely experience less killer whale predation have shown weak trends in mean size and age (14). Finally, harvest rates have not declined uniformly across space. Because our model is not spatially explicit, it cannot distinguish regional differences in how factors such as predation, harvest, hatcheries, competition, and ocean conditions have affected the demographic structure of Chinook salmon. The model could serve as a starting point for population-specific models that explore how regional factors may have contributed to the coast-wide decline in Chinook salmon body size.

While increasing predation pressure is likely contributing to declining average sizes in Chinook salmon, some populations of fish-eating killer whales may in turn be negatively affected by reduced abundances and body sizes of their prey. A decline of ~10% in mean length, as indicated by our data, implies a reduction in caloric value of an average-sized Chinook salmon of about 30 to 40% (56). Food limitation may be one of the factors responsible for the recent decline in the abundance of the southern resident killer whales (SRKW; refs. 57–59), the only population of fish-eating killer whales in the northeast Pacific Ocean that is not thriving. This emphasizes the importance of considering the complex interactions between predators and their prey as well as intra- and interspecific interactions among predators. In particular, interactions between SRKW and the expanding populations inhabiting more northerly waters appears to be an important component of understanding the concerning demographic status of SRKW. Some Chinook salmon populations originating from central and southern parts of their North American range are protected under the US Endangered Species Act, and fish-eating killer whales are protected under the US Marine Mammal Protection Act and the Canadian Species at Risk Act (40, 60, 61). The potential trade-off between management objectives, namely maintaining or increasing abundances of both predators and their prey, poses a challenge to conservation. Fisheries management which provides harvest opportunities for tribal, subsistence, sport, and commercial fisheries, is faced with additional challenges due to the resurgence of marine mammal predators. It is thus important to acknowledge trade-offs between conservation and benefits to fisheries when determining management goals. Interestingly, protecting marine mammals by rebuilding fisheries is increasingly proposed as a target conservation strategy (62). Rebuilding salmon might be more challenging for populations that have experienced severe declines in mean size and thus spawner quality. If killer whales are causing changes in Chinook salmon demographics through undesirable changes in phenotypic traits that might propagate to affect population productivity and their fisheries, future conservation conflicts seem inevitable.

## Materials and Methods

**Data Analysis.** The analysis of changes in body size of Chinook salmon relies on data for wild and hatchery populations from central California to western Alaska available in agency databases and the Regional Mark Information System (RMIS). Detailed descriptions for synthesizing these data for the purposes of size at age and age composition analyses can be found in a previous study (14). We fit linear mixed effects models to individual observations of size (fork length, in millimeters) of Chinook salmon covering the brood years 1971 to 2010. Chinook salmon have a complex life history with fish returning to spawn after 0 to 2 y in freshwater and 1 to 5 y in the ocean, meaning the fish returning in any given year represent a mix of fish originating from different brood years. Analyses of changes in mean size were performed by brood year, the years when eggs of a particular cohort of fish were deposited in the gravel, to avoid confounding effects of variation in year class strength of multiple returning cohorts in a given run year. We only used samples of individuals that were considered part of the escapement, that is, fish that have escaped the fisheries and returned to freshwater habitats to spawn (~900,000 samples). This was done to ensure that the results would not depend on the inclusion of potentially selective fishery data and that the estimated time series would reflect postremoval trends in mean size.

We considered the categorical fixed effects of brood year, rearing type (hatchery/wild), sampling method (fishery code, eight levels), run type (spring, summer, fall, late fall, upriver bright), and freshwater age (0, 1, 2) in the case of age-specific models, while day of year of sampling was considered as a continuous variable (for further details on the variables see ref. 14). Categories with at least five observations and populations with at least 5 y of data were included in the analysis. Random intercepts for each year nested within population were used to account for the lack of independence of data within years and populations. The mixed-effects models had the form  $L_i = \beta_0 + \beta_1 FE_1 + \dots + \beta_n FE_n + b_{p|y} + \epsilon_i$ , where  $\beta_0$  is the intercept,  $\beta_1, \dots, \beta_n$  are regression coefficients of the fixed effects (FE),  $b_{p|y} \sim N(0, \sigma_b^2)$  is a normally distributed random effect for year (y) nested in population (p), and  $\epsilon_i \sim N(0, \sigma^2)$  is a normally distributed error term. Models were fit using the package nlme (v.3.1-128) (63) in R (v.3.5.1) (64). Inclusion of nested random effects was supported by a likelihood ratio test. Inclusion of fixed effects was determined using Akaike information criterion-based multimodel inference using the MuMIn package (v.1.24.1) (65) by evaluating the complete set of models with all possible combinations of fixed effects. Models with different fixed effects were compared using maximum likelihood estimation, and models with different random effects and the final model were fit using restricted maximum likelihood. The selected mean size model included all fixed effects but no interactions. Based on the selected model, year predictions were made for wild fall-run Chinook salmon.

Estimates of consumption by fish-eating killer whales were taken from a recent study on marine mammal predation of Chinook salmon (23) and were lagged by 5 y to match the brood year of Chinook salmon, because most fish consumed are 5 to 6 y old (Fig. 1).

**Simulation Model.** We simulate how changes in predation pressure and fishery exploitation would be expected to alter the age and size composition of returning Chinook salmon over time, with the main goal of identifying ecological conditions that might have caused demographic changes similar to those observed in North American Chinook salmon. Our dynamic age- and size-based population model for Chinook salmon allows for the gradual evolution of traits related to growth and maturation. Specifically, the asymptotic average size of individuals in the population and a correlated trait that determines the probability of maturing at a given age and size can evolve in response to changes in survival probability due to size-selective harvest and/or predation.

**Model Functions and Parameters.** The model functions and parameter values reflect the typical life history of Chinook salmon in the northeast Pacific Ocean. We defined a set of default parameter values based on available literature and empirical data on Chinook salmon, but our model analysis explores deviations in parameter values within ranges that were considered biologically reasonable (SI Appendix, Table S1), including simultaneous random draws of all model parameters.

**Reproduction.** Fecundity in Chinook salmon depends on female body size. The number of eggs (E) produced by a female was thus assumed to depend on female length (L) according to a power function  $E = a_F L^{b_F}$ , where  $a_F$  is the fecundity constant and  $b_F$  is the fecundity exponent (SI Appendix, Fig. S2). Parameter values were informed by literature data (66). Recruitment (R) of smolts was based on a 1:1 sex ratio in the population and depended on the

total number of eggs produced according to an asymptotic Beverton–Holt-type relationship,  $R = E / \left( \frac{1}{a_R} + \frac{E}{b_R} \right) e^{\epsilon_R}$ , where  $a_R$  is the productivity and  $b_R$  is the capacity parameter of the density dependence function (SI Appendix, Fig. S2), and recruitment variability is assumed to be log-normally distributed with  $\epsilon_R \sim N(0, \sigma_R)$ . Recruitment variability had a minor effect on trait dynamics and changes in mean size, and the default value was set to a moderate level of recruitment variation (67). The productivity parameter was based on literature values (10), and smolt capacity was set to ensure a sufficient number of individuals in each category to calculate statistical averages in any given year. Marine survival was assumed to be independent of population density.

**Growth.** The von Bertalanffy growth function was used to model individual growth. The growth increment ( $g_{y,i}$ ) of individual  $i$  from 1 y (y) to the next is  $g_{y,i} = k_i (L_{\infty,i} - L_{y-1,i}) e^{\epsilon_G}$ , where  $k_i$  is the growth rate coefficient (or growth rate),  $L_{\infty,i}$  is the asymptotic average length (or maximum length),  $L_{y-1,i}$  is previous length, and  $\epsilon_G \sim N(0, \sigma_G)$  describes growth variation due to stochastic environmental effects with variance  $\sigma_G$  (SI Appendix, Fig. S2). The length of individual  $i$  in year  $y$  is then  $L_{y,i} = L_{y-1,i} + g_{y,i}$ , where  $L_{y-1,i}$  in the first year of life was defined as the average smolt length  $L_S$ . Annual growth increments were thus assumed to be stochastic and drawn from a lognormal distribution around the deterministic growth increment as determined by growth parameters  $k_i$  and  $L_{\infty,i}$ . Reference growth parameters were chosen such that the individual growth trajectories together with the age- and size-dependent maturation probabilities produced size distributions in the return that resembled the size distributions in the empirical data (14). The growth rate coefficient of an individual was further assumed to be correlated with the asymptotic average length,  $k_i = k_{ref} - \beta_g L_{\infty,ref} + \beta_g L_{\infty,i}$ , where  $L_{\infty,ref}$  and  $k_{ref}$  are the reference values of maximum size and growth rate, respectively, and  $\beta_g$  is the slope of the relationship between the two parameters (SI Appendix, Fig. S2). The growth parameters trade-off was based on an estimated correlation between the two growth parameters using values reported in a stock assessment model used to manage Chinook salmon populations on the west coast of the United States and Canada (Fishery Regulation Assessment Model) (68). We thus assume that the range of possible individual growth trajectories is constrained by a trade-off between average asymptotic length and growth rate.

**Evolution.** The asymptotic average length was modeled as a quantitative trait that evolved gradually in response to selection due to size-dependent survival (and was assumed to be correlated to the maturation schedule, discussed below). Its initial value was set to approximate the equilibrium mean trait value under default values of all other parameters (10, 55). The evolutionary dynamics depend on the variances in asymptotic size and growth rate that together determine trait heritability, which was not a parameter in the model. Heritability was calculated as the amount of expected deterministic variance in size at age over the amount of stochastic variance in size at age for ocean age-1 fish (SI Appendix, Fig. S5), which was the age group least affected by size-selective removals. We assumed constant genetic variance in the population, which implies a time-invariant mutation–segregation–recombination kernel, as done elsewhere (69, 70). Offspring trait values were drawn from a normal distribution around the mean parental trait value with constant variance (truncated at zero), although recent evidence suggests that age at maturation in salmonids may be controlled by a single locus (29, 71). Variances in asymptotic size and growth rate were set to reflect heritability values for length- and age-related traits in Chinook salmon, which are typically around 0.20 to 0.35 (27, 30). The emergent heritability for size at ocean age 1 at equilibrium dynamics in our model (without fishing and predation) using default parameter values was around 0.22.

**Maturation.** The maturation process was modeled using a probabilistic maturation reaction norm. Probabilities of maturing at a given age (a) and size (s) are given by a logistic function,  $P_{M,a,s} = 1 / \left( 1 + \exp \left( -\frac{L - L_{M50,a}}{\sigma_M} \right) \right)$ , where  $L_{M50,a}$  are the reaction norm midpoints describing the age-specific lengths at which maturation probability is 50%, and  $\sigma_M$  determines the width of the reaction norm. The default value of the variance term  $\sigma_M$  was set to resemble the relative widths of reaction norms used in other studies (17, 72). The reaction norm midpoints are given by  $L_{M50,a} = \alpha_M + \beta_M a$ , where  $\alpha_M$  and  $\beta_M$  are the intercept and slope (SI Appendix, Fig. S2), respectively. We assumed a negative slope of the maturation reaction norm such that faster-growing fish mature at a younger age compared to slower-growing fish, in line with other studies (17, 48, 49). Default values were set such that the resulting proportions of maturing individuals were in line with the literature (17, 73) and resembled typical age proportions of maturing fish with ocean ages 2 to 4 being the dominant age groups in the return (14). The maturation reaction norm intercept  $\alpha_M$  was correlated to maximum size,  $\alpha_{M,i} = \alpha_{M,ref} - \gamma (L_{\infty,ref} - L_{\infty,i})$ , where  $\alpha_{M,ref}$  is the reference intercept and  $\gamma$  is

the slope of the relationship (SI Appendix, Fig. S2). While there is evidence for sex-specific evolution of age and size at maturity in salmonids (29, 71), trait evolution in our model was not sex-specific and we assumed that the resulting evolutionary changes reflect average trait changes of both sexes. We modeled trait changes in the reaction norm intercept because available studies suggest that evolution is more likely to shift the intercept than the slope of the maturation reaction norm (72). Because the strength of the trait correlation was uncertain, we tested a wide range of values, ranging from no correlation to a strong correlation that would imply rapid evolution of the maturation schedule with changes in maximum size (SI Appendix, Table S1).

**Survival.** Size-independent annual survival was assumed to be low during the first year at sea and relatively high in subsequent years of marine residence (74, 75). Size-dependent survival due to size-selective predation and harvest occurred after maturation.

Predation removals were based on the predation rate in a given year ( $PR_y$ ) and the size selectivity of predation ( $S_{p,s}$ ). Selectivity was modeled as a sigmoid function given by  $S_{p,s} = 1 / (1 + \exp(-\beta_p(L - L_{p50})))$ , where  $L_{p50}$  is the selection midpoint at which selectivity is half of its maximum, and  $\beta_p$  determines the steepness of the selectivity curve (SI Appendix, Fig. S2). The selectivity parameters were based on available data of killer whales feeding on Chinook salmon (76) and selectivity curves estimated from those data (25). Because the selectivity function was estimated from empirical data, other functional forms were not tested. This logistic form is flexible in allowing a wide range of selectivity patterns, from gradual to knife-edge, and we explore a wide range of values for the midpoint and steepness. Predation rate was simulated to increase over the last 50 y of the simulations. We tested a wide range of plausible predation rates (SI Appendix, Table S1). Observed size declines could also result from the accumulating effects of selection under constant predation (SI Appendix, Fig. S10); however, this scenario was considered highly unlikely, because predator abundances have increased continuously over the past few decades (23).

Harvest removals were based on the harvest rate in a given year ( $HR_y$ ) and the size selectivity of harvest ( $S_{H,s}$ ). Harvest selectivity was modeled as a unimodal function with specified variances to reflect different degrees of selectivity,  $S_{H,s} = \exp(-(\ln(L) - \ln(L_{H,max}))^2 / 2\sigma_H^2)$ , where  $L_{H,max}$  is the length at maximum selectivity and  $\sigma_H$  is the SD on log scale, which determines the

degree of selectivity (SI Appendix, Fig. S2). We used a value of  $\sigma_H = 0.25$  to represent a selective (gillnet) fishery, a value of  $\sigma_H = 0.5$  to represent a mixed (troll, gillnet, and seine) fishery, and a value of  $\sigma_H = 2$  to represent a largely unselective (troll) fishery. The unimodal form was based on previously estimated selectivity curves for Chinook salmon gillnet fisheries, where the length at maximum selectivity resembled different mesh sizes used in typical gillnet fisheries, with values of 625, 725, and 825 mm representing 6.5-, 7.5-, and 8.5-inch mesh sizes, respectively (77). We tested a wide range of harvest rates (SI Appendix, Table S1).

**Model Simulations.** The simulation model tracks individuals of a given age, size, and trait in each year and by "state" (immature, mature, preyed upon, returned, harvested, and escaped). We discretized the size and trait space using a resolution of 10 mm and model five ocean age groups, where the oldest is a plus group such that individuals that do not mature by ocean age 5 (less than 0.1% of a given cohort) remain in this age group until they reach maturity. Space is implicit in the model: Reproduction and density-dependent juvenile survival occur in freshwater, somatic growth and maturation occur during ocean residence, and predation and harvest mortality occur after maturation during the return migration, prior to reproduction in freshwater habitats. Each year individuals grow, experience size-independent mortality, some individuals in each age group reach maturity, and these individuals subsequently experience size-dependent predation and fishing mortality, or escape to reproduce and then die. Details of how the model keeps track of individuals by age, size, trait, and state are provided in SI Appendix, Supplementary Methods: Model Simulations.

Code for the simulation model is available from the corresponding author upon request. Data used to analyze changes in Chinook salmon body size were presented in an earlier study (14), available from the RMIS (<http://www.rmis.org/>) and the respective state agencies (Alaska Department of Fish and Game and Washington Department of Fish and Wildlife).

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