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ARTICLE

Using hierarchical models to estimate stock-specific and seasonal variation in ocean distribution, survivorship, and aggregate abundance of fall run Chinook salmon

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Abstract: Ocean fisheries often target and catch aggregations comprising multiple populations or groups of a given species. Chinook salmon (*Oncorhynchus tshawytscha*) originating from rivers throughout the west coast of North America support mixed-stock ocean fisheries and other ecosystem components, notably as prey for marine mammals. We construct the first coastwide state-space model for fall Chinook salmon tagged fish released from California to British Columbia between 1977 and 1990 to estimate seasonal ocean distribution along the west coast of North America. We incorporate recoveries from multiple ocean fisheries and allow for regional variation in fisheries vulnerability and maturation. We show that Chinook salmon ocean distribution depends strongly on region of origin and varies seasonally, while survival showed regionally varying temporal patterns. Simulations incorporating juvenile production data provide proportional stock composition in different ocean regions and the first coastwide projections of Chinook salmon aggregate abundance. Our model provides an extendable framework that can be applied to understand drivers of Chinook salmon biology (e.g., climate effects on ocean distribution) and management effects (e.g., consequences of juvenile production changes).

Résumé : Il est fréquent que les pêches océaniques visent et exploitent des concentrations de poissons comprenant plusieurs populations ou groupes d'une même espèce. Les saumons quinnats (*Oncorhynchus tshawytscha*) originaires des rivières le long de la côte ouest de l'Amérique du Nord supportent des pêches océaniques de stocks mélangés et d'autres éléments des écosystèmes, en tant que proies de mammifères marins, notamment. Nous avons élaboré le premier modèle d'espace d'états à l'échelle de la côte pour les saumons quinnats à migration automnale marqués relâchés de la Californie à la Colombie-Britannique de 1977 à 1990 pour estimer leur répartition océanique saisonnière le long de la côte ouest de l'Amérique du Nord. Nous incorporons les individus récupérés de plusieurs pêches océaniques et permettons des variations régionales de la vulnérabilité et de la maturation des ressources. Nous démontrons que la répartition océanique des saumons quinnats dépend fortement de la région d'origine et varie selon la saison, alors que leur survie présente des variations régionales dans le temps. Des simulations incorporant des données sur la production de juvéniles fournissent la composition proportionnelle des stocks dans différentes régions de l'océan et les premières projections à l'échelle de la côte de l'abondance cumulative des saumons quinnats. Notre modèle fournit un cadre évolutif pouvant être utilisé pour évaluer l'influence de différents facteurs sur la biologie des saumons quinnats (p. ex. effets du climat sur leur répartition océanique) et les effets de la gestion (p. ex. conséquences de changements à la production de juvéniles). [Traduit par la Rédaction]

Introduction

Migratory species present unique challenges for conservationists and managers. A diversity of taxa from insects through mammals occupy and migrate across vast areas of the Earth's surface (Martin et al. 2007; Block et al. 2011), and the movements of many marine fish, marine mammal, and sea turtle species pose challenges for sustainable management as multiple regulatory bodies must collaborate on fishing and management.

Population structure, where individuals in a given area consist of multiple, distinct groups, may further complicate marine management. Particular populations, subpopulations, or life-history types within a single population often co-occur (e.g., Schindler et al. 2010; Teel et al. 2015; Satterthwaite and Carlson 2015), but the contribution of each group to the aggregate abundance in migratory species may vary spatially and temporally, and therefore the importance of a given component in one region often differs from the same component in another. Portfolio theory (Markowitz 1952; Koellner and Schmitz 2006) has shown that population complexes with a diverse set of contributing groups will result in reduced variation in aggregate abundance (Hilborn et al. 2003; Schindler et al. 2010, 2015). Most applications of portfolio theory to natural systems have emphasized the temporal attributes of aggregate abundance, showing how increased diversity among components (Moore et al. 2010; Thorson et al. 2014; Satterthwaite and Carlson 2015) or life-history diversity (Hilborn et al. 2003; Schindler et al. 2010; Greene et al. 2010) lead to resilience and stability in aggregate.

For migratory species, it is important to recognize that the portfolio framework is relevant in a spatial as well as temporal context

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(Griffiths et al. 2014). Movement may create a shifting mosaic in which the distribution of both the aggregate abundance and the individual contributors to abundance shift in space and time. Furthermore, while fisheries are often focused on maintaining robust aggregate abundances over the long term, conservation decisions are often focused on avoiding low abundance for component populations or sub-populations. Management actions to protect or conserve these less productive stocks is generally referred to as "weak stock" management. Thus, conflict between managing aggregate abundance and the protection of a particular population may arise, and strategies for spatial and temporal management must consider this conflict.

Chinook salmon (*Oncorhynchus tshawytscha*) are a highly migratory species native to the Pacific coast of North America. In the eastern Pacific, Chinook salmon occur along the continental shelf and into the open ocean, ranging from central California to Alaska (Healey 1991), where they support extensive and economically valuable fisheries (PFMC 2016*a*; PSC 2016). Chinook salmon also serve important roles in the ecosystem, as prey for both marine predators such as sharks, pinnipeds, and killer whales (Chasco et al. 2017) and terrestrial predators including birds and bears (Good et al. 2007; Schindler et al. 2013). Chinook salmon inhabiting any given coastal area are comprised of fish from multiple stocks (Healey 1991; Norris et al. 2000; Weitkamp 2010). Understanding the spatial and temporal dynamics of Chinook salmon throughout their range is critical, as some populations of the northeast Pacific are depleted and listed under the US Endangered Species Act (ESA) or Canadian Species At Risk Act (SARA).

While Chinook salmon are one of the iconic species of the northeast Pacific and subject to large-scale fisheries and extensive research (Ruckelshaus et al. 2003), their marine spatial distribution and migration patterns are poorly understood. Some stock-specific distributions for juvenile Chinook salmon are available from research surveys (Trudel et al. 2009; Tucker et al. 2011; Burke et al. 2013), while others have provided stock-specific estimates of ocean distribution using coded-wire tags (CWT; Norris et al. 2000; Nandor et al. 2010; Weitkamp 2010) or genetic stock identification (Winans et al. 2001; Bellinger et al. 2015; Satterthwaite et al. 2015). The vast majority of these tagging and sampling programs are a result of decades of intensive marking and tagging of hatchery-raised fish (Nandor et al. 2010; Weitkamp 2010; Satterthwaite et al. 2013). Fisheries management models such as those developed and used annually by the Pacific Salmon Commission's Chinook Technical Committee (CTC; e.g., CTC 2015) use information from CWT recoveries in many fisheries along the coast in concert with spawning escapement to provide information about the abundance and status of Chinook salmon stocks from Oregon to Alaska. The CTC's work provides vital fisheries management advice annually, but it does not include information on Chinook salmon stocks from California and does not provide direct estimates of spatial distribution.

In the most comprehensive peer-reviewed coastwide study to date, Weitkamp (2010) examined tag recoveries for 93 Chinook salmon stocks in ocean fisheries from California to the Bering Sea to produce the only comprehensive description of inferred stock-specific spatial distributions. While Weitkamp (2010) was groundbreaking in its breadth and scope, it did not account for fishing effort nor changes in seasonal distribution, meaning that estimated distributions may be biased by uneven fishing and fisheries sampling efforts in space and time. Because of differences in stock-specific tagging rates, numbers of tag recoveries could not be compared among stocks to infer relative densities. More targeted studies have inferred season-specific local densities from catch per unit effort (CPUE), typically involving fewer stocks, a smaller spatial range, and only considering one gear type at a time (Norris et al. 2000; Sharma et al. 2013; Satterthwaite et al. 2013, 2015). Although Newman (1998) developed a state-space framework for integrating spatial data on tag recoveries into a demographic model including mortality and movement, there are limited applications of this approach to empirical data sets aside from a coho salmon (*Oncorhynchus kisutch*) stock in Washington (Newman 2000).

Here we explore the spatiotemporal dynamics of fall run Chinook salmon occurring along the Pacific coast of North America using an integrated modeling approach. We use tag release and recovery data from ocean harvest along with data on commercial and recreational fishing efforts to estimate a spatiotemporal model for fall Chinook salmon. By modeling all stocks simultaneously, our model shares information among stocks in a biologically reasonable way and leverages the fact that fish derived from different rivers swim in the same areas of the coastal ocean to improve estimates of shared processes. We provide estimates of seasonal ocean distribution and abundance for Chinook salmon populations representing the full geographic extent of North American fall Chinook salmon. To our knowledge, this is the first coastwide analysis of seasonal patterns in density that simultaneously accounts for multiple axes of biological variation among Chinook stocks (differences in maturation, variation in ocean distribution, and spatiotemporal variation in early ocean survival), variation in detection probabilities due to fisheries effort and gear type vulnerabilities, and both measurement and process error. After estimating our biological model, we combine estimates of Chinook salmon ocean distribution with regional estimates of juvenile Chinook salmon production to generate estimates of the cumulative abundance and distribution of fall Chinook salmon abundance along the entire west coast of North America on a seasonal basis. This unifying statistical framework improves our understanding of Chinook salmon biology and provides a methodology from which it is possible to explore changing ocean distributions, spatiotemporal variation in mortality, and interactions with other species and fisheries.

Methods

Study species

Chinook salmon (*O. tshawytscha*) are the largest of the northeast Pacific salmon, and native populations spawn in rivers along the northern Pacific Ocean from northern Japan to Siberia along the Asian coast and central California to Alaska along the North American coast (Healey 1991; Quinn 2005). Although considerable life-history diversity exists both across and within watersheds, populations are typically classified based on the season when adults return to their natal rivers to spawn (run timing, generally designated as fall, winter, spring, and summer runs). Adult run timing may be a good predictor of additional aspects of life history, including the timing of major events in the freshwater phase of the life cycle (Healey 1991). The life-history variation in run timing for adults also translates into differences in when juveniles of each run type migrate to the ocean. For example, fall run Chinook salmon juveniles typically emigrate to sea during their first year of life, while spring run fish typically spend an extra year in fresh water before emigrating. There can be considerable variation within runs, and variability in run timing appears to have evolved independently many times (Waples et al. 2004; Moran et al. 2013). Adults typically spend 2–4 years at sea with northern populations more often maturing at older ages (Myers et al. 1998; Quinn 2005).

Considerable loss and degradation of freshwater habitat, along with a desire to supplement harvest, has led to the establishment of numerous hatchery programs coastwide (Naish et al. 2007). Hatchery production now substantially exceeds natural production in many regions (refer to online Supplementary data, Table S3.1[1]). Many hatchery fish (and a small number of wild fish) are tagged with CWT (Johnson 1990), which contain a numeric identifier unique to each batch of fish, providing information on stock-of-origin, time of release, and other details about a hatchery release group or wild fish collection event.

Data

Although there are multiple Chinook salmon run types on the west coast of North America, fall Chinook salmon are the most dominant and data rich (both in terms of population size and tagging programs). Thus we restricted our analysis to developing models of fall Chinook salmon ocean distribution, with the idea that these general methods are extendable and applicable to other life-history types and species. We used three sources of data to estimate ocean abundance and distribution. First, we extracted information on CWT releases from the Regional Mark Information System (RMIS; http://www.rmis.org/rmis_login.php?action=Login&system=cwt). We extracted information from tagged releases from 43 major hatcheries spanning central California to Vancouver Island British Columbia and representing fish released between 1978 and 1991 (from brood years 1977 to 1990). Fall Chinook salmon are rare in rivers north of British Columbia, where the majority of Chinook salmon runs are spring run. The range of years analyzed was constrained primarily by the availability of fishing effort data (see below) and the high intensity of fishing effort during this period. If the model failed for years with substantial fishing effort, it would likely fail for more recent years, which have seen coastwide declines in Chinook salmon fisheries. For central Oregon to Canada, we selected hatcheries based on their previous identification as major hatcheries associated with indicator stocks by the Pacific Salmon Commission (CTC 2015). Major hatcheries from southern Oregon and California were selected based on the indicator stocks used by the Pacific Fishery Management Council (PFMC 2016*b*). Table S1.1[1] presents a complete list of hatcheries included in the analysis.

For this set of years and hatcheries, we identified 2196 unique CWT tag codes to include, representing approximately 83 million CWT fish released during the study period (see Table S1.6[1] for a complete list). This list of tag codes excludes releases where comments indicated major problems with the release (e.g., high disease prevalence). We then aggregated tag codes released by individual hatcheries, brood year, brood stock, release year, and release season. For hatcheries that released fall Chinook salmon at multiple points during the year (i.e., they release both fingerling and yearling Chinook salmon), we categorized tag release into two groups based on season of release. This consolidation resulted in 454 unique hatchery – brood year – release season combinations (see Table S1.1[1]), each of which we refer to as a "release" in subsequent sections.

Second, we compiled recovery information for each identified tag code from RMIS. We noted the recovery date, location code, and port at which the fish were sampled. As each tag recovery in the RMIS database has an associated expansion that aims to correct for the proportion of the catch sampled, we used the expanded number reported for each of the tag codes in the RMIS database. Using the expanded number helps account for temporal and spatial variation in the sampling intensity of the fisheries catch. For marine recoveries, we assigned each recovery to the fishing gear type used to one of 17 coastal regions (Fig. 1) and to one of four seasons (spring: April–May; summer: June–July; fall: August–October; winter: November–March). Ocean recovery areas were derived largely from those used by Weitkamp (2010). The division of seasons was informed by both the biology of fall Chinook salmon (they enter their natal rivers to begin their spawning migration in the fall) and practical considerations (there is much less information about the spatial distribution of fish in the winter due to reduced salmon fishing effort; see Figs. S1.1–S1.4[1]). We only include recovery information from the three fishing gear types for which we have effort information (see below). In total, this included an estimated 527 711 ocean recoveries for the focal release groups. In addition to the ocean recoveries, we use freshwater recoveries (both from river fisheries and escapement to hatcheries and natural spawning areas) reported in RMIS to parameterize some model components (see Observation Model below). As illustrative examples, we provide recovery data from the commercial troll fishery for two releases (Fig. 2).

Third, we compiled data on commercial and recreational fishing effort from the United States and Canadian government sources. For commercial troll, treaty troll, and recreational fisheries along the outer coast of Washington, Oregon, and California, we used the PFMC "blue book" (http://www.pcouncil.org/salmon/background/document-library/historical-data-of-ocean-salmon-fisheries/). Recreational effort in Puget Sound, Washington was extracted from published WDFW reports (e.g., WDFW 1979). Alaska troll effort was supplied through a data request to the Alaska Department of Fish and Game (ADFG) and included both power troll and hand troll gear types. We detail how we combine these two effort types in Supplementary data S2[1]. We acquired Canadian troll effort through a data request to Fisheries and Oceans Canada (DFO) for 1982–1995. Earlier years of Canadian troll effort were extracted from official Canadian government data reports (British Columbia Catch Statistics, available at http://www.pac.dfo-mpo.gc.ca/stats/comm/ann/index-eng.html). The lack of publically available data describing Canadian commercial troll fishing effort targeting Chinook salmon between 1996 and 2004 limited our analysis to 1979–1995 and to brood years 1977–1990. We hope to expand the time-frame in future analyses. Recreational fishing effort data for the study period were also not available from Canada (except for some years in the Strait of Georgia; Fig. S1.4[1]) or from Alaskan waters. We describe how we accounted for these gaps in the model description section below. Complicating matters, each type of effort is reported in different units; recreational effort is reported in units of angler-days in the United States and boat-days in Canada, troll effort is reported in units of boat-days, and treaty troll in units of deliveries (see Supplement data S1 and S2[1] for fishing effort for each gear type).

Troll, treaty troll, and recreational fisheries account for >95% of CWT ocean recoveries for our release groups. The remaining recoveries were largely from commercial gillnet and seine fisheries with a few other rare types (e.g., test fisheries). Many gillnet and seine fisheries incidentally catch Chinook salmon, but some are active in fisheries in the mouth of the natal river or near the hatchery ("terminal" fisheries). Since many net fisheries only catch fish from individual sources, they are not a representative sample of multiple stocks within regions, and including them could affect model inferences about ocean distribution of Chinook salmon. Therefore we did not incorporate data from these sources but address the implications for these missing fisheries in the methods and discussion.

Model

To estimate the seasonal abundance and distribution of fall Chinook salmon, we simultaneously model the abundance and distribution of hatchery fall Chinook salmon released into 10 of the 17 ocean regions (Fig. 1) over 14 years (brood years 1977–1990). Our model tracks the abundance of fish from the spring of age 2 (defined as calendar year minus brood year) to fall of age 6, encompassing 19 seasonal time steps. As conventions for describing the age of Chinook salmon are confusing and vary regionally and

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[1] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2017-0204.

Fig. 1. Map of study area, hatchery locations (black dots), and 17 coastal regions used in the study. Locator map (left) attribution: Esri, DeLorme, General Bathymetric Chart of the Oceans (GEBCO), National Oceanic and Atmospheric Administration National Geophysical Data Center (NOAA NGDC), and other contributors. Main map attribution: Esri, NOAA NGDC, NOAA Global Self-consistent, Hierarchical, High-resolution Geography Database (GSHHG), and other contributors. Refer to text for descriptions of acronyms used in the figure. [Colour online.]

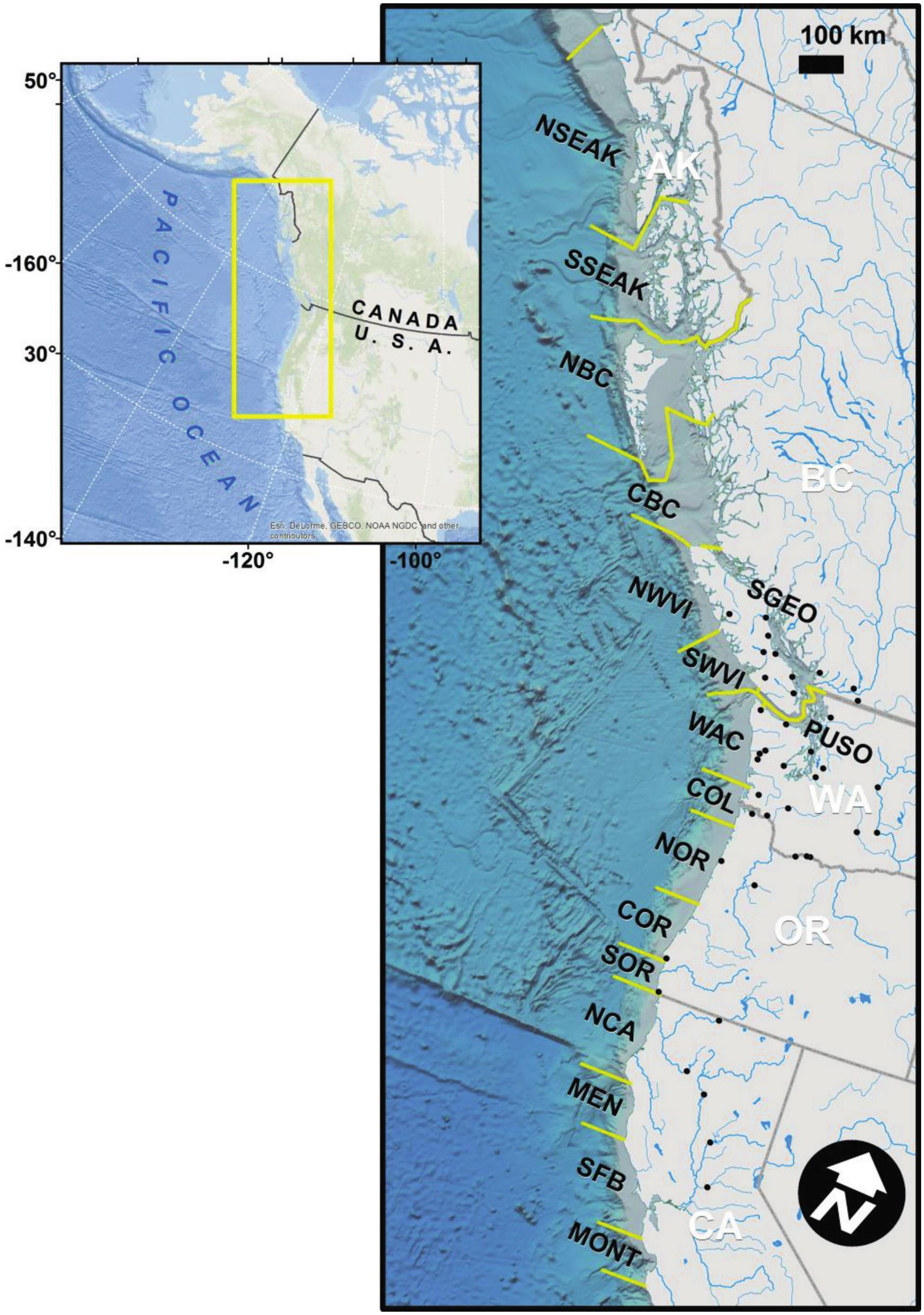
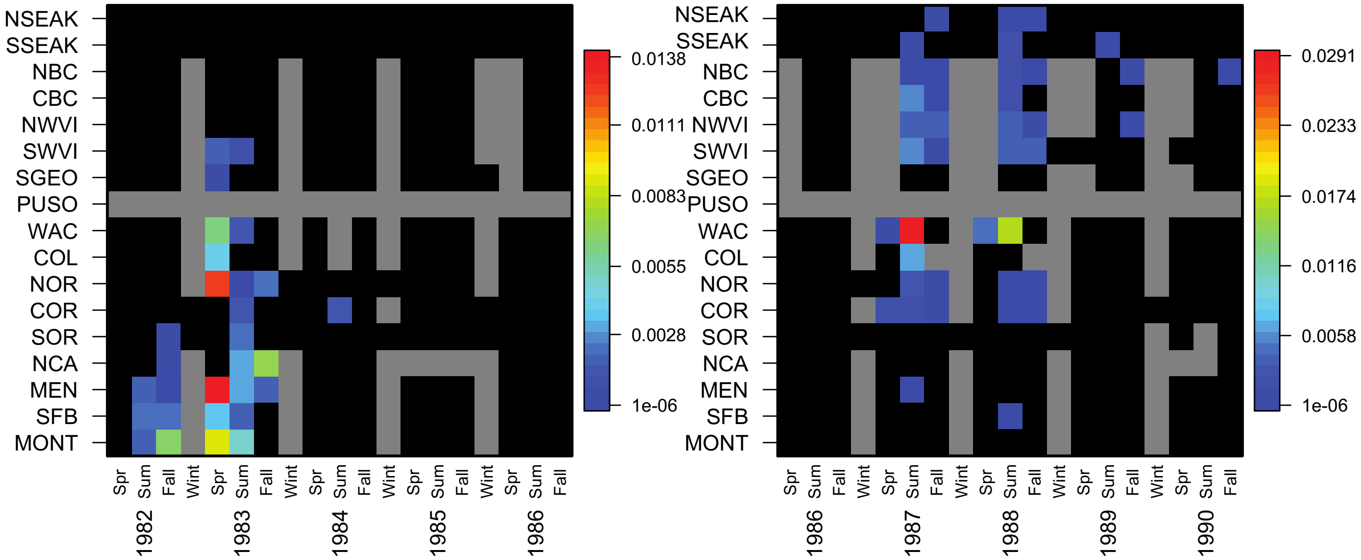


Fig. 2. Example raw CPUE data for two releases. (Left panel) Observed CPUE (fish per boat-day) from commercial troll fisheries for fall Chinook salmon released from Coleman National Fish Hatchery (SFB region) in 1980 (N = 393 932 at release). Black indicates region–season combinations with commercial troll fisheries but zero observed catches. Grey indicates no commercial troll fishery occurred in a region–season combination. (Right panel) Observed CPUE from commercial troll fisheries for fall Chinook released from Lyons Ferry (UPCOL region) released in 1984 (N = 234 985 at release). Note that the color ramp differs between panels.



by run type, we provide a table outlining fall Chinook salmon age classification used here (Table S1.2[1]). Unfortunately some model components such as fishing mortality vary and are reported by calendar year and season, not model season, and so have appropriate subscripts to reflect this complexity.

To generate estimates of the abundance of fall Chinook salmon from distinct regions, we need to quantify at least six core processes: (*i*) the number fish entering the ocean from natal rivers, (*ii*) the natural mortality of juvenile fish, (*iii*) the natural mortality of adult fish, (*iv*) fishing mortality by age and region, (*v*) the spatial distribution of fish in the ocean, and (*vi*) the age-specific loss of fish from the ocean due to maturation (salmon leaving the ocean and returning to their natal streams to spawn). We use a state-space framework that separates the biological processes (fish moving, dying from natural causes or fisheries, etc.) from what we observe about these fish populations (generally fisheries catches). This allows us to explicitly account for and make inferences about populations in locations and areas which may have no observations or missing data.

Using parameter estimates from the model and estimates of the number of juvenile fall Chinook salmon, we make projections of the number of Chinook salmon in each ocean region for fish originating from different regions and by age class (see section on Projected ocean distribution of fall Chinook salmon). Owing to the complexity of the model we outline the process and observation models briefly in the main text and highlight model components that are novel to this work. We present a comprehensive model description in online Supplement S2[1]. We provide a full list of parameters and subscripts used in model description in Table S2.1[1].

Process model

We track the number and distribution of each Chinook salmon release for the entirety of its life cycle. Each release is associated with a particular natal region, brood, and release year. Because we use hatchery releases, the initial number of fish in each release group is treated as known without error. We estimate an independent juvenile mortality rate, spanning the period from date of release to season 1 of the model, for each release and denote it ϕ_i for release i. During the 19 seasonal time steps of the model (subscript a; Table S1.2[1]), we model the total abundance of each release coastwide as an unobserved, latent variable, $N_{i,a}$. In each season, fish are subjected to age-specific natural mortality rate, M_a and are captured in commercial and recreational fisheries at fishing mortality rates, $F\_$ (subscripts suppressed, see below) that are determined by the fishing effort in a particular region and the age- and gear-specific vulnerability. Both natural and fishing mortality are modeled as density-independent processes and modeled as occurring simultaneously. An important assumption of the model is that fish of the same age in the same spatial region and season are considered to be equivalently vulnerable to ocean fisheries occurring in that spatial box and season. We incorporate information on retention size limits for each year, season, and spatial region (see Table S1.5[1]). Additionally, we include a process variability term to incorporate additional, unmodeled aspects of fisheries and the environment.

The distribution of Chinook salmon among the 17 ocean regions varies among seasons and is estimated within our population dynamic model. We let $\theta_{r,l,s}$ be the proportion of fish from natal region r, present in ocean region l, at the beginning of season s, and estimate $\theta_{r,l,s}$ within the model. For a given natal region and season, across all locations, the proportions must sum to 1. We assume that fish from the same natal region, but potentially different rivers or hatcheries, have identical ocean distributions in a given season, and that ocean distributions within a season are the same across Chinook salmon ages. Weitkamp (2010) suggested that ocean distribution may vary with ocean age (ocean age = recovery year – release year) with very young fish (ocean age = 1) found closer to their natal river mouth than older fish (ocean ages 2 to 5), but with the older age classes being broadly similar in distance from their natal river (their tables 5, 6). As our model starts well into ocean age 1 (using Weitkamp's (2010) age accounting; see Table S1.2[1]) and focuses on modeling older fish, those that are susceptible to ocean fisheries, this model assumption matches available information. Although results from Satterthwaite et al. (2013) indicates modest differences in age-specific distributions of older fish from a single stock, the statistical significance of these differences was not assessed. Therefore, modifications that allow for age dependence in ocean distribution should be an important consideration in future work but are unlikely to fundamentally change our conclusions.

In the fall, adult Chinook salmon leave the ocean to return to the freshwater spawning grounds. We model spawning as the proportion of fish leaving the ocean in the middle of the fall season. We define a small number of ocean regions near the river mouth from which fish can enter their river to spawn (see Table S1.3[1]). This ensures that fish cannot instantaneously jump thousands of kilometres into their natal river but does acknowledge that fish from several ocean regions may contribute spawning fish. This assumption differs substantially from other Chinook salmon models that do not explicitly consider spatial distributions (e.g., CTC 2015). We model the proportion of mature fish leaving the ocean as a logistic function of age in years. Again, we acknowledge alternate formulations for leaving the ocean to spawn may be appropriate.

Observation model

There are few direct, fisheries-independent surveys of Chinook salmon in the ocean, but Chinook salmon were caught coastwide across a range of fisheries (but see surveys of very young Chinook salmon; Trudel et al. 2009; Burke et al. 2013). We use spatially explicit recovery data from three fisheries gear types in our analysis (commercial troll, recreational hook and line, and commercial treaty troll) to calculate the expected catch of fish from release *i*, gear *g*, ocean region *l*, season *s*, and calendar year *c* as a function of the number of age *a* Chinook salmon present and fishing mortality in each region. For winter, spring, and summer seasons (seasons without fish escaping to fresh water), the catch follows the Baranov catch equation (Baranov 1918; Beverton and Holt 1957):

$$(1)\qquad \mu_{i,a,l,g} = \frac{F_{a,s,c,l,g}}{(M_a + \Sigma_g F_{a,s,c,l,g})} N_{i,a}\theta_{r,l,s}\{1 - \exp[-(M_a + \Sigma_g F_{a,s,c,l,g})]\}$$

For the fall season, let $N_{i,a,l,S}$ be the number of Chinook salmon present in the ocean after spawning fish enter the river midway through the season. Then catch for the entire fall season is

$$(2)\qquad \mu_{i,a,l,g} = \frac{F_{a,s,c,l,g}}{(M_a + \Sigma_g F_{a,s,c,l,g})} N_{i,a}\theta_{r,l,s}\{1 - \exp[-0.5(M_a + \Sigma_g F_{a,s,c,l,g})]\} + \frac{F_{a,s,c,l,g}}{(M_a + \Sigma_g F_{a,s,c,l,g})} N_{i,a,l,S}\{1 - \exp[-0.5(M_a + \Sigma_g F_{a,s,c,l,g})]\}$$

We use two likelihoods to connect the estimated catch ($\mu_{i,a,l,g}$) to the observed catch. First, for all year–season–location–gear combinations for which we have either documented fishing effort and catches (all troll fisheries and recreational fisheries in the California, Oregon, Washington, and part of British Columbia) or only observed catches (recreational fisheries in most of Canada and Alaska), we model the probability of observing greater than zero Chinook salmon as a Bernoulli random variable:

$$(3)\qquad G_{i,l,g,a} \sim \text{Bernoulli}(\text{logit}^{-1}[\text{logit}(W_{l,s,c,g}\pi_0) + \pi_1 \log(\mu_{i,a,l,g})])$$

where *G* takes on a value of 1 if the observed catch *C* is positive, and a value of 0 otherwise. Here, $W_{l,s,c,g}$ is the fraction of the catch sampled as extracted from the RMIS database (see Table S1.5[1]). The parameters π_0 and π_1 serve to transform the catch to the logit scale and acknowledge that some stocks may be present and caught in fisheries even if the sampling of the catch does not observe them. As sampling effort for CWT has varied both spatially and through time, we calculated the observed sampling fraction from the RMIS database for each tag recovery and aggregated them by season, spatial region, and gear type. We calculated the median value for the sampling fraction among all reported catches in each region and season and set $W_{l,s,c,l}$ to be the median sampling fraction. We estimate a single offset, π_0, which is a proportion bounded between 0 and 1 to account for potential non-independence among individual sampled fish in the catch. Finally, we estimate a slope, π_1, to scale how observation probability increases with increases expected catch.

The second component of the likelihood consists of linking the observed catches to the estimated catches if greater than zero Chinook salmon were observed.

$$(4)\qquad C_{i,l,g,a} \sim \text{LogNormal}(\log(\mu_{i,a,l,g}), \exp[\sigma_0 + \sigma_1 \log(\mu_{i,a,l,g})]) \quad \text{if } C_{i,l,g,a} > 0$$

Here the observation error term for the dispersion between observed and predicted catch has two parameters (σ_0, σ_1) and allows the observation error to vary with larger values of predicted catch.

As expressed in eqs. 3 and 4, our models explicitly acknowledge that our observations of fisheries catches of particular release groups are uncertain (i.e., there is observation error). This contrasts with some models used in salmon management (e.g., CTC 2015) and cohort reconstruction approaches used by other authors (e.g., Coronado and Hilborn 1998; Kilduff et al. 2014) that assume error-free observation of catches.

In addition to recoveries from fisheries, we need to account for the Chinook salmon that leave the ocean and return to their natal river or hatchery and complete their life cycle. Ideally, we would have a likelihood component corresponding to the observed fish in rivers and hatcheries for each release group. Unfortunately, preliminary examination of the RMIS database revealed notable deficiencies in the freshwater recovery data; we identified some individual tag groups from throughout the study region with many ocean recoveries but zero or near zero freshwater recoveries. Such discrepancies have been noted by other authors (e.g., Baker and Morhardt 2001). Furthermore, we compared freshwater recoveries reported in RMIS with recoveries used in several stock assessments. For example, we were unable to reproduce the results reported for Iron Gate and Trinity River hatcheries in Hankin and Logan (2010), which we know included substantial quality control and additions to the data beyond the raw RMIS data. We could not identify which RMIS freshwater recovery data were reliable and which were not, and so we elected to incorporate only information about the relative occurrence of different age Chinook salmon in freshwater recoveries, not the actual expanded numbers of total observed freshwater recoveries. We detail these approaches in the online supplement and provide the mean estimated proportion returning at each age for each region in Table S1.4[1]. This aspect of our model is important because by not using information about in-river recoveries we rely on catches in ocean fisheries to estimate both spatial distributions and the various parameters that scale overall abundance (e.g., juvenile survivorship and gear specific catchability). As a result, our estimates of parameters that the scale total abundance of Chinook salmon, including most prominently juvenile survival and catchabilities, are difficult to estimate and likely mis-estimated by an unknown factor. However, this factor will apply to all modeled releases and thus does not change the relative order of survivorships among releases. We note that virtually all other estimates of survivorship for salmon based on cohort reconstructions face this problem as well (Coronado and Hilborn 1998; Kilduff et al. 2014, 2015; CTC 2015).

Finally, we added two constraints to penalize biologically unreasonable life histories within the model and help account for our imprecision in freshwater recovery data (see Supplement data S2[1] for details). First, we constrained the model so that on average, between ages 1 and 6 greater than 99% of individuals are assumed to leave the ocean by the final model time step. They must either die from natural causes or fisheries or leaving the ocean for fresh water. This ensures the model avoids parameter spaces where there are a large number of old fish present in the ocean (age 7+) and which accords with Chinook salmon biology. Second, we constrained the model so that the total number of fish from a single cohort surviving from release to make a spawning migration to fresh water average (all ages summed) nearly 2%. For both constraints, we allow for substantial variation among releases so individual releases may differ substantively from these average rates (Supplementary data S2[1]).

Estimation

We implemented the above state-space model in STAN (Gelman et al. 2015, Carpenter et al. 2017) as implemented in the R statistical language (R Core Team 2016; Stan Development Team 2016). STAN uses a Hamiltonian Monte Carlo (HMC) sampling (Neal 2011; Hoffman and Gelman 2014; see Monnahan et al. 2016 for a description targeted at ecologists). Table S2.1[1] provides a description of all parameters and prior distributions. STAN estimates the joint posterior distribution of parameters and latent states. For all results reported here we used five chains using a warmup period of 300 iterations and 2000 monitoring iterations. We used model diagnostics such as checks for divergent transitions, comparisons among chains (Gelman–Rubin statistics), and posterior predictive checks.

Analysis of juvenile survival estimates

After estimation of the juvenile mortality rate for each of the 454 release groups, we constructed a linear mixed model to understand drivers juvenile variation. We used $\log(\phi_i)$ as the response variable and explained variation in survivorship using number of months between release and model start (n_month) as a continuous fixed effect and year, origin region, and n_month nested within origin region as random effects. This model allows fish from different origin regions and fish that spend more time at liberty in the river and ocean to have different juvenile survivorships. Past analyses comparing early mortality among releases have often ignored such attributes (Coronado and Hilborn 1998; Kilduff et al. 2014, 2015).

Projected ocean distribution of fall Chinook salmon

The above model provides estimates of many parameters that are important for determining the abundance and distribution of Chinook salmon. However, since hatchery releases of Chinook salmon are not tagged with CWT at constant rates, and hatchery-versus natural-origin fish make up substantially different proportions of different stocks, CWT data alone cannot be used to generate estimates of Chinook salmon abundance in the ocean. We use model estimates in conjunction with estimates of out-migrating juvenile Chinook salmon leaving rivers and hatcheries to provide predicted fall Chinook salmon abundances in space and time. We outline an approach to simulating Chinook salmon using model estimates and show how both the proportional contribution of individual stocks and aggregate abundance change under two illustrative scenarios.

Generating predicted fall Chinook salmon distributions require specifying three model components. First, we need estimates of the number of juvenile fall Chinook salmon produced by each origin region (including both hatchery and wild). Second, we need to specify the fishing mortality occurring in space and time. Finally, we need to determine scenarios for juvenile mortality.

For the first scenario, we compiled available information on juvenile fall Chinook salmon production from hatchery and wild sources for each origin. We present approximate estimates of juvenile production in Table S3.1[1] and detail the methods and data sources used for each area estimate in Supplement S3[1]. For fishing mortality, we used the median mortality for each area and season estimated across the observed time-series (1979–1995). For juvenile mortality, we used a simple assumption: all juvenile fish experience the same mortality regardless of their origin. Together these assumptions are designed to reflect the distribution of fall Chinook salmon in the ocean under typical ocean conditions, not the distribution and abundance in a particular year. We refer to this as the "base" scenario.

For the second scenario, we used the same value of fishing mortality (median) and juvenile mortality (mean, spatially invariant) as the base scenario. But for Chinook salmon production, we reduced hatchery production in Puget Sound (PUSO) by half from 37 to 18.5 million. We then compare the abundance and distribution of Chinook salmon in the ocean under the base and "PUSO hatchery" scenarios to illustrate the consequences of changing aspects of hatchery production for ocean abundance and distribution. Other assumptions and simulations could be used to generate distributions and abundance under other scenarios, but we provide a relatively simple, hypothetical scenario here as an example of the possibilities of this approach.

For both scenarios, we use Monte Carlo methods to sample from the posterior estimates of estimated parameters and simulate abundance and distribution through time. As we have fixed juvenile survival, fishing mortality, and the number of juveniles arising from each region, variation only reflects uncertainty in the spatial distribution and in the parameters associated with spawning. Thus the simulations underestimate the overall uncertainty in abundance and distribution. We also use the average process error for each origin region (Fig. S1.7[1]), which further underestimates uncertainty.

Results

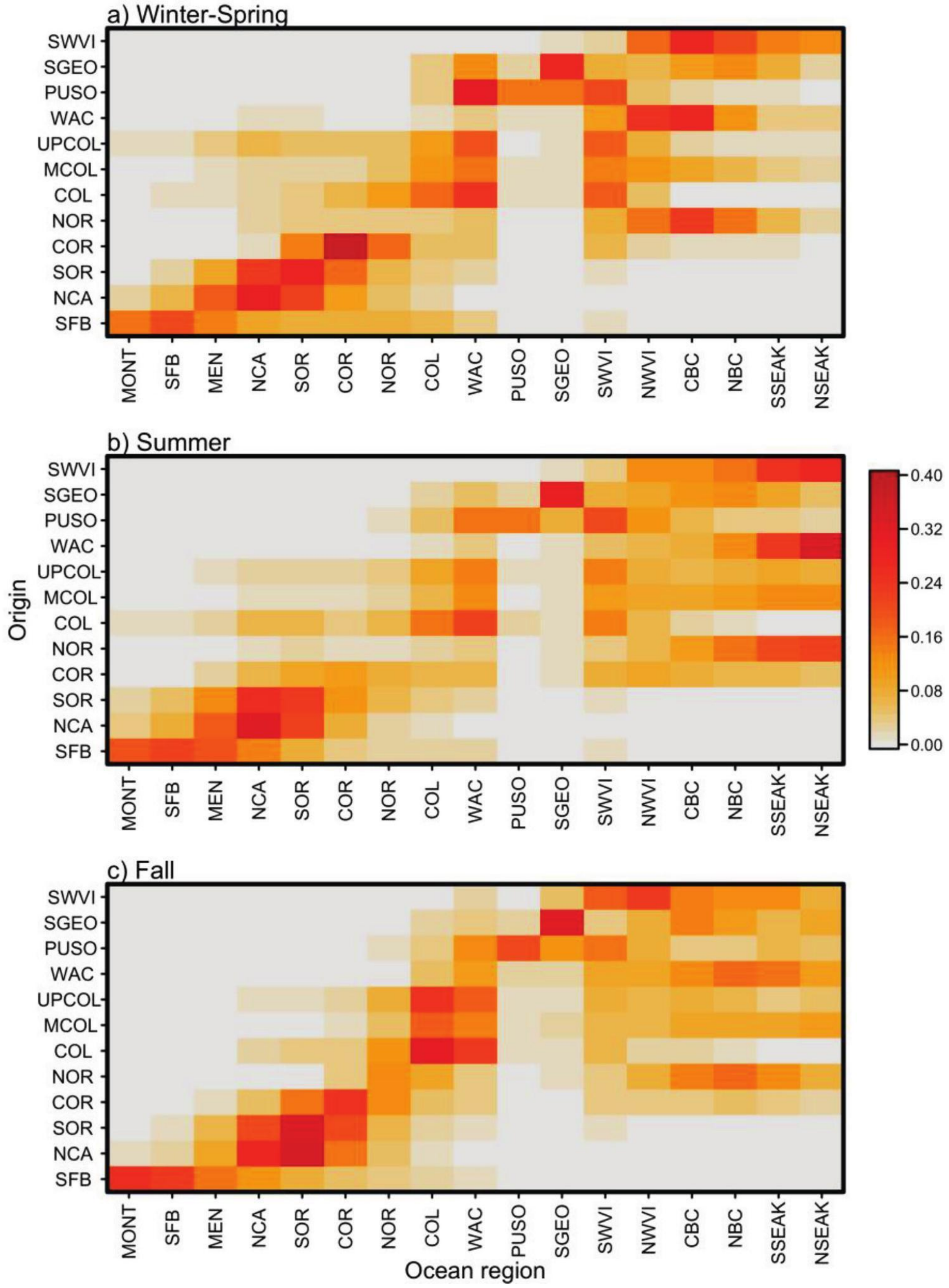
Despite the large amount of data and many latent states and parameters, the model converged and produced reasonable biological estimates for parameters. The effective sample size for all parameters was greater than 1000 and maximum $\hat{R}$ (a measure of model convergence) was less than 1.01. We focus on two model components in the main text before turning to two simple scenarios to understand the attributes of Chinook salmon ocean aggregations using simulations. We present posterior estimates of model parameters in the online supplement along with figures of other major model components.

Spatial distribution of Chinook salmon by origin and season

We detected strong differences in seasonal ocean distribution among different origin regions for fall Chinook salmon (Fig. 3). A common pattern across stocks was that fish were generally distributed near their origin region. For example, fish originating between California and southern Oregon (SFB, NCA, SOR) remained in United States waters south of the British Columbia border (regions WAC and south) and were observed rarely in Canadian and Alaskan waters in our data set. Fish from the most northern region, SWVI, were almost never present south of their origin and were estimated to be almost exclusively in Alaska and Canada. Fish from the Columbia River basin (COL, MCOL, and UPCOL) showed the broadest spatial distribution with significant proportions present in areas from California to Alaska. Virtually all fish estimated to be present in the Salish Sea (PUSO, SGEO) originated there, indicating few Chinook salmon from the outer coast migrate into the Salish Sea.

There was a signature of seasonal distributions in fish from nearly all regions. Fish from a given ocean region tended to be more northerly distributed in summer than in winter–spring, and due to spawning migrations Chinook salmon tend to be located near their region of origin during the fall. Ocean distributions also tend to be spatially less concentrated in the winter–spring. In part, this may reflect the uneven length of the seasons in our model as winter–spring spans seven months (November–May) while summer spans only two (June–July).

Fig. 3. Estimated proportional spatial distribution by season of fall Chinook salmon originating from 11 different regions ($\theta_{i,r,s}$). Each row represents the proportion of fish from a region present in each ocean region (rows sum to 1). Posterior means are shown.



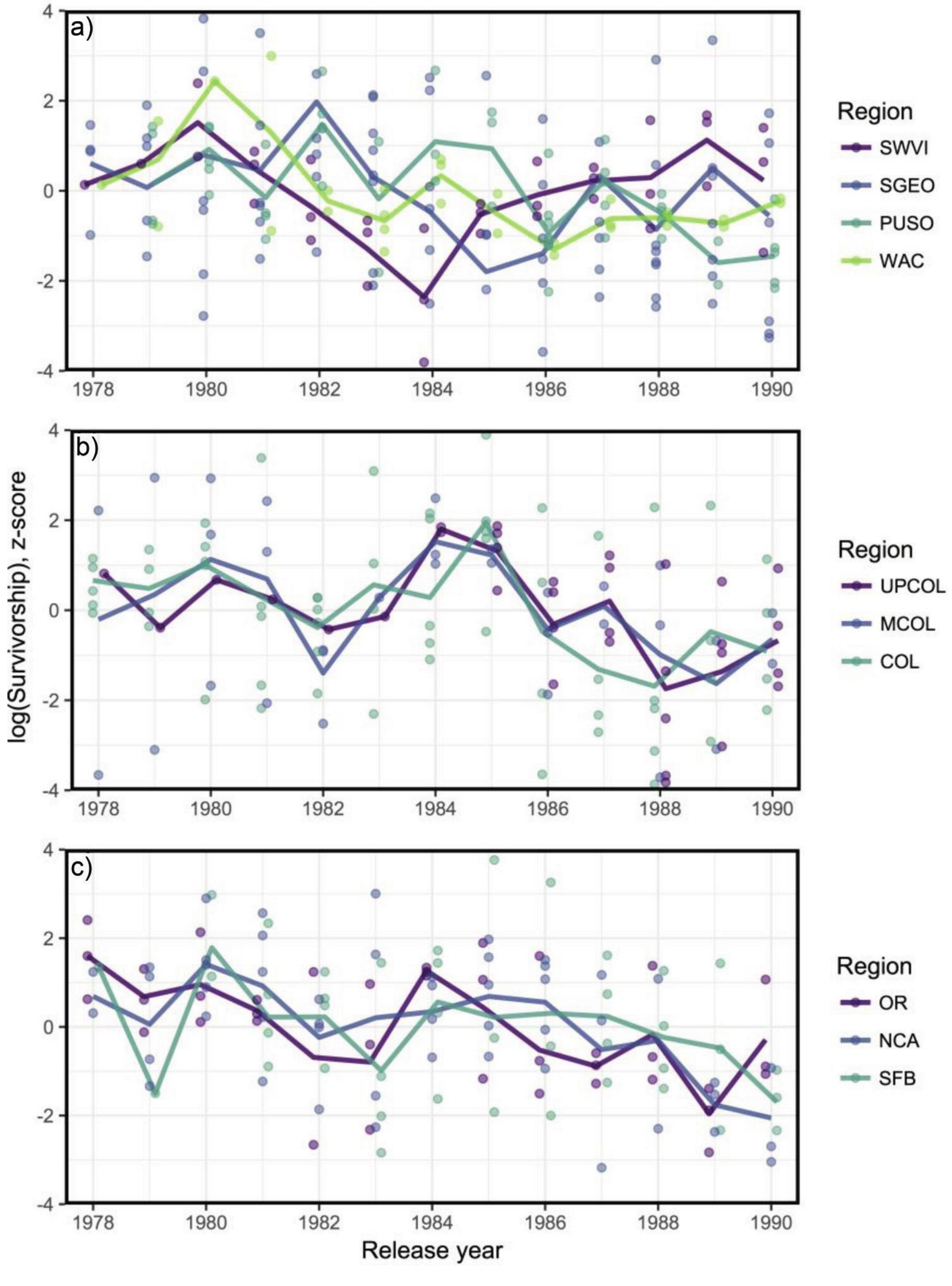
Variation in early mortality

Estimates of mortality for each of the 454 release groups showed wide variation in mortality rates among releases (range of posterior medians for ϕ_i: 1.39 to 3.29; across release mean = 2.02) corresponding to a range of survivorship of 0.037 to more than 0.248 for the period between release and the start of the model in April of brood year + 2. As this range includes releases from all origin regions and years, and thus includes releases with vastly different lengths of time between release and the start of the model (from 1 to 13 months), such large variation is not unexpected. We further summarized model estimates of early mortality in two ways.

The linear mixed effect model showed a large effect of n_month on $\log(\phi_i)$ with longer time periods associated with increase mortality (slope estimate for n_month: 0.002 (0.002); mean(SE)), indicating that on average, an increase of one month resulted in an increase of 0.002 in $\log(\phi_i)$. There was strong among-region variation in the overall mortality intercept (SD among regions = 0.053) and variation among years (SD = 0.033). This result coincides with intuition — fish that spend more time in the river and ocean should have greater mortality — but this result does highlight that many past analyses comparing early mortality among releases have ignored such attributes (Coronado and Hilborn 1998; Kilduff et al. 2014, 2015).

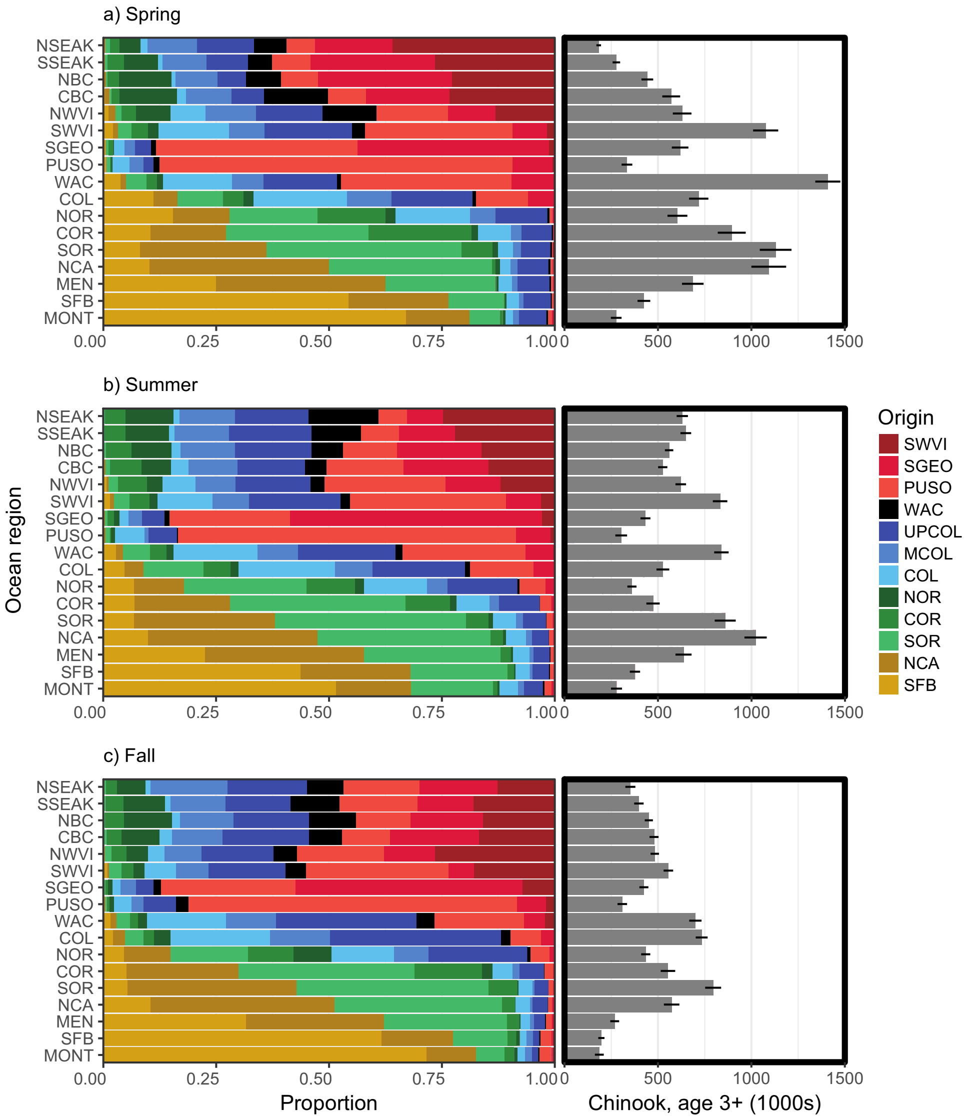
Second, to make our results comparable to estimates of previous analyses of Chinook salmon early survivorship (Kilduff et al. 2014), we used estimated model parameters to calculate estimated survivorship to the beginning of fall season, age 2. We estimated survivorship for each release in the absence of fishing which accounted for juvenile mortality, natural mortality, and estimated

Fig. 4. Survivorship trends for juvenile Chinook salmon from release to 1 August, brood year +2 for different origin regions between 1978 and 1990. Raw survivorship scores have been converted to *z* scores (subtract the among-year mean, divide by the standard deviation) to make trends in survival comparable among regions. Panels show weighted mean for Chinook from northern regions (*a*), the Columbia basin (*b*), and southern regions (*c*; see also Fig. 1). Individual points show mean estimates for individual release groups. Owing to low numbers of release groups in Oregon regions (NOR, COR, SOR), we combined Oregon releases into a single "OR" region. [Colour online.]



process error, $S_i = \exp(-\phi_i - \sum_{a=1}^{a=2}[M_a + \omega_{i,a}])$, where $\omega_{i,a}$ is the estimated process variability. For region combinations that had at least three releases in a given year, we calculated a weighted mean and weighted standard deviation for each region and converted estimated survivorship to *z* scores (subtracted the among-year mean, divided by the standard deviation among years; Fig. 4). We use *z* scores to emphasize that our results should not be used as estimates of absolute survivorship, as we do not include release-specific information about freshwater recoveries or recoveries from marine net fisheries. Owing to relatively few releases in SOR, COR, and NOR, we combined these three regions to calculate a single mean for the Oregon coast (denoted "OR"). Survivorship between release and age 2 was highly variable among regions and both within and among years. Interestingly, most regions show substantial temporal variation in survivorship, but years of high and low survivorship are not coincident among regions. Survivorship trends from the Columbia River tended to be fairly coincident (Fig. 4*b*), as did fish from Oregon and California (Fig. 4*c*), but similar trends among northern stocks were less obvious (Fig. 4*a*). Overall there was very high variability within regions in some years (e.g., SFB in 1985) indicating strong differences in survivorship among hatchery releases. As our model does not include abundances of CWT recoveries from fresh water or the small number of recoveries from nontarget fisheries, we expect these esti-

Fig. 5. Distribution and abundance of fall Chinook salmon age 3 and older in the ocean. We show proportional contribution of age 3+ fish to each ocean region (left panels) and total abundance (right panels) at the beginning of spring (*a*), summer (*b*), and fall (*c*) seasons. Results arise from simulations assuming median fishing mortality for each area and season (see Fig. S1.9[1]) and a single juvenile mortality rate shared across all regions.



mated survivorships biased from their true values. However, the patterns of relative survivorship across time and among regions should be correct.

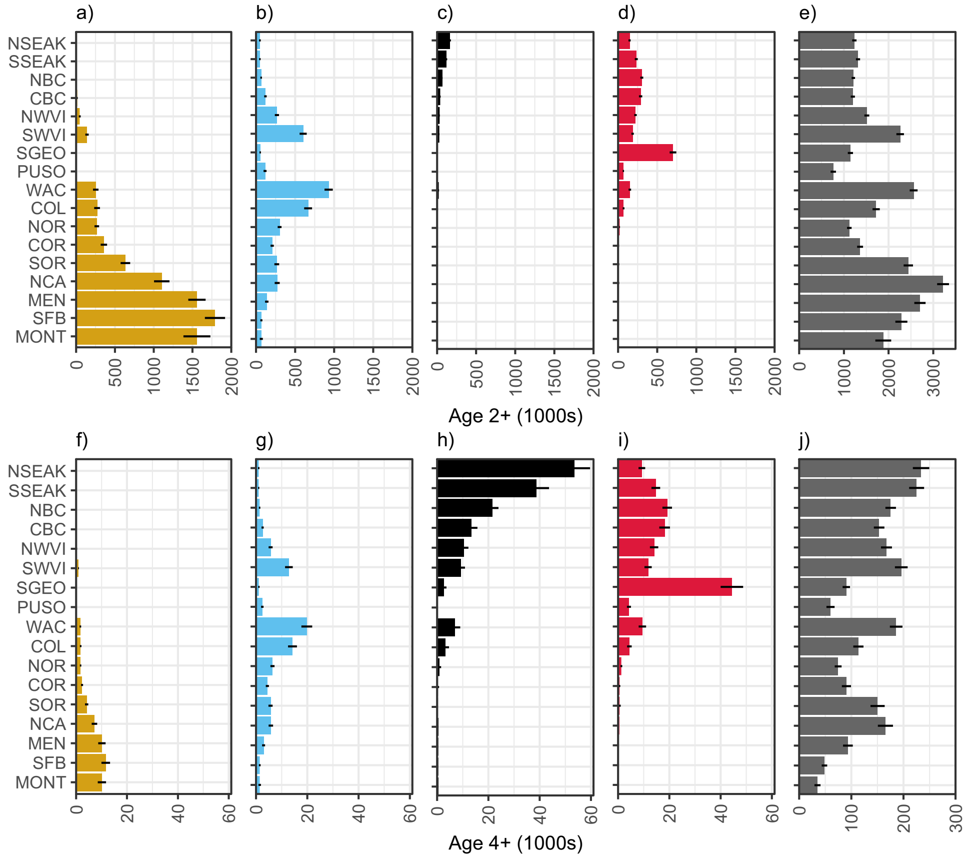
Comparing distributions and cumulative abundance

Given the varied production of Chinook salmon among origin regions (Table S3.1[1]), and the distinct ocean distributions of these fish (Fig. 3), it is not surprising that ocean areas vary substantially in proportional compositions and aggregate abundance of Chinook salmon (Fig. 5). In terms of proportional contribution, seasonal variation is present but not striking. For example, the two southeast Alaska regions (NSEAK and SSEAK) are comprised predominantly of fall Chinook salmon from Canada, Washington, and the Columbia River basin in all seasons, though the proportion from Columbia basin increases notably from spring to summer. The Salish Sea (regions PUSO and SGEO) are dominated by fish originating in those regions in all seasons, while the Californian ocean regions (MONT, SFB, MEN, and NCA) all have close to or more than 50% of fish present originating from California rivers in all seasons (Fig. 5).

While the proportional composition of a given area may be relatively consistent across seasons, the distribution changes for many origin regions simultaneously, resulting in substantial difference among seasons in the cumulative abundance of fall Chinook salmon (Fig. 5). Notably, the southern most regions (MONT and SFB) and PUSO have the lowest total abundance in all seasons. In contrast, the northern regions (SSEAK and NSEAK) have relatively low abundance in the spring (Fig. 5*a*), but the abundance increases markedly during the summer (Fig. 5*b*) reflecting a northerly shift in distributions of most Chinook salmon stocks (Fig. 3).

The cumulative abundance and distribution of fall Chinook salmon also depend strongly on the age range of Chinook salmon considered. For example, the cumulative abundance of fish age 2 and older is substantially different from the distribution of fish age 4 and older (compare Figs. 6*e* and 6*j*). Old and large fish are notably more abundant in the northern regions, whereas young and small fish are more available in the southern parts of the range. Note that this change in distribution is not driven by changes in the distribution of fish with age (fish of different ages

Fig. 6. Summer distribution and abundance of fall Chinook salmon from four representative regions and two age groups under the base scenario. Areas SFB (*a*, *f*), COL (*b*, *g*), WAC (*c*, *h*), SGEO (*d*, *i*), and aggregate abundance across all stocks (*e*, *j*). [Colour online.]



are modeled as having identical ocean distributions; see Methods) but is due instead to strong differences in maturation probability among origin regions. Fish originating from northern areas tend to mature at older ages (Fig. S1.8[1]; Table S1.4[1]). This is readily apparent in comparing the increasing contribution of WAC and SGEO origin fish to total age 4+ fish relative to age 2+ and the concomitant decline of SFB and COL fish (Fig. 6).

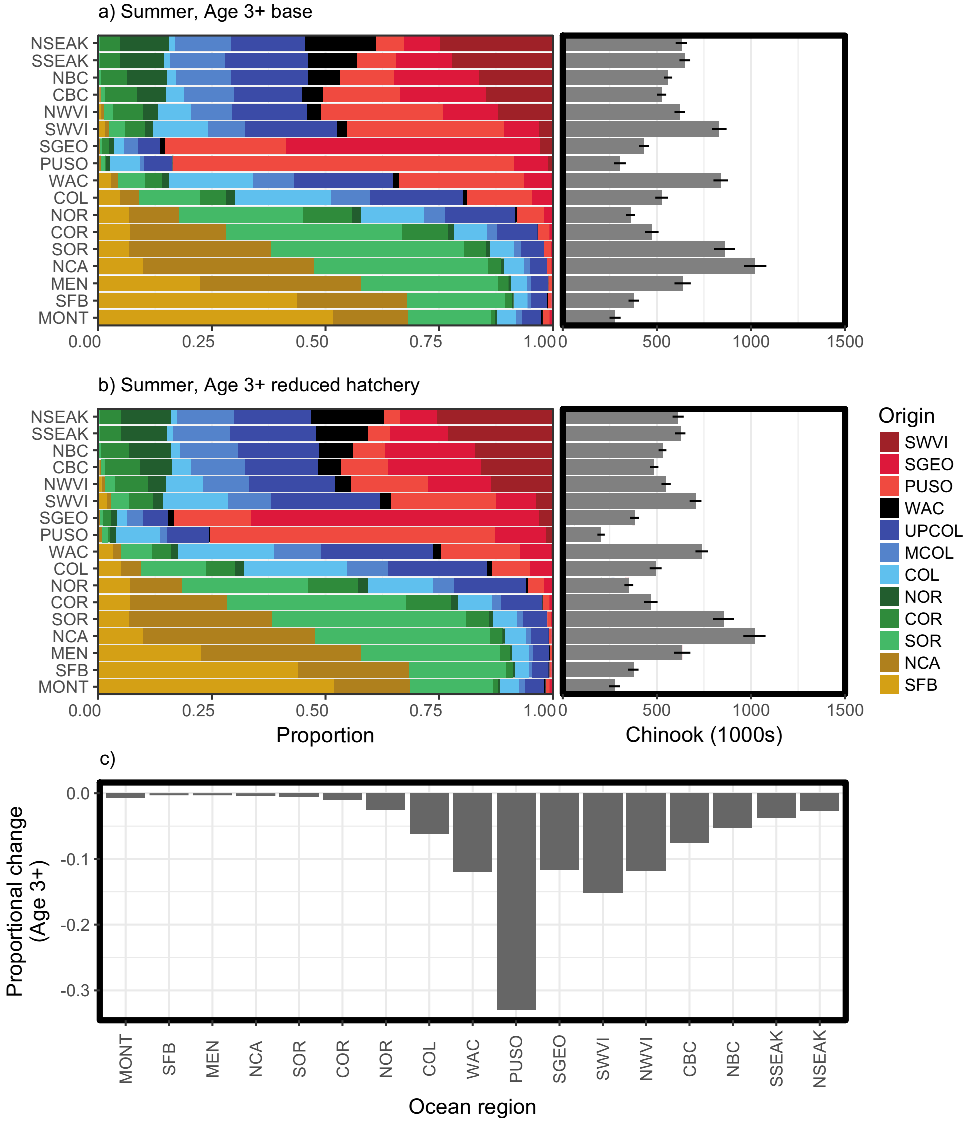
Finally, comparisons of the base and PUSO hatchery scenarios reveal how changes in management have ramifications beyond the region of origin. We contrast the projected abundance in total abundance between scenarios for age 3+ during the summer (Fig. 7). From a fisheries perspective, most Chinook salmon are vulnerable to both commercial and recreational fisheries by summer age 3 (model season 10; Table S1.2[1]; Fig. S1.6[1]), and we can consider the changes between the two scenarios as affecting the number of fish potentially available to fisheries in a given region. We clearly show that a reduction of hatchery production by half is predicted to change Chinook salmon abundance most dramatically in Puget Sound,a decline in abundance by nearly one-third between base and PUSO hatchery scenarios,but declines of more than 10% are predicted along the Washington coast (WAC) and southern Canadian regions (SGEO, SWVI, NWVI) as well. Changes to PUSO hatchery production are predicted to have a limited effect on the most southerly and northerly regions.

Discussion

We present a coastwide model for fall Chinook salmon that simultaneously models populations originating from California to British Columbia and accounts for biological variation among populations and across time. We explicitly account for the fisheries effort and sampling of fisheries that affect the detection of Chinook salmon populations in the ocean. Our model provides a joint estimate of salmon spatial distribution, juvenile mortality, and spatiotemporal estimates of fisheries mortality; processes that are typically estimated and discussed separately (e.g., Weitkamp 2010; Kilduff et al. 2014; CTC 2015). By estimating a joint time-series model that includes populations spanning much of the northeastern Pacific, we are able to move beyond comparisons of CPUE of different Chinook salmon stocks derived from CWT (Satterthwaite et al. 2013; Norris et al. 2000) or Genetic Stock Identification (GSI; Bellinger et al. 2015; Satterthwaite et al. 2015) and translate information from fisheries catch into estimates of spatial distribution and total abundance. Importantly, our work explicitly accounts for missing data, locations and times where no one was fishing and therefore no sampling of Chinook salmon occurred, and thus expands on previous examinations of salmon ocean distribution. Our work is a tool that has broad application for understanding patterns of spatiotemporal variation among Chinook salmon and other tagged salmonid populations. Additionally, it is a simulation platform for exploring the consequences of biological variation and management decisions on an important marine resource.

We present a step toward understanding the portfolio of Chinook salmon populations contributing to each coastal region in each season. A full exploration of spatial portfolios of Chinook salmon would involve accounting for factors contributing to variation within and covariation among populations and is beyond the scope of this paper. However, basic tenets of portfolio theory do allow us to begin to discuss the implications of the spatial patterns. Broadly, portfolio theory suggest that regions that are more highly reliant on fish originating from one or a few areas would experience more temporal variability than areas with more contributing populations. In the base scenario, three areas had greater than 50% of their abundance derived from a single region in all seasons: two in California (MONT, SFB) and Puget Sound,

Fig. 7. Comparison of two simulation scenarios. (*a*, *b*) Proportional contribution of age 3+ fish to each ocean region (left panels) and total abundance (right panels) at the beginning of summer under the base scenario (*a*) and under reduced hatchery production from the PUSO region (*b*). Panel (*c*) shows the proportional change in total abundance from base to PUSO hatchery scenarios for age 3+ Chinook salmon.



Washington (PUSO). Additionally, these three areas are also estimated to have the lowest total Chinook salmon abundance. Together these facts suggest these regions with low stock diversity are likely susceptible to periods of especially low abundance. Indeed, the ocean fishery in California and southern Oregon was recently closed for two consecutive years due to poor production of Sacramento River fall Chinook salmon (Lindley et al. 2009; Carlson and Satterthwaite 2011), and our simulation of reduced hatchery production highlights the sensitivity of PUSO to changes in local hatchery production (Fig. 7). In contrast, other regions are composed of fish from diverse sources and have a more balanced contribution (e.g., NOR, SWVI, NWVI, NBC, SSEAK, NSEAK) and would be expected to have more stable portfolios over the long term. Interestingly, these areas largely correspond to locations with important and historically productive Chinook salmon troll fisheries (Southeast Alaska, west coast Vancouver Island, and Oregon coast).

From the perspective of predator populations, increased stock diversity (and stability) may translate to increased growth rates. Anecdotally, piscivorous killer whale populations with higher latitude distributions tend to have higher population growth rates (Ward et al. 2013). When considering portfolios, though, it is important to note that this analysis does not include other Chinook salmon life-history types. Spring run Chinook salmon are the other major life-history type in the northeastern Pacific; other run types such as winter run Chinook salmon are confined to California rivers and relatively rare (Quinn 2005), though in some locations summer runs are also present. Spring Chinook become more abundant with increasing latitude as all Chinook originating from Alaskan and northern British Columbian rivers are spring run. Thus, while this analysis presents a reasonable approximation of the Chinook portfolio in California, it dramatically underestimates both the total number of Chinook and life-history diversity present in British Columbia and Alaskan waters in particular. Further work must be done to incorporate the range of life histories of Chinook salmon into ocean portfolios. Overall however, portfolio approaches have clear potential for examining the consequences of aggregate patterns of abundance, how they may affect directed fisheries or incidental catch in nondirected fisheries, ecosystem considerations for species dependent upon aggregate abundance such as killer whales or other marine mammal predators, and how portfolio properties vary in response to management or environmental changes.

While the outlined model incorporates many important attributes of Chinook biology, it necessarily makes simplifying assumptions to accommodate missing or incomplete data and ensure model identifiability. Several major aspects of our estimation model should be the foci of future improvement and research. Most importantly, reliable data pertaining to tag recoveries in the escapement of Chinook to fresh water would greatly improve estimates of both maturation probabilities and ocean survivorship. Such information would have the largest impact on the juvenile survivorship estimates (Fig. 4) and the catchability coefficients (*q*; see Supplementary data S2[1]) as they serve to scale the overall abundance of fish available in the ocean for fisheries. However, corralling and verifying such data coastwide is a major task that is beyond the scope of this project. Other reasonable and important extensions to the model include (*i*) allowing for age-specific or oceanographic driven changes to seasonal distributions, (*ii*) accounting for population specific growth rate and (or) temporal variation in growth that would translate into population difference in vulnerability to fishing gear types, (*iii*) including the fishing effort data necessary to expand the study time-window to include data from 1996 onward, and (*iv*) incorporating information from non-mixed stock fisheries such as terminal gillnet and seine fisheries that are not equally likely to capture fish from different origins. Projections of total Chinook salmon abundance could be substantially improved with improved information about the outmigration of juvenile Chinook salmon from rivers coastwide.

Much of the interannual dynamics of ocean mortality for Chinook tends to happen very early after migrating downstream, when size and growth play a large role in survival (Beamish et al. 2004; Duffy and Beauchamp 2011). These complex ecological dynamics vary by season and year and require much more data to describe than we could include in this model. Moreover, disentangling juvenile salmon mortality rates in different habitats (rivers, estuaries, coastal ocean) is an ongoing effort. We applied a simple approach, allowing juvenile survival to be independent of adult survival and vary by release, but did not model the full mechanistic processes underlying variation in juvenile mortality. Given the importance of early life stages on overall population dynamics, connecting this model more closely to early survivorship is likely one of the more crucial aspects to tackle in future work.

An important additional consideration for ocean distribution modeling is understanding how to incorporate information from both physical tagging using older technologies (CWT) and information derived from more recently developed and applied genetic stock identification tools (GSI; Satterthwaite et al. 2014; Bellinger et al. 2015). In practice, GSI data provides information about the proportional contribution of fish from different origins in a given area or catch per unit effort information for different stocks. Using GSI data alone without an accompanying analysis of scales or otoliths lacks information about age structure. As the age structure will strongly affect the estimated stock composition of any given ocean region, GSI information alone may provide difficult to interpret patterns (Fig. 6). Overall, however, our predictions (Figs. 5–7) should provide predictions for proportional compositions that can be compared directly to GSI studies. Integrating GSI and CWT data in a single integrated framework is an exciting and important area for future work.

Beyond data and model complexity, computational limitations do present a challenge for large models like ours. In theory, there is no constraint upon how many releases can be modeled simultaneously, but the 454 releases modeled here require estimation of nearly 8600 latent states and incorporate over 228 000 observations for the binomial likelihood (the total number of releases–location–season–gear type combinations) and over 17 000 observations for the log-normal component. Expanding the number of releases substantially would require substantially improving computational resources or moving away from full Bayesian estimation toward approximations of the posterior distribution such as Laplace approximations (Rue et al. 2009).

Overall, we provide a framework to integrate information from multiple fall Chinook salmon stocks to simultaneously estimate parameters from a complex population dynamic model. We emphasize the spatiotemporal attributes of the parameters here, particularly estimates of ocean distribution and regional patterns in juvenile survival, and provide illustrative examples of how these estimates can be used to simulate scenarios and that these scenarios may be useful in a variety of management and ecosystem contexts in the future.

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