

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

3

4 Andrew Olaf Shelton<sup>1</sup>

5 William H. Satterthwaite<sup>2</sup>

6 Eric J. Ward<sup>1</sup>

7 Blake E. Feist<sup>1</sup>

8 Brian Burke<sup>3</sup>

9

10 <sup>1</sup> Conservation Biology Division, Northwest Fisheries Science Center, National Marine  
11 Fisheries Service, National Oceanic and Atmospheric Administration, 2725 Montlake  
12 Blvd. E, Seattle, WA 98112, U.S.A.

13

14 <sup>2</sup> Fisheries Ecology Division, Southwest Fisheries Science Center, National Marine  
15 Fisheries Service, National Oceanic and Atmospheric Administration, 110 McAllister  
16 Way, Santa Cruz, CA 95060, USA

17

18 <sup>3</sup> Fish Ecology Division, Northwest Fisheries Science Center, National Marine Fisheries  
19 Service, National Oceanic and Atmospheric Administration, 2725 Montlake Blvd. E,  
20 Seattle, WA 98112, U.S.A.

21

22

23 Keywords: *Oncorhynchus tshawytscha*, portfolio theory, ocean distribution, spatio-  
24 temporal models

25

26

27 Supplement S1: Supplemental Tables and Figures

28 Supplement S2: Detailed methods

29 Supplement S3: Smolt outmigrant data description

30 **Abstract**

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

## 46 **Introduction**

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

52           Population structure, where individuals in a given area consist of multiple, distinct  
53 groups, may further complicate marine management. Particular populations, sub-  
54 populations, or life-history types within a single population often co-occur (e.g. Schindler  
55 et al. 2010; Teel et al. 2015; Satterthwaite and Carlson 2015), but the contribution of each  
56 group to the aggregate abundance in migratory species may vary spatially and temporally  
57 and therefore the importance of a given component in one region often differs from the  
58 same component in another. Portfolio theory (Markowitz 1952; Koellner and Schmitz  
59 2006) has shown that population complexes with a diverse set of contributing groups will  
60 result in reduced variation in aggregate abundance (Hilborn et al. 2003; Schindler et al.  
61 2010, 2015). Most applications of portfolio theory to natural systems have emphasized  
62 the temporal attributes of aggregate abundance, showing how increased diversity among  
63 components (Moore et al. 2010; Thorson et al. 2014; Satterthwaite and Carlson 2015) or  
64 life-history diversity (Hilborn et al. 2003; Schindler et al. 2010; Greene et al. 2010) lead  
65 to resilience and stability in aggregate.

66           For migratory species, it is important to recognize that the portfolio framework is  
67 relevant in a spatial as well as temporal context (Griffiths et al. 2014). Movement may  
68 create a shifting mosaic in which the distribution of both the aggregate abundance and the

69 individual contributors to abundance shift in space and time. Furthermore, while fisheries  
70 are often focused on maintaining robust aggregate abundances over the long term,  
71 conservation decisions are often focused on avoiding low abundance for component  
72 populations or sub-populations. Management actions to protect or conserve these less  
73 productive stocks is generally referred to as ‘weak stock’ management. Thus, conflict  
74 between managing aggregate abundance and the protection of a particular population  
75 may arise and strategies for spatial and temporal management must consider this conflict.

76 Chinook salmon (*Oncorhynchus tshawytscha*) are a highly migratory species  
77 native to the Pacific coast of North America. In the eastern Pacific, Chinook salmon  
78 occur along the continental shelf and into the open ocean, ranging from central California  
79 to Alaska (Healey 1991), where they support extensive and economically valuable  
80 fisheries (PFMC 2016a; PSC 2016). Chinook salmon also serve important roles in the  
81 ecosystem, as prey for both marine predators such as sharks, pinnipeds, and killer whales  
82 (Ford 2012; Chasco et al. 2017) and terrestrial predators including birds and bears (Good  
83 et al. 2007; Schindler et al. 2013). Chinook salmon inhabiting any given coastal area are  
84 comprised of fish from multiple stocks (Healey 1991; Norris et al. 2000; Weitkamp  
85 2010). Understanding the spatial and temporal dynamics of Chinook salmon throughout  
86 their range is critical, as some populations of the northeast Pacific are depleted, and listed  
87 under the US Endangered Species Act (ESA) or Canadian Species At Risk Act (SARA).

88 While Chinook salmon are one of the iconic species of the northeast Pacific and  
89 subject to large-scale fisheries and extensive research (Ruckelshaus et al. 2003), their  
90 marine spatial distribution and migration patterns are poorly understood. Some stock-  
91 specific distributions for juvenile Chinook salmon are available from research surveys

92 (Trudel et al. 2009; Tucker et al. 2011; Burke et al. 2013) while others have provided  
93 stock-specific estimates of ocean distribution using coded-wire tags (CWT; Norris et al.  
94 2000; Nandor et al. 2010; Weitkamp 2010) or genetic stock identification (Winans et al.  
95 2001; Bellinger et al. 2015; Satterthwaite et al. 2015). The vast majority of these tagging  
96 and sampling programs are a result of decades of intensive marking and tagging of  
97 hatchery raised fish (Nandor et al. 2010; Weitkamp 2010; Satterthwaite et al. 2013).  
98 Fisheries management models such as those developed and used annually by the Pacific  
99 Salmon Commission's Chinook Technical Committee (CTC; e.g., CTC 2015) use  
100 information from CWT recoveries in many fisheries along the coast in concert with  
101 spawning escapement to provide information about the abundance and status of Chinook  
102 salmon stocks from Oregon to Alaska. The CTC's work provides vital fisheries  
103 management advice annually, but it does not include information on Chinook salmon  
104 stocks from California and does not provide direct estimates of spatial distribution.

105         In the most comprehensive peer-reviewed coastwide study to date, Weitkamp  
106 (2010) examined tag recoveries for 93 Chinook salmon stocks in ocean fisheries from  
107 California to the Bering Sea to produce the only comprehensive description of inferred  
108 stock-specific spatial distributions. While Weitkamp (2010) was groundbreaking in its  
109 breadth and scope, it did not account for fishing effort nor changes in seasonal  
110 distribution, meaning that estimated distributions may be biased by uneven fishing and  
111 fisheries sampling effort in space and time. Because of differences in stock-specific  
112 tagging rates, numbers of tag recoveries could not be compared among stocks to infer  
113 relative densities. More targeted studies have inferred season-specific local densities from  
114 catch per unit effort (CPUE), typically involving fewer stocks, a smaller spatial range,

115 and only considering one gear type at a time (Norris et al. 2000; Sharma et al. 2013;  
116 Satterthwaite et al. 2013, 2015). Although Newman (1998) developed a state-space  
117 framework for integrating spatial data on tag recoveries into a demographic model  
118 including mortality and movement, there are limited applications of this approach to  
119 empirical datasets aside from a coho salmon (*Oncorhynchus kisutch*) stock in  
120 Washington (Newman 2000).

121         Here we explore the spatio-temporal dynamics of fall-run Chinook salmon  
122 occurring along the Pacific coast of North America using an integrated modeling  
123 approach. We use tag release and recovery data from ocean harvest along with data on  
124 commercial and recreational fishing effort to estimate a spatio-temporal model for fall  
125 Chinook salmon. By modeling all stocks simultaneously, our model shares information  
126 among stocks in a biologically reasonable way and leverages the fact that fish derived  
127 from different rivers swim in the same areas of the coastal ocean to improve estimates of  
128 shared processes. We provide estimates of seasonal ocean distribution and abundance for  
129 Chinook salmon populations representing the full geographic extent of North American  
130 fall Chinook salmon. To our knowledge, this is the first coastwide analysis of seasonal  
131 patterns in density that simultaneously accounts for multiple axes of biological variation  
132 among Chinook stocks (differences in maturation, variation in ocean distribution, and  
133 spatio-temporal variation in early ocean survival), variation in detection probabilities due  
134 to fisheries effort and gear type vulnerabilities, and both measurement and process error.  
135 After estimating our biological model, we combine estimates of Chinook salmon ocean  
136 distribution with regional estimates of juvenile Chinook salmon production to generate  
137 estimates of the cumulative abundance and distribution of fall Chinook salmon

138 abundance along the entire west coast of North America on a seasonal basis. This  
139 unifying statistical framework improves our understanding of Chinook salmon biology  
140 and provides a methodology from which it is possible to explore changing ocean  
141 distributions, spatio-temporal variation in mortality, and interactions with other species  
142 and fisheries.

143

## 144 **METHODS**

### 145 *Study Species*

146 Chinook salmon (*Oncorhynchus tshawytscha*) are the largest of the northeast  
147 Pacific salmon and native populations spawn in rivers along the northern Pacific Ocean  
148 from northern Japan to Siberia along the Asian coast and central California to Alaska  
149 along the North American coast (Healey 1991; Quinn 2005). Although considerable life-  
150 history diversity exists both across and within watersheds, populations are typically  
151 classified based on the season when adults return to their natal rivers to spawn (run  
152 timing, generally designated as fall, winter, spring, and summer runs). Adult run timing  
153 may be a good predictor of additional aspects of life-history including the timing of major  
154 events in the freshwater phase of the lifecycle (Healey 1991). The life history variation in  
155 run-timing for adults also translates into differences in when juveniles of each run type  
156 migrate to the ocean. For example, fall run Chinook salmon juveniles typically emigrate  
157 to sea during their first year of life while spring run fish typically spend an extra year in  
158 freshwater before emigrating. There can be considerable variation within runs, and  
159 variability in run timing appears to have evolved independently many times (Waples et

160 al. 2004; Moran et al. 2012). Adults typically spend 2-4 years at sea with northern  
161 populations more often maturing at older ages (Myers et al. 1998; Quinn 2005).

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

169

#### 170 ***Data***

171         Although there are multiple Chinook salmon run types on the west coast of North  
172 America, fall Chinook salmon are the most dominant and data rich (both in terms of  
173 population size and tagging programs). Thus, we restricted our analysis to developing  
174 models of fall Chinook salmon ocean distribution, with the idea that these general  
175 methods are extendable and applicable to other life-history types and species. We used  
176 three sources of data to estimate ocean abundance and distribution. First, we extracted  
177 information on CWT releases from the Regional Mark Information System (RMIS;  
178 [http://www.rmis.org/rmis\\_login.php?action=Login&system=cwt](http://www.rmis.org/rmis_login.php?action=Login&system=cwt)). We extracted  
179 information from tagged releases from 43 major hatcheries spanning central California to  
180 Vancouver Island British Columbia and representing fish released between 1978 and  
181 1991 (from brood years 1977 to 1990). Fall Chinook salmon are rare in rivers north of  
182 British Columbia, where the majority of Chinook salmon runs are spring run. The range



183 of years analyzed was constrained primarily by the availability of fishing effort data (see  
184 below) and the high intensity of fishing effort during this period. If the model failed for  
185 years with substantial fishing effort, it would likely fail for more recent years which have  
186 seen coastwide declines in Chinook salmon fisheries. For central Oregon to Canada, we  
187 selected hatcheries based on their previous identification as major hatcheries associated  
188 with indicator stocks by the Pacific Salmon Commission (CTC 2015). Major hatcheries  
189 from southern Oregon and California were selected based on the indicator stocks used by  
190 the Pacific Fishery Management Council (PFMC 2016b). Table S1.1 presents a complete  
191 list of hatcheries included in the analysis.

192 For this set of years and hatcheries, we identified 2,196 unique CWT tag codes to  
193 include, representing approximately 83 million CWT fish released during the study  
194 period (see Table S1.6 for a complete list). This list of tag codes excludes releases where  
195 comments indicated major problems with the release (e.g. high disease prevalence). We  
196 then aggregated tag codes released by individual hatcheries, brood year, brood stock,  
197 release year, and release season. For hatcheries that released fall Chinook salmon at  
198 multiple points during the year (i.e., they release both fingerling and yearling Chinook  
199 salmon), we categorized tag release into two groups based on season of release. This  
200 consolidation resulted in 454 unique hatchery-brood year-release season combinations  
201 (see Table S1.1), each of which we refer to as a “release” in subsequent sections.

202 Second, we compiled recovery information for each identified tag code from  
203 RMIS. We noted the recovery date, location code, and port at which the fish were  
204 sampled. As each tag recovery in the RMIS database has an associated expansion that  
205 aims to correct for the proportion of the catch sampled, we used the expanded number

206 reported for each of the tag codes in the RMIS database. Using the expanded number  
207 helps account for temporal and spatial variation in the sampling intensity of the fisheries  
208 catch. For marine recoveries, we assigned each recovery to the fishing gear type used, to  
209 one of 17 coastal regions (Fig. 1), and to one of four seasons (spring: April-May;  
210 summer: June-July; fall: August-October; winter: November-March). Ocean recovery  
211 areas were derived largely from those used by Weitkamp (2010). The division of seasons  
212 was informed by both the biology of fall Chinook salmon (they enter their natal rivers to  
213 begin their spawning migration in the fall) and practical considerations (there is much  
214 less information about the spatial distribution of fish in the winter due to reduced salmon  
215 fishing effort; see Fig. S1.1-S1.4). We only include recovery information from the three  
216 fishing gear types for which we have effort information (see below). In total, this  
217 included an estimated 527,711 ocean recoveries for the focal release groups. In addition  
218 to the ocean recoveries, we use freshwater recoveries (both from river fisheries and  
219 escapement to hatcheries and natural spawning areas) reported in RMIS to parameterize  
220 some model components (see *Observation Model* below). As illustrative examples, we  
221 provide recovery data from the commercial troll fishery for two releases (Fig. 2).

222 Third, we compiled data on commercial and recreational fishing effort from the  
223 United States and Canadian government sources. For commercial troll, treaty troll, and  
224 recreational fisheries along the outer coast of Washington, Oregon, and California, we  
225 used the PFMC ‘blue book’ ([http://www.pcouncil.org/salmon/background/document-  
226 library/historical-data-of-ocean-salmon-fisheries/](http://www.pcouncil.org/salmon/background/document-library/historical-data-of-ocean-salmon-fisheries/)). Recreational effort in Puget Sound,  
227 Washington was extracted from published WDFW reports (e.g., WDFW 1979). Alaska  
228 troll effort was supplied through a data request to the Alaska Department of Fish and

229 Game (ADFG) and included both power troll and hand troll gear types. We detail how we  
230 combine these two effort types in Supplement S2. We acquired Canadian troll effort  
231 through a data request to the Canadian Department of Fisheries and Oceans (DFO) for  
232 1982-1995. Earlier years of Canadian troll effort were extracted from official Canadian  
233 government data reports (British Columbia Catch Statistics, available at  
234 <http://www.pac.dfo-mpo.gc.ca/stats/comm/ann/index-eng.html>). The lack of publically  
235 available data describing Canadian commercial troll fishing effort targeting Chinook  
236 salmon between 1996 and 2004 limited our analysis to 1979-1995 and to brood years  
237 1977-1990. We hope to expand the time-frame in future analyses. Recreational fishing  
238 effort data for the study period were also not available from Canada (except for some  
239 years in the Strait of Georgia, Fig. S1.4) or from Alaskan waters. We describe how we  
240 accounted for these gaps in the model description section below. Complicating matters,  
241 each type of effort is reported in different units; recreational effort is reported in units of  
242 angler-days in the United States and boat-days in Canada, troll effort is reported in units  
243 of boat-days, and treaty troll in units of deliveries (see Supplement S1 and S2 for fishing  
244 effort for each gear type)

245         Troll, treaty troll, and recreational fisheries account for >95% of CWT ocean  
246 recoveries for our release groups. The remaining recoveries were largely from  
247 commercial gillnet and seine fisheries with a few other rare types (e.g. test fisheries).  
248 Many gillnet and seine fisheries incidentally catch Chinook salmon, but some are active  
249 in fisheries in the mouth of the natal river or near the hatchery (“terminal” fisheries).  
250 Since many net fisheries only catch fish from individual sources, they are not a  
251 representative sample of multiple stocks within regions, and including them could affect

252 model inferences about ocean distribution of Chinook salmon. Therefore, we did not  
253 incorporate data from these sources, but address the implications for these missing  
254 fisheries in the methods and discussion.

255

## 256 **Model**

257 To estimate the seasonal abundance and distribution of fall Chinook salmon, we  
258 simultaneously model the abundance and distribution of hatchery fall Chinook salmon  
259 released into 10 of the 17 ocean regions (Fig. 1) over 14 years (brood years 1977-1990).  
260 Our model tracks the abundance of fish from the spring of age 2 (defined as calendar year  
261 minus brood year) to fall of age 6, encompassing 19 seasonal time steps. As conventions  
262 for describing the age of Chinook salmon are confusing and vary regionally and by run  
263 type, we provide a table outlining fall Chinook salmon age classification used here (Table  
264 S1.2). Unfortunately, some model components such as fishing mortality vary and are  
265 reported by calendar year and season, not model season, and so have appropriate  
266 subscripts to reflect this complexity.

267 To generate estimates of the abundance of fall Chinook salmon from distinct  
268 regions, we need to quantify at least six core processes: 1) the number fish entering the  
269 ocean from natal rivers; 2) the natural mortality of juvenile fish; 3) the natural mortality  
270 of adult fish; 4) fishing mortality by age and region; 5) the spatial distribution of fish in  
271 the ocean; and 6) the age-specific loss of fish from the ocean due to maturation (salmon  
272 leaving the ocean and returning to their natal streams to spawn). We use a state-space  
273 framework which separates the biological processes (fish moving, dying from natural  
274 causes or fisheries, etc.) from what we observe about these fish populations (generally

275 fisheries catches). This allows us to explicitly account for and make inferences about  
276 populations in locations and areas which may have no observations or missing data.

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

285

### 286 *Process Model*

287 We track the number and distribution of each Chinook salmon release for the  
288 entirety of its life-cycle. Each release is associated with a particular natal region, brood  
289 and release year. Because we use hatchery releases, the initial number of fish in each  
290 release group is treated as known without error. We estimate an independent juvenile  
291 mortality rate – spanning the period from date of release to season 1 of the model – for  
292 each release and denote it  $\phi_i$  for release  $i$ . During the 19 seasonal time steps of the model  
293 (subscript  $a$ ; Table S1.2), we model the total abundance of each release coastwide as an  
294 unobserved, latent variable,  $N_{i,a}$ . In each season, fish are subjected to age-specific natural  
295 mortality rate,  $M_a$ , and are captured in commercial and recreational fisheries at fishing  
296 mortality rates,  $F_-$  (subscripts suppressed, see below) that are determined by the fishing  
297 effort in a particular region and the age- and gear-specific vulnerability. Both natural and

298 fishing mortality are modeled as density-independent processes and modeled as occurring  
299 simultaneously. An important assumption of the model is that fish of the same age in the  
300 same spatial region and season are considered to be equivalently vulnerable to ocean  
301 fisheries occurring in that spatial box and season. We incorporate information on  
302 retention size limits for each year, season, and spatial region (see Table S1.5).  
303 Additionally, we include a process variability term to incorporate additional, unmodeled  
304 aspects of fisheries and the environment.

305         The distribution of Chinook salmon among the 17 ocean regions varies among  
306 seasons and is estimated within our population dynamic model. We let  $\theta_{r,l,s}$  be the  
307 proportion of fish from natal region  $r$ , present in ocean region  $l$ , at the beginning of  
308 season  $s$ , and estimate  $\theta_{r,l,s}$  within the model. For a given natal region and season, across  
309 all locations the proportions must sum to 1. We assume that fish from the same natal  
310 region, but potentially different rivers or hatcheries, have identical ocean distributions in  
311 a given season and that ocean distributions within a season are the same across Chinook  
312 salmon ages. Weitkamp (2010) suggested that ocean distribution may vary with ocean  
313 age (ocean age = recovery year – release year) with very young fish (ocean age = 1)  
314 found closer to their natal river mouth than older fish (ocean ages 2 to 5), but with the  
315 older age classes being broadly similar in distance from their natal river (their Tables 5,  
316 6). As our model starts well into ocean age 1 (using Weitkamp’s (2010) age accounting;  
317 see Table S1.2) and focuses on modeling older fish – those that are susceptible to ocean  
318 fisheries – this model assumption matches available information. Although results from  
319 Satterthwaite et al. (2013) indicates modest differences in age-specific distributions of  
320 older fish from a single stock, the statistical significance of these differences was not

321 assessed. Therefore, modifications that allow for age-dependence in ocean distribution  
322 should be an important consideration in future work, but are unlikely to fundamentally  
323 change our conclusions.

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

334

### 335 *Observation Model*

336 There are few direct, fisheries independent surveys of Chinook salmon in the  
337 ocean, but Chinook salmon were caught coastwide across a range of fisheries (but see  
338 surveys of very young Chinook salmon; Trudel et al. 2011; Burke et al. 2013). We use  
339 spatially explicit recovery data from three fisheries gear types in our analysis  
340 (commercial troll, recreational hook and line, and commercial treaty troll) to calculate the  
341 expected catch of fish from release  $i$ , gear  $g$ , ocean region  $l$ , season  $s$ , and calendar year  $c$   
342 as a function of the number of age  $a$  Chinook salmon present and fishing mortality in  
343 each region. For winter, spring, and summer seasons (seasons without fish escaping to

344 freshwater), the catch follows the Baranov catch equation (Baranov 1918; Beverton and  
 345 Holt 1957)

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

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

$$\begin{aligned} \mu_{i,a,l,g} = & \frac{F_{a,s,c,l,g}}{(M_a + \sum_g F_{a,s,c,l,g})} N_{i,a} \theta_{r,l,s} \left\{ 1 - \exp \left[ -0.5 \left( M_a + \sum_g F_{a,s,c,l,g} \right) \right] \right\} \\ & + \frac{F_{a,s,c,l,g}}{(M_a + \sum_g F_{a,s,c,l,g})} N_{i,a,l,S} \left\{ 1 - \exp \left[ -0.5 \left( M_a + \sum_g F_{a,s,c,l,g} \right) \right] \right\} \end{aligned} \quad (2)$$

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

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

357 where  $G$  takes on a value of 1 if the observed catch,  $C$ , is positive, and a value of 0  
 358 otherwise. Here,  $W_{l,s,c,g}$  is the fraction of the catch sampled as extracted from the RMIS  
 359 database (see Table S1.5). The parameters  $\pi_0$  and  $\pi_1$  serve to transform the catch to the  
 360 logit scale and acknowledge that some stocks may be present and caught in fisheries even  
 361 if the sampling of the catch does not observe them. As sampling effort for CWT has



362 varied both spatially and through time, we calculated the observed sampling fraction  
 363 from the RMIS database for each tag recovery and aggregated them by season, spatial  
 364 region, and gear type. We calculated the median value for the sampling fraction among  
 365 all reported catches in each region and season and set  $W_{l,s,c,l}$  to be the median sampling  
 366 fraction. We estimate a single offset,  $\pi_0$ , which is a proportion bounded between 0 and 1  
 367 to account for potential non-independence among individual sampled fish in the catch.  
 368 Finally, we estimate a slope,  $\pi_1$ , to scale how observation probability increases with  
 369 increases expected catch.

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

$$372 \quad C_{i,l,g,a} \sim \text{LogNormal}(\log(\mu_{i,a,l,g}), \exp(\sigma_0 + \sigma_1 \log(\mu_{i,a,l,g})))$$

$$373 \quad \text{if } C_{i,l,g,a} > 0 \quad (4)$$

374 Here observation error term for the dispersion between observed and predicted catch has  
 375 two parameters ( $\sigma_0, \sigma_1$ ) and allows the observation error to vary with larger values of  
 376 predicted catch.

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

382 In addition to recoveries from fisheries, we need to account for the Chinook  
 383 salmon that leave the ocean and return to their natal river or hatchery and complete their  
 384 life-cycle. Ideally, we would have a likelihood component corresponding to the observed  
 385 fish in rivers and hatcheries for each release group. Unfortunately, preliminary

386 examination of the RMIS database revealed notable deficiencies in the freshwater  
387 recovery data; we identified some individual tag groups from throughout the study region  
388 with many ocean recoveries but zero or near zero freshwater recoveries. Such  
389 discrepancies have been noted by other authors (e.g. Baker and Morhardt 2001).  
390 Furthermore, we compared freshwater recoveries reported in RMIS with recoveries used  
391 in several stock assessments. For example, we were unable to reproduce the results  
392 reported for Iron Gate and Trinity River hatcheries in Hankin and Logan (2010), which  
393 we know included significant quality control and additions to the data beyond the raw  
394 RMIS data. We could not identify which RMIS freshwater recovery data were reliable  
395 and which were not and so we elected to incorporate only information about the relative  
396 occurrence of different age Chinook salmon in freshwater recoveries, not the actual  
397 expanded numbers of total observed freshwater recoveries. We detail these approaches in  
398 the online supplement and provide the mean estimated proportion returning at each age  
399 for each region in Table S1.4. This aspect of our model is important because by not using  
400 information about in river recoveries we rely on catches in ocean fisheries to estimate  
401 both spatial distributions and the various parameters that scale overall abundance (e.g.  
402 juvenile survivorship and gear specific catchability). As a result, our estimates of  
403 parameters that the scale total abundance of Chinook salmon – including most  
404 prominently juvenile survival and catchabilities – are difficult to estimate and likely mis-  
405 estimated by an unknown factor. However, this factor will apply to all modeled releases  
406 and thus does not change the relative order of survivorships among releases. We note that  
407 virtually all other estimates of survivorship for salmon based on cohort reconstructions

408 face this problem as well (Coronado and Hilborn 1998; Kilduff et al. 2014, 2015; CTC  
409 2015).

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

422

#### 423 *Estimation*

424 We implemented the above state-space model in STAN (Gelman et al. 2015,  
425 Carpenter et al. 2016) as implemented in the R statistical language (R Core Team 2016,  
426 Stan Development Team 2016). STAN uses a Hamiltonian Monte Carlo (HMC) sampling  
427 (Neal 2011; Hoffman and Gelman 2014; see Monnahan et al. 2016 for a description  
428 targeted at ecologists). Table S2.1 provides a description of all parameters and prior  
429 distributions. STAN estimates the joint posterior distribution of parameters and latent  
430 states. For all results reported here we used five chains using a warmup period of 300

431 iterations and 2000 monitoring iterations. We used model diagnostics such as checks for  
432 divergent transitions, comparisons among chains (Gelman-Rubin statistics), and posterior  
433 predictive checks.

434

#### 435 *Analysis of juvenile survival estimates*

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

445

#### 446 *Projected ocean distribution of fall Chinook salmon*

447 The above model provides estimates of many parameters that are important for  
448 determining the abundance and distribution of Chinook salmon. However, since hatchery  
449 releases of Chinook salmon are not tagged with CWT at constant rates, and hatchery-  
450 versus natural-origin fish make up substantially different proportions of different stocks,  
451 CWT data alone cannot be used to generate estimates of Chinook salmon abundance in  
452 the ocean. We use model estimates in conjunction with estimates of out-migrating  
453 juvenile Chinook salmon leaving rivers and hatcheries to provide predicted fall Chinook

454 salmon abundances in space and time. We outline an approach to simulating Chinook  
455 salmon using model estimates and show how both the proportional contribution of  
456 individual stocks and aggregate abundance change under two illustrative scenarios.

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

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

472         For the second scenario, we used the same value of fishing mortality (median) and  
473 juvenile mortality (mean, spatially invariant) as the base scenario. But for Chinook  
474 salmon production, we reduced hatchery production in Puget Sound (PUSO) by half from  
475 37 to 18.5 million. We then compare the abundance and distribution of Chinook salmon  
476 in the ocean under the base and “PUSO hatchery” scenarios to illustrate the consequences

477 of changing aspects of hatchery production for ocean abundance and distribution. Other  
478 assumptions and simulations could be used to generate distributions and abundance under  
479 other scenarios but we provide a relatively simple, hypothetical scenario here as an  
480 example of the possibilities of this approach.

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

488

## 489 **Results**

490 Despite the large amount of data and many latent states and parameters, the model  
491 converged and produced reasonable biological estimates for parameters. The effective  
492 sample size for all parameters was greater than 1,000 and maximum  $\hat{R}$  (a measure of  
493 model convergence) was less than 1.01. We focus on two model components in the main  
494 text before turning to two simple scenarios to understand the attributes of Chinook  
495 salmon ocean aggregations using simulations. We present posterior estimates of model  
496 parameters in the online supplement along with figures of other major model  
497 components.

498

499 *Spatial distribution of Chinook salmon by origin and season*

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

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

519

#### 520 *Variation in early mortality*

521 Estimates of mortality for each of the 454 release groups, showed wide variation  
522 in mortality rates among releases (range of posterior medians for  $\phi_i$ : 1.39 to 3.29; across

523 release mean = 2.02) corresponding to a range of survivorship of 0.037 to more than  
 524 0.248 for the period between release and the start of the model in April of brood year + 2.  
 525 As this range includes releases from all origin regions and years, and thus includes  
 526 releases with vastly different lengths of time between release and the start of the model  
 527 (from 1 to 13 months), such large variation is not unexpected. We further summarized  
 528 model estimates of early mortality in two ways.

529         The linear mixed effect model showed a large effect of  $n\_month$  on  $\log(\phi_i)$  with  
 530 longer time periods associated with increase mortality (slope estimate for  $n\_month$ :  
 531 0.002(0.002); mean(SE)), indicating that on average, an increase of one month resulted  
 532 in an increase of 0.002 in  $\log(\phi_i)$ . There was strong among region variation in the  
 533 overall mortality intercept (SD among regions = 0.053) and variation among years (SD =  
 534 0.033). This result coincides with intuition – fish that spend more time in the river and  
 535 ocean should have greater mortality– but this result does highlight that many past  
 536 analyses comparing early mortality among releases have ignored such attributes  
 537 (Coronado and Hilborn 1998; Kilduff et al. 2014, 2015).

538         Second, to make our results comparable to estimates of previous analyses of  
 539 Chinook salmon early survivorship (Kilduff et al. 2014), we used estimated model  
 540 parameters to calculate estimated survivorship to the beginning of fall season, age 2. We  
 541 estimated survivorship for each release in the absence of fishing which accounted for  
 542 juvenile mortality, natural mortality, and estimated process error,  $S_i = \exp(-\phi_i -$   
 543  $\sum_{a=1}^{a=2}[M_a + \omega_{i,a}])$ , where  $\omega_{i,a}$  is the estimated process variability. For region  
 544 combinations that had at least three releases in a given year, we calculated a weighted  
 545 mean and weighted standard deviation for each region and converted estimated



546 survivorship to z-scores (subtracted the among-year mean, divided by the standard  
547 deviation among years; Fig. 4). We use z-scores to emphasize that our results should not  
548 be used as estimates of absolute survivorship as we do not include release-specific  
549 information about freshwater recoveries or recoveries from marine net fisheries. Due to  
550 relatively few releases in SOR, COR, and NOR, we combined these three regions to  
551 calculate a single mean for the Oregon coast (denoted “OR”). Survivorship between  
552 release and age 2 was highly variable among regions and both within and among years.  
553 Interestingly, most regions show substantial temporal variation in survivorship, but years  
554 of high and low survivorship are not coincident among regions. Survivorship trends from  
555 the Columbia River tended to be fairly coincident (Fig. 4b), as did fish from Oregon and  
556 California (Fig. 4c), but similar trends among northern stocks were less obvious (Fig. 4a).  
557 Overall there was very high variability within regions in some years (e.g. SFB in 1985)  
558 indicating strong differences in survivorship among hatchery releases. As our model does  
559 not include abundances of CWT recoveries from freshwater or the small number of  
560 recoveries from non-target fisheries, we expect these estimated survivorships biased from  
561 their true values. However, the patterns of relative survivorship across time and among  
562 regions should be correct.

563

#### 564 *Comparing distributions and cumulative abundance*

565         Given the varied production of Chinook salmon among origin regions (Table  
566 S3.1), and the distinct ocean distributions of these fish (Fig. 3), it is not surprising that  
567 ocean areas vary substantially in proportional compositions and aggregate abundance of  
568 Chinook salmon (Fig. 5). In terms of proportional contribution, seasonal variation is

569 present but not striking. For example, the two southeast Alaska regions (NSEAK and  
570 SSEAK) are comprised predominantly of fall Chinook salmon from Canada, Washington,  
571 and the Columbia River basin in all seasons, though the proportion from Columbia basin  
572 increases notably from spring to summer. The Salish Sea (regions PUSO and SGEO) are  
573 dominated by fish originating in those regions in all seasons, while the Californian ocean  
574 regions (MONT, SFB, MEN, and NCA) all have close to or more than 50% of fish  
575 present originating from California rivers in all seasons (Fig. 5).

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

584 The cumulative abundance and distribution of fall Chinook salmon also depend  
585 strongly on the age range of Chinook salmon considered. For example, the cumulative  
586 abundance of fish age 2 and older is substantially different from the distribution of fish  
587 age 4 and older (compare Fig. 6e and 6j). Old and large fish are notably more abundant  
588 in the northern regions, whereas young and small fish are more available in the southern  
589 parts of the range. Note that this change in distribution is not driven by changes in the  
590 distribution of fish with age (fish of different ages are modeled as having identical ocean  
591 distributions; see *Methods*) but is due instead to strong differences in maturation

592 probability among origin regions. Fish originating from northern areas tend to mature at  
593 older ages (Fig. S1.8; Table S1.4). This is readily apparent in comparing the increasing  
594 contribution of WAC and SGEO origin fish to total age 4+ fish relative to age 2+ and the  
595 concomitant decline of SFB and COL fish (Fig. 6).

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

609

## 610 **Discussion**

611 We present a coast-wide model for fall Chinook salmon that simultaneously  
612 models populations originating from California to British Columbia and accounts for  
613 biological variation among populations and across time. We explicitly account for the  
614 fisheries effort and sampling of fisheries that affect the detection of Chinook salmon

615 populations in the ocean. Together, our model provides a joint estimate of salmon spatial  
616 distribution, juvenile mortality, and spatio-temporal estimates of fisheries mortality;  
617 processes that are typically estimated and discussed separately (e.g. Weitkamp 2010;  
618 Kilduff et al. 2014; CTC 2015). By estimating a joint time-series model that includes  
619 populations spanning much of the northeastern Pacific, we are able to move beyond  
620 comparisons of CPUE of different Chinook salmon stocks derived from CWT  
621 (Satterthwaite et al. 2013; Norris et al. 2000) or Genetic Stock Identification (GSI;  
622 Bellinger et al. 2015; Satterthwaite et al. 2015) and translate information from fisheries  
623 catch into estimates of spatial distribution and total abundance. Importantly, our work  
624 explicitly accounts for missing data – locations and times where no one was fishing and  
625 therefore no sampling of Chinook salmon occurred – and thus expands on previous  
626 examinations of salmon ocean distribution. Our work is a tool has broad application for  
627 understanding patterns of spatio-temporal variation among Chinook salmon and other  
628 tagged salmonid populations. Additionally, it is a simulation platform for exploring the  
629 consequences of biological variation and management decisions on an important marine  
630 resource.

631         We present a step toward understanding the portfolio of Chinook salmon  
632 populations contributing to each coastal region in each season. A full exploration of  
633 spatial portfolios of Chinook salmon would involve accounting for factors contributing to  
634 variation within and covariation among populations and is beyond the scope of this paper.  
635 However, basic tenets of portfolio theory do allow us to begin to discuss the implications  
636 of the spatial patterns. Broadly, portfolio theory suggest that regions that are more highly  
637 reliant on fish originating from one or a few areas would experience more temporal

638 variability than areas with more contributing populations. In the base scenario, three areas  
639 had greater than 50% of their abundance derived from a single region in all seasons: two  
640 in California (MONT, SFB) and Puget Sound, Washington (PUSO). Additionally, these  
641 three areas are also estimated to have the lowest total Chinook salmon abundance.  
642 Together these facts suggest these regions with low stock diversity are likely susceptible  
643 to periods of especially low abundance. Indeed, the ocean fishery in California and  
644 southern Oregon was recently closed for two consecutive years due to poor production of  
645 Sacramento River fall Chinook salmon (Lindley et al. 2009; Carlson and Satterthwaite  
646 2011), and our simulation of reduced hatchery production highlights the sensitivity of  
647 PUSO to changes in local hatchery production (Fig. 7). In contrast, other regions are  
648 composed of fish from diverse sources and have a more balanced contribution (e.g. NOR,  
649 SWVI, NWVI, NBC, SSEAK, NSEAK) and would be expected to have more stable  
650 portfolios over the long-term. Interestingly, these areas largely correspond to locations  
651 with important and historically productive Chinook salmon troll fisheries (Southeast  
652 Alaska, west coast Vancouver Island, and Oregon coast).

653         From the perspective of predator populations, increased stock diversity (and  
654 stability) may translate to increased growth rates. Anecdotally, piscivorous killer whale  
655 populations with higher latitude distributions tend to have higher population growth rates  
656 (Ward et al. 2013). When considering portfolios, though, it is important to note that this  
657 analysis does not include other Chinook salmon life-history types. Spring-run Chinook  
658 salmon are the other major life-history type in the northeastern Pacific; other run-types  
659 such as winter run Chinook salmon are confined to California rivers and relatively rare  
660 (Quinn 2005), though in some locations summer runs are also present. Spring Chinook

661 become more abundant with increasing latitude as all Chinook originating from Alaskan  
662 and northern British Columbian rivers are spring-run. Thus, while this analysis presents a  
663 reasonable approximation of the Chinook portfolio in California, it dramatically  
664 underestimates both the total number of Chinook and life-history diversity present in  
665 British Columbia and Alaskan waters in particular. Further work must be done to  
666 incorporate the range of life-histories of Chinook salmon into ocean portfolios. Overall,  
667 however, portfolio approaches have clear potential for examining the consequences of  
668 aggregate patterns of abundance, how they may affect directed fisheries or incidental  
669 catch in non-directed fisheries, ecosystem considerations for species dependent upon  
670 aggregate abundance such as killer whales or other marine mammal predators, and how  
671 portfolio properties vary in response to management or environmental changes.

672         While the outlined model incorporates many important attributes of Chinook  
673 biology, it necessarily makes simplifying assumption to accommodate missing or  
674 incomplete data and ensure model identifiability. Several major aspects of our estimation  
675 model should be the foci of future improvement and research. Most importantly, reliable  
676 data pertaining to tag recoveries in the escapement of Chinook to freshwater would  
677 greatly improve estimates of both maturation probabilities and ocean survivorship. Such  
678 information would have the largest impact on the juvenile survivorship estimates (Fig. 4)  
679 and the catchability coefficients ( $q$ ; see Supplement S2) as they serve to scale the overall  
680 abundance of fish available in the ocean for fisheries. However, corraling and verifying  
681 such data coast-wide is a major task that is beyond the scope of this project. Other  
682 reasonable and important extensions to the model include: *a*) allowing for age-specific or  
683 oceanographic driven changes to seasonal distributions; *b*) accounting for population

684 specific growth rate and/or temporal variation in growth which would translate into  
685 population difference in vulnerability to fishing gear types; c) including the fishing effort  
686 data necessary to expand the study time-window to include data from 1996 onward; and  
687 d) incorporating information from non-mixed stock fisheries such as terminal gillnet and  
688 seine fisheries that are not equally likely to capture fish from different origins.

689 Projections of total Chinook salmon abundance could be substantially improved with  
690 improved information about the outmigration of juvenile Chinook salmon from rivers  
691 coastwide.

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

703         An important additional consideration for ocean distribution modeling is  
704 understanding how to incorporate information from both physical tagging using older  
705 technologies (CWT) and information derived from more recently developed and applied  
706 genetic stock identification tools (GSI; Satterthwaite et al. 2014; Bellinger et al. 2015). In

707 practice, GSI data provides information about the proportional contribution of fish from  
708 different origins in a given area or catch per unit effort information for different stocks.  
709 Using GSI data alone without an accompanying analysis of scales or otoliths lacks  
710 information about age-structure. As the age-structure will strongly affect the estimated  
711 stock composition of any given ocean region, GSI information alone may provide  
712 difficult to interpret patterns (Fig. 6). Overall, however, our predictions (Fig. 5-7) should  
713 provide predictions for proportional compositions that can be compared directly to GSI  
714 studies. Integrating GSI and CWT data in a single integrated framework is an exciting  
715 and important area for future work.

716       Beyond data and model complexity, computational limitations do present a  
717 challenge for large models like ours. In theory, there is no constraint upon how many  
718 releases can be modeled simultaneously, but the 454 releases modeled here require  
719 estimation of nearly 8,600 latent states and incorporate over 228,000 observations for the  
720 binomial likelihood (the total number of release-location-season-gear type combinations)  
721 and over 17,000 observations for the log-normal component. Expanding the number of  
722 releases substantially would require substantially improving computational resources or  
723 moving away from full Bayesian estimation toward approximations of the posterior  
724 distribution such as Laplace approximations (Rue et al. 2009).

725       Overall, we provide a framework to integrate information from multiple fall  
726 Chinook salmon stocks to simultaneously estimate parameters from a complex population  
727 dynamic model. We emphasize the spatio-temporal attributes of the parameters here –  
728 particularly estimates of ocean distribution and regional patterns in juvenile survival –  
729 and provide illustrative examples of how these estimates can be used to simulate



730 scenarios and that these scenarios may be useful in a variety of management and  
731 ecosystem contexts in the future.

732

### 733 **Acknowledgements**

734 We thank L. Weitkamp and R. Kope for their expertise with the CWT and fishing effort  
735 datasets and for comments throughout the creation of this paper, J. Carlile for providing  
736 Alaska Department of Fish and Game fishing effort data and M. O’Farrell for information  
737 about Californian salmon runs and fisheries. We thank M. Ford, J. Samhoury, L. Barnett,  
738 and two anonymous reviewers for comments on earlier versions of the manuscript. We  
739 acknowledge U.S. Navy, Commander, U.S. Pacific Fleet for partial support (MIPR  
740 N00070-16-MP-4C872).

741

### 742 **References**

- 743 Baker, P.F. and Morhardt, E. 2001. Survival of Chinook salmon smolts in the  
744 Sacramento-San Joaquin Delta and Pacific Ocean. *In*: R.L. Brown, ed. Contributions  
745 to the biology of Central Valley salmonids. Fish Bull. 179: Volume 2. California  
746 Department of Fish and Game, Sacramento. pp. 163-182
- 747 Baranov, T.I. 1918. On the question of the biological basis of fisheries. Nauch. Issledov.  
748 Iktiolog. Inst. Izv. I 1: 81–128.
- 749 Beamish, R.J., Mahnken, C., Neville, C.M. 2004. Evidence that reduced early marine  
750 growth is associated with lower marine survival of coho salmon. Trans. Am. Fish.  
751 Soc. 133: 26-33
- 752 Bellinger, M.R., Banks, M.A., Bates, S.J., Crandall, E.D., Garza, J.C., Sylvia, G., and

- 753 Lawson, P.W. 2015. Geo-referenced, abundance calibrated ocean distribution of  
 754 Chinook salmon (*Oncorhynchus tshawytscha*) stocks across the West Coast of North  
 755 America. PLoS ONE 10(7): e0131276. doi:10.1371/journal.pone.0131276.
- 756 Beverton, R.J.H., and Holt, S.J. 1957. On the dynamics of exploited fish populations.  
 757 Chapman & Hall.
- 758 Block, B.A., Jonsen, I.D., Jorgensen, S.J., Winship, A.J., Shaffer, S.A., Bograd, S.J.,  
 759 Hazen, E.L., Foley, D.G., Breed, G.A., Harrison, A.L., Ganong, J.E., Swithenbank,  
 760 A., Castleton, M., Dewar, H., Mate, B.R., Shillinger, G.L., Schaefer, K.M., Benson,  
 761 S.R., Weise, M.J., Henry, R.W., and Costa, D.P. 2011. Tracking apex marine  
 762 predator movements in a dynamic ocean. Nature 475(7354): 86–90.  
 763 doi:10.1038/nature10082.
- 764 Burke, B.J., Liermann, M.C., Teel, D.J., and Anderson, J.J. 2013. Environmental and  
 765 geospatial factors drive juvenile Chinook salmon distribution during early ocean  
 766 migration. Can. J. Fish. Aq. Sci. 70: 1167–1177. doi:10.1139/cjfas-2012-0505.
- 767 Carlson, S.M., and Satterthwaite, W.H. 2011. Weakened portfolio effect in a collapsed  
 768 salmon population complex. Can. J. Fish. Aq. Sci. 68: 1579–1589.  
 769 doi:10.1139/f2011-084.
- 770 Carpenter, B., Gelman, A., Hoffman, M., Lee, D., Ben Goodrich, Betancourt, M.,  
 771 Brubaker, M.A., Guo, J., Li, P., and Riddell, A. 2017. Stan: A probabilistic  
 772 programming language. J. Stat. Softw. 76:1-32 doi:10.18637/jss.v076.i01
- 773 Chasco, B., I. Kaplan, A.C. Thomas, A. Acevedo-Gutiérrez, D Noren , M.J. Ford, M.B.  
 774 Hanson , Mr. J. Scordino , S. Jeffries, K.N. Marshall, A.O. Shelton, C. Matkin, B.  
 775 Burke, E.J. Ward. 2017. Competing tradeoffs between increasing marine mammal

- 776 predation and fisheries harvest of Chinook salmon. Scientific Reports. 7: 15439.  
777 doi:10.1038/s41598-017-14984-8.
- 778 Coronado, C. and Hilborn, R. 1998. Spatial and temporal factors affecting survival in  
779 coho and fall Chinook salmon in the Pacific Northwest. Bulletin of Marine Science  
780 62:409–425.
- 781 CTC 2015. 2014 Exploitation Rate Analysis and Model Calibration Volume One. Pacific  
782 Salmon Commission Joint Chinook Technical Committee. Available at:  
783 [http://www.psc.org/publications/technical-reports/technical-committee-](http://www.psc.org/publications/technical-reports/technical-committee-reports/chinook/)  
784 [reports/chinook/](http://www.psc.org/publications/technical-reports/technical-committee-reports/chinook/)
- 785 Duffy, E.J. and Beauchamp D.A. 2011. Rapid growth in the early marine period  
786 improves the marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in  
787 Puget Sound, Washington. Can. J. Fish. Aquat. Sci. 68(2):232–240.
- 788 Gelman, A., Lee, D., and Guo, J. 2015. Stan: A probabilistic programming language for  
789 Bayesian inference and optimization. J. Educ. Behav. Stat. 40(5): 530–543.  
790 doi:10.3102/1076998615606113.
- 791 Good, T.P., M.M. McClure, B.P. Sandford, K.A. Barnas, D.M. Marsh, B.A. Ryan, and E.  
792 Casillas. 2007 Quantifying the effect of Caspian tern predation on threatened and  
793 endangered Pacific salmon in the Columbia River estuary. Endangered Species  
794 Research 3:11-21.
- 795 Greene, C.M., Hall, J.E., Guilbault, K.R., and Quinn, T.P. 2010. Improved viability of  
796 populations with diverse life-history portfolios. Biol. Lett. 6(3): 382–386.  
797 doi:10.1098/rsbl.2009.0780.
- 798 Griffiths, J.R., Schindler, D.E., Armstrong, J.B., Scheuerell, M.D., Whited, D.C., Clark,

- 799 R.A., Hilborn, R., Holt, C.A., Lindley, S.T., Stanford, J.A., and Volk, E.C. 2014.  
800 Performance of salmon fishery portfolios across western North America. *J. Appl.*  
801 *Ecol.* 51(6): 1554–1563. doi:10.1111/1365-2664.12341.
- 802 Hankin, D.G. and Logan, E. 2010. A preliminary analysis of Chinook salmon coded-wire  
803 tag recovery data from Iron Gate, Trinity River and Cole Rivers Hatcheries, brood  
804 years 1978–2004. Prepared for The Hoopa Valley Tribal Council and the Arcata  
805 Office, U.S. Fish and Wildlife Service. Available at:  
806 [https://www.fws.gov/arcata/fisheries/reports/technical/IGHTRH.CWTanalysis2009%](https://www.fws.gov/arcata/fisheries/reports/technical/IGHTRH.CWTanalysis2009%20Hankin%20Rpt.pdf)  
807 [20Hankin%20Rpt.pdf](https://www.fws.gov/arcata/fisheries/reports/technical/IGHTRH.CWTanalysis2009%20Hankin%20Rpt.pdf)
- 808 Healey, M.C. 1991. Life history of Chinook salmon (*Oncorhynchus tshawytscha*). *In*:  
809 Groot, C. and Margolis, L., eds. Pacific salmon life histories. Vancouver, BC. pp.  
810 311–394.
- 811 Hilborn, R., Quinn, T.P., Schindler, D.E., and Rogers, D.E. 2003. Biocomplexity and  
812 fisheries sustainability. *P. Natl. Acad. Sci. USA.* 100(11): 6564–6568.  
813 doi:10.1073/pnas.1037274100.
- 814 Hoffman, M.D., and Gelman, A. 2014. The No-U-turn sampler: adaptively setting path  
815 lengths in Hamiltonian Monte Carlo. *J. Mach. Learn. Res.* 15: 1593–1623.
- 816 Johnson, J.K. 1990. Regional overview of coded wire tagging of anadromous salmon and  
817 steelhead in northwest America. *Am. Fish. Soc. Symp.* 7: 782–816.
- 818 Kilduff, D.P., Botsford, L.W., and Teo, S.L.H. 2014. Spatial and temporal covariability  
819 in early ocean survival of Chinook salmon (*Oncorhynchus tshawytscha*) along the  
820 west coast of North America. *ICES J. Mar. Sci.* 71(7): 1671–1682.  
821 doi:10.1093/icesjms/fsu031.

- 822 Kilduff, D.P., Di Lorenzo, E., Botsford, L.W., and Teo, S.L.H. 2015. Changing central  
823 Pacific El Niños reduce stability of North American salmon survival rates. *P. Natl.*  
824 *Acad. Sci.* 112(35): 10962–10966. doi:10.1073/pnas.1503190112.
- 825 Koellner, T., and Schmitz, O.J. 2006. Biodiversity, ecosystem function, and investment  
826 risk. *BioScience* 56(12): 977–985. doi:10.1641/0006-  
827 3568(2006)56[977:BEFAIR]2.0.CO;2.
- 828 Lindley, S.T., Grimes, C.B., Mohr, M.S., Peterson, W., Stein, J., Anderson, J.T.,  
829 Botsford, L.W., Bottom, D.L., Busack, C.A., Collier, T.K. et al. 2009. What caused  
830 the Sacramento River fall Chinook stock collapse? NOAA Tech. Memo. NOAA-TM-  
831 NMFS-SWFSC-447.
- 832 Markowitz, H. 1952. Portfolio selection. *J. Financ.* 7(1): 77–91. doi:10.1111/j.1540-  
833 6261.1952.tb01525.x.
- 834 Martin, T.G., Chadès, I., Arcese, P., Marra, P.P., Possingham, H.P., and Norris, D.R.  
835 2007. Optimal conservation of migratory species. *PLoS ONE* 2(8): e751.  
836 doi:10.1371/journal.pone.0000751.
- 837 Monnahan, C.C., Thorson, J.T., and Branch, T.A. 2016. Faster estimation of Bayesian  
838 models in ecology using Hamiltonian Monte Carlo. *Meth. Ecol. Evol.* 8: 339-348.  
839 doi:10.1111/2041-210X.12681.
- 840 Moore, J.W., McClure, M., Rogers, L.A., and Schindler, D.E. 2010. Synchronization and  
841 portfolio performance of threatened salmon. *Conserv. Lett.* 3(5): 340–348.  
842 doi:10.1111/j.1755-263X.2010.00119.x.
- 843 Moran, P., Teel, D.J., Banks, M.A., Beacham, T.D., Bellinger, R.M., Blankenship, S.M.,  
844 Candy, J.R., Garza, J.C., Hess, J.E., Narum, S.R., Seeb, L.W., Templin, W.D.,

- 845 Wallace, C.G., and Smith, C.T. 2012. Divergent life-history races do not represent  
846 Chinook salmon coast-wide: the importance of scale in Quaternary biogeography.  
847 *Can. J. Fish. Aq. Sci.* 70: 415–435. doi:10.1139/cjfas-2012-0135.
- 848 Myers, J.M., Kope, R.G., Bryant, G.J., and Teel, D. 1998. Status review of Chinook  
849 salmon from Washington, Idaho, Oregon, and California. NOAA Technical Memo  
850 NMFS-NWFSC-35.
- 851 Naish, K.A., Taylor, J.E., III, Levin, P.S., Quinn, T.P., Winton, J.R., Huppert, D., and  
852 Hilborn, R. 2007. An evaluation of the effects of conservation and fishery  
853 enhancement hatcheries on wild populations of salmon. *Adv. Mar. Biol.* 53: 61–194.  
854 doi:10.1016/S0065-2881(07)53002-6.
- 855 Nandor, G.F., Longwill, J.R., and Webb, D.L. 2010. Overview of the coded wire tag  
856 program in the greater Pacific region of North America. *In*: Wolf, K.S. and O’Neal,  
857 J.S., eds., PNAMP special publication: tagging, telemetry, and marking measures for  
858 monitoring fish populations. Pacific Northwest Aquatic Monitoring Partnership  
859 Special Publication 2010-002. pp. 5-46.
- 860 Neal, R.M. 2011. MCMC using Hamiltonian dynamics. *In*: Brooks, S., Gelman, A.,  
861 Jones, G.L., and Meng, X.-L. eds. *Handbook of Markov Chain Monte Carlo*.  
862 *Handbook of Markov Chain Monte Carlo*. pp. 113–162. CRC Press.
- 863 Newman, K.B. 1998. State-space modeling of animal movement and mortality with  
864 application to salmon. *Biometrics* 54(4): 1290. doi:10.2307/2533659.
- 865 Newman, K.B. 2000. Hierarchic modeling of salmon harvest and migration. *J. Agr. Biol.*  
866 *Envir. St.* 5(4): 430-455. doi:10.2307/1400659.
- 867 Norris, J.G., Hyun, S.Y., and Anderson, J.J. 2000. The ocean distribution of the

- 868 Columbia River upriver bright fall chinook salmon stocks. North Pacific  
869 Anadromous Fish Commission Bulletin, 2: 221–232.
- 870 PFMC (Pacific Fishery Management Council). 2016a. Review of 2015 Ocean Salmon  
871 Fisheries Stock Assessment and Fishery Evaluation Document for the Pacific Coast  
872 Salmon Fishery Management Plan. Pacific Fishery Management Council, 7700 NE  
873 Ambassador Place, Suite 101, Portland, OR 97220-1384, USA.
- 874 PFMC (Pacific Fishery Management Council). 2016b. Pacific Coast salmon fishery  
875 management plan for commercial and recreational salmon fisheries off the coasts of  
876 Washington, Oregon, and California as revised through amendment 19. Pacific  
877 Fishery Management Council, 7700 NE Ambassador Place, Suite 101, Portland,  
878 Oregon 97220-1384.
- 879 Pacific Salmon Commission. 2016. Joint Chinook Technical Committee annual report of  
880 catch and escapement for 2015. Report TCCHINOOK (16)-3. Pacific Salmon  
881 Commission, 600 - 1155 Robson Street, Vancouver, B.C., Canada V6E 1B5
- 882 Quinn, T.P. 2005. The Behavior and Ecology of Pacific Salmon and Trout. University of  
883 Washington Press, Canada.
- 884 R Core Team. 2016. R: A language and environment for statistical computing. R  
885 Foundation for Statistical Computing, Vienna, Austria. URL [https://www.R-](https://www.R-project.org/)  
886 [project.org/](https://www.R-project.org/).
- 887 Ruckelshaus, M.H., Levin, P., Johnson, J.B., and Kareiva, P.M. 2003. The Pacific salmon  
888 wars: what science brings to the challenge of recovering species *Annu. Rev. Ecol.*  
889 *Syst.* 33:665–706. doi:10.1146/annurev.ecolsys.33.010802.150504.
- 890 Rue, H., Martino, S., Chopin, N. 2009. Approximate Bayesian inference for latent

- 891 Gaussian models using integrated nested Laplace approximations (with discussion).  
892 J. Roy. Stat. Soc. B. 71:319-392.
- 893 Satterthwaite, W.H., and Carlson, S.M. 2015. Weakening portfolio effect strength in a  
894 hatchery-supplemented Chinook salmon population complex. Can. J. Fish. Aq. Sci.  
895 72: 1860-1875. doi:10.1139/cjfas-2015-0169.
- 896 Satterthwaite, W.H., Ciancio, J., Crandall, E., Palmer-Zwahlen, M.L., Grover, A.M.,  
897 O'Farrell, M.R., Anderson, E.C., Mohr, M.S., and Garza, J.C. 2015. Stock  
898 composition and ocean spatial distribution inference from California recreational  
899 Chinook salmon fisheries using genetic stock identification. Fish. Res. 170: 166–178.  
900 doi:10.1016/j.fishres.2015.06.001.
- 901 Satterthwaite, W.H., Mohr, M.S., O'Farrell, M.R., and Wells, B.K. 2013. A comparison  
902 of temporal patterns in the ocean spatial distribution of California's Central Valley  
903 Chinook salmon runs. Can J Fish Aq Sci 70(4): 574–584. doi:10.1139/cjfas-2012-  
904 0395.
- 905 Satterthwaite, W.H., Mohr, M.S., O'Farrell, M.R., Anderson, E.C., Banks, M.A., Bates,  
906 S.J., Bellinger, M.R., Borgerson, L.A., Crandall, E.D., Garza, J.C., Kormos, B.J.,  
907 Lawson, P.W., and Palmer-Zwahlen, M.L. 2014. Use of genetic stock identification  
908 data for comparison of the ocean spatial distribution, size at age, and fishery  
909 exposure of an untagged stock and its indicator: California Coastal versus Klamath  
910 River Chinook salmon. Trans. Am. Fish. Soc. 143: 117–133.  
911 doi:10.1080/00028487.2013.837096.
- 912 Schindler, D.E., Armstrong, J.B., and Reed, T.E. 2015. The portfolio concept in ecology  
913 and evolution. Front. Ecol. Env. 13: 257–263. doi:10.1890/140275.

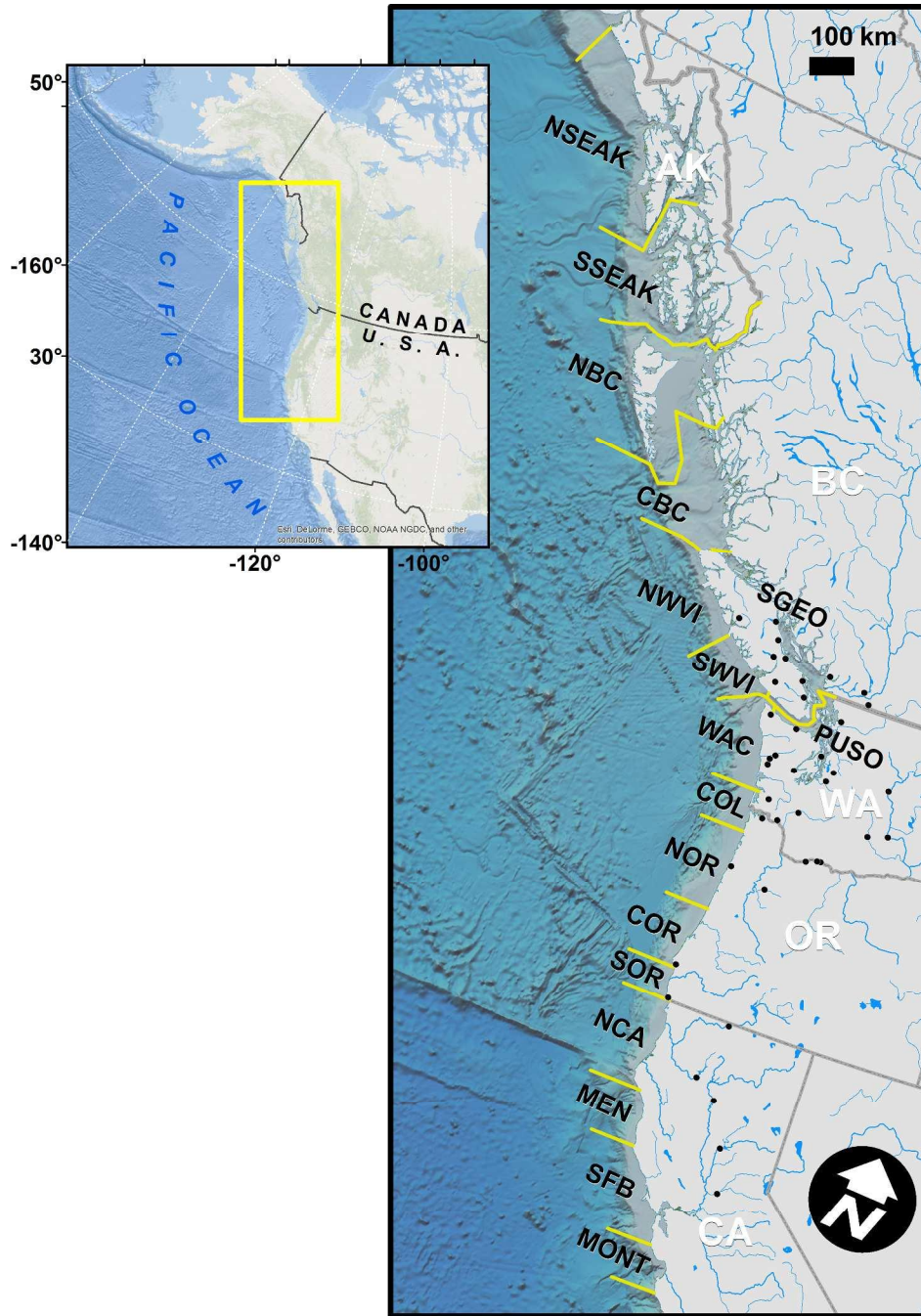


- 914 Schindler, D.E., Armstrong, J.B., Bentley, K.T., Jankowski, K., Lisi, P.J., and Payne,  
915 L.X. 2013. Riding the crimson tide: mobile terrestrial consumers track phenological  
916 variation in spawning of an anadromous fish. *Biol. Lett.* 9:20130048.  
917 doi:10.1098/rsbl.2013.0048.
- 918 Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., and  
919 Webster, M.S. 2010. Population diversity and the portfolio effect in an exploited  
920 species. *Nature* 465: 609–612. doi:10.1038/nature09060.
- 921 Sharma, R., Vélez Espino, L.A. , Wertheimer, A.C., Mantua N., and Francis, R.C. 2013.  
922 Relating spatial and temporal scales of climate and ocean variability to survival of  
923 Pacific Northwest Chinook salmon (*Oncorhynchus tshawytscha*). *Fisheries*  
924 *Oceanography* 22: 14–31. doi:10.1111/fog.12001.
- 925 Stan Development Team. 2016. *RStan: the R interface to Stan*, Version 2.10.1. [http://mc-](http://mc-stan.org)  
926 [stan.org](http://mc-stan.org).
- 927 Teel, D.J., Burke, B.J., Kuligowski, D.R., Morgan, C.A., and Van Doornik, D.M. 2015.  
928 Genetic identification of Chinook Salmon: stock-specific distributions of juveniles  
929 along the Washington and Oregon coasts. *Mar. Coast. Fish.* 7:274–300  
930 doi:10.1080/19425120.2015.1045961.
- 931 Thorson, J.T., Scheuerell, M.D., Buhle, E.R., and Copeland, T. 2014. Spatial variation  
932 buffers temporal fluctuations in early juvenile survival for an endangered Pacific  
933 salmon. *J. Anim. Ecol.* 83(1): 157–167. doi:10.1111/1365-2656.12117.
- 934 Trudel, M., Fisher, J., Orsi, J.A., Morris, J.F.T., Thiess, M.E., Sweeting, R.M., Hinton,  
935 S., Fergusson, E.A., and Welch, D.W. 2009. Distribution and migration of juvenile  
936 Chinook salmon derived from coded wire tag recoveries along the continental shelf

- 937 of western North America. *Trans. Am. Fish. Soc.* 138(6): 1369–1391.
- 938 doi:10.1577/T08-181.1.
- 939 Tucker, S., Trudel, M., Welch, D.W., Candy, J.R., Morris, J.F.T., Thiess, M.E., Wallace,  
940 C., and Beacham, T.D. 2011. Life history and seasonal stock-specific ocean  
941 migration of juvenile Chinook Salmon. *Trans. Am. Fish. Soc.* 140(4): 1101–1119.  
942 doi:10.1080/00028487.2011.607035.
- 943 Waples, R.S., Teel, D.J., Myers, J.M., and Marshall, A.R. 2004. Life-history divergence  
944 in Chinook salmon: historic contingency and parallel evolution. *Evolution* 58(2):  
945 386–403. doi:10.1111/j.0014-3820.2004.tb01654.x.
- 946 WDFW (Washington Department of Fisheries). 1979. Washington State sport catch report.  
947 Available at: <http://wdfw.wa.gov/fishing/harvest/>
- 948 Weitkamp, L.A. 2010. Marine distributions of Chinook salmon from the west coast of  
949 North America Determined by coded wire tag recoveries. *Trans. Am. Fish. Soc.*  
950 139(1): 147–170. doi:10.1577/T08-225.1.
- 951 Winans, G.A., Viele, D., Grover, A., Palmer-Zwahlen, M., Teel, D., and Van Doornik, D.  
952 2001. An update of genetic stock identification of Chinook salmon in the Pacific  
953 Northwest: test fisheries in California. *Rev. Fish. Sci.* 9(4): 213–237.  
954 doi:10.1080/20016491101753.
- 955

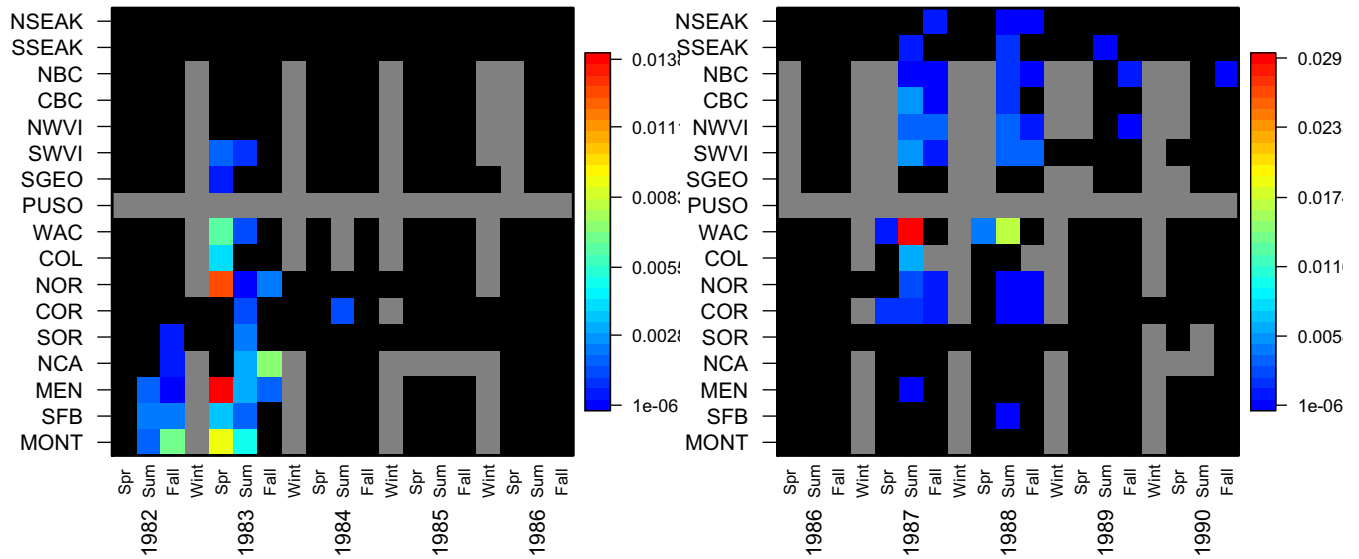
956  
957  
958  
959  
960  
961  
962

Figure 1: Map of study area, hatchery locations (black dots), and 17 coastal regions used in the study. Locator map (left) attribution: Esri, DeLorme, GEBCO, NOAA NGDC, and other contributors. Main map attribution: Esri, NOAA NGDC, NOAA GSHHG, and other contributors.



963

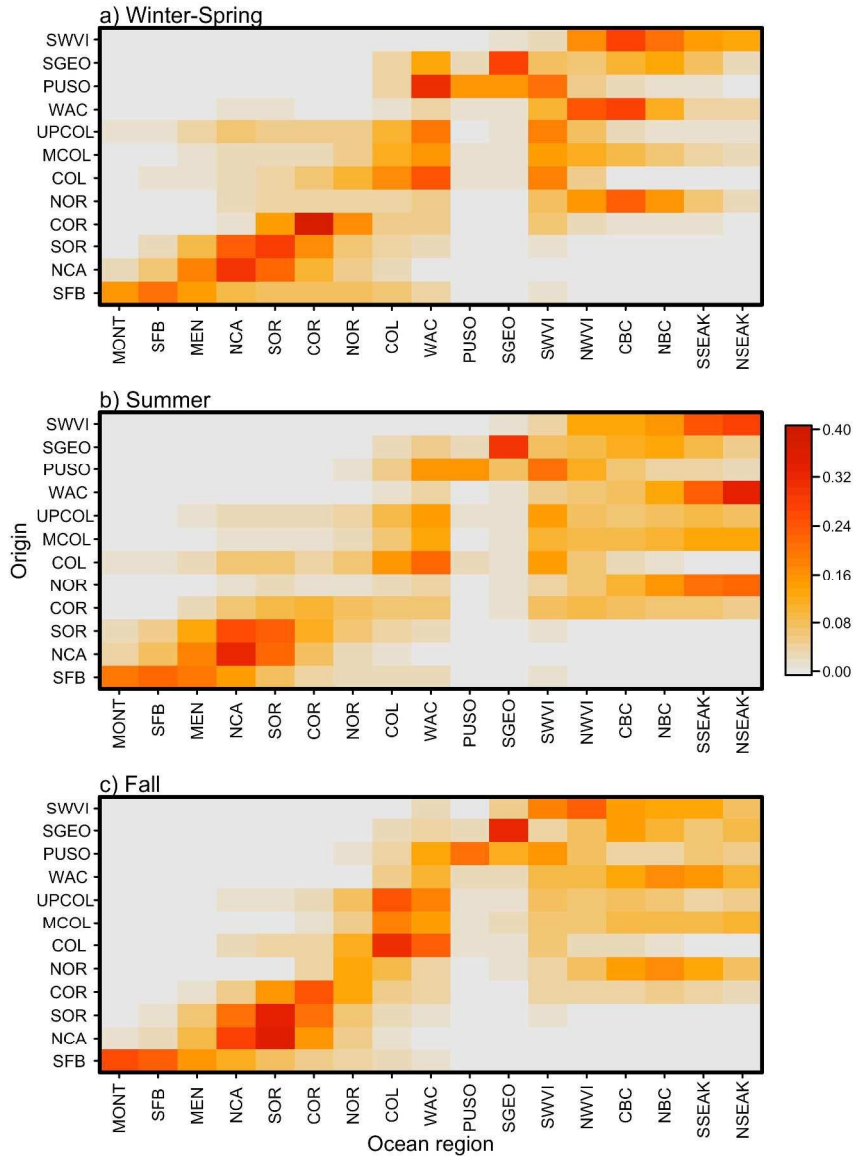
964 Figure 2: Example raw CPUE data for two releases. *Left panel*: Observed CPUE (fish per  
 965 boat-day) from commercial troll fisheries for fall Chinook salmon released from Coleman  
 966 National Fish Hatchery (SFB region) in 1980 (N=393,932 at release). Black indicates  
 967 region-season combinations with commercial troll fisheries but zero observed catches.  
 968 Grey indicates no commercial troll fishery occurred region-season combination. *Right*  
 969 *panel*: Observed CPUE from commercial troll fisheries for fall Chinook released from  
 970 Lyons Ferry (UPCOL region) released in 1984 (N=234,985 at release). Note that the  
 971 color ramp differs between panels.  
 972  
 973



974  
 975

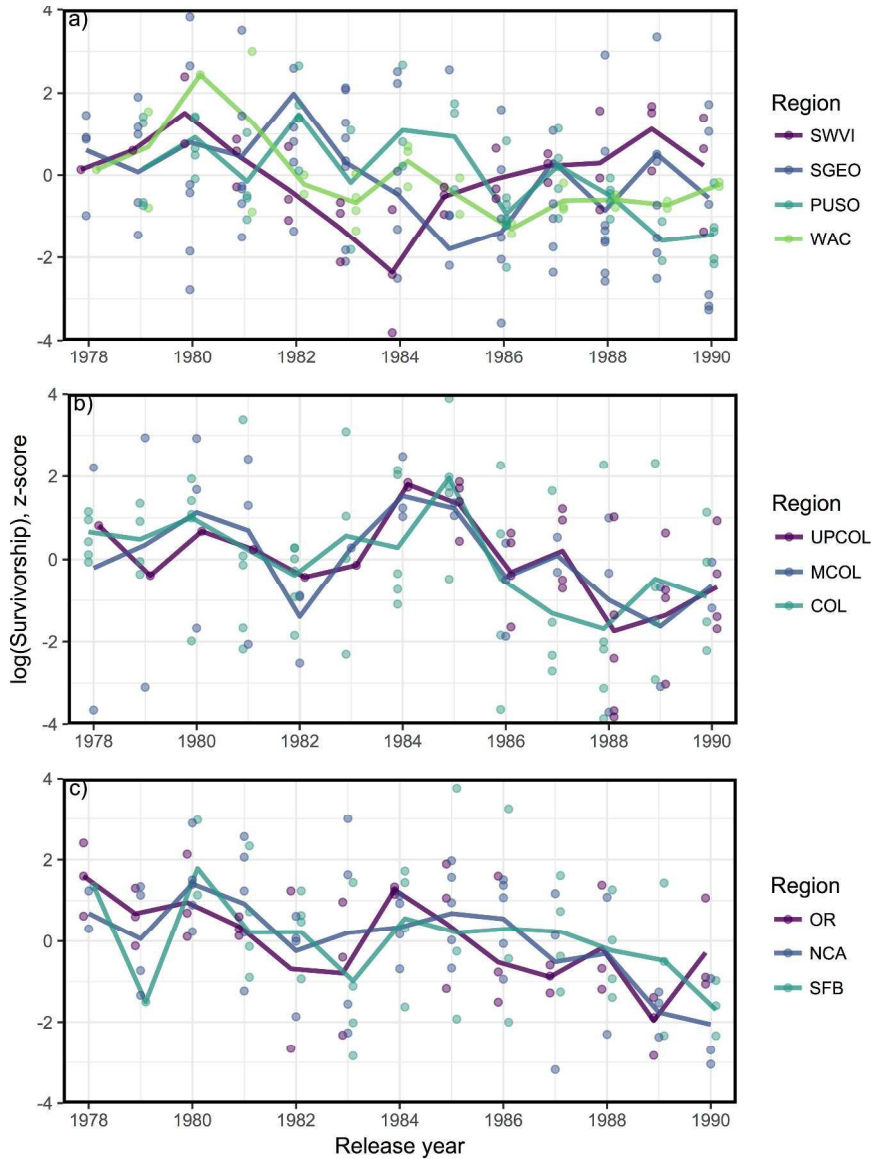
976  
 977  
 978  
 979  
 980  
 981

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



982  
 983  
 984

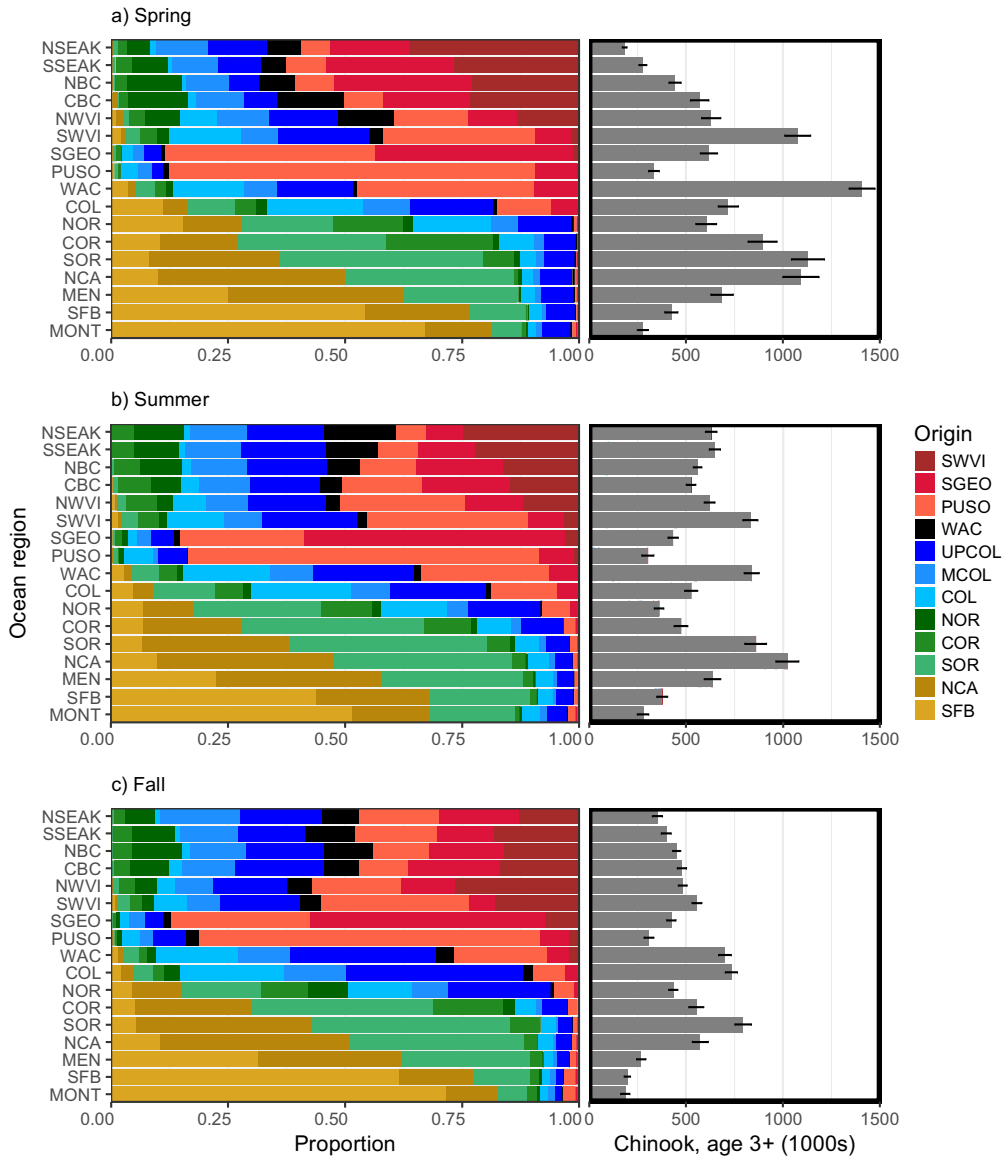
985 Figure 4: Survivorship trends for juvenile Chinook salmon from release to August 1,  
 986 brood year +2 for different origin regions between 1978 and 1990. Raw survivorship  
 987 scores have been converted to z-scores (subtract the among-year mean, divide by the  
 988 standard deviation) to make trends in survival comparable among regions. Panels show  
 989 weighted mean for Chinook from northern regions (*a*), the Columbia basin (*b*), and  
 990 southern regions (*c*; see also Fig. 1). Individual points show mean estimates for  
 991 individual release groups. Due to low numbers of release groups in Oregon regions  
 992 (NOR, COR, SOR), we combined Oregon releases into a single “OR” region.  
 993



994  
 995  
 996

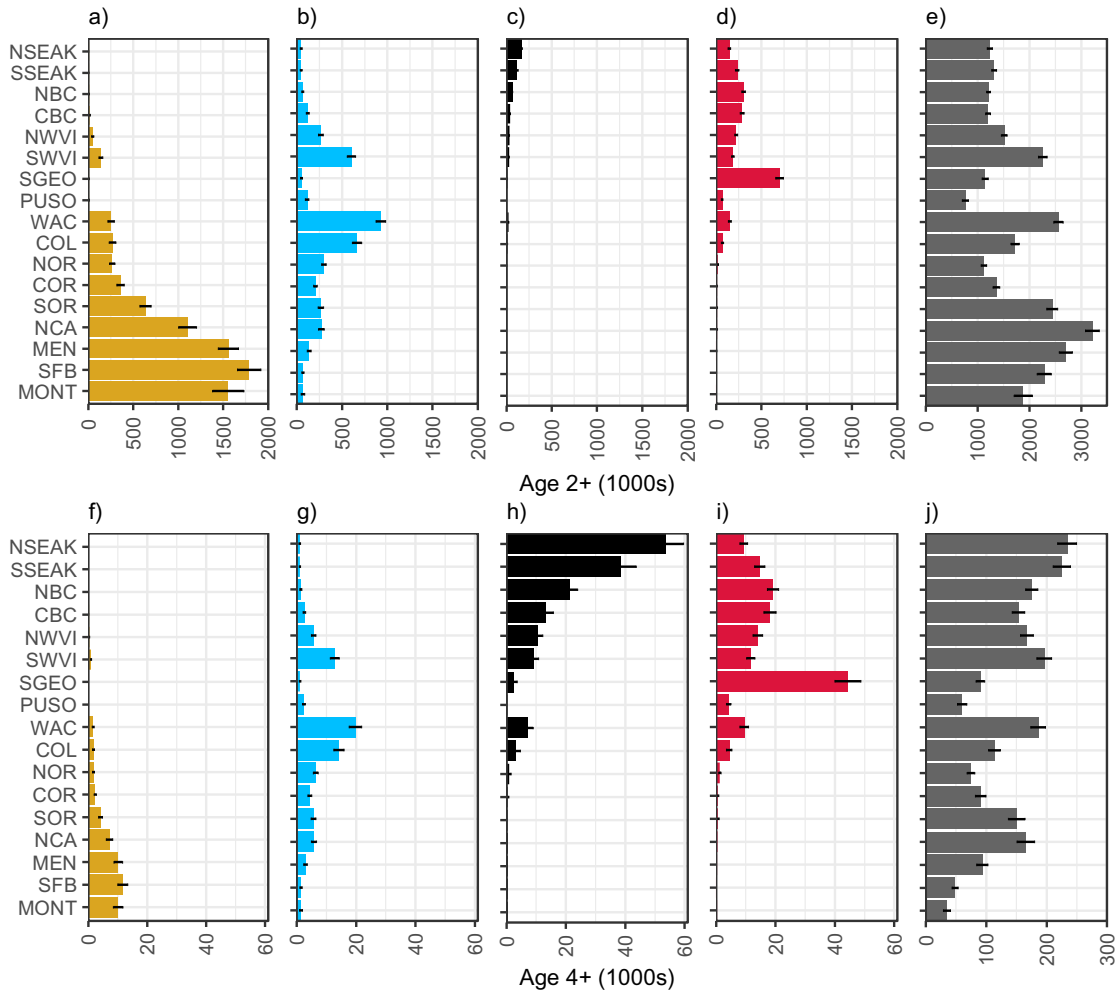
Can. J. Fish. Aquat. Sci. Downloaded from www.nrcresearchpress.com by National Marine Mammal Lab Lib on 06/15/18  
For personal use only. This Just-IN manuscript is the accepted manuscript prior to copy editing and page composition. It may differ from the final official version of record.

997 Figure 5: Distribution and abundance of fall Chinook salmon age 3 and older in the  
 998 ocean. We show proportional contribution of age 3+ fish to each ocean region (left  
 999 panels) and total abundance (right panels) at the beginning of spring (a), summer (b), and  
 1000 fall (c) seasons. Results arise from simulations assuming median fishing mortality for  
 1001 each area and season (see Fig. S1.9) and a single juvenile mortality rate shared across all  
 1002 regions.  
 1003



1004  
 1005  
 1006  
 1007

1008 Figure 6. Summer distribution and abundance of fall Chinook salmon from four  
 1009 representative regions and two age groups under the base scenario. Areas SFB (*a,f*),  
 1010 COL(*b,g*), WAC (*c,h*), SGEO (*d,i*), and aggregate abundance across all stocks (*e,j*)  
 1011

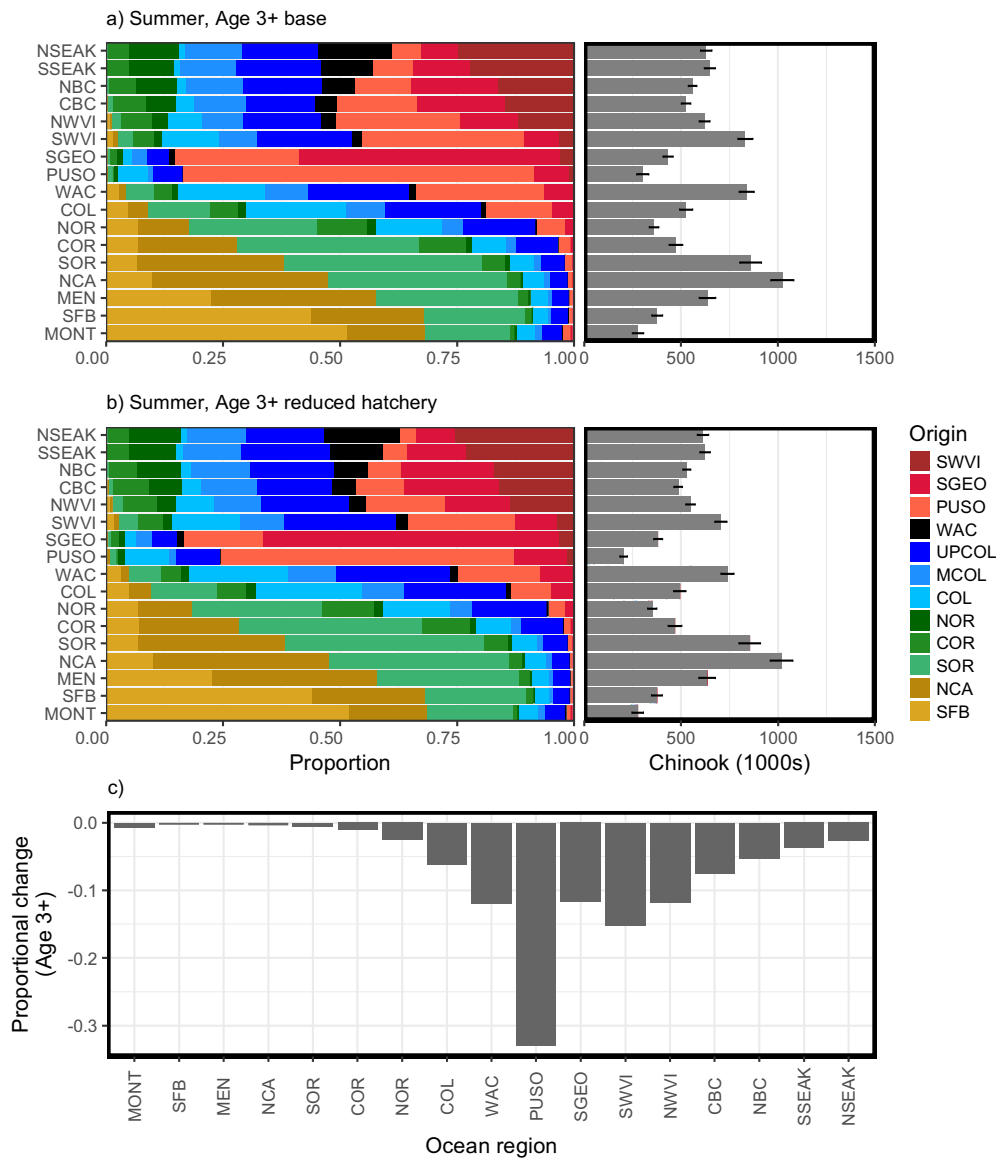


1012  
 1013

Can. J. Fish. Aquat. Sci. Downloaded from www.nrcresearchpress.com by National Marine Mammal Lab Lib on 06/15/18  
 For personal use only. This Just-IN manuscript is the accepted manuscript prior to copy editing and page composition. It may differ from the final official version of record.



1014 Figure 7: Comparison of two simulation scenarios. (a,b) Proportional contribution of age  
 1015 3+ fish to each ocean region (left panels) and total abundance (right panels) at the  
 1016 beginning of summer under the base scenario (a) and under reduced hatchery production  
 1017 from the PUSO region (b). Panel (c) shows the proportional change in total abundance  
 1018 from base to PUSO hatchery scenarios for age 3+ Chinook salmon.  
 1019



1020

1021